UNIVERSITY OF SOUTHAMPTON

ASPECTS OF THE MICROPALAEONTOLOGY OF DEVONIAN STRATA OF NORTH DEVON

A thesis presented for the degree of
Doctor of Philosophy

By

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ABSTRACT

FACULTY OF SCIENCE

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An integrated micropalaeontological investigation has been made of a *ca.*3km thick continuous sequence of Devonian strata in north Devon (S.W. England), encompassing the Lynton Formation, Hangman Sandstone Group, Ilfracombe Slates and Morte Slates. The sequence comprises interdigitated marine and non-marine sediments of low greenschist metamorphic facies: fossils have previously been considered rare in this succession.

Low abundance, icriodid-dominated conodont faunas have been recovered from the Lynton Formation and the Ilfracombe Slates: in total, 33 pectiniform conodont taxa are reported. Polygnathids are confined in their recovery to the Ilfracombe Slates. Despite the uniformly low total organic carbon content of the rocks (0.1-0.3%), diverse palynofloras have been isolated from the marine, or marine-influenced sediments. Initial problems of the oxidation and temporary stability of opaque phytoclasts were overcome, and assemblages found to be dominated by well preserved, terrestrially-derived organic matter, comprising miospores, tetrads, and wood. Acritarchs, chitinozoa and scolecodonts are infrequent. Over 130 species of miospore are described, in addition to 29 acritarch taxa, 11 forms of chitinozoa, and a diverse suite of scolecodont and wood morphotypes. The influence of reworking proved difficult to assess, due to the low yields and generally good preservation of the material.

Age determinations are based largely on the miospore assemblages, although conodonts provide independent corroborative evidence. The palynostratigraphy established for north Devon is compared with the zonal schemes of Richardson & McGregor (1986) and Streel *et al.*, (1987). Based on miospore data, the Lynton Formation is interpreted as no older than latest Emsian in age, with the uppermost horizons and overlying Hollowbrook Formation of possibly earliest Eifelian age. Conodont faunas recovered from the isolated, inland section at Watersmeet (of uncertain stratigraphic position, but ?located within the lower third of the exposed Lynton Formation), are of early Eifelian aspect. The nonmarine Trentishoe Formation and the majority of the Rawns Formation proved barren. The sediments of the upper Hangman Sandstone Group yielded comparatively abundant, diverse miospore assemblages of ?mid-late Eifelian age. The overlying lower Ilfracombe Slates are interpreted as earliest Givetian in age. Conodont faunas recovered from the Rillage, Holey, Combe Martin Beach and David's Stone Limestone Members are indicative of the Lower/Middle *varcus* conodont Subzones (≈mid Givetian). The upper Combe Martin Slates are considered late Givetian in age, with the conformably overlying Kentisbury Slates attributable to the Frasnian Stage. A marked depletion in the miospore assemblages approximates to the Kentisbury/Morte Slates boundary. The Morte Slates yielded miospores and acritarchs typical of the Frasnian Stage, although the topmost horizons may possibly be of earliest Famennian age.

The conodont faunas are interpreted as pectiniform lags. The sole recovery or predominance of *Icriodus* over narrow-platformed polygnathids suggests that a shallow-water marine environment prevailed during the deposition of parts of the Ilfracombe Slates. A detailed palynofacies study of the sequence was limited by the paucity of indigenous marine palynomorphs. However, a distinct dependency between scolecodont occurrence and the more proximal, shallow-marine facies has been observed.

An extensive geothermometry study integrated conodont C.A.I values and vitrinite reflectance data. Vitrinite reflectivity is uniformly high throughout the studied sequence, and the lack of dependency of *Rm* on stratigraphic position suggests that coalification was syn-orogenic. By applying the time independent conversion formula of Barker & Pawlewicz (1986) to this vitrinite data, the sediments are interpreted as having been influenced by temperatures in excess of 300°C.

This study demonstrates the value of integrating both palynological and conodont data in a regional biostratigraphical study, and furthermore identifies the Devonian sequence of north Devon as an important, continuous reference section for Devonian miospore palynostratigraphy.

CONTENTS

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TAXONOMIC DISCLAIMER. This publication is not deemed to be valid for taxonomic purposes (refer to the *International Code of Zoological Nomenclature,* 1985: edited by W.D.Ride *et al.*).

"If I have ever made any valuable discoveries,
it is owing more to patient attention,
than to any other talent." - Sir Isaac Newton.

To M and D.

CHAPTER 1.

INTRODUCTORY CHAPTER.

1.1. GENERAL INTRODUCTION.

Strata of Devonian age are extensively developed in southwest Britain and include a wide range of clastic and carbonate lithotypes. The Hercynian orogeny caused widespread stratigraphical dislocation within coeval sequences of the Southwest, but has only marginally disrupted the interdigitated marine and nonmarine Devonian continuum that crops-out along part of the north Devon coast. Indeed, due to its ease of access and comparatively simple structure, the sediments of north Devon provide what potentially is one of the best Devonian sections in the British Isles through which to take a continuous palaeontological sample profile.

Although Devon provided the nominal type locality for the Devonian System of Sedgwick and Murchison (1839), interest in the area has dwindled largely due to the paucity and sporadic distribution of macrofossils. This is particularly true for north Devon, where the Devonian succession has been formally differentiated merely according to lithological variation, with little regard for the (palaeontologically constrained) position of Devonian Stage boundaries. This has made comparison and the direct correlation with other contemporaneous sequences in and outside the British Isles problematical. In view of the limited Devonian macropalaeontology reported from north Devon, a detailed micropalaeontological investigation was the only untested, and considered potentially viable means of addressing and possibly solving this problem. Until the present study, previous endeavours had proved largely inconclusive.

In recent years, geological interest in north Devon has been revitalised following the detailed sedimentological studies of Tunbridge (1986, and earlier papers listed therein) and Pound (*in prep.*). These sedimentological investigations, coupled with the independent doctorate studies of Holwill (1965) and Jeffery (1971) for the Ilfracombe Slates, facilitated the systematic sampling of part of the Devonian sequence for micropalaeontological study.

Miospores and conodonts are the two principal correlative indices that form the basis of the biostratigraphical evaluations proposed herein. These two fossil groups were chosen, primarily because they are relatively diverse and abundant, but also because internationally, conodonts and miospores are currently the most widely used microfossils in Devonian biostratigraphical schemes. Therefore, coeval faunas and palynofloras documented within the geographically close "type" European Devonian sections may prove potential correlatives with north Devon.

The content of this thesis is divisible into two main parts: the study, comprising the systematic recovery and description of microfossils from the studied section, followed by a review of their application (and utility) in biostratigraphical, palaeoenvironmental, and maturity evaluations. This introductory chapter outlines the geological and geographical context of the study area, as well as introducing the principal microfossils studied. The techniques employed in microfossil extraction, isolation and analysis, together with a resumé of microfossil preservation are discussed in Chapter 2. The systematic palaeontology (Chapter 3) is concerned largely with the description of miospores from the fully marine, or marine-influenced sediments of north Devon. Conodonts, acritarchs, scolecodonts and chitinozoa occur intermittently within similar facies. The temporal distribution of these microfossils was evaluated, and collectively (but with a miospore bias) provides a somewhat clearer picture of the chronostratigraphical relationships for the sequence studied. The spatial distribution of certain microfossils indigenous to the marine environment was documented, allowing speculative evaluations to be made of palaeoenvironmental conditions. An extensive study of organic maturity has allowed tentative estimates of burial depth, and an assessment of the hydrocarbon source-rock potential of the Devonian strata of north Devon.

1.2 RATIONALE AND OBJECTIVES.

North Devon offers a unique opportunity to evaluate the palaeontology of a thick, presumed continuous stratigraphical interval of Devonian sediments. Traditional macropalaeontological investigations have proved inconclusive for the precise determination of relative age relationships within this sequence. Corals, brachiopods, bivalves and fish are widely used Devonian zonal indices, and collectively, or in isolation, have allowed correlation of marine and/or nonmarine strata. As House & Dineley (1985) recently remarked, the paucity of such fauna has limited the resolution of Devonian Series boundaries within certain marine Devonian successions of the British Isles. Indeed, in many areas in the Southwest, these have yet to be accurately resolved: this is particularly true of north Devon.

The need for some form of palaeontological constraint on the differentiation of the Devonian succession of north Devon has long been apparent. A number of cursory micropalaeontological studies have been attempted in this area, although apart from that of Orchard (1979), all have proved inconclusive. With this backdrop the current research programme was conceived, involving a more detailed systematic study of any microfossils recovered.

Initial, generalised aims were as follows;

(i) To recover and systematically document any microfossils from the Devonian sediments of north Devon.

(ii) To plot the temporal distribution of these microfossils through the studied sequence.

(iii) If possible, to recognise faunal and floral "events" within the Devonian sediments of north Devon which have been defined within coeval marine and nonmarine Devonian sequences around the globe.

(iv) Where possible, integrate and test the comparability of biostratigraphical data made available by these microfossils.

(v) If feasible, evaluate the palaeoenvironmental distribution of indigenous marine microfossils through the sequence studied.

Miospores and conodonts were primarily targeted, and proved the most valuable biostratigraphical indices. However, the general direction of the current research programme was dictated largely by the availability and quality of miospores and conodonts. Although locally important, conodonts have restricted stratigraphical distribution and therefore are of limited regional biostratigraphical use. Conversely, miospores have proved comparatively widespread, giving subsequent biostratigraphical evaluations a distinct miospore bias. Where possible conodont data was taken into consideration, and used as an independent biostratigraphical control on the age determinations inferred from the palynology.

As a matter of course, current problems entrenched in conodont and dispersed miospore systematics were addressed. Recent developments in the technique of measuring vitrinite reflectance (refer to Chapter 6), coupled with the availability of suitable microfossil material proved an additional bonus, allowing speculation as to the thermal evolution of the study area.

1.3. THE STUDY AREA.

The location of the study area, the local lithostratigraphy and also the outcrop pattern of the Devonian sequence studied are illustrated on the accompanying Figures 1.1 & 1.2. In part, north Devon forms the southern margin to the Bristol Channel (Figure 1.1). Approximately thirty-six kilometres of coastline between Lynmouth (SS 724494) in the east and Woolacombe (SS 458439) to the west provide a cross-strike section through, at a conservative estimate, 3km[1] of presumed conformable Devonian sediments (Figure 1.2). This succession comprises intercalated marine and non-marine facies. The topography is highest in the eastern part of the study area, in places forming precipitous cliffs, but becomes increasingly subdued in the west. Overall accessibility is good, though variable east of Combe Martin. Sample collection from the main exposures of the Trentishoe Formation necessitated the use of a boat.

Lithostratigraphical nomenclature follows that of Edmonds *et al.* (1985) except for the use of "Lynton Formation" following Pound (*in prep.*), in preference to the traditional terminology of the "Lynton Beds". Although this unit has, as yet, to be formally designated "formation" status, the definition of Pound is followed largely for reasons of conformity, as unpublished data made available by Pound proved integral in the sampling of this lowermost unit. Of further note is the definition of the boundary between the Kentisbury and Morte Slates, which as defined by Edmonds *et al.* (1985) is located southwest of Brandy Cove Point (SS 502471) - see remarks in Orchard (1979, p. 129) and House & Dineley (1985, p. 306).

For a review of the lithostratigraphic divisons of the geology within north Devon, and details of regional correlation refer to House *et al.,* (1977), bearing in mind the modifications outlined above.

1.4. GEOLOGY.

1.4.1 Palaeogeography.

During Silurian-Devonian times southern Britain lay at a latitude of between 20 S and 30 S (Drewry *et al.*, 1974; Ziegler *et al.*, 1977). The sediments of southern Britain were deposited in an arid to semi-arid environment (Allen 1974a, 1974b, 1979) with the limestones of southwest England having accumulated in a warm, tropical sea (House, 1975). Based upon palaeomagnetic data, the

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[1] This thickness excludes the Pickwell Down Sandstones, the Upcott Slates, Baggy Sandstones and the Devonian part to the Pilton Shales - collectively, these units and those listed earlier form part of the conformable Devonian sequence of north Devon, which naturally exceeds 3 km in total thickness.

FIGURE 1.1 LOCATION AND REGIONAL GEOLOGY OF THE STUDY AREA.

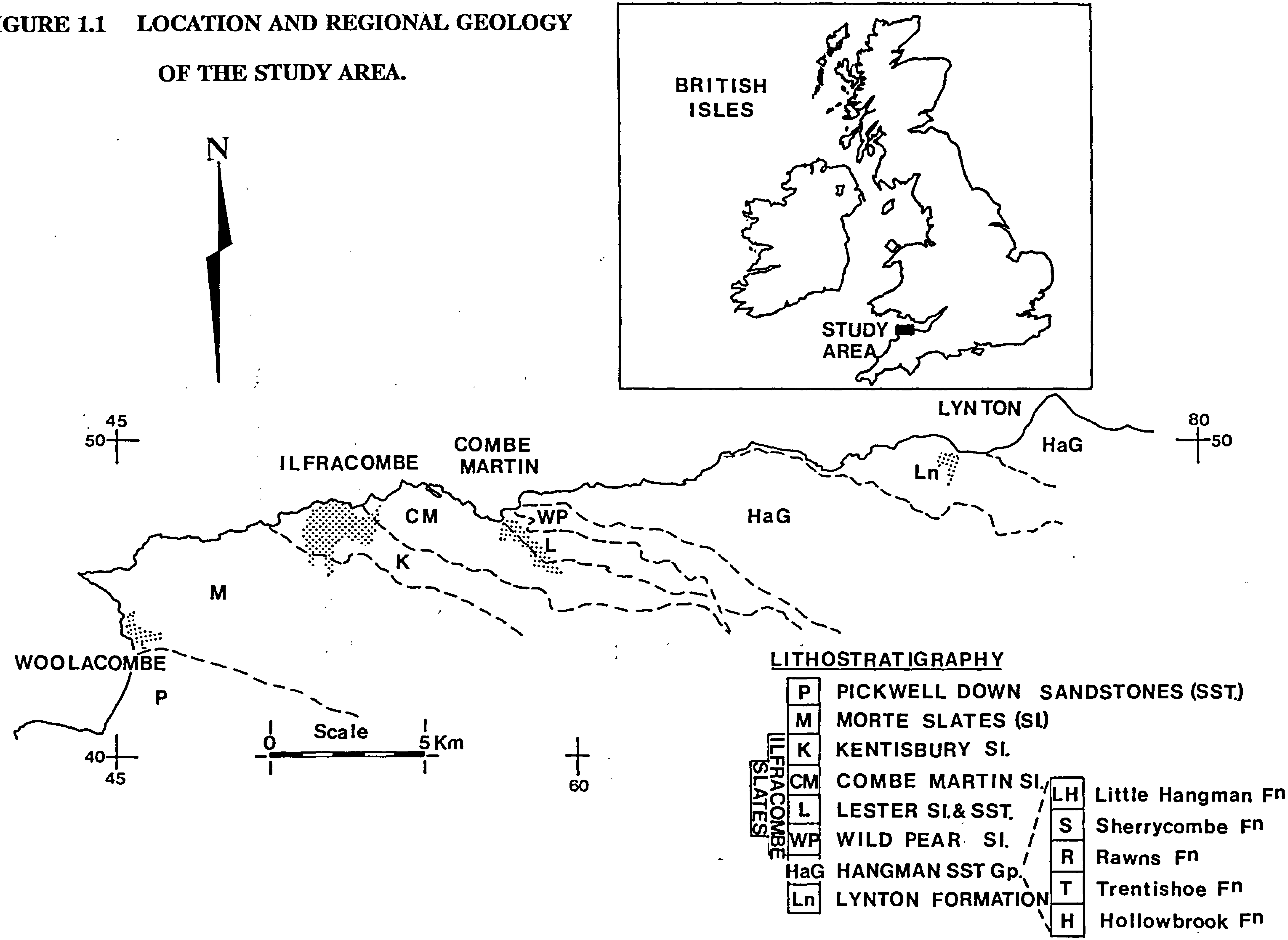
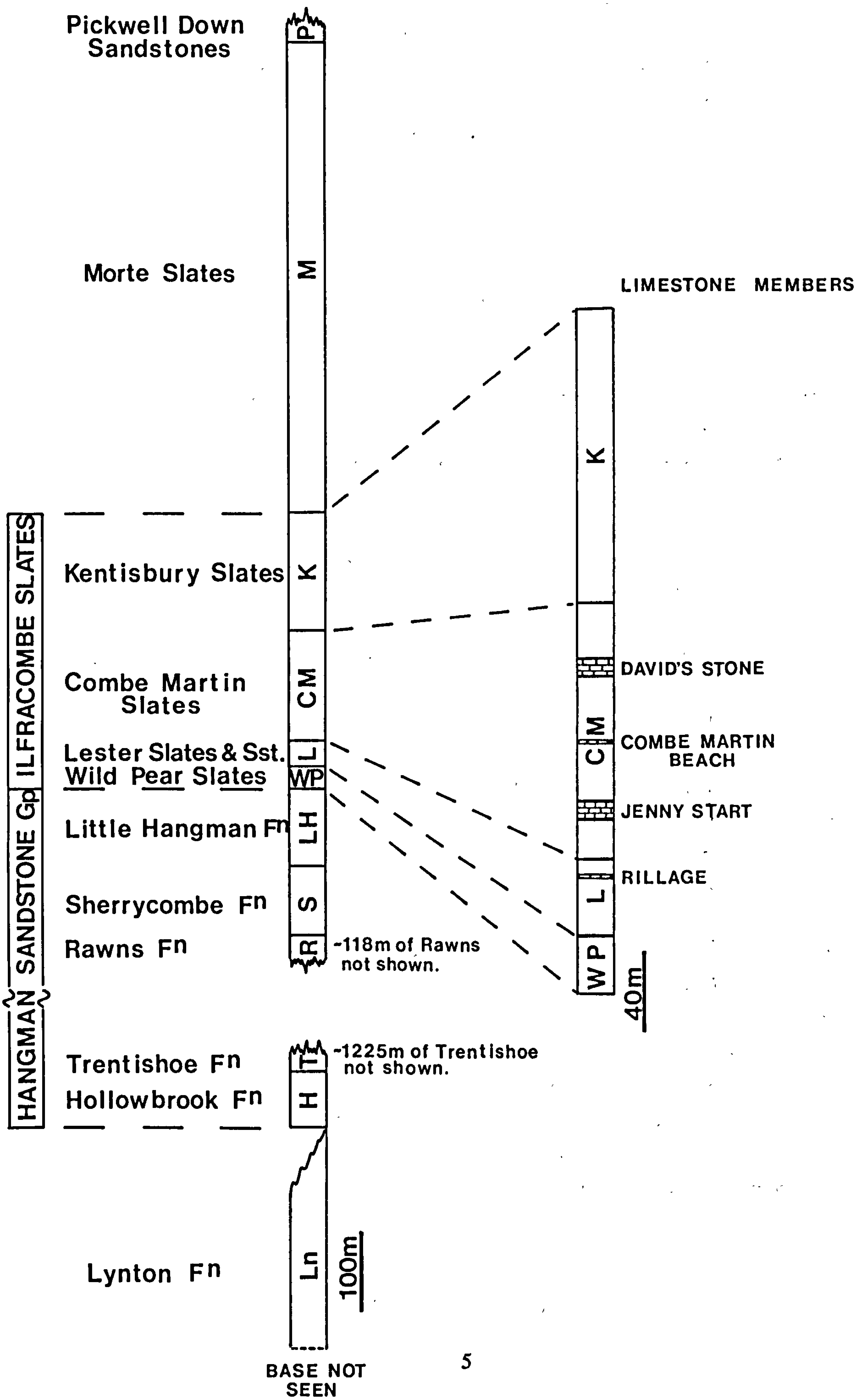


FIGURE 1.2 LITHOSTRATIGRAPHY OF THE DEVONIAN (PARS)

OF NORTH DEVON.



palaeogeographic reconstruction of Smith *et al.* (1973) for the Lower Devonian places Britain at approximately 25°S on the western margin of the "Rheic ocean". Scotese *et al.*, (1985), however, located Britain nearer to the palaeoequator, although this interpretation has not been widely accepted, largely due to disparities with known sedimentological evidence. Briden *et al.*, (1984) supplemented palaeomagnetic data for the British Isles, corroborating the earlier evaluation of Smith *et al.* (1973).

Recently, Tsien (1989) constructed twelve palaeogeographical maps for the Cornwall-Ardenno-Rhenish Basins, and spanning the Devonian Period. Of interest is the location of southwest England during the middle Givetian (Figure 1, p.342), which according to Tsien (1989) is placed at a somewhat lower latitude (*c.* 10°S) than previously defined.

1.4.2 The geological succession.

With the closure of the Palaeozoic Iapetus Ocean (Harland & Gayer, 1972; McKerrow & Ziegler, 1972; Dineley, 1973, 1975) and the collision of the North American and European plates towards the end of the Silurian Period, the Caledonian "geosyncline" was subsequently transformed into an orogenic belt extending from New York State to Spitsbergen. This newly created landmass (the "Old Red Continent", but also known as "North Atlantis") covered a substantial surface area. On a more local scale, the destruction the Welsh "geosyncline" resulted in a landmass extending over part of Wales, the West Midlands and southern England. As a consequence the marine environment that had so dominated sedimentation within the Welsh Basin was displaced southwards, and became restricted to present day Devon and parts of Cornwall (George, 1970 p. 51). This new landmass persisted throughout the Devonian and into the Carboniferous[2] Period. Indeed, with the exception of parts of southern Cornwall, it is widely accepted that Devonian sedimentation in southwest England was initiated on continental crust forming the southern margin to this Caledonian Continent.

The term "Old Red Sandstone" was coined by Conybeare and Phillips (1822), and the first continental Palaeozoic rocks present in southern Britain were considered of "Old Red" affinity (Allen, 1974a). This Anglo-Welsh Platform spanned from Anglesey to north Devon and southern England, and from southwest Dyfed (Pembrokeshire) to the west Midlands (Allen, 1974a, Fig. 4). Allen (1974a) also perceived sediment supply to north Devon to be from the north. On the basis of subsurface data this platform can be extrapolated into eastern England (Wills, 1973, 1978). In the extreme south, a sea extended across a large area of southern England, Belgium, France, and Germany (Goldring *et al.* 1968). From Pragian times onwards, the progressive northward onlap of marine sediments in Southwest Britain was accompanied by the differential subsidence of the shelf, with Ford (1972) interpreting the marine sediments of southern England to represent the precursor of the Amorican "geosyncline". By noting regional variability in the conodont faunas, Matthews (1977) defined four discrete, major sedimentary basins in the Southwest, which were bounded by E-W trending fault zones: the Roseland, Tevone and Bude Basins and the Exmoor "sink". These extensional basins developed and filled sequentially from south to north ahead of an advancing deformation front. Goldring & Langenstrassen (1979) later suggested that the marine Devonian of southwest England was deposited in a tectonically unstable setting, comparable to sequences within the Rhenish Schiefergebirge.

[2] land, emergent during this Period, is commonly referred to as "St. Georges Land".

Devonian rocks in Southwest Britain are currently disposed about the Culm (Carboniferous) Trough. In the north (present-day north Devon), thick continental sequences which were derived from the adjoining continental landmass are intercalated with near-shore marine deposits. The Devonian outcrop south of the Culm sediments (present-day south Cornwall) comprises offshore and basinal marine sediments, in a much more complex tectonic setting.

Provided below are details of the known sedimentology and palaeontology for each major lithostratigraphical unit studied in the present research programme: encompassing the Lynton Formation, Hangman Sandstone Group, and the Ilfracombe and Morte Slates.

1.4.2a. *The Lynton Formation.*

The oldest Devonian rocks exposed in north Devon are traditionally referred to as the Lynton Beds (Simpson, 1964; Scrutton, 1978; Evans 1980, 1983; Edmonds *et al.* 1985). In this study, the Lynton Beds are assigned formation status following the re-evaluation of Pound (*in prep.*). This basal lithostratigraphic unit comprises shallow marine, heterolithic mudstones and predominantly fine grained sandstones. Bioturbation is common, with wave-rippled cross-bedded and hummocky cross-bedded units widespread. The sedimentology suggests deposition on a wave-dominated shelf, in water depths mainly between storm and fair weather wave base. The base of this unit is not seen (*e.g.* Edmonds *et al.,* 1985), and the top is believed to be diachronous (Pound, *in prep.*). To the east of the area, adjacent to the Lynmouth-East Lyn Fault (Edmonds *et al.* 1985), Pound (*in prep.*) estimates the thickness of the sequence to be 200m, and thickening away from the fault to ≈250m. Correlation through the succession is problematical as units are visually indistinguishable and of uncertain lateral continuity, although three localised members have been recognised by Pound (*in prep.*; the Lee Stone, Watersmeet, and Woody Bay Members). In the eastern outcrop of the Lynton Formation, near to the western end of the onshore portion of the Lynmouth-East Lyn Fault[3] (which is believed to be a splay from the Bristol Channel fault system; Pound, *in prep.*), Tunbridge (1986) reported a matrix supported intraformational conglomerate, which he termed the Lyn Conglomerate. This conglomerate was interpreted to represent submarine debris flows, and the product of sediment sliding down a local syn-sedimentary fault scarp.

A recent detailed sedimentological study by Chris Pound (*in prep.*) has significantly supplemented current understanding of the Lynton Formation. Besides identifying three members within this Formation (as cited above), Pound (*in prep.*) recognised distinct seasonality in sedimentation for parts of the lower Lynton Formation. Sand-body morphology was controlled by the combination of palaeoslope/palaeoshoreline trend (which dipped to the SSW), and seasonal variability in trade wind patterns. Sandbodies migrated offshore in response to oblique-offshore directed (S.E.) geostrophic currents (generated by onshore-directed trade winds of sustained velocity), with mud sedimentation predominating during the summer monsoonal months (unsteady monsoonal winds directed offshore).

Pound (*in prep.*) has recognised three distinct sandy lithofacies associations, interrupting background muddy shelf deposition:

(1) The Lee Stone Member - comprising flaser and cross-bedded fine grade sandstones, and

[3] Based on geophysical evidence, Lloyd *et al.* (1973) continue this fault offshore into the Bristol Channel.

representing the migration of a linear sandbody moulded by semi-permanent trade winds, inducing geostrophic flow and weak tidal currents.

(2) The Watersmeet Member - comprising poorly sorted, cross-bedded, medium grade sandstones, moulded by currents similar to those responsible for the deposition of the Lee Stone Member.

(3) The Woody Bay Member - comprising hummocky cross-stratified fine grade sandstones, emplaced by storm events and becoming amalgamated to form extensive sandbodies.

The Lynton Formation reflects deepening in the palaeoenvironment though its lower and middle horizons (Pound, *pers. comm.*), followed by a progressive shallowing and marked ultimately at the top by the development of sandy shoreline sediments (Tunbridge, 1983). According to Bluck *et al.* (1989) the Lynton Formation may be regarded as the northern equivalent of the Meadfoot Beds of South Devon and represent part of a late Pragian to Emsian transgressive event.

At the top of the formation the sediments represent a phase of regressive deposition, contrary to the known eustatic transgression recognised within coeval sediments of late Emsian-early Eifelian age around the globe (House, 1983). This transition, from marine to essentially non-marine sedimentation, was heralded by the predominance of thick grey sandstones over finer grained deposits. As anticipated, the ichnofossils reflect this changes in sea-level, but according to Pound (*pers. comm.*) the transition between the Lynton and overlying Hollowbrook Formations cannot be gauged by the disappearance of *Chondrites*, as was earlier claimed by Tunbridge (1978, and subsequent papers). According to Pound (*in prep.*), the ichnofossil referred to by Tunbridge (1978) as *Chondrites* and preserved within the Lynton/Hollowbrook transition beds is more indicative of the taxon *Palaeophycus tubularis*, and occurs across this lithostratigraphic boundary.

Apart from the accounts of Phillips (1841), Whidborne (1901) and more recently Evans (1980, 1983), little palaeontology has been described from the Lynton Formation. Etheridge (1867) included a listing of fossils in his study of the Lynton "Slates", which was later supplemented by Hamling (1908). Despite tectonic distortion and the generally poor, fragmentary condition of the fauna, the Lynton Formation was referred to the Lower Devonian, although Simpson (1964) considered components of the fauna to be possibly early Eifelian in age. Subsequently, a number of authors (*inter alia* House & Selwood, 1966; House *et al.*, 1977) viewed the top of the Lynton Formation to be attributable to the Eifelian Stage, although Goldring *et al.*, (1968), and Edmonds *et al.*, (1985) maintain this formation to be exclusively Emsian in age. Based on brachiopod evidence, Evans (1980, 1983) advocated a late Emsian age for the Lynton Formation, although did not discount the possibility that the uppermost levels may be earliest Eifelian in aspect. Spore assemblages recovered from the Lynton Formation by Richardson and Hassan (*pers. comm.*, in Pound, 1984; Pound *in prep.*) confirmed a late Emsian age, although no specific details were provided.

1.4.2b *The Hangman Sandstone Group.*

A Middle Devonian, latest Caledonian uplift in South Wales generated a major clastic wedge in north Devon, resulting in the development of the Hangman Sandstone Group (Tunbridge 1978, 1983, 1984, 1986). Allen (1979) traced the development of "magnafacies" in the Old Red Sandstone of Ireland and Britain, and defined four incursion episodes of coarse clastics which he believed to be tectonically controlled. The development of the Hangman Sandstone Group is related to the third phase as defined by Allen (1979): this is reported as being a widely erosional and regressive event spanning the Eifelian to earliest Givetian interval.

The Hangman Sandstone Group exceeds 1,500m in thickness, and comprises regressive sediments at the base and transgressive strata at the top. Tunbridge (1978) formalised the nomenclature for this Group, differentiating five formations. The lowermost Hollowbrook Formation represents the transition from shelf to foreshore deposition (sandy shoreline conditions), with the progradation of terrigenous clastic sediment from the north swamping the marine environment to the south. This unit is considered to be ≈70m in thickness, and is conformably overlain by the Trentishoe Formation. This latter formation is ≈1250m in thickness and comprises sandy sheetflood and clay playa facies, largely indicative of ephemeral, low sinuosity stream sedimentation (Tunbridge 1981a, 1984, 1986). The source material for these lithic arenites was derived principally from the erosion of the highest Lower Old Red Sandstone sequences in South Wales (Tunbridge, 1986). Following a short, mud-dominated pedogenic interval (the Yes Tor Member of Tunbridge, 1980) localised uplift to the north shed coarse clastics into north Devon (as recorded by the Rawns Formation). The Rawns Formation comprises ≈120m of sediment that cannot be equated petrographically to any potential source area in Wales, and may therefore have been derived from Lower Palaeozoic or Precambrian rocks believed located at a shallow depth to the north, in the Bristol Channel Fault Zone. Indeed, these facies have been interpreted as being sourced from an intermittent "Bristol Channel Landmass" (Anderton *et el.,* 1979), although Tunbridge (1986, 1987) suggested that these sediments were in fact generated by more localised strike-slip movement within the Bristol Channel area (thus proving relatively short-lived sources of coarse clastic material). Wilson *et al.* (1989) remarked upon similar conglomeratic sediments present in south Wales (*e.g.* the Lindsway Bay Formation, Allen 1974; Woodhill Bay Conglomerate, Wallis 1927, Tunbridge 1986). Recently, Gayer & Jones (1989) question whether complex strike-slip tectonics were in fact responsible for triggering certain phases of sedimentation in the north Devon and south Wales area. Based upon an appraisal of seismic reflection data, Brooks *et al.* (1988) consider the Late Palaeozoic "strike-slip fault", cited by Tunbridge (1986) as having controlled Mid-Devonian sedimentation, to represent a major southerly-dipping Variscan thrust. From seismic data, Gayer & Jones (1989) commented that it is impossible to determine whether a pre-thrust fault existed in this area controlling Devonian sedimentation, although they did speculate that this feature may well have been an extensional fault. Consequently, Gayer & Jones (1989) considered the inversion of an extensional fault (producing the observed thrust) to be mechanically easier than the inversion of a vertical strike-slip fault (*sensu* Tunbridge, 1986).

The Rawns Formation is succeeded by transgressive, partly muddy sediments colloquially known as the Sherrycombe and Little Hangman Formations, which are ≈190m in combined thickness and signify the end of terrestrially-dominated sedimentation in north Devon. This rise in sea-level during the Middle Devonian stemmed the flood of clastics down from the north, and allowed the deposition of barrier island and shoreface sands and muds. Within the Sherrycombe Formation a number of minor transgressive-regressive events have been traced against an overall transgressive phase (Tunbridge, 1978), and according to Tunbridge (1978) this formation may also represent the establishment of estuarine or possible delta-fan conditions.

Little reliable palaeontological evidence has been documented from the Hangman Sandstone Group. Plant remains identified as *Calamites* and *Psilophyton* were reported by Evans (1922), Evans & Stubblefield (1929) and Tunbridge (1978). Evans (1922) also remarked on the presence of "obscure fish fragments". Evans (1922, in Evans & Stubblefield, 1929) recorded a *Coccosteus* scale and plant remains from the Rawns Beds. Within the overlying Sherrycombe Formation, Lane (1965) detailed a comparatively diverse fauna, including *Myalina*, *Naticopsis*, *Bellerophon* and a suite of corals. Prior to Lane (1965), distorted *Myalina* valves preserved within this unit were identified as *Stingocephalus* (refer to Evans, 1922). Lane (1965) also reported *Myalina*, *Naticopsis* and bryozoans within the topmost unit of the Hangman Sandstone Group, namely the Little Hangman Formation.

In view of their position overlying the Lynton Formation and beneath the Ilfracombe Slates, the Hangman Sandstone Group have traditionally been perceived to be largely (if not entirely) of Middle Devonian age: that is to say almost exclusively Eifelian, with some possible Givetian strata in the uppermost levels.

1.4.2c *The Ilfacombe Slates.*

The Ilfracombe Slates are believed to conformably overly the Hangman Sandstone Group, although the junction exposed on the coast to the east of Combe Martin is acknowledged to be structurally complex (Edmonds *et al.*, 1985). Furthermore, the precise stratigraphy of the Ilfracombe Slates has proved difficult to elucidate, due to intense tectonic deformation, and in certain parts, sedimentological monotony. The lithostratigraphical nomenclature for the Ilfracombe Slates adopted in the present study follows that defined by Edmonds *et al.* (1985). This appraisal of Edmonds *et al.* (1985) incorporated the proposals of Evans (1922), Evans & Stubblefield (1929), Holwill (1962), Webby (1966a,b) and Holwill *et al.* (1969). At a conservative estimate, this marine succession comprises ≈335m of silicate and carbonate lithotypes (Edmonds *et al.* 1985), and has been informally subdivided into four units: in ascending order, the Wild Pear Slates (≈30m thick), the Lester Slates and Sandstone (≈35-40m thick), the Combe Martin Slates (≈119.34-134.84m) and the Kentisbury Slates (≤150m thick).

The sedimentology of this sequence has still to be studied in any great detail. Independently, Webby (1966a,b), Tunbridge (*pers. comm.*, 1988), Bluck *et al.* (1989) and Pound (*pers. comm.*, 1989) have offered speculative palaeoenvironmental models for the evolution of this sequence: the following is based largely upon these observations. In summary, despite minor fluctuations in the rate of subsidence and sediment supply, sedimentation occurred on a shallow marine shelf: the shoreline was located to the north. Most of the thick argillaceous and arenaceous deposits of the Ilfracombe and overlying Morte Slates were interpreted by Webby (1966b) as having accumulated in a shallow-water prodelta and delta-platform environmental setting. Bluck *et al.* (1989) consider the lowest Wild Pear Slates to comprise cleaved, bioturbated mudstones and thin-bedded sandstones, which represent deposition near to, or below, storm wave base. According to Bluck *et al.* (1989) the overlying Lester Slates and Sandstones contain calcareous cross-bedded sandstones, siltstones and bioclastic limestones (the Rillage and Holey Limestone Members), indicative of a shallowing in the environment, with deposition occurring between fair weather and storm wave-base. Webby (1966a,b) interpreted the thin, predominantly biostromal limestones within the Combe Martin Slates (in ascending order: the Jenny Start, Combe Martin Beach & David's Stone Limestone members) as indicating deposition in relatively shallow water, although Webby believed variation in the composition of the preserved coral assemblages suggested subtle fluctuations in water-depth. Indeed, Webby (1966b) defined the "Combe Martin biotope" (centred around the development of the Combe Martin Beach Limestone), representing deposition in weakly turbulent, slightly deeper-water conditions. Recently, Bluck *et al.* (1989) have remarked that the Combe Martin Slates comprise cleaved, wavy and lenticular bedded mudstones, and hummocky cross-bedded, fine-grained sandstones, in association with the three distinctive limestone units listed earlier. According to Bluck *et al.*, (1989), these sediments collectively indicate deposition on a storm worked shelf, that contained a complex of sand shoals and patch reefs, with ooid banks developing in front of the reefs and lagoonal lime-muds accumulating on the landward side. The youngest formation of the Ilfracombe Slates, the Kentisbury Slates, comprises hummocky cross-bedded and bioturbated heterolithic storm deposits. Small scale sandy incursions are believed to reflect onshore deposition, derived from the reworking and shoreward transportation of older beach and fluviatile sands (Webby 1966a,b).

As remarked by Edmonds *et al.* (1985, p. 12) the fossils from this unit are sparse and in general poorly preserved. Holwill (1963; 1964a,b; 1965; 1968) described and illustrated corals from the Ilfracombe Slates, and interpreted the rich rugose coral fauna of the Jenny Start Limestone (and equivalent Roadwater Limestone of the Brendon Hills, west Somerset; Webby, 1964) as being of Givetian age. In contrast, the coral faunas of the Combe Martin Beach and David's Stone Limestones were on balance broadly comparable, and according to Holwill (1963, 1964b, 1965) of probable early Frasnian age. Webby (1966b) questioned this age evaluation, believing there to be no faunal evidence to substantiate an absolute Frasnian age (see also remarks in Scrutton 1975, p.132). Unlike Holwill (1963, 1964b, 1965), who perceived the differential coral faunas preserved within the Jenny Start, Combe Martin Beach and David's Stone Limestones to have chronological significance, Webby (1966b) viewed such faunal differences as indicating ecological rather than temporal variation. Orchard (1979) subsequently reported on a conodont fauna of *varcus* Zone age, recovered from a level ≈50m below the top of the Kentisbury Slates.

Further to Webby (1966b) and Orchard (1979), the Ilfracombe Slates have by and large been regarded as Givetian in age.

1.4.2d *The Morte Slates, and associated Upper Devonian lithostratigraphical units in north Devon.*

A pronounced deepening in the water column followed the deposition of the Kentisbury Slates, and thus defines the onset of the delta-front deposits of the Morte Slates. The fourth "magnafacies" episode of Allen (1979) coincides approximately with the development of the upper Ilfracombe Slates and overlying Morte Slates. This phase in sedimentation reflects predominantly deeper-water deposition, and was initiated during late Givetian times, continuing through into the Frasnian.

The cleaved, graded siltstones of the Morte Slates are on the whole devoid of macrofossils and are currently believed to be, at a conservative estimate, approximately 600m in thickness (Edmonds *et al.* 1985). According to Webby (1966b), the sedimentology of the Morte Slates reflects a number of minor regressional and transgressional phases in sedimentation within an overall regressive pulse, that culminated in the development of the overlying, more proximal deltaic facies of the Pickwell Down Sandstones. Note: Johnson *et al.* (1986) identified a mainly Late Devonian (late Givetian to early Carboniferous) major transgressive-regressive cycle in the strata of western Canada, western

United States, New York, Belgium and Germany, and which broadly correlates with the sediments in north Devon.

In common with the rest of the studied sequence, the Morte Slates have yielded an impoverished and poorly preserved fauna. The faunal data catalogued by Gregory (1897) and Evans & Pocock (1912) collectively suggests a Frasnian-Famennian age for these sediments. Based upon a fish fauna, Selwood and Durrance (1982) deduced the age of the overlying Pickwell Down Sandstones to be early Famennian.

Neither the early macropalaeontological work, nor the more recent evidence documented by Edmonds *et al.* (1985) can confirm Webby's (1966b) interpretation that the Morte Slates were the product of pro-delta or delta-platform sedimentation.

The Pickwell Down Sandstones overly the Morte Slates, and are believed to be 1,200m in thickness. This unit comprises broadly upward coarsening siliclastics, their lower parts displaying a series of deltaic sequences, and in the higher levels incorporating sandy low-sinuosity fluvial deposits (Bluck *et al.,* 1989). Unlike the Hangman Sandstone Group, at present the Pickwell Down Sandstones cannot be demonstrated to be the product of sourceland tectonics, but are related simply to Famennian regression (House *et al.* 1977; Clayton *et al.* 1986).

The coastal mud-flat deposits of the Upcott Slates overly the Pickwell Down Sandstones, which are in turn succeeded by the distributary channel sandstones and deltaic sequences of the Baggy Beds. These sediments are overlain by the neritic through to deeper-water sandstones and shales of the Pilton Beds. Consideration of the entire Devonian sequence of north Devon indicates that this continuum reflects the intercalation of transgressive and regressive sediments, deposited on the southern shelf of the Old Red Sandstone continent.

1.4.3. Local structural setting.

Hobson & Sanderson (1983), and more recently Edmonds *et al.*, (1985) review the structural geology preserved within the Devonian sequence of north Devon. The major structure to the north of the district is the Lynton Anticline, the axis of which trends east-southeast from Lynmouth Bay. North of this fold axis, small-scale folds and associated faults define the southern boundary of the Bristol Channel trough (Edmonds *et al.*, 1985). To the south the general structure appears far simpler. The progressive increase in the inclination of the slaty cleavage towards the south, across the southern limb of the Lynton Anticline and through progressively younger strata reflects the northward vergence of this major anticlinal structure. The oldest sediments, those of the Lynton Formation, crop out in the east of the study area, and delineate the core of this Exmoor "Anticline". In a geotraverse to the southwest, from the Lynton Formation, one passes up through increasingly younger Devonian strata, and ultimately into the Lower Carboniferous deposits located to the SSW.

Holwill (1965), Jeffery (1978) and Edmonds *et al.*, (1985) remarked on localised repetition in the stratigraphy through folding. Holwill *et al.*, (1969) commented that intense thrusting is significant in the localised dislocation of the stratigraphy, although this mechanism has been disputed by Edmonds *et al.* (1985). Edmonds *et al.*, (1985) remarked on the intensity of small-scale folding in relation to lithology, being particularly severe in the dominantly argillaceous Ilfracombe and Morte Slates, and less influential on the more competent, sandstone-dominated strata of the Hangman

Sandstone Group. In general, fold axes are sub-horizontal, or show gentle westerly or easterly plunges. The fold attitudes change in disposition from northward-overturned in the north of the area, to upright in the southwest.

Numerous north-westerly trending dextral wrench faults pervade throughout this area (Shearman, 1962). These faults do not have a large displacement (with the exception of the Little Hangman-Parracombe Fault), and with the associated NE-SW trending set are more probably "late-normal" in origin (Pound *pers. comm.*). The Lynmouth-East Lyn Fault and the Little-Hangman Parracombe Fault are major strike-slip faults that are slightly oblique to the described regional fault trend, being more ESE-WNW and not structurally associated with these wrench faults.

Edmonds *et al.* (1985) postulated that the main structures in the area were attributable to a single orogenic phase of late Carboniferous age, and that in general, faults post-date folds. During the later Alpine orogeny it has been suggested that there was some small scale reactivation of fractures (Dearman, 1964; Shearman, 1967; Edmonds *et al.* 1975).

1.4.4 Regional setting of the Devonshire Variscides.

According to Tsien (1989) the Variscan "geosyncline" that extended across Northwestern and Central Europe may be differentiated into a northern and southern sector, of which the Devonian sediments of southwest England can be related to the Ardenno-Rhenish Basins. This "geosyncline" extended over southwestern Ireland, southern England, northern France (Boulonnais), Belgium, Germany, and Poland. Tsien (1989) defined twelve palaeogeographical scenarios spanning the Devonian , and there-upon mapped the complex spatial distribution of six major sedimentary facies. Within all of these reconstructions, the Devonian sediments of north Devon are shown to be in continuity with marine and nonmarine facies of Europe. The presumed proximity and correlation of the Variscides of Belgium and Germany with the Devonian of southwest England has a particular relevance to this study, largely because of the extensive Devonian micropalaeontology that has been reported from the former two regions.

Following orogensis, the Devonian and Carboniferous sediments of north Devon formed part of a much larger orogenic belt, the Rhenohercynian Variscides, the geotectonic character of which is problematical. Holder & Leveridge (1986a,b) speculate that the Rhenohercynian Variscides of Belgium, Germany and southwest England were in tectonic continuity prior to the Late Carboniferous, and where subsequently offset along the putative Bristol Channel-Bray Fault : the evolutionary modelling of this orogenic belt is, however, still uncertain. Holder & Leveridge (1986a,b) envisaged significant subduction in an essentially oceanic setting, whereas Badham (1982) and Barnes & Andrews (1986) perceived the region to have evolved through predominantly strike-slip tectonics in an essentially intra-cratonic setting.

1.5 THE SUBDIVISIONS OF THE DEVONIAN SYSTEM AND THEIR RECOGNITION IN NORTH DEVON.

In 1982 the Subcommission on Devonian Stratigraphy adopted the standard conodont zonation (and associated terminology) as the basic framework to which series boundaries could be related (Ziegler and Klapper, 1982). By necessity these refer to successions outside the British Isles that encompass predominantly pelagic sediments, being the most favourable source of conodont elements (although critical index taxa have been recognised within a variety of other sediment-types, including neritic sediments).

In the present study the international standard stage and series terminology presented by Ziegler & Klapper (1985), and summarised by House (1988), is used (as shown in Figure 1.3). Figure 4.1 (of Chapter 4) shows the comparability with and resolution of major chronostratigraphical (stage) boundaries using the miospore zonal schemes of Richardson & McGregor (1986) and Streel *et al.* (1987), as well as indicating those parts of the standard conodont zonational scheme relevant to the present study.

SERIES	STAGE
UPPER	FAMENNIAN
	FRASNIAN
MIDDLE	GIVETIAN
	EIFELIAN
LOWER	EMSIAN
	PRAGIAN
	LOCHKOVIAN

Figure 1.3 Nomenclature of the Devonian System, after Ziegler & Klapper (1985) and House (1988).

The tripartite Series division of the Devonian System into Lower, Middle and Upper has proved comparatively stable. However the concept and application of sub-series divisions varied considerably around the globe, until the terminology was rationalised and consolidated in 1982 (refer to the discussion by Ziegler & Klapper, 1985). The Gedinnian, Siegenian and Emsian Stage terminology for the Lower Devonian, established within the Ardennes and Eifel regions, has been widely applied in clastic sequences in and outside western Europe. However, following the detailed description of Czech sequences by Chlupac *et al.* (1972) and Chlupac & Turek (1983), the terminology comprising Lochkovian, Pragian, Zlichovian, and Dalejian for carbonate facies has been advocated and adopted in western North America, Asia and Australia (the Subcommission on Devonian Stratigraphy retained the term "Emsian", which circumscribes the latter two divisions). The Middle Devonian Stage names of Eifelian and Givetian were proposed in Germany, with the French preferring the terms Couvinien and Givetien for approximately the same time interval. The Upper Devonian interval has been differentiated into the Frasnian and Famennian Stages, although again the definition and application of each has differed quite significantly.

Many Devonian palynologists have expressed a preference for the retention of the Rheinish stage terminology for part of the Lower Devonian (namely the Gedinnian and Siegenian), even subsequent to the recommendations of the Subcommission in 1982 (note the remarks in McGregor, 1979a p. 164, and Richardson and McGregor, 1986 p. 2). Streel *et al.* (1987) however adopt the revised terminology (as illustrated above in Fig. 1.3) in proposing their miospore zonal scheme for the Devonian of the marine Ardenne-Rhenisch regions of Western Europe. However, as Richardson & McGregor (1986) remark, the temporal distribution of spores is poorly known in the Czechoslovakian Lower Devonian, and thus the precise relationship between the Rheinish spore-bearing facies and the pelagic facies of Czechoslovakia is currently uncertain.

The correlation of Devonian rocks for the British Isles, compiled by House *et al.*, (1977) is still widely applicable today. In relation to the Devonian of north Devon, the only modifications subsequently proposed are those of House & Dineley (1985). Figure 1.4 (overleaf) shows the resolution of the Devonian Stages relative to the lithostratigraphy of north Devon, after House *et al.*, (1977) and the later emendations summarised in House & Dineley (1985). For comparison, the results of the present study are included, with a detailed discussion provided in Chapter 4, Section 4.7 (note oblique or dashed boundary lines imply uncertainty, rather than diachroneity).

1.6 PREVIOUS MICROPALAEONTOLOGICAL STUDIES ON THE MARINE DEVONIAN OF NORTH DEVON AND ASSOCIATED AREAS IN BRITAIN.

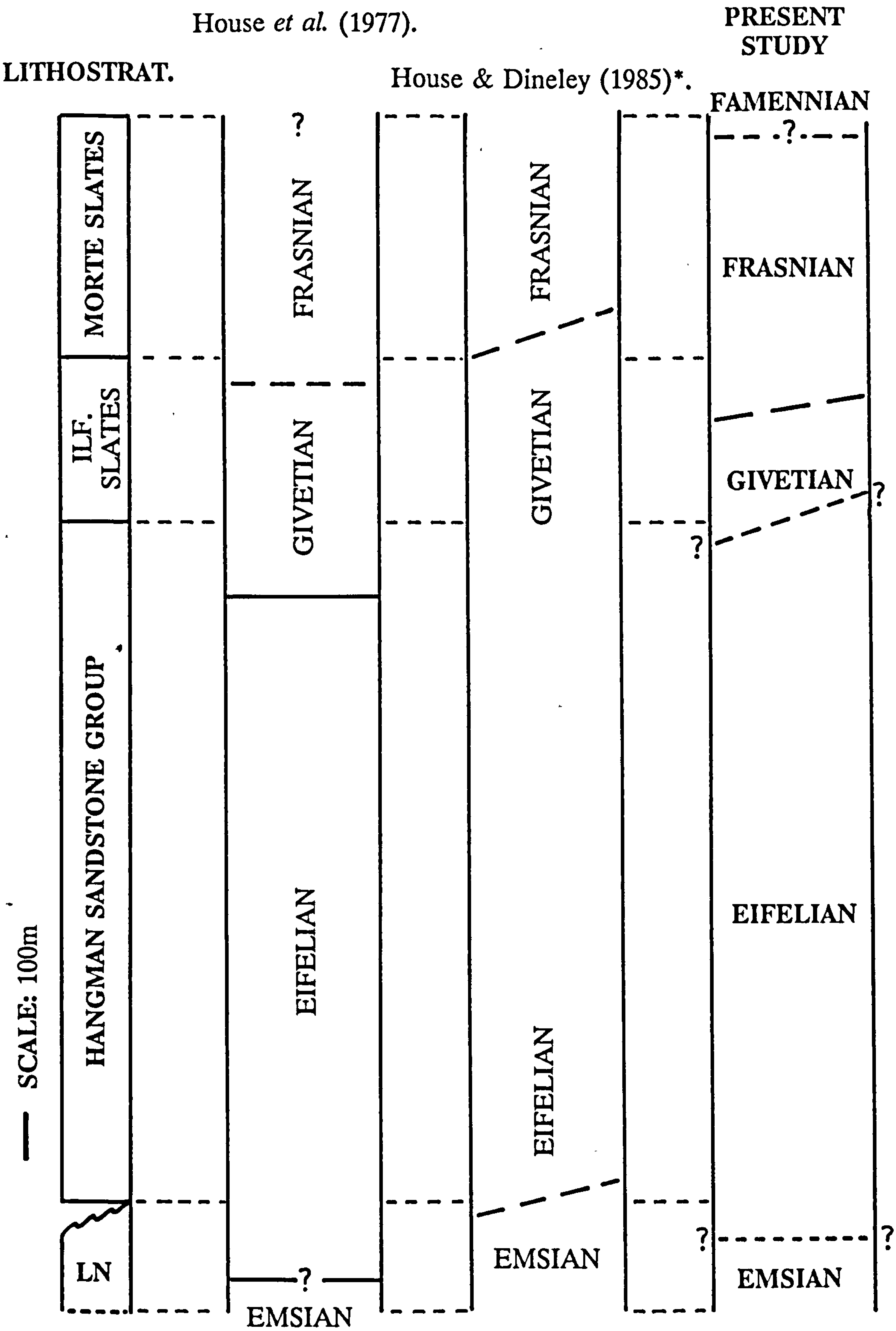
1.6.1 Introduction.

In view of the micropalaeontological perspective to the current research programme, and the general paucity of published macropalaeontological data for the north Devon, the following section outlines only certain aspects of micropalaeontology reported from the Devonian of Britain (with particular reference to north Devon). For a generalised resumé of macropalaeontology, refer to Evans (1983), Edmonds *et al.*, (1985) and the synopsis included in Section 1.4.

1.6.2 Conodont research.

With the exception of the Baggy and Pilton Shales (Williams, 1970; Sandberg and Dreesen, 1984, respectively), negligible detailed conodont research has been based on the marine Devonian sediments of north Devon (refer to localities listed by Dineley & Rhodes, 1956; Rhodes *et al.* 1957a,b; Austin *et al.*, 1970; Rhodes *et al.* 1973). Orchard (1979) reported on five conodont localities in north Devon, four of which from the Lester Slates & Sandstones yielded monospecific faunas that comprised *Icriodus* aff. *difficilis*. The fifth fauna, that of sample K2, was collected towards the top of the Kentisbury Slates and contained a comparatively diverse and abundant fauna, comprising 100 listed elements that included *Icriodus latecarinatus*, *I. ?brevis*, *I.* cf. *difficilis*, *Polygnathus varcus* group, *P. linguiformis linguiformis* (gamma morphotype) and *Spathognathodus semialternans*. Orchard interpreted an age no younger than the *varcus* Zone for this K2 fauna (see discussion in Chapter 4, Section 4.2.3b). Subsequently, Austin *et al.* (1985, p. 113) reported three new conodont localities from the Ilfracombe Slates: from the Combe Martin Beach Limestone (Combe Martin Beach SS 577474, & Haggington Beach, SS 540482) and the David's Stone Limestone (Sandy Bay, SS 596474). Poorly preserved icriodids predominate over rare polygnathids, but no details of assemblage composition were provided. Austin *et al.* (1985, p. 113-114) also reported eight new collections from the Brendon and Quantock Hills of west Somerset (the sediments in this area laterally equivalent to those that crop-out in north Devon). Constituents of these faunas recovered by Orchard were kindly made available

Figure 1.4. Previous synoptic age assessments for the Devonian of north Devon, compared with the findings of the present study.



KEY.

ILF = Ilfracombe Slates.
LN = Lynton Formation.

*based essentially upon Orchard (1979) & Evans (1983).

to the present author, and are illustrated herein (Plate 3.8). Prior to the present study, no conodonts have been reported from the Lynton Formation.

Conodonts have been quite extensively detailed from south Devon (*inter alia* Orchard, 1975, 1978a; Castle, 1982), and from both north Cornwall (*e.g.* Kirchgasser, 1970; Mouravieff, 1977) and south Cornwall (*e.g.* Hendriks *et al.* 1971; Sadler, 1973a). *Inter alia*, Stewart (1981a,b) remarked on conodont faunas from inland east Cornwall. For a more extensive literature review and discussion refer to Austin *et al.*, (Chapter 4; in Higgins and Austin, 1985).

Due largely to the lack of conodont research upon the marine Devonian of the British Isles, faunas recovered in the present work from the Lynton Formation, were best compared with coeval assemblages reported from sections elsewhere around the globe (*inter alia*: Weddige, 1977, 1982). Sadler (1973a, *pars*) documents a coeval fauna from southern Cornwall, but lacks the specific icriodids recovered in the present study. Kirchgasser (1970), Orchard (1975, 1978a) and Castle (1982) describe, in part, conodont faunas comparable in age to those reported herein from the Ilfracombe Slates. However, by virtue of the composition of these conodont faunas recovered from the Ilfracombe Slates, the material correlated more closely with contemporaneous faunas documented from outside the British Isles (*e.g.* the Eifel region, Weddige 1977; Morocco and the Ardennes, Bultynck 1987).

1.6.3 Palynology.

Excluding the Late Devonian palynology of the Baggy and Lower Pilton Beds (Dolby, 1970b: note the re-interpretation by Higgs *et al.*, 1988, p. 45), negligible palynology has been reported (or even attempted) for the Devonian sediments of north Devon. Owens (in Edmonds *et al.*, 1985 p. 6) remarked on recovering carbonized plant spores, including probable *Hystricosporites* spp., from the northern flanks of the Valley of the Rocks, west of Lynton. Richardson and Hassan (in Pound 1984; Pound, *in prep.*) noted palynomorph assemblages recovered from the Lynton Formation indicated a late Emsian age (although provided no details of assemblage composition). Coincidental with the remapping of sheets 277 and 293, the British Geological Survey prepared 15-20 samples, representative of the entire sequence, for palynological study. Internal reports kindly made available by Dr. B. Owens describe sparse, carbonized phytoclast assemblages. "Wood" and "?hystricospores" were recovered from Hollerday Hill (most probably the same material as mentioned by Owens, above). Abundant, carbonized woody debris was reported from the upper Kentisbury Slates at Brandy Cove Point, with wood and rare spores (identified as *Lycospora* spp. and *Lophotriletes* spp.) detailed from the Morte Slates. Samples collected from Mill Rock (of the Pickwell Down Sandstones) proved barren.

Comparatively little palynological research has been published from Devonian sediments in the British Isles, relative to coeval sections elsewhere in Europe. Lang (1925) pioneered research into the palynology of the Old Red Sandstone, in a study of Orcadian Basin floras. Richardson subsequently produced a series of papers (1960, 1962, 1965) on the palynology of the classic Orcadian area. Richardson (1967) reported a number of Lower Devonian spore assemblages from Scotland, England and the Welsh Borderland. Mortimer (1967, 1969) and Mortimer & Chaloner (1967, 1972) published the first detailed systematic studies of the Devonian palynology of subsurface marine Devonian sediments in southern England. Chaloner & Streel (1968) detailed Early Devonian spores from south Wales. Dolby (1970a,b), Dolby & Neves (1970), and Utting & Neves (1970) contemporaneously reported on Late Devonian-Early Carboniferous palynofloras from southern and southwest Britain.

A number of publications followed, providing details of palynology from surface and subsurface Devonian sediments. Gayer *et al.* (1973) described a well preserved, Late Devonian miospore and megaspore assemblage from a plant bearing siltstone 20m below the top of the Old Red Sandstone in the Taff Gorge, south Wales. Owens, Downie & Reynolds (1977) reported on subsurface palyniferous horizons within the Steeple Aston Borehole, and Richardson & Rasul (1978a,b) detailed Lower Devonian palynomorphs from the Apley Barn Borehole. Turner *et al.* (1979) reported sparse palynomorph assemblages of Famennian age from the subsurface Mylor Slates of the Mount Wellington Borehole, Cornwall. The age of the lowermost, sparse palynomorph assemblages recovered from the Knap Farm Borehole described by Mitchell *et al.* (1982), were re-evaluated by Higgs *et al.* (1988) and attributed to the Late Devonian. Le Gall *et al.* (1985) used palynological data documented from the Gramscatho Group (Cornwall) in the palaeogeographical and geodynamic modelling of the Lizard Front. Allen & Marshall (1981), Marshall & Allen (1982) and Marshall (1988) supplemented Richardson's earlier studies of the palynology of the Orcadian basin. McNestry (1988) reported on latest Devonian-Lower Carboniferous palynology from two borehole sections in south Wales, and more recently Dean (1989a,b) has recovered Devonian palynomorphs from south Devon and east Cornwall. Wilkinson & Knight (1989) report late Famennian palynomorphs from the "Mylor-type" sediments that crop out near Porthleven, south Cornwall.

For this study, the palynological research of Mortimer & Chaloner (1972) and in part Richardson & Rasul (1978a,b) on British marine Devonian proved particularly useful, as did the studies of Richardson (1960, 1962, 1965), Marshall & Allen (1982) and Marshall (1988) of the palynology of the nonmarine strata Orcadian Basin. Due to the lack of comparative literature of British Devonian palynology, the bulk of taxonomic and biostratigraphical evaluations have relied upon comparison with assemblages documented outside the British Isles. The zonal schemes of Richardson & McGregor (1986) and Streel *et al.* (1987) synthesise current perceptions of the temporal distribution of miospores through the Devonian System and were applied in the present study.

Although our knowledge of Devonian palynology within the British Isles is accumulating, very little is known of the detailed stratigraphic distributions of taxa. This would clearly impose limitations on any subsequent, palynologically-based regional correlation. The current data-base is based largely on disjunct subsurface borehole data, or isolated surface outcrops, with little understanding of how these sequences and their associated palynology are related. Although the sequence of north Devon includes a substantial interval of non-recovery, the sedimentary continuum is sufficiently extensive to provide a partial insight into the temporal distribution of dispersed miospores through the marine (and also non-marine) Devonian sediments of Britain. Consequently, the palynostratigraphy established for this area may prove significant, acting as a template in the partial consolidation of British Devonian palynology - Note Mortimer & Chaloner (1972, p. 3) remark that the miospore assemblages recovered from the various subsurface Devonian strata in southern Britain had characteristics all of their own, and could not be related palynologically.

1.7 INTRODUCTION TO THE MICROFOSSILS DOCUMENTED.

1.7.1 The Conodonta.

Pander (1856) described a suite of phosphatic microfossils ("conodonts") of what he believed were the skeletal fragments of fish, with each morphologically distinctive "element" representative of a distinct species. So was established the discrete element (or form) classification system for conodonts, which until recently, provided the basis of all systematic studies. It is now known that a variety of conodont elements often occurred in the same vermiform animal: this has given rise to a second "multielement" classification system. The conodont host animal formed an integral and often prolific component of the Palaeozoic and earliest Mesozoic marine biota, and has been reported in considerable abundance from a diversity of palaeoenvironments. Hence, conodonts have considerable biostratigraphical potential, as is shown by the many intricate zonational schemes that have been formulated.

The exact zoological affinity of the conodont animal (*sensu stricto* Briggs *et al.*, 1983) is still the subject of much debate, as this extinct fossil group has no close analogues in the living biosphere. Aldridge *et al*, (1986) considered new soft-bodied finds from the Granton Shrimp Bed to negate the feasibility of a chaetognath affinity, with these specimens appearing more consistent with a chordate model. Currently, the most attractive hypothesis is that conodonts represent a separate group of jawless craniates (Aldridge & Briggs, 1986). The soft-tissue of these animals is rarely preserved, and so the study of the dissociated elements forms the basis of most conodont research. It is known that conodont elements commonly occurred in bilateral "apparatuses" in the head region of these animals, but their exact function is still much debated (see below).

Conodont elements exhibit a diversity of morphology, and have been recovered over a spectrum of sizes - from the millimeteric scale (13mm in Aldridge *et al.*, 1988) to 10's of microns ($<80\mu m$; Nicoll 1983, Swift, 1986). Pietzner *et al.* (1968) reported these elements to be largely composed of calcium phosphate (francolite, a variety of apatite) with some organic matter (amino acids - Pietzner *et al.*, 1968; Savage *et al.*, 1988). Mode of growth and related structural complexity have allowed a broad categorisation of conodont elements into three types: protoconodonts, paraconodonts and euconodonts (Bengtson, 1976; Szaniawski, 1987). Knowledge of only the most advanced forms, the euconodonts, is appropriate to this study. Euconodonts are the most common and widely studied type of conodont element, with somewhat tenuous phylogenetic links to the more primitive paraconodonts and protoconodonts (Dzik, 1986, Aldridge 1987). Elements have further been differentiated according to shape and position within the multielement apparatus of the animal (refer to Sweet 1981, pp.W5-W16; Sweet, 1988). Ultrastructural studies have revealed the growth of euconodonts to be centrifugal, which is believed to indicate secretion within an epithelial "pocket" (Bengtson, 1976).

Much of the discussion of conodont apparatus function has been centred upon polygnathacean taxa. Some workers perceive condonts to have performed as teeth, actively used in the acquisition of food (*e.g.* Briggs *et al.*, 1983; Sweet, 1985; Dzik, 1986; Aldridge *et al.*, 1987). Others have considered ramiforms to have been supports for tentacular ciliate tissue that sieved particulate food matter, and which was then gently crushed by the posteriorly situated pectiniform elements (Nicoll, 1985, 1987; Nicoll & Rexroad, 1987). Furthermore, Nicoll (1987) postulated that variation in element design may have reflected differences in the type of food particles consumed by various conodont species.

Over the past few decades the concept of conodont biofacies has developed, which comprise different, distinct but coeval conodont assemblages. A multitude of conodont biofacies models have thus been proposed, especially for the Late Devonian and Early Carboniferous intervals (*e.g* Dreesen *et al.*, 1986). Within these models, specific conodont taxa are acknowledged to have occupied certain specialised ecological niches, influenced by factors such as temperature, salinity and water circulatory patterns. Devonian conodont palaeoecology is discussed in Chapter 5, appropriate to the age and faunal character of the assemblages detailed from north Devon. The application of conodonts to thermal maturation evaluation in discussed Chapter 6.

1.7.2 Miospores

Many plants (vascular land plants included) incorporate the dispersal of spores to propagate species. For a detailed synopsis of spore (and pollen) biology and related reproductive strategies, refer to Traverse (1988, Chapter 4).

Dispersed spores with tetrad marks are believed to be derived from terrestrial plants and have been reported in abundance and of considerable morphological variety from around the globe in sediments of Llandovery to Recent age (*inter alia*, McGregor 1984; Richardson & McGregor, 1986). A number of authors have claimed to have isolated spores and tetrads from sediments of pre-Llandovery age (*inter alia*, Timofeev, 1966; Combaz, 1967; Smith, 1975), but such discoveries are widely treated with caution. However, Gray *et al.*, (1982) reported *Ambitisporites*-like dissociated spores and tetrad configurations from sediments of Caradocian (Late Ordovician) age, and more recently Nohr-Hansen & Bundagaard Koppelhus (1988) document Ashgillian (Late Ordovician) ornamented, dispersed miospores from Washington Land, north Greenland. Unfortunately, within the Palaeozoic fossil record it has proved often impossible to equate many dispersed spore parataxa to their parent plant. Interpretative problems have been compounded by discoveries such as Moore (1946), who remarked upon an immense diversity in spore morphology within a selection of Carboniferous sporangia. In this study of some 30 sporangia, Moore noted that the spores contained within an individual sporangium differed markedly in size, construction and ornamentation, and believed this to reflect different stages of maturity or growth.

The transition of plant organisms from inhabiting an aqueous environment to the comparatively harsh subaerial environment required morphological reorganisation, to overcome the adversities of dehydration (Edwards, 1982) and possibly ultra-violet damage (Beerbower, 1985). To maintain homiohydry throughout the plant, specialised structures such as tracheids and cuticles were developed, and the recovery of such fragments within kerogen isolates may be used to suggest an earliest terrestrial flora. In illustration, Edwards and Davies (1976) reported *in situ* tracheids from sediments of Ludlow age, and thus substantiated claims of an early land flora.

Miospores are composed of an unusual organic substance, referred to as sporopollenin. Zetsche and Kalin (1931) established an approximate empirical formula of $C_{90}H_{142}O_{27}$ for *Lycopodium* sporopollenin. Recently, Brooks *et al.*, (1971) have suggested sporopollenin to be a copolymer of ß-carotene and fatty acids, although Given (1984) and Given *et al.*, (1985) dispute these claims. What is widely accepted is that sporopollenin is a highly inert C-H-O compound, that is comparatively transparent at low temperatures. With an increase in temperature (or rank) the colour deepens through yellow to black, with an associated increase in reflectance. Chemically this equates to the loss of oxygen and hydrogen with an associated increase in carbon, and is considered analogous to the coalification process noted for other organic matter. Sporopollenin is acknowledged to be a remarkably resiliant compound, although Elsik (1966), amongst others, has shown that some fungi can digest sporopollenin (as evidenced by microbial scars on pollen and spores).

Spores are usually differentiated into two broadly defined categories dependant upon size: miospores have a diameter arbitrarily taken as less than 200μm in diameter (and for heterosporous plants reflect the smaller male gametophyte), whereas megaspores display a mean diameter exceeding 200μm. Spores display immense variability in construction, and due to their mondial distribution and considerable abundance, have proved ideal as biostratigraphical indices. The distribution of spores within both continental and marine facies, coupled with their rapid evolutionary rates makes them particularly useful. Amongst others, Stanley (1969) and Tschudy (1969) have addressed the relationship between sedimentary facies and spore distribution. The greatest concentration and diversity in dispersed spore assemblages appears to occur in the inner neritic zone, although (excluding deltas) slightly more off-shore. Spores are reported from distal, deep-water environments, but are commonly small, depleted in abundance and diversity, and are usually poorly preserved.

1.7.3 The Acritarcha.

The Acritarcha (Evitt, 1963) is a polyphyletic group of organic-walled microplankton organisms of uncertain biological affinity (Deflandre, 1945; Downie *et al.*, 1963). These microfossils range in age from Late Precambrian to Holocene, but achieved their greatest abundance and morphological diversity in the Cambrian to Devonian interval, with an apparent acme in development within the Ordovician (Loeblich, 1970; Tappan & Loeblich, 1971). Few studies have been made of wall composition, but optically they resemble spores and dinoflagellates in being generally singular and homogeneous (some laminar or double-layered walls do occur). Eisenack (1963) reviewed a number of crude chemical tests he had preformed upon acritarchs, and subsequently confirmed that the material was similar to that of spores. Kjellström (1971) examined tasmanitids using infrared spectrometry, and showed the substance to probably be polymerised lipids. After an extensive study of the chemistry of *Parka* and *Chuaria*, Niklas & Chaloner (1976) concluded the wall substance to be plant in origin and similar to the sporopollenin.

Taxonomically, acritarchs are treated as an informal *incertae sedis* "Group", the Acritarcha (Evitt, 1963 - expounded by Downie, Evitt & Sarjeant 1963), which follow the tenets of the International Code of Botanical Nomenclature. This cautious approach to systematic treatment was to prevent unwarranted or unjustified assumptions being made in their taxonomic differentiation. Downie *et al.* (1963) initially defined 13 sub-groups, with subsequent workers proposing in total an additional 13: many of these have in fact been re-allocated to other formal groupings with elucidation of their true biological affinity. The Acritarcha are known to include an immense diversity of form genera and species. Taxa are differentiated primarily upon vesicle & process dimensions, ultrastructural ornamentation, style of excystment, process disposition & attachment, and the nature of process terminations.

Downie (1973) remarked that the Acritarcha contains probable cyst-remains of marine planktonic algae, with some most probably affiliated to the dinoflagellates (Note: prior to the rationalisation of Downie *et al.*, (1963) acritarchs and dinoflagellates were unsatisfactorily differentiated). Current consensus favours the Acritarcha to represent the encystment ("resting") stage of some algae, being the product either of some form of sexual reproduction, or alternatively as a response to adverse environmental conditions.

At present very little is known of the palaeoenvironmental distribution of Palaeozoic acritarch palynofloras (refer to the discussion in Chapter 5, Section 5.3.1).

1.7.4 The Chitinozoa.

Eisenack (1931) was the first to describe an unusual group of "flask-shaped" microfossils that had a chitinoid appearance (amber-brown at low rank), based upon specimens isolated from glacial erratics in the Baltic region. Despite the implication from their name, however, *Chitinozoa* contain no chitin (Voss-Foucart & Jeuniaux, 1972). Collinson & Schwab (1955) suggested that they are probably composed of pseudochitin, and Goodarzi (1985a) remarked that they may be similar in composition to graptolites, although the optical properties of the two groups differ quite substantially (Goodarzi, 1984; 1985a,b). Any relationship may be merely superficial. Chitinozoa-like microfossils have been reported from the Precambrian of Arizona (Bloesser *et al.*, 1977) with unequivocal representatives first noted in the Tremadocian. The group ranges into Late Devonian/earliest Carboniferous times, with Permian records considered questionable (?reworked). Chitinozoa are exclusive to the Palaeozoic, having no modern anologue and are thus of problematical biological affinity. Early research indicated the morphological organisation of chitinozoa to be relatively simplistic, comprising hollow organic-walled tests displaying longitudinal radial symmetry. Chitinozoa tests have been discovered in aggregates (*inter alia*, Taugourdeau & Magloire, 1964; Jenkins, 1970b; Legault, 1973a; Wrona, 1980) and also cocooned clusters. These observations, coupled with the realisation that the oral structure may be markedly more complicated, has changed the perception of this group from being a simple microfossil category, to one of substantially greater complexity. Despite the discovery of the aforementioned aggregates, there is still little consensus as to the exact biological affiliation of this group. In the literature Chitinozoa have been variously attributed to the protozoa (Eisenack 1931, 1932), or interpreted to represent metazoan egg-capsules (Koslowski 1963), fungi (Locquin, 1977), phytoplankton (Obut, 1973) and even the pre-prosicula stage in the graptolite life-cycle (Jenkins, 1970b).

Taxonomically, Chitinozoa have been differentiated primarily according to variation in the shape of the test, nature of the surface ornament and the character of the aboral surface. The possession of an operculum or prosome was at one time considered significant in the supra-generic differentiation of taxa, although Bockelie (1978, 1981) questioned this approach, noting certain forms to display both a prosome and operculum. Attributes including rapid evolution, global distribution and morphological diversification have enhanced their potential as biostratigraphical indices, particularly within the times of their acme (*e.g.* the zonation proposed by Achab 1989 for the Ordovician strata of Quebec and Newfoundland).

Interest in Devonian chitinozoa has traditionally lapsed behind that of Lower Palaeozoic faunules. The demise of the group within the Devonian , as reflected by the reduction in abundance and diversity, limits their biostratigraphical and palaeoenvironmental utility. Furthermore, the progressive terrestrialisation by plants in Silurian times, which became increasingly complex during the Devonian Period and subsequently through the later Phanerozoic, has made available alternative correlatives indices (namely dispersed spores and later pollen).

In common with the Acritarcha, little is know of the spatial distribution of Chitinozoa (refer to the discussion in Chapter 5, Section 5.3.1).

1.7.5 Scolecodonts.

Scolecodonts are dentate microfossils, ranging in size from <50μm to several millimetres, and are believed to represent the fossilised jaw-elements of marine annelids. The term "scolecodont" was first applied for isolated polychaete jaws in an abstract by Croneis & Scott (1933). Almost a century earlier, Eichwald (1854), Massalango (1855) and Pander (1856) independently published accounts of these dissociated fossil elements. Both Eichwald (1854) and Pander (1856) described such elements from the Lower Palaeozoic of the Baltic region, believing them to be fish denticles. However, little subsequent interest has been expressed in scolecodonts, as can be gauged by the limited literature available.

Within the phylum Annelida (segmented worms) only two classes, the Polychaeta and Oligochaeta produce mineralised, resiliant jaw-like teeth. The development of a differentiated jaw-apparatus is virtually unique to the Eucinidae, an order of polychaetes. Therefore, scolecodonts are thought to be the acid-resistant cuticulinous jaws of polychaete annelids, occurring predominantly in Palaeozoic rocks with sparse Mesozoic records linking this fossil form with Recent species. Although compositionally and functionally different, scolecodonts share the same nomenclatural difficulties as conodonts, as they are commonly preserved as dissociated elements with natural assemblages scarce.

Schwab (1966, p. 416) claimed polychaete jaws to be composed of chitinous material, although Desiere & Jeunieux (1968) noted only 0.13% (dry weight) of chitin in the scolecodont element. Voss-Foucart *et al.,* (1973) similarly disputed the compositional predominance of chitin by demonstrating Recent polychaete jaws to be composed of scleroprotein. Olive (1980, p. 572, 580) reviewed the variable composition of jaw material, comprising tanned protein, aromatic amino acids, glycerine, hystidine, and an assortment of metals including iron, zinc and copper. Colbath & Larson (1980) remarked upon a "chitinous" layer covering an inner calcium carbonate layer in fossil polychaete jaws. (calcium carbonate is a noted component of some modern scloecodont elements, particularly in mandibles which bear anterior calcareous plates). Studies concerned exclusively with element composition are few, but according to data currently available it would seem reasonable to deduce that fossil scolecodonts comprised both organic and mineral fractions.

The growth of scolecodont jaw elements may have been continuous or elements may have been replaced (shed). Amongst others, Paxton (1980) demonstrated continuous growth in mandibles, although recently Colbath (1987a) contested the continuous growth of maxillae in eunicoid polychaetes. The moulting of jaws in Recent annelids is well documented (*inter alia* Kielan-Jaworowska 1966, p. 49-51), but for obvious reasons difficult to verify in the fossil record. Kielan-Jaworowska (1966, p. 50-51) suggests that the jaw-within-a-jaw arrangement of morphologically identical elements in the placognaths may indicate moulting, and Schwab (1966, p.420) remarked that the first and second element configuration within placognath jaws of *Staurocephalites* is analogous with tooth replacement in mammals. However, Schwab (1966) could not discount the possibility that this configuration was due to growth abnormalities. Mierzejewski (1978a) discussed the feasibility of the physiological replacement of scolecodont elements, and commented that the element size of eunicids jaws increases during ontogeny. Recently Colbath (1987a, p. 447) verified element replacement in jawed fossil polychaetes, by drawing analogy with Recent material.

Four natural assemblage-types have been defined based on the presence and combination of various element types. Placognath apparatus-types are known from Ordovician to Late Devonian strata, with the remaining three apparatus-types (namely the ctenognathid, labidognathid, and prionognathid) spanning the Ordovician to Recent interval. Scolecodonts have been detailed quite extensively from Palaeozoic strata, in particular Ordovician (*e.g.* Hadding, 1913, 1915), Silurian (*e.g.* Eisenack, 1975; Bergman 1989), Devonian (*inter alia*, Lange 1949; Taugourdeau 1970b, 1971; Jansonius & Craig 1974;) and Permian strata (*e.g.* Szaniawski, 1968). Published accounts of scolecodonts from Mesozoic and Tertiary strata are far fewer. Of the 168 papers listed by Taugourdeau (1978) only 20 deal with post-Palaeozoic forms. Fossil polychaete jaw apparatuses or disjunct elements are almost completely unknown from the Cenozoic interval. Jan du Chene & Gorin (1974) described isolated elements from Eocene flysch sediments in France, as did Germeraard (1980) from Cenozoic strata of Jamaica. Recently Szaniawski & Wrona (1987) documented polychaete jaws from the Cape Melville Formation (Lower Miocene) of King George Island, West Antarctica.

As was typical of conodont taxonomy until the latter part of the 1960's, a dualism still exists in scolecodont taxonomy, with the continued application of both discrete element (form) and multielement (apparatus) approaches. The desirability of revising form-taxonomic categories is undisputed, but as yet is far from complete. Kozur (1970, 1972) attempted a synthesis of the two taxonomic systems into one unified scheme, but this has not been widely accepted.

As current knowledge stands, scolecodonts have limited stratigraphic and palaeoenviromental utility. Edgar (1984) remarked on the potential of scolecodont maxillary jaws as stratigraphic indices, although to date there is no scheme available, based solely on these microfossils. Very little is known of the palaeoecology of polychaete eucinids, except that they were exclusive to the marine environment. In an extensive study of Silurian paulinitid polychaetes from Gotland, Bergman (1989) remarked on the association between certain taxa and particular sedimentary facies. Low abundance, low-diversity faunas, dominated by small specimens, were apparently indicative of fairly deep water. Lagoon and other restricted environments probably offered the optimal conditions for paulinitid polychaete habitation (Bergman 1989, p. 25). However, no detailed bathymetric or palaeo-environmental data were provided.

1.8. SUMMARY.

Due to the minimal amount of palaeontological data reported from the study area, most current age assessments are poorly based. An integrated micropalaeontological study was considered the only viable means of resolving series boundaries within that part of the Devonian succession of north Devon under investigation.

CHAPTER 2.

MATERIALS, METHODS & GENERAL REMARKS.

2.1 INTRODUCTION.

This chapter briefly introduces the criteria and notational scheme adopted in present work when sampling lithotypes for certain microfossils. The methodology applied in the extraction and subsequent analysis of particular organic-walled and phosphatic microfossils is discussed. General remarks are also made in relation to sample productivity, microfossil preservation, the viability of a quantitative palynofacies study, and also innovative taxonomy.

2.2 SAMPLE NOTATIONAL SCHEME.

Samples collected and examined in this study are referenced according to a comparatively simplistic notational scheme, being referred to the appropriate lithostratigraphical unit by a prefix of alphabetical character(s). The numerical suffix to each sample code refers to a specified stratigraphic level or alternatively a particular geographic location within the identified unit. Samples were usually numbered from base upwards, with an increase in "value" usually relating to a "younger" sample station. As an illustration, samples representative of the Combe Martin Slates are identifiable by the prefix "CM", with CM02 referring to a sample taken close to the base of this unit. A synopsis of the code prefixes are provided below.

Lithostratigraphic unit	Abbreviation*
Morte Slates	M
Kentisbury Slates	K
Combe Martin Slates	CM
Lester Slates & Sandstones	L
Wild Pear Slates	WP
Little Hangman Formation	LH
Sherrycombe Formation	S
Rawns Formation	R
Trentishoe Formation	T
Hollowbrook Formation	H
Lynton Formation	LN

* As applied in this study

Figure 2.1 Sample nomenclature (lithostratigraphic abbreviations) applied in the present study.

Certain horizons were sampled or recollected from at times other than the main field seasons. This may account for any disparity in the numerical ordering of samples. Both conodont and palynomorph samples were integrated into a single notational scheme.

2.3 CONODONT SAMPLE COLLECTION AND PREPARATION.

2.3.1 Sample collection.

Details of sections sampled for conodonts and quantities of specific taxa recovered from each productive sample are provided within Appendix I. Details are also included of faunas recovered during reconnaissance sampling in 1986, as well as assemblages documented from material collected during the detailed sampling programmes undertaken in 1987 and 1988.

Of all rock types, Collinson (1965) remarked that limestones are usually the most reliable to yield large numbers of well preserved conodonts. With this in mind, and because the probability of isolating conodonts randomly from a slate-dominated sequence is comparatively low, calcareous sandstones or carbonates within the Lynton Formation and Ilfracombe Slates were preferentially sampled. Sampling intervals were governed by limestone thicknesses, with local stratigraphic continuity dependant largely upon structural complexity (note details in Appendix I, and sample positions marked upon the synoptic biostratigraphic charts of Chapter 4 - Figs. 4.2 & 4.3). The limestones members exposed at the nominate localities of the David's Stone and the Jenny Start cliffs were not sampled, principally due to problems of intense localised structural deformation and also inaccessibility. Alternative, lateral equivalents of these units were studied instead. On average 1-2kg samples were collected from each sample station. In total, approximately one quarter of a metric tonne of limestone was processed. Sample characteristics and subsequent yields are also provided in Appendix I.

2.3.2 Conodont sample preparation.

Stone (1987) succinctly reviews current techniques applied by contemporary conodontologists in the extraction, concentration and subsequent analysis of conodont specimens. Loosely following the methodology outlined therein, samples collected in the present study were crushed to coarse pebble or cobble sized fragments (4mm-64mm), weighed and standardly immersed in a 10% solution of acetic acid. 20g of calcium acetate were added to buffer the solution and so prevent, or at least minimise the corrosion or complete dissolution of any potential conodont fauna contained therein. Where samples proved particularly resiliant to such digestion, they were treated with 7% formic acid (the solution buffered with calcium formate). Such treatment was implemented for lithotypes with a low carbonate component, such as the calcareous sandstones of the Lee Stone Member, and also the highly ferruginous, ferroan dolomites of the Combe Martin Beach Limestone Member. As a matter of course, after 2-3 days the spent acid solution and insoluble slurry were passed through a sieve stack incorporating 75μm, 125μm and 700μm sieves. Once thoroughly washed, the coarse fraction (>700μm) was re-acidised (to a maximum of 6 times). The fine residues were retained and oven dried at 60 C.

Conodonts were subsequently concentrated using a variety of media. Bromoform (with specific density [S.D.]= 2.894 at 20 C), tetrabromoethane (S.D.= 2.96) and diiodomethane (S.D.= 3.325 at 20 C) were used to isolate conodonts from the associated insoluble gangue mineral fraction. If a bromoform separation proved unsatisfactory, tetrabromoethane was used. Diiodomethane was only applied for residues enriched with pyrite (refer to Swift 1987, p.66). The bulky residues were further reduced in volume using either a Davis magnetic separator (kindly made available by Dr. R. J. Aldridge, formerly of Nottingham University) or a conventional Franz-type electromagnetic separator (see Stone 1987, p.26-27).

All final heavy fractions were scanned using an Olympus SZH binocular microscope and conodont elements isolated using a fine, moistened brush. Microfossils found in association with the conodont faunas were retained, and the entire microfossil assemblage stored within labelled slides. A representative quarter of all light fractions were also analysed, but yielded negligible skeletal material.

2.4 PALYNOLOGICAL SAMPLE COLLECTION AND PREPARATION.

2.4.1 Introduction.

The collection of potentially productive palynological samples is still highly speculative. There are no irrefutable means of predetermining palynomorph presence within a sampled horizon. Informal guide-lines exist which aspire to constrain indiscriminate sampling, and thus improve the probability of recovering palynomorphs (note observations in Cross, 1964; Schopf, 1964). Finer grained lithotypes and a tendency towards a black colouration are considered the optimum visual means of identifying a potentially productive palynological host lithotype. The subsequent methods of demineralisation and kerogen concentration are well established, although oxidation procedures applied commercially and in academe still appear to be relatively conservative (oxidation is commonly only implemented if organic matter is visually translucent or opaque). As a result of oxidation, some form of chemical or physical modification of organic substances (*e.g.* sporopollenin) is suggested by the changes in palynomorph colouration observed during this processes. However, the exact mechanism of "oxidation" to date remains enigmatic (refer to the discussion in Traverse, 1988, p.43-44).

2.4.2 Sample collection.

The principal sections sampled for palynology are detailed in Appendix II, along with an approximate indication of the composition of the kerogen isolate. The synoptic biostratigraphical charts presented in Chapter 4 schematically order palyniferous sample stations sequentially through the lithostratigraphic column. Figures 2.2 and 2.3 depict the geographical location of samples collected through the Kentisbury Slates and overlying Morte Slates. Within these two lithostratigraphic units, it is at present virtually impossible to chronologically order samples between isolated sections, largely due to local structural complexity and in part to the sedimentological monotony of the succession. As will be mentioned in Chapter 4, palynological assemblages recovered from these two units were merely tabulated with no inference as to the relative ordering of samples.

During the course of this palynological study, over 450 samples were processed. This data base includes reconnaissance samples collected in 1986, and material from the subsequent detailed sampling surveys of 1987 and 1988. Only a representative selection, which provide the basis of the results documented herein, are systematically detailed.

Fine grained, indurated lithotypes (slates) constitute a high percentage of the Devonian

FIGURE 2.2. THE GEOGRAPHICAL LOCATION OF PALYNOLOGICAL SAMPLES COLLECTED FROM THE KENTISBURY SLATES

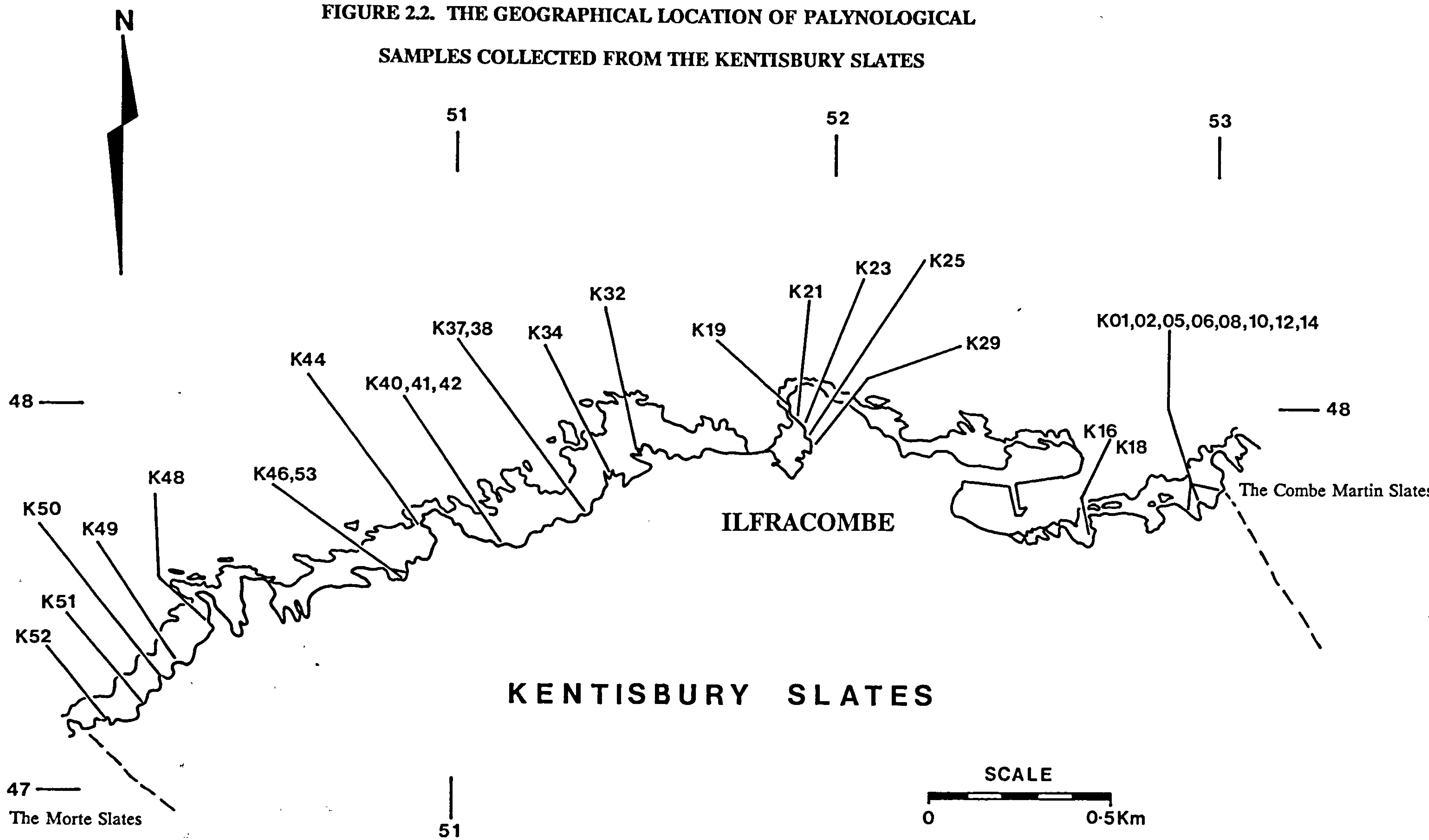


FIGURE 2.3 THE GEOGRAPHICAL LOCATION OF PALYNOLOGICAL SAMPLES COLLECTED FROM THE MORTE SLATES.

sediments that outcrop in North Devon. During the course of this study all the lithostratigraphical units from the basal Lynton Formation through inclusive to the Morte slates were extensively sampled, intervals ranging from the centimetre scale to 10's of metres (dependant upon the local availability of suitable horizons, inconjunction with structural complexity): weathered exposures were avoided, as well as structural features such as faults, intensely veined sections, and fold closures. Excluding parts of the Morte Slates and the ephemeral stream deposits within the Hangman Sandstone Group, the finer grained, homogeneous dark blue-grey slates were preferentially collected (palynomorphs were nearly always recovered from samples displaying these visual and textural characteristics). This sampling bias followed reconnaissance sampling and an initial investigation during the latter part of 1986, during which a suite of different lithotypes of variable colouration and grain size were processed. As a consequence, this optimum palyniferous lithotype was identified in the study area.

In addition to sample preparation for conodonts, a number of limestones were processed for palynology but their organic component proved negligible. Subsequent palynological sampling was therefore restricted to silicate lithologies. In part the Morte Slates comprise olive green lithologies, with the middle Hangman Sandstone Group containing a predominance of reddish tinged sediments: both either proved barren or yielded an impoverished organic component.

2.4.3 Palynological sample preparation.

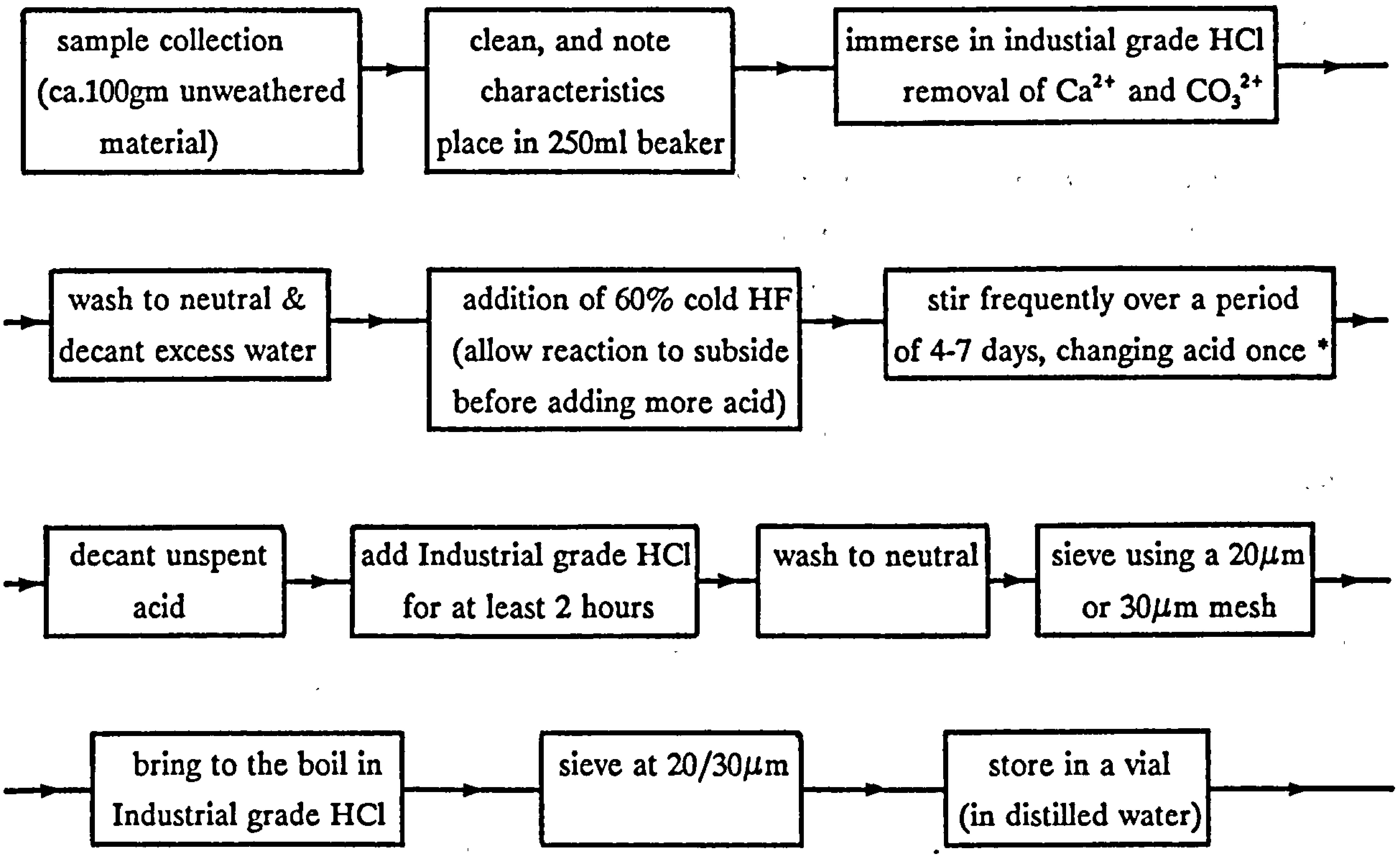
Phipps & Playford (1984) provide a comprehensive guide to the variety of chemical and physical techniques available for the extraction and subsequent concentration of palynomorphs from sediments. These were followed in part by the present author. Prior to treatment with hydrofluoric acid, the colouration and additional hand specimen characteristics of the sediment were noted (see colouration and carbonate content tabulated within Appendix II). Figure 2.4 provides a resumé of the standard extractional methodology applied in this study. Approximately 100g of cleaned, unweathered sample was demineralised. The highly indurated nature of the sediment necessitated two stages of immersion in cold 60% hydrofluoric acid, with the sample sieved in between to reduce the volume of the residue (and thus facilitate further digestion), and the acid subsequently replenished. The vast majority of disaggregated samples were sieved through a 20μm filter mesh, although occasionally a 30μm mesh was used, depending whether or not samples proved highly siliceous and/or difficult to sieve. Mesh sizes were chosen with discretion, as during preliminary trials the minimum diameter of structured palynomorphs appeared by and large to exceed 25-30μm. Although occasionally enriched in pyrite, the final kerogen extracts were generally devoid of undissolved mineral, such that further concentration using heavy liquids (zinc bromide) was not required. Subsequent treatment with fuming Schultz solution removed any pyrite. All palynological samples were free of amorphous organic matter, so the use of an ultrasonic probe was not required. Prepared kerogens were stored and only oxidised immediately prior to transmitted light microscopy.

The high rank and associated opacity of all organic matter recovered from the Devonian sediments of north Devon necessitated oxidation, to permit any form of systematic study in transmitted light. Initial applications of Schultz solution (30ml saturated $KClO_3$ solution : 90ml concentrated HNO_3, Phipps and Playford 1984, p. 13) proved ineffective in increasing palynomorph transparency. Amongst others, Playford & Helby (1968), Deunff (1977) and Coquel & Deunff (1977) have detailed methodologies for oxidising carbonized palynomorphs, although the techniques outlined by these

Figure 2.4

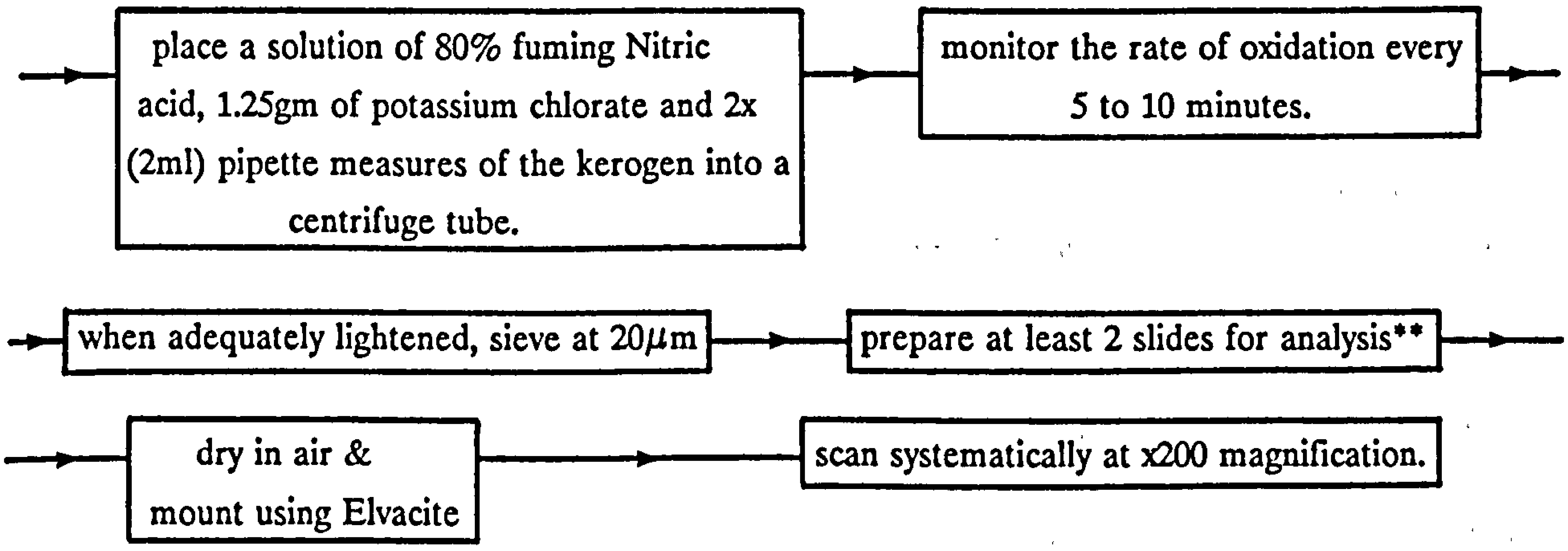
Procedure employed in the extraction and subsequent preparation of dispersed organic matter from the palyniferous Devonian sediments of north Devon.

DEMINERALISATION



* duration of acidisation is largely dependant upon the silicate content of the sample, its grain size and metamorphic facies. A simple test to determine whether the sample is sufficiently demineralised is to feel the texture of the residue, whilst stiring with the glass stiring rod.

OXIDATION AND MOUNTING



** no dispersal agents were used.

workers do appear somewhat time intensive and overly complicated. In a palynological study of Devonian sediments on Shetland, Marshall (1980) remarked that to successfully macerate high rank spore assemblages the oxidising media should be selected with care, with emphasis accorded to both the concentration of the system and the duration of the reaction. By adopting the approach of Marshall (1980), the optimum oxidation medium suitable to the material recovered from north Devon was recognised.

Extensive experimentation with the oxidation process incorporated the controlled variation in the relative percentages of cold potassium chlorate solution and fuming nitric acid. 80% fuming nitric acid and 1.25g of potassium chlorate proved adequate for the standard oxidation of all organic kerogen isolates, irrespective of stratigraphic position (also listed in Appendix II are specific details relating to the duration of oxidation for each sample). Although certain kerogen constituents responded differently to the influence of oxidation (refer to discussion in Section 2.7) the above reagent mixture was considered the most effective, with the duration of oxidation simply varied in a number of separate treatments, so as to attempt the clearing of all the kerogen components. Oxidation times were commonly between 30-90 minutes (rarely greater). Personal observations suggested that the main phase of clearing appears to take place either instantaneously, or well within the first 15-30 minutes of treatment. Prolonged and vigorous exposure usually proved ineffective, presumably because the potency of the solution decreases with time. The observed variation in the duration of oxidation is difficult to explain, although this may reflect subtle, finite variability in the intensity of organic metamorphism. However, no discernible relationship was recognised between the duration of oxidation and vitrinite reflectance (refer to Chapter 6). Furthermore, the time of exposure proved different for successive samples within individual sections. On the rare occasion that a kerogen isolate was over oxidised, the organics tended to flocculate, but using an ultrasonic probe (for a matter of seconds) the particulate matter was dispersed.

At regular intervals throughout each oxidation treatment, the translucency and associated changes in colour of the organic matter was checked, and when considered sufficiently transparent the reaction was neutralised with distilled water and slides prepared. As a matter of course, two slides were produced per sample in accordance with standard methodology. No dispersive agents were used, with the kerogen isolates (in distilled water) simply pipetted evenly onto a cover-slip and allowed to dry at room temperature. Evaporation of the distilled water was not enhanced by use of a hotplate, to avoid inducing re-darkening. Once thoroughly dry, coverslips were mounted using the comparatively inert mounting medium "Elvacite 2044".

An as yet unexplained phenomenon of oxidised, initially opaque organic matter is its instability and comparatively short "shelf-life". This phenomenon has been remarked upon by Dolby (1970b), Marshall (1980) and Van der Zwan (1980). Phytoclasts oxidised according to the methodology discussed above did not remain transparent indefinitely. Indeed, material prepared in this manner could only be studied for a period of up to (approximately) three months (maximum) after oxidation, during which time the material degraded and eventually either regained its original opacity or finally appeared too turbid to allow honest taxonomic appraisal. In extreme cases and during periods of high atmospheric humidity the "shelf-life" proved as short as 24 hours - the storage of oxidised strewn slides in a refrigerator after analysis seemingly retarded this re-darkening process. As will be discussed in Section 2.8, it was for this reason that no new taxa were formally proposed, as no type material could be designated and stored for posterity. Preliminary investigations upon re-darkened material using infra-red microscopy proved inconclusive, but despite the inevitable re-darkening of this material, specimens were logged and location coordinates noted (refer to the plate descriptions). Future innovations to infra-red microscopy may allow re-examination at some later date.

The only reservation about the technique outlined above concerns comparisons between dimensions of palynomorphs listed herein with type specimens from coeval, presumed lower rank sediments. Workers should be aware of potential specimen swelling and/or contraction induced either collectively or individually from diagenesis, coalification and/or subsequent specimen extraction/oxidation (Smith & Butterworth, 1967; Pierart 1974, 1978). Indeed, Johnson (1985) has advised caution when quantifying oxidised organic matter, as substantial exinal swelling may occur. From a number of personal communications, it appears palynologists are by and large averse to the prolonged oxidation of organic matter, fearing the destruction of certain kerogen constituents. Although these considerations are acknowledged and in certain instances justified, faced with the dilemma of oxidation and the potential destruction of certain (?minor) components versus non-oxidation and negligible taxonomic work, the author naturally favoured the former approach. The quality of the material illustrated in Chapter 3 clearly demonstrates that with the careful application of strong oxidising reagents, initially opaque organic matter may be sufficiently lightened and not destroyed. Furthermore, the type and concentration of the reagents applied in the present study were considered to have negligible corrosive or other detrimental effect upon primary palynomorph structure. This is somewhat surprising, as at such elevated rank, palynomorphs have traditionally been perceived to be brittle and easily fragmented (*e.g.* Correia, 1967; Cramer, 1972).

2.4.3a *A rapid technique for palynomorph extraction.*

Magné & Dufaure (1964) outlined a technique for the rapid recovery of radiolaria from siliceous sediments, involving the combined application of HF acid and hydrogen peroxide (refer to the resumé in Stone 1987, p. 25). This technique was successfully applied by the present author in the recovery of Ordovician conodonts from a suite of Scottish cherts (material supplied by Prof. Ray Ethington, University of Missouri). Although the reaction is extremely violent, strongly exothermic and incorporates an oxidising reagent, the writer further considers it a potential means for recovering palynomorphs from siliceous sediments. 100g of five, partially pulverised slate samples (known to be palyniferous) were treated with a mixture comprising 200ml of 48% H_2O_2 and 300ml of 60% industrial grade HF. The reaction became strongly exothermic and peaked after 5-10 minutes (noted in Stone as 20-30 minutes). Once this reaction subsided, unspent acid was decanted, the residue neutralised with distilled water and the slurry subsequently sieved. Neoformed fluorides were removed using conventional techniques (*i.e.* boiling in industrial grade hydrochloric acid). The kerogen isolate was retained and the opaque palynomorphs oxidised using the procedure outlined earlier. Kerogens extracted in this manner were compared with material recovered from the same samples using the standard methodology of simple, cold HF immersion (taking up to 4-5 days). Both mounted isolates contained palynomorph assemblages which appeared near identical in preservation and composition. Although expensive, this technique may prove to be a viable and commercially attractive means of extracting organics from lower rank sediments. Indeed, although this method clearly needs further investigation, it may prove of particular interest to commercial palynology, where time is of the essence.

2.5 MICROPALAEONTOLOGICAL MICROSCOPY AND PHOTOGRAPHY.

2.5.1 Binocular microscopy.

All conodont residues were scanned using an Olympus SZH binocular microscope. Attempts were made to photograph a selection of different conodont elements so as to convey the high conodont Colour Alteration Indices (C.A.I.) using this binocular microscope and daylight colour film. Specimens were illuminated with a strong oblique incident light source, with a blue filter fitted to the camera to compensate for the artificial lighting. Unfortunately, the resolution obtained and the quality of the subsequent prints were considered to be inadequate for use herein.

2.5.2 Transmitted light microscopy.

Palynological slides were logged at x200 magnification on an Olympus BHS 313 microscope (Serial No. 582701) housed in the Department of Geology, University of Southampton. Detailed taxonomic observations were made using a x100 oil immersion objective, with all systematic descriptions undertaken at x1000 magnification. All prepared slides and unoxidised kerogens isolates are similarly stored at the above address.

2.5.3 Transmitted light microphotography.

All phytoclasts (encompassing woody detritus and palynomorphs) were photographed using the aforementioned Olympus BHS 313 microscope and an Olympus C-35AD-2 camera (plus associated PM-10ADsp colour monitor attachment and AD automated exposure control unit). The majority of specimens were photographed initially at x1000 magnification, or if exceptionally large by using the x40 objective. For high resolution work a x6 objective was housed within the PM-10ADsp camera turret. Kodak 35mm Panatomic X (32 ASA) black & white film (or equivalent), of reciprocity 2 was used. Exposure times varied according to the opacity of the specimen: the duration was usually of the order of ≈1-5 seconds (most thin walled, transparent acritarchs and miospores), and rarely exceeded 30 seconds (typical for opaque hystricospores and virtually the entire chitinozoa faunule). Spot metering compensated for variability in oxidised spore transparency ("oxidised colour"). For description and photography, all specimens were mounted in "Elvacite 2044", as the obtained optical resolution proved far better than that found using water strewn mounts.

2.5.4 Reflected light microscopy.

The preparatory techniques and methodology applied in rank determinations are outlined by Hillier & Marshall (1988) and comprehensively detailed within Chapter 6 (the present study). A Zeiss UMSP 50 (Photospectrophotometer) and IBM monitor, driven by the "SLAP" programme, allowed the measurement of organic reflectance. Photographs were taken using a Contax RTS II Quartz camera, and Kodak 35mm Panatomic X (32 ASA) black and white film. Exposure time was automated and maintained constant for all specimens, irrespective of pleochroic colour and orientation.

2.5.5 Scanning Electron Microscopy.

2.5.5a *Introduction.*

Extensive use was made of an ISI-60A Scanning Electron Microscope (SEM) for the analysis of the conodont faunas and palynofloras recovered from north Devon. Having gold coated the specimens under vacuum and configured the microscope to the optimum settings (working distance 8mm or 24mm; voltage 16kV; contrast and brightness dependant upon specimen size, orientation and adhesion to the stub), photographs were taken using Ilford FP4 120 black & white film. In all cases the electron microscope provided an invaluable insight into ultrastructural detail as well as more generalised evaluations of gross morphology.

2.5.5b *Conodonts and miscellanea.*

SEM stubs were initially coated with Wax-W, a black background medium standardly used in conodont photography. Elements representative of the conodont faunas were fixed to the SEM stubs using Leit-C Plast (carbon based) adhesive. Once gold coated, specimens were viewed from a variety of orientations; principally "upper view" for Pa elements as the morphography of this surface is of prime taxonomic use. Specimens were initially photographed at two basic orders of magnification, namely x110 and x70 (dependent upon size). Uniformity in magnification allowed an appreciation of size variation between variants of probable ontogenetic lineages (*e.g. Icriodus brevis*, Plate 3.2, figs. 1-11). Representatives of the associated microfauna were also photographed using this microscope, and are illustrated on Plate 3.7.

2.5.5c *Palynology.*

Representative kerogen isolates from all the principal lithostratigraphic units were mounted as an aqueous strewn directly onto polished stubs, allowed to dry and subsequently gold coated. A variety of procedures were initially tried, in preparing organic-walled microfossils for analysis using the SEM. These included first mounting a kerogen isolate onto a cover slip which was then secured to the stub with electrically conductive paint, or mounting an organic isolate directly onto a stub coated with Wax-w (as used in conodont photography). However these two preparatory techniques did not markedly improve the quality of the resulting image. Single specimen-mounts were also analysed. Detailed observations provided by the scanning electron microscopy were integrated into the descriptive systematics.

The application of scanning electron microscopy to Devonian palynological research is by no means a recent innovation (*e.g.* Riegel, 1968). Indeed in the context of the British Isles, Le Gall *et al.* (1985) based a number of miospore identifications on SEM observations (in a study of the Upper Devonian palynology of the Gramscatho Group, the Lizard, South Cornwall).

Recently Dean (1989a,b) has demonstrated the viability of palynological investigations in Southwest England based solely upon SEM work. For the Lower Devon (Emsian) miospore assemblage illustrated by Dean (1989a) from south Devon, such a technique is clearly viable, being revolutionary in a sense as such sediments have traditionally been considered undatable. Subsequently, Dean (1989b) illustrates a comparatively diverse but again morphologically simplistic palynomorph assemblage of (?)Famennian aspect from east Cornwall.

From personal observations the applicability of an exclusively SEM-based investigation of Devonian miospores (*e.g.* Dean 1989a,b) has severe limitations. At present, Devonian miospore systematics rely heavily on transmitted light observation and by necessity require comparatively transparent material (note in principal the remarks of Playford 1977, p. 9-10). With the increase in morphological complexity of spores from late Emsian/early Eifelian times onwards, it is doubtful whether at present (and bearing in mind the current status of the literature) assemblages of such an age could be objectively evaluated based solely upon SEM analysis. According to Dean (*pers.comm.*, 1989) specimens were not manipulated once mounted on SEM stubs (although this has been achieved in other studies *e.g* Walker & Walker, 1984): in Dean's research the identification of miospores is therefore dependent largely upon the original orientation of the (strewn) mounted specimen. Furthermore, by relying simply upon the SEM it is unlikely whether certain subtle internal structures can be resolved (such as the intexinal granulation noted for *Insculptospora confossa*, unless of course the exoexine is fortuitously ruptured). Clearly the two techniques still need to be used collaboratively, and as the current research programme has demonstrated, with careful but somewhat unconventional oxidation, palynomorphs extracted from indurated, high rank sediments can be sufficiently lightened. Therefore, even when confronted with material of such elevated rank, observations using the SEM can be integrated with transmitted light microscopy.

2.6 SAMPLE PRODUCTIVITY.

2.6.1 Conodonts.

Samples collected from the Lynton Formation and Ilfracombe Slates were processed for conodonts. The yields from these carbonates proved relatively low, the faunas poorly preserved and of comparatively low diversity. Of the 82 horizons sampled, 53 yielded conodonts. Thirty-three Pa pectiniform taxa were documented, plus a variety of (presumed) vicarious coniform, ramiform and Pb elements. All the faunas were dominated by icriodids, with polygnathids recovered exclusively from the Ilfracombe Slates. Yields for the fossiliferous samples (corrected to number of elements per kilogram) varied from as little as <1 element/kg to, in an exceptional case (sample K53), 282 elements/kg (refer to Appendix I). The icriodid to polygnathid ratios also differ quite substantially, from comprising exclusively icriodids, to a 3:1 ratio. The low diversity, abundance, and isolated occurrence of the faunas, coupled with the absence of a number of important zonal polygnathid taxa limited the biostratigraphical utility of the conodont faunas for the sequence as a whole.

2.6.2 Palynomorphs.

As the work of Pflug & Reitz (1987) recently demonstrated, organic-walled microfossils can survive comparatively intense metamorphism. This is clearly the case for the palynofloras recovered from the Devonian of north Devon, as the sediments in this area are of lower greenschist facies (chlorite grade).

Palynomorphs proved by far the most ubiquitous microfossil group within the marine or marine-influenced sediments. 238 samples provide the basis of the palynological aspect to this current research programme, of which 74% yielded miospores, 42% miospore tetrads, 23% acritarchs, 37% chitinozoa and 43% scolecodonts. Over 130 species of miospore, 29 acritarch taxa, 11 forms of chitinozoa, 5 morphotypes of scolecodonts and 4 heterogeneous groupings of wood were documented.

The relative components of the kerogen isolates and the palaeoenvironmental implications thereof are discussed in Chapter 5. There is minimal evidence to support differential palynomorph sorting.

The method of visually quantifying the various components within a palynological assemblage is still somewhat arbitrary and prone to human error. Preliminary absolute counts of particulate organic matter within prepared slides were considered unrepresentative (largely due to variable oxidation and poor preservation), with related estimates of palynomorph yield per gram of sediment considered inaccurate. In very broad terms, the kerogen isolates were noted to contain a predominance of terrestrially derived organic matter (miospores, tetrads and wood debris), with marine organic-walled microfossils proving infrequent or absent (refer to Chapter 5).

In an attempt to objectively evaluate the organic component within the Devonian sediments of north Devon, twelve samples were chosen at random from the 238 sample set. Using a Carlo Erba Instruments EA 1108 Elemental Analyser (CHNS-O), the Total Organic Carbon (T.O.C.) component was assessed (for methodology refer to Appendix IV). The results are plotted on Figure 2.5. T.O.C. levels are clearly very low, ranging between 0.1-0.3%. Unfortunately an insufficient number of samples was analysed to confirm any relationship between T.O.C. content and sedimentary facies.

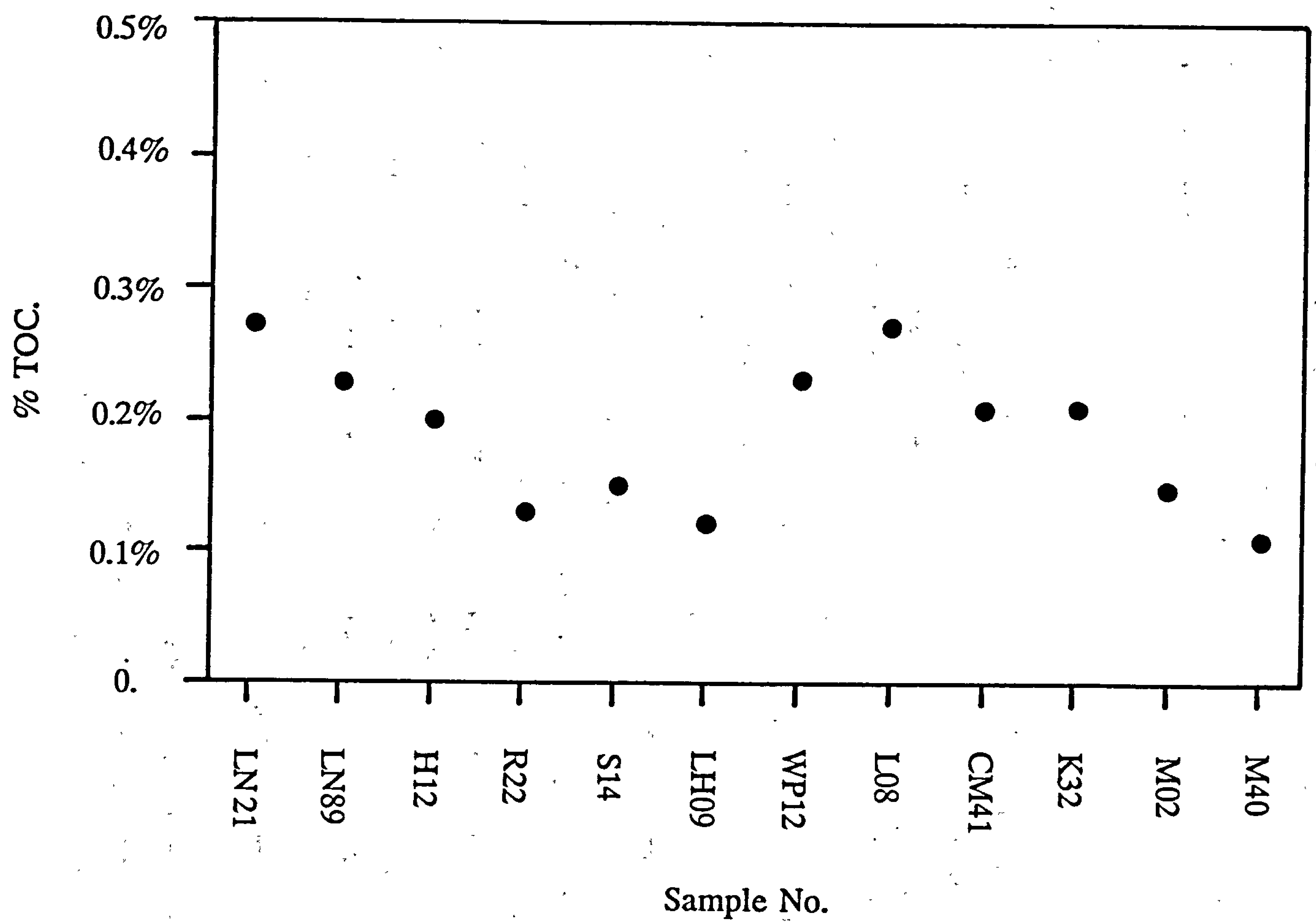
2.7 MICROFOSSIL PRESERVATION.

2.7.1 Conodonts.

The preservation of conodont elements recovered in the present study varied considerably, and when notably poor, limited detailed taxonomy (refer also to the discussion of conodont preservation in Chapter 6). Aware of the potential damage inflicted upon conodont elements through energetic and thoughtless processing, great care was taken to ensure that both chemical and mechanical degradation was kept to a minimum. Through buffering and the use of sample suspension-meshes (which elevated the coarse fraction above the base of the bucket, and also facilitated subsequent washing), the faunas were recovered in what was considered their optimum condition. As a consequence the fragmented, fragile, or etched condition of the conodont elements was attributed to factors other than sample demineralisation (*e.g.* diagenesis or regional metamorphism).

Tectonically deformed conodonts have been reported in the literature (*e.g* Kovacs & Arkai, 1987; Plate 13.5). The recovery of deformed conodonts in the present study was a clear indication of the severity of regional tectonic influences upon conodont preservation (refer to Plate 3.7, figs. 1-4 herein). Certain icriodids appear to have been either longitudinally deformed (*e.g* the elongate element illustrated in Pl. 3.7, fig. 1), or transversely sheared (Pl. 3.7, figs. 2, & 3). The narrow platformed polygnathid (Pl. 3.7, fig. 4, = *Polygnathus rhenanus*) displays an essentially intact but sigmoidal free blade: this sinuosity is a clear indication of tectonic distortion. In addition, a large percentage of the fauna were highly fragile (*e.g.* note the cracks apparent in the specimen of *Polygnathus linguiformis linguiformis*, Pl. 3.6, figs. 1 a,b,c). In rare cases, specimens displayed "crack-seal" textures (*e.g.* the Pb element, Pl. 3.6, figs. 7 a,b). Amongst others, Müller & Nogami (1971) have reported the organic repair of broken conodont elements, but the scale and severity of the breaks referred to above are considered far too extensive to be attributed to such organic "re-setting" by the host animal. Rather, these features further demonstrate the influence of tectonism on the fauna. Furthermore, virtually all conodont elements recovered were incomplete, with the anterior

Figure 2.5 Total Organic Carbon (T.O.C.) content representative of the Devonian sediments of north Devon.



free-blades of most polygnathids partially or entirely missing (note general preservation of the polygnathids illustrated on Plate 3.5). The *Icriodus* faunas also displayed highly fragmentary lower surfaces (attributable ?largely to abrasion and fragmentation during sedimentation).

Surface alteration textures were noted on some conodonts, and indeed element "corrosion" was a widespread characteristic. Rejebian *et al.* (1987) illustrate a similar "etched" surface-texture, attributing this to the influence of regional metamorphism. In the present study, elements occasionally appeared so intensely corroded that even generic identification was not immediately obvious. The remnants of diagenetic alteration of organic apatite were occasionally noted. Near-cubic or polyhedral crystal-growths were occasionally recorded "embedded" in to the conodont elements (refer to Pl. 3.7, fig. 9: note the polygonal crystals discernible between the spindle denticulation).

2.7.2 Palynomorphs.

2.7.2a *Introduction.*

The small dimensions and the usually compressed form of dispersed fossil palynomorphs can cause problems to taxonomy, which may be further inhibited by the opacity and adverse preservation of phytoclasts. The preservation of organic-walled microfossils documented in the present study proved highly variable, either within a single assemblage or between successive samples. Although plate 3.9 may more appropriately have been included within this chapter, it precedes the palynomorph plates of Chapter 3 to show that despite adverse preservation and high Thermal Alteration Indices (T.A.I., *sensu* Staplin 1969), the quality of most oxidised palynomorphs is moderate to exceptional.

Of the lithostratigraphical units studied, in general the Lynton and Little Hangman Formations and the Wild Pear and Combe Martin Slates yielded the least well preserved palynomorphs. Intense, highly localised structural deformation may partly account for such poor preservation (as was earlier suggested to account for the variability in the duration of oxidation). However, assuming vitrinite reflectivity to be a means of gauging the intensity of metamorphism (either burial or otherwise), no direct relationship was established between the occurrence of poorly preserved assemblages, and those samples with an elevated vitrinite reflectance signature. In the context of north Devon, specimens of comparable preservation were recovered from both the "lower rank" (Rm $\approx$ 4.5%) and "higher rank" (Rm $\approx$ 7.5%) sediments. Similarly, the predominant sediment-type of a sampled section appears to have had minimal influence, as equally well preserved phytoclasts were isolated from sequences dominated by either argillaceous or sandy lithotypes. The negligible recovery of organics from carbonate lithologies precluded any meaningful comparison.

Within the dispersed organic isolates recovered from north Devon, five categories of preservation were defined, namely; (i) opacity, (ii) pyrite damage, (iii) foreign sporopollenin adhesions, (iv) exine turbidity and corrosion, and (v) palynomorph fragmentation. These are discussed below.

2.7.2b *Opacity* (Pl. 3.9, figs. 1 & 2).

Palynomorph "colour" is discussed in Chapter 6, relative to vitrinite reflectance studies and conodont C.A.I. evaluation. Palynomorph colouration (subjectively calibrated according to the Thermal Alteration Index (T.A.I.) of Staplin, 1969) is mentioned here, however, as initial opacity and on occasion the translucency of oxidised specimens proved a major limitation in the thorough documentation of palynomorph assemblages. As already briefly mentioned, a further limitation to the prolonged analysis of the palynofloras proved the instability of the oxidised kerogen isolates (refer to the earlier discussion in Section 2.4.3). In the present study, oxidation appears to have had a highly variable effect upon most kerogen isolates: within individual assemblages some morphotypes were seemingly unaffected by the process, whereas others may conceivably have been damaged (realistically, specimen damage attributable to oxidation is believed negligible). The ability to lighten opaque organic-walled microfossils may be dependent on palynomorph construction, although in practice this is often difficult to gauge. However, in general terms thick-walled phytoclasts usually proved difficult to lighten, relative to thinner-walled specimens (refer to Section 2.8 below).

The progressive change in palynomorph transparency has provided the basis of countless geothermometric evaluations, since the realisation that besides inherent pigmentation, palynomorph colour is controlled by the influence of temperature on the encasing sediment (*e.g.* Staplin, 1969; Barnard *et al.*, 1976; Brooks, 1981). A comparison of the colour of unoxidised organic material (recovered from all the palyniferous units studied) with the maturation index of Staplin (1969) reveals values of 5, irrespective of sedimentary facies and more significantly, stratigraphic position. This uniformity in phytoclast colouration in the study area suggests that the organics throughout the region have been influenced by high temperatures. This observation corroborates the extreme C.A.I. values (*sensu* Epstein *et al.*, 1977) and the widespread, persistently high levels of vitrinite reflectance similarly noted through this sequence.

It is worth noting that high rank (and related organic opacity) does not necessarily equate to poor specimen preservation (*i.e.* although opaque, palynomorphs encased in thermally mature sediments may, further to oxidation, appear well preserved). This observation is confirmed by findings of the present study

2.7.2c *Pyrite damage* (Pl. 3.9, figs. 3-7).

The most common, secondary feature noted within the oxidised palynomorph assemblages were the remnant polygonal pits produced by the once-growth of pyrite crystals into such organic wall. The kerogens isolated from north Devon were inclusively treated with fuming nitric acid (and potassium chlorate), which not only increased the transparency of the organic matter, but also removed any such pyrite crystals originally embedded in this organic material. Only regular, polygonal cavities were left, and thus observed in oxidised kerogen strewn mounts. Pyrite "pitting" affected a substantial percentage of the particulate organic matter recovered in this study, being most severe within the assemblages recorded from the middle Lynton Formation, the Little Hangman Formation, the Wild Pear Slates and sporadically throughout the Combe Martin and the Kentisbury Slates. Such corrosion is comparatively easy to recognise by the distinct symmetry of indentations/perforations, and is readily distinguishable from primary foveolation, which tends to be more smooth and rounded in morphology (as noted upon the distal hemisphere of *Emphanisporites foveolatus*). Virtually all the different organic microfossil groups documented in the present study were affected by this phenomenon, although to varying degrees. As well as miospores and acritarchs, wood phytoclasts appear to have been common nucleation centres for the growth of pyrite. However, and specific to north Devon, chitinozoa tests and scolecodont elements were usually free from pyrite cavities, which may be a reflection of the differences in wall chemistry. However, amongst others, Paris (1981) illustrates intense pyrite damage to chitinozoa tests: this makes the absence of pyrite damage to such microfossils in north Devon all the more unusual.

The degree of pyrite damage proved highly variable within constituents of an individual assemblage. Palynomorphs of all shapes, sizes and constructions were indiscriminately influenced. Pyrite relics in palynomorphs have been discussed in the literature by Love (1958; 1962, p. 447) and more extensively by Neves & Sullivan (1964). Neves & Sullivan (1964) in particular recognised three distinct morphotypes of pyrite relic, and believed anaerobic bacterial attack to have induced such mineral growth in organic matter. Pyrite damage is known to influence material of quite variable rank. For the studied material, there was no means of assessing whether pyrite growth in fossil palynomorphs was largely attributable to diagenesis, or the effect of regional metamorphism.

2.7.2d *"Foreign" sporopollenin adhesions.* (Pl. 3.9, figs. 8, 9, ?13 & 14).

Occasionally, a veneer of "foreign" sporopollenin material was easily recognisable in the present study, observed adhering (preferentially) to the exine of miospores. Such features were only confirmed as secondary when specimens of *Insculptospora confossa* were recovered bearing a variably developed "apiculose, sculptured veneer" on the outside of the exoexine (refer to Pl. 3.9, figs. 8, 9 herein). By definition, this generic complex displays a sculptured inner body and an untextured exoexine (Marshall, 1985), so that any "ornament" on the outer layer is clearly not a primary facet. Such tapetal residue may have fused to the spore coat whilst contained within the parent sporangium (immediately prior to dispersal), or alternatively may have "developed" either during dispersal, encasement within the sediment, or through the subsequent extraction and oxidation of the specimen.

In the case of *Insculptospora confossa* (Richardson) Marshall 1985 this surficial texture was readily identifiable as a secondary attribute. With other specimens this was not so easy to deduce, and on occasion it proved almost impossible to differentiate primary apiculose ornamentation form a veneer of "foreign" sporopollenin matter. Indeed, a complex of simple, finely apiculate miospores of believed negligible stratigraphic utility, were noted sporadically throughout the studied sequence. However, unless the ornament was interpreted as obviously primary (as with forms attributed to *Apiculatisporis* spp. or *Cyclogranisporites* spp.) and in view of the described pseudo-sculpture to *Insculptospora confossa*, such a texture was regarded as secondary in origin.

2.7.2e *Microbial scars, "parasitic borings" and exine turbidity* (Pl. 3.9, figs. 10 and 11).

The microbial scarring of pollen and spore exines has been extensively reported (*inter alia*, Love, 1962; Moore, 1963; Elsik, 1966, 1971). The occurrence of such features in this study proved on the whole rare, although the ?miospore fragment illustrated as figure 11 on plate 3.9 does display a number of well defined, subcircular, ±perforated scars, of probable microbial affinity. Representatives of the acritarch palynoflora displayed similar, subcircular perforations in the vesicle wall, which may well represent bacterial degradation (*e.g Maranhites perplexus,* Pl. 3.31, fig. 13).

Parasitic borings have been widely reported and illustrated in the literature (*e.g.* Eisenack 1931, p. 86; Laufeld, 1967 p. 316, 1974 p. 119 (in part); Jenkins 1967, p. 458; Wrona 1980, p. 138-142; Paris, 1981). A number of chitinozoa recovered in the present study displayed isodiametric perforations (e.g. Pl. 3.33, figs. 3, 13). There is some question whether these perforations represent the remnants of broken appendages, or are truly parasitic borings, although Paris (1981), amongst others, has demonstrated the tests of Chitinozoa to be solid, and lacking lumen when appendages break. It seems improbable that such rounded perforations were inorganically derived, although Martin (1971, p. 11-12) attributed features of similar morphology to the disintegration of framboidal pyrite.

In transmitted light some miospore exines appeared markedly turbid (note the degraded specimen of *Geminospora boleta*, Pl. 3.9 fig. 10). Such a reduction in wall transparency may reflect inorganic (chemical) or alternatively organic (bacterial) degradation, or merely represent inadequate oxidation.

2.7.2f *Palynomorph fragmentation.*

Naturally, the compression of any three dimensional object is most likely to induce some form of distortion, and during the present investigation, certain palynomorphs were consistently recovered in a particular mode of preservation. Theoretically tectonism may induce the fragmentation of organic matter on a millimetric scale, particularly if the material is coalified and therefore "brittle". Indeed, Clayton & Graham (1974) attributed the fracturing of large spores recovered from the Sherkin Formation, Southern Ireland, to a penetrative cleavage. In the present study certain, large, thick-walled palynomorphs were recovered in variable modes of preservation, ranging from severely fragmented to virtually intact and complete. If such spore-types fragment, they tend to rupture or tear irregularly. Conversely thinner-walled, acamerate palynomorphs showed a tendency to crumple or collapse quite passively. For camerate spores the exinal layers were noted to distort and/or disintegrate either independent of, or conversely in sympathy with, one another. The degree of cameration was influential in this respect, with the continuity of attachment between the two or on occasion three exinal layers, the exact positioning of detachment and the nature of the exinal sculpture influencing the extent/type of exinal distortion or fragmentation.

The typical preservation of hystricospores recovered from the Devonian sediments of north Devon (Pl. 3.24, figs. 1-5) illustrates the need to be aware of the severity of palynomorph fragmentation. In the Lynton and Hollowbrook Formations, hystricospores were notably prolific, but only in exceptional cases were specimens recovered complete. Bifurcate terminations to the processes are a morphological attribute of taxonomic significance in the identification of *Hystricosporites* spp. and *Ancyrospora* spp. Invariably these were missing. Conceivably this may have occurred either during initial dispersal (fluid or organism transportation), or as a result of mechanical abrasion during sedimentation, lithification and/or subsequent tectonism. Oxidation may also have influenced such appendage preservation. Occasionally, the poor preservation of hystricospores proved them virtually indistinguishable from species of *Grandispora* spp., that display a closely appressed, laminate wall structure.

Ruptured laesurae were a widespread feature, irrespective of miospore morphology, rank or stratigraphic level. This may have been a primary (germination) or secondary (compressional) attribute, although the exact cause is impossible to ascertain.

2.8. THE VIABILITY OF QUANTITATIVE PALYNOLOGY AND INNOVATIVE TAXONOMY.

Attempts were initially made to classify and quantify the various kerogen constituents logged during standard slide analyses. Qualitative yields of palynomorphs per gram of sediment were estimated, but in light of the more absolute, quantitative T.O.C. evaluations, such data were disregarded. As mentioned earlier, a recurrent problem proved the incomplete lightening of certain phytoclasts. Furthermore, oxidised palynomorph transparency proved highly variable within single assemblages. Unfortunately, the duration of oxidation was never optimised so as to sufficiently and simultaneously lighten both thick and thin walled palynomorphs. Usually, two separate oxidations were necessary to allow the documentation of both thick- and thin- 'walled palynomorphs (*e.g.* hystricospores and calamospores respectively). If left unmonitored, the time taken to increase the transparency of thick-walled phytoclasts not only over macerated a large proportion of the associated kerogen isolate, but also tended to partially damage(?) such thick-walled palynomorphs. Besides specimen opacity, identification was further limited by the ?bacterial degradation, pyritisation and fragmentation of organic matter (as introduced in Section 2.7 above). Clearly, high rank and adverse palynomorph preservation made both quantitative palynology and the formal designation of new taxa unfeasible. Once oxidised, all organic matter was noted to progressively degenerate and eventually re-darken. This instability proved a major limitation to the prolonged study of oxidised kerogen isolates, and furthermore merited proportional and relative counts of palynomorphs (particularly miospores) unviable.

Although no detailed quantitative palynology was attempted, a qualitative assessment is provided of the numbers of each miospore taxon recovered. As will be outlined in the preamble to the palynomorph systematics (in Chapter 3), the methodology outlined by Balme (1988, p. 119) was adopted to subjectively convey generalised proportions of specific palynomorphs within an assemblage. Nomenclature referring to the stratigraphic distribution of taxa through lithostratigraphical units was considered ambiguous and unnecessary.

Despite the reservations noted above, a number of palynomorphs unreported in the literature and thus "unique" to the Devonian sediments of north Devon, were described (refer to Chapter 3 of the present study). Due to the aforementioned problems of oxidised specimen stability, such new morphotypes were simply logged, described and illustrated, but have been left within informal open nomenclature.

2.9 STORAGE OF MATERIALS.

The conodont faunas recovered in this study are held in Department of Geology, The University of Southampton: specimens illustrated herein are referenced to a particular storage window within each storage slide. Untreated rock samples and extracted but unoxidised palynological kerogens are also housed at the same address, as are the oxidised palynological strewn mounts which formed the basis of the current research project. Unfortunately, the instability of the material makes it most improbable that specimens can be re-examined in transmitted light at a later date. Specimens coordinates are provided to allow potential, infra-red microscopy in the future.

2.10. SUMMARY.

In the past, problems of poor microfossil preservation, low palynomorph yields, coupled with high T.A.I values, has limited the viability and applicability of micropalaeontological research in structurally deformed Hercynides (as remarked upon by Orchard 1979, and Streel 1986). In the present study, techniques standardly applied in the extraction and subsequent preparation of various microfossils from indurated sediments, were applied to samples collected from north Devon. Great care was taken not only to limit the unnecessary corrosion and abrasion of microfossils during extraction, but also in carefully monitoring subsequent organic oxidation reactions.

Conodonts proved the principal microfossil-types extracted from the sampled carbonates, although yields were uniformly low. T.O.C levels were similarly low throughout the siliclastic sediments sampled. By the application of standard oxidative reagents (fuming Schultz) but in a somewhat unorthodox manner, opaque palynomorphs were successfully lightened. This technique is believed to have minimal corrosive affect upon organic-walled microfossils.

Irrespective of sedimentary facies, terrestrially-derived material forms the predominant constituent of the isolated palynofloras. The miospore assemblages have the greatest biostratigraphical utility throughout the region, by virtue of their immense diversity and comparative abundance.

CHAPTER 3.

SYSTEMATIC PALAEONTOLOGY.

3.1 INTRODUCTION

This chapter provides systematic descriptions of an assortment of microfossils recovered from the Devonian sediments of north Devon. Conodonts and miospores have the greatest biostratigraphical utility, and are accordingly covered in the greatest detail. The conodont elements are described alphabetically by genera, using single element classification (*sensu formo*). The paucity in ramiform and coniform elements precluded the extensive application of multielement terminology. Following this section, the miospore population is systematically described. A brief resumé is also provided of other organic-walled microfossils found in association (but in reduced numbers) with the miospores. Where considered appropriate, introductory comments have been included for certain key conodont and miospore genera. Due to the comparatively low abundance, poor preservation and the lack of comparative publications, the acritarch, chitinozoa, and scolecodont assemblages, coupled with their limited biostratigraphical potential (relative to the miospores), the descriptions of these microfossils are by necessity brief.

Where established species have been recognised within the microfossil assemblages recovered from north Devon, the related synonymy lists comprise the first description of the taxon, coupled with alterations to the name or species-concept, and also more recent or considered important references. Synonymy lists have been kept to a minimum, and are acknowledged to be far from comprehensive, as the present study was concerned more with the practical applications of microfossils than with their detailed taxonomy. Non-nomenclatural characters are related to entries in the synonymy lists, based on the suggestions of Richter (1948) and Matthews (1973):

1990 No sign(s) in front of the year. Responsibility may or may not be accepted here for the inclusion of this reference: identification is considered valid.

? 1990 Question mark in front of the year. This reference is included with some uncertainty.

p 1990 p in front of the year. Only part of the reference refers to the species under discussion.

non 1990 non in front of the year. The figured specimens are considered atypical of the original intent of the designating author.

Recently Bengtson (1988) has reasserted the importance, viability and application of open nomenclatural schemes to systematic palaeontology. Based on this study, the following characters are used to convey the level of conviction by which generic or specific categories have been recognised in the present study.

- No notational prefix before either generic or specific name implies that the taxon is definitively identified by the author.

cf. - The identification is provisional, *i.e.* the form documented is similar to, but not identical with, an established taxon. The uncertainty may reflect poor preservation.

aff.- The form described is considered a new, previously undescribed species or subspecies. The material is insufficient for formal description, and best compared with the taxon referenced. The application of this term does not necessarily involve uncertainty.

? - Indicates that the identification is uncertain.

sp. (or sp.A, etc...) - Indicates species identification is impossible, and has not been attempted, or that the form illustrated cannot be associated with any known species. The use of sp. A, sp. B, *etc.* allows differentiation of more than one such taxon.

Details of the occurrence of each microfossil type are provided. The range charts presented within Chapter 4 (with reference to Appendix I & II) plot the temporal distribution of these taxa through the studied sequence.

Conodont data kindly provided by Dr. M. Orchard (*pers. comm.*, 1989) are integrated into the findings of the present study (with permission): details of the scanning electron photomicrographs supplied by Orchard are referenced in the text and illustrated independently (Plate 3.8 - "The Orchard Collection"). This material was recovered a number of years ago by Orchard from limestone units within Somerset, that are presumed contemporaneous with those that crop out within north Devon. These data were never published).

3.2 CONODONTS.

3.2.1 Conodont classification.

A multielement configuration of conodont elements is not a recent concept, being remarked upon as early as Hinde (1879). However recent discoveries of the rarely preserved conodont animal tissue (*e.g.* Briggs *et al.*, 1983), in conjunction with the documentation of exceptionally well preserved, fused clusters of conodont elements (*e.g.* Nicoll 1983, 1985) have greatly strengthened the case for the widespread adoption of a multielement classificatory scheme. Furthermore, Klapper & Philip (1971, p. 439) commented that continued usage of form taxonomy is not only biologically unrealistic but also retards a more comprehensive evaluation of conodonts. Despite these factors, there is still a degree of confusion within the classificatory schemes applied by contemporary Devonian conodont workers, largely due to the application of multielement taxonomy without the complete removal or rationalisation of traditional form taxonomic concepts. This dualism is however gradually being suppressed as form taxa are rationalised, junior synonymies eliminated and the transition to multielement classification finalised.

In the past, many Devonian form species have been defined upon minor and often ambiguous criteria, illustrating how unsatisfactory the current single element classification scheme can be. For example, the *Icriodus* plexus has undergone quite intense and seemingly (biologically) unjustifiable speciation. Although still highly contested, Nicoll (1983) recently proposed what the present author considers to be the most realistic element configuration for the apparatus of the *Icriodus* animal. In comparison, the multielement apparatus of the Polygnathidae is widely documented and reasonably well accepted (*e.g.* Lange 1968; Klapper and Philip 1971; Ziegler 1972; Sparling 1981; Nicoll 1985). In general ramiform elements are believed to have had a vicarious habit, and thus many (Devonian) conodont species are differentiated based solely upon the variability of pectiniform element morphology.

By and large, reconstructed Devonian multielement apparatuses have been determined by the statistical and visual equation of dissociated elements, incorporating data from studies of diagenetically fused clusters. Unfortunately few Devonian bedding plane assemblages have been documented (*e.g.* Mashkova, 1972), with the clusters reported by Lange (1968) considered to be coprolitic in origin (Ziegler, 1972). Despite such problems, the limited number of multielement "structural plans" in conjunction with homomorphy in elemental types has facilitated the recognition of Devonian multielement apparatuses.

In recent years increased attention has been focused on conodont palaeoecology, although the influences of dimorphism, ontogeny and ecological preference of certain generic complexes is still problematical, proving difficult to evaluate.

Within north Devon many of the limestones are rich in allochems, which suggested to Webby (1966b) deposition in an agitated water column. In the present study, many of these limestone have yielded conodonts. Recently McGoff & Briggs (1988; *pers. comm.* 1989) evaluated the hydrodynamic properties of different conodont element types, and deduced that even very low-energy flow regimes may be sufficient to induce breakage or simply differentially sort conodont elements (refer to discussion in Chapter 5, section 5.2.4). The disproportionate relative numbers of conodont elements recovered, coupled with their abraded and fragmentary form supported the idea that postmortem sorting was probably significant. Quite often, conodont faunas may be anticipated to have been subjected to spatial and/or temporal mixing, although within north Devon this proved difficult to gauge. In spite of this, the faunal composition noted in the present study may in part reflect some primary distributional pattern, equatable to relationships (biofacies) recognised within coeval European and American Devonian palaeoenvironments (refer to the review in Chapter 5, section 5.2.2).

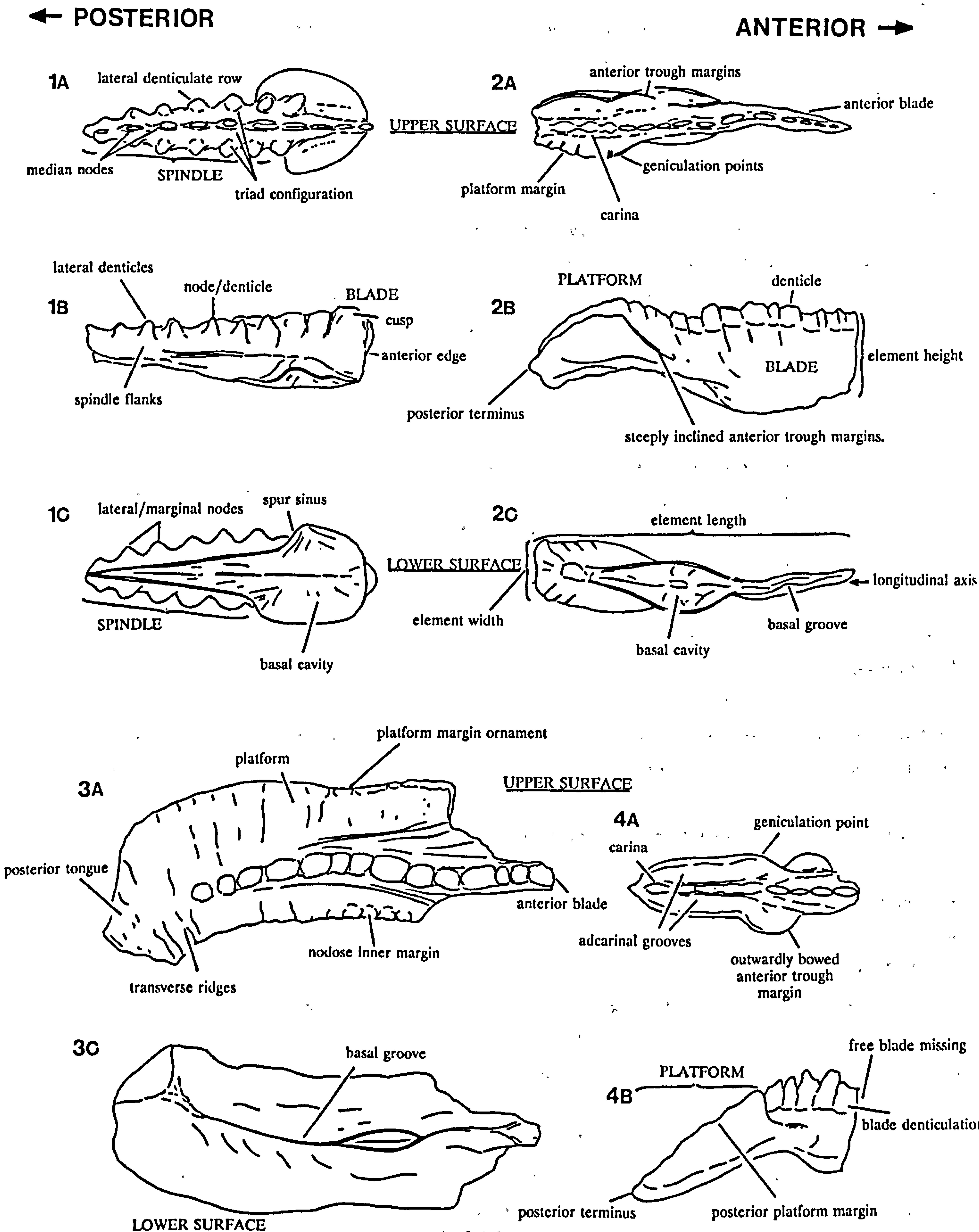
In view of the poor quality of the faunas, the low yields and also the preference still of many icriodid researchers to recognise form species, it would be unrealistic to adopt a multielement approach. The fragmentary form of most of the conodont elements limited the precise recognition of established species, and although many forms recovered were distinguishable from one another, a number did not readily fit into any established species concept. The icriodid fauna was particularly prone to fragmentation, with the lower surface usually poorly preserved or missing. Weddige & Ziegler (1979, p. 161) refute the importance attached to lower surface morphology in differentiating icriodids, which therefore validates the majority of identifications made within the present study (being based largely upon upper and lateral element morphology). Although ramiform and pectiniform elements of polygnathids were recovered (albeit in limited numbers), their precise inter-relationship remains problematical in the present study.

3.2.2 Orientation and nomenclature of conodont elements.

Figure 3.2.1 details the terminology and element orientation used in describing dissociated conodont elements in the present study. The traditional orientation of icriodid Pa elements (Ziegler 1975, p. 67; Robison 1981, p. W15) is not adopted, in view of the work by Nicoll (1983) on the fused

FIGURE 3.2.1

CONODONT MORPHOLOGICAL TERMINOLOGY & ORIENTATION



A. = upper view.
B. = lateral (side) elevation - element profile.
C. = lower view

1 = *Icriodus* spp.
2 = narrow-platformed polygnathid (*Polygnathus varcus* Group)
3 = broad-platformed polygnathid (*Polygnathus linguiformis* complex)
4 = narrow-platformed polygnathid (*Polygnathus varcus* Group): blade missing

clusters of *Icriodus expansus* from the Canning Basin, W. Australia. Although contrary to the traditional view, the orientation and apparatus composition proposed by Nicoll for this plexus is more compatible with other known Devonian multielement configurations. Indeed, Nicoll (1983) perceived the multielement *Icriodus* apparatus to be broadly consistent with the polygnathacean design.

All polygnathid elements are detailed in accordance with established methodology and nomenclature (Sweet, p. W14, in Robison 1981). Where appropriate, the terminology proposed by Klapper *et al.* (1970, p. 652) for the systematic description of narrow platformed polygnathids is applied.

Appendix I details sample characteristics, the total conodont yield from each sampled horizon, and the absolute numbers of each taxon subsequently recovered. Based on the data-base presented overleaf, Chapter 4 (and associated figures) discusses the stratigraphical distribution of taxa through the key carbonate horizons within north Devon, with Chapter 5 addressing palaeoevironmental conditions as gauged in part by the conodont faunas.

3.2.3 The *Icriodus* plexus.

3.2.3a *Introduction.*

In the Treatise, the genus *Icriodus* is assigned to the Family Icriodontidae Müller & Müller (1957), and affiliated with genera such as *Icriodella* Rhodes (1953), *Pedavis* Klapper & Philip (1971), and *Pelekysgnathus* Thomas (1949). The *Icriodus* plexus is believed polyphyletic (Sweet, 1988) and stratigraphically ranges from Pridoli (latest Silurian) to the Famennian (Robison, 1981, p. W125). Indeed, this group is commonly cited as an "index fossil" of the Devonian Period (Sweet 1988, p. 70), being particularly important stratigraphically in shallow-water Devonian biofacies. Despite numerous problems in their taxonomy and phylogeny still remaining unsolved, the Icriodontidae have proved important zonal indices in the resolution and correlation of Lower Devonian strata. With the subsequent inception and proliferation of the Polygnathidae (being the favoured correlative indices for the late Lower, Middle and Upper Devonian) the biostratigraphical significance attached to the *Icriodus* plexus has dwindled.

Several interpretations of the multielement configuration of *Icriodus* have been proposed. Lange (1968) described early Upper Devonian coprolitic cluster of ($\approx$30) acodinan and (1 pair of) icriodid elements. Subsequently Klapper & Philip (1971, 1972) believed the apparatus of the *Icriodus* animal comprised scaphate platform elements in association with an assortment of tiny pyramidal or pastinate coniform elements (categorised as a Type 4 apparatus). Based upon a study of Middle Devonian *Icriodus* assemblages from the Ardennes, Bultynck (1972) statistically reconstructed 13 assemblages and proposed an *Icriodus* apparatus formed entirely of segminiscaphate elements. Each assemblage was composed either exclusively of one form species of *Icriodus*, or a morphological transition series consisting of between two or three. Ziegler (1972) assigned *Icriodus* to a Lower Devonian Apparatus Type b category, being similar to the Type 4 class defined by Klapper & Philip: comprising icriodid and acodinan elements. Ziegler (1972) also concurred with Klapper & Philip (1971, p. 439) in believing the number of icriodid elements probably exceeded acodinan elements. However, the association of *Icriodus* and acodinan elements in the gut of a palaeoniscoid fish (Nicoll, 1977) and more recently in fused clusters (Nicoll, 1983) suggest that the true multielement apparatus of the *Icriodus* animal in fact comprised icriodid and acodinan elements. Furthermore Nicoll (1983) suggested that the apparatus of the *Icriodus* animal, and perhaps other members of the Icriodontidae, comprised a pair of scaphate Pa elements and a multitude of cones (which may have exceeded 140 in number). Nicoll (1983) perceived each cone as possibly homologous to a single denticle on ramiform elements representative of a Type 1 apparatus, and therefore interpreted the *Icriodus* apparatus to be very similar in function to those of polygnathacean genera. Based on a study of *Icriodus woschmidti woschmidti* recovered from Sardinia, Serpagli (1983) supported the hypothesis that the multielement configuration of this species comprised six distinct constituents, and not two as had previously been interpreted. Furthermore, the apparatus included several ramiform elements.

The differentiation of species within the *Icriodus* plexus is often founded on subtle variations in a few morphological characteristics (*e.g.* refer to the differentiation of the *Icriodus brevis* "plexus" by Bultynck 1987, p. 158-159). As mentioned earlier, lower surface morphology was once considered significant in species discrimination (*e.g.* the proposal of *Icriodus corniger, sensu* Wittekindt 1966, p. 629; *Icriodus introlevatus* after Bultynck 1970, p. 113). More recently however, Weddige & Ziegler (1979) considered this feature to have minimal taxonomic significance. This stance is supported herein, and therefore in the following conodont systematics *Icriodus* speciation relies principally on upper/lateral element morphology.

Icriodids form an appreciable constituent of the faunas recovered from the carbonates of north Devon, and for certain strata were the only conodonts reported. Almost 20 years ago Schumacher (1971, p. 90) remarked that the genus was in urgent need of revision, with Rhodes *et al.* (1973, p. 130) later referring to icriodid systematics as a "nomenclatorial jungle". Despite the comparative faunal diversity, problems of identifying established species were compounded by the current instability in *Icriodus* systematics, coupled with the poor quality and low abundance of the faunas from north Devon. It was thus felt that collectively these factors did not justify a detailed rationalisation of *Icriodus* systematics.

3.2.3b *Descriptive systematics*. The format of the following systematics is in accordance with the approach outlined within the "Treatise" (Robison, 1981), in preference to that of Sweet (1988).
PHYLUM/CLASS : Conodonta, Eichenberg 1930; ORDER : Conodontophorida, Eichenberg 1930; Superfamily : Prioniodontacea Bassler, 1925.

Family : Icriodontidae Müller & Müller, 1957.

Genus : *Icriodus* Branson & Mehl, 1938.

Type species : *Icriodus expansus* Branson & Mehl, 1938.

Icriodus arkonensis Stauffer

Plate 3.8, figs. 1, 2. "The Orchard Collection".

1938 *Icriodus arkonensis* Stauffer, p.429, Pl. 52, figs. 10, 15.
p 1938 *Icriodus expansus* Branson & Mehl, in Stauffer, Pl. 52, fig. 25.
1977 *Icriodus arkonensis* Stauffer, in Weddige, p. 284-285, Pl. 2, figs. 26-29.
1980 *Icriodus arkonensis* Stauffer, in Klapper & Johnson, Pl. 3, fig. 24.
1985 *Icriodus arkonensis* Stauffer, in Austin *et al.*, Pl. 4.3 , fig. 11.
p 1988 *Icriodus arkonensis* Stauffer, in Sparling, Fig 18, 2.

Description. Spindle ≈broadly biconvex to pyriform in shape; the anterior portion may appear slightly laterally expanded, with the maximum width anterior of midlength. The upper surface displays a distinctive style of denticulation; the marginal nodes are laterally opposed, transversely elongate and contiguous with the median row. The median row denticles are low and form an irregular "ridge" extending from the anterior to the posterior tip. The lateral nodal-pairings are subdued, squat, subround, transversely elongate to wedge-shaped and longitudinally discrete. The anterior blade is weakly (if at all) developed, and does not obviously project beyond the spindle; comprises one markedly subdued ill-developed denticle, or is defined by two or three confluent nodes.

In lateral view the element is straight to slightly arcuate in profile. The lower surface appears deep and widely excavated, and may exhibit a weak spur & sinus (as visible in upper elevation).

Occurrence. *Roduish Limestone;* - The Orchard Collection (refer to Plate 3.8 description for specific details).

Remarks. The record of recovery and illustrations of this taxa were provided by Orchard (*pers. comm.*). Only lateral and upper view photomicrographs were provided.

Comparisons. *Icriodus expansus* resembles *I. arkonensis*, but differs in the gross morphology of the spindle. According to Klapper (in Ziegler, 1975) *I. expansus* lacks a prominent spur and related sinus, although the *I. expansus* group does embrace forms both with and without a spur. Therefore, the two may be differentiated upon the nature and disposition of the denticulation(lower surface morphology aside); for *I. arkonensis* the middle platform displays conspicuous but discrete transverse bridges, with the denticles seemingly well aligned. Anteriorly the median row of *I. retrodepressus* lies in a depression, and is not conspicuously "ridged" (for example refer to the figured specimens of Plate 3.1, fig. 15, 16). The denticulation of *Icriodus amabilis* Bultynck & Hollard (1980) and *I. obesus* Bultynck (1987) appear more discrete and well defined. *Icriodus* sp. A (of Weddige, 1977; Pl. 3, figs. 48-49) bears well defined transverse ridges on the upper surface.

Icriodus ?arkonensis Stauffer

Plate 3.4, fig. 1.

? p 1988 *Icriodus arkonensis* Stauffer, in Sparling, Fig. 17, 3.

Description. Spindle outline variable; triangular to rounded-triangular biconvex. Denticulation on the upper surface longitudinally discrete, indistinct; comprises 6-7 laterally-paired, subrounded to ovate nodes (commonly enlarged and ±contiguous with the median nodes). Towards the posterior terminus the median nodes become increasingly contiguous longitudinally, resembling a more or less angular, irregular ridge. The lateral denticles may be transversely aligned, or orientated oblique to the median row. Maximum spindle width is anterior of midlength. The denticulation on the anterior spindle is commonly diffuse, ill-defined. The anterior blade comprises up to 6 ill-defined, irregular nodes of variable height and dimensions. The blade may constitute over one third the total element length.

In lateral view the element is straight and the anterior edge is erect to slightly reclined. In profile the denticulation varies from well rounded to pointed and the median row ?depressed or equal in height. The lower surface is deeply excavated, with the trace of a spur and associated sinus perceptible.

Occurrence. Sample 86.067.

Remarks. Specimens are only tentatively attributed to *I. arkonensis*, as the blade appears comparatively distinct, and more significantly the spindle denticulation is not demonstrably contiguous with the median row.

The spindle triads commonly appear chevroned, closing anterior-wards.

Comparisons. The spindle morphology of *Icriodus* aff. *arkonensis* (in Bultynck, 1987, Pl. 6, figs. 29) is similar, but the nodes towards the anterior part of the spindle/blade appear better defined.

Icriodus brevis Stauffer
Plate 3.2, figs. 1-11, 20; Pl. 3.7, figs. 1 (?).
Pl. 3.8, figs. 3, 4, 6(?), 12(?).

1940 *Icriodus brevis* Stauffer, p.424, Pl. 60, figs. 30, 43, 44, 52.
1940 *Icriodus cymbiformis* Branson and Mehl, in Stauffer, Pl. 60, figs. 37, 51, 56-58, 68.
1970 *Icriodus brevis brevis* Stauffer, in Seddon, p.735-736, Pl. 12, figs. 12-15.
p 1972 *Icriodus eslaensis* assemblage Bultynck, p.81, figs. 14 B-C.
1976 *Icriodus brevis* Stauffer, in Ziegler *et al.*, p. 117, Pl. 1, figs. 10-16
1977 *Icriodus brevis* Stauffer, in Weddige, p. 285, Pl. 2, fig. 37.
1978 *Icriodus brevis* Stauffer, in Uyeno, p. 18, Pl. 4, figs. 28-44
p 1979 *Icriodus latecarinatus* Bultynck, in Orchard, Pl. 1, figs. 17, 22.
1987 *Icriodus brevis* Stauffer, in Bultynck, p. 158, Pl. 6, figs. 1-14.
1988 *Icriodus brevis* Stauffer, in Sparling, Fig. 17 (13); Fig.18 (4).

Description. Scaphate, broadly biconvex to elongate-triangular element: ≈bilaterally symmetrical. Longitudinal axis straight or crescentic in upper view. The upper surface displays well defined denticulation; the spindle bears two to six triads (commonly 4-5). When preserved the posterior terminus appears pointed. The 3-6 lateral denticle pairs are longitudinally discrete, subcircular to ovate in plan outline and rarely coalesce with (although may be closely appressed to) the median row. In adult specimens the anteriormost lateral nodes on the spindle appear ovate and/or ridged. The denticles are occasionally aligned, although generally tend to alternate. Maximum element width is usually anterior of midlength, or one third the distance from the anterior terminus (commonly coincides with the anteriormost triad on the spindle). The anterior blade comprises 2-4 longitudinally contiguous median row denticles, which appear strongly ovate and usually indistinguishable. The blade constitutes between 1/4 and 1/3 the entire element length and the anteriormost cusp is enlarged (commonly twice the dimensions of the other blade denticles). The median row nodes are transversely compressed, discrete and/or confluent longitudinally. Denticle fusion is most notable anteriorly.

In lateral view the element axis may be straight, or the upper surface ≈convex upwards. The upper surface denticulation appears relatively constant, and in profile the nodes are subrounded to angular. The denticles on the anterior blade may be aligned with, or displaced below the level of the spindle (such that in profile the blade may appear broadly crescentic). The cusp is distinct, enlarged, and with an erect to slightly reclined anterior edge. The lower surface is asymmetric in outline: anteriorly a laterally enlarged "bowl" incorporating a weak spur & sinus, tapering posteriorly as a constricted groove. The cavity appears "deepest" underlying the blade.

Occurrence: The Lester Slates & Sandstones; *the Rillage and Holey limestones.* The Combe Martin Slates; *the Combe Martin Beach and David's Stone Limestones.* The Kentisbury Slates; *K53.* "The Orchard Collection".

Remarks. The illustrations of *I. brevis, I. eslaensis* and *I. lindensis* in the present study represent end members of a recognised intergrading complex. However, these species are maintained as discrete due to their biostratigraphical utility (*sensu* Bultynck, 1987).

Denticle disposition and form, and gross element morphology were highly variable, and the lower surface and posterior terminus commonly fragmented. Both mature (adult) and juvenile forms of *Icriodus brevis* were recovered. Indeed, the juveniles of *I. latecarinatus* figured by Orchard (1979) are attributed herein to *I. brevis.*

Comparisons. The morphology and disposition of the anterior blade (in lateral view) allows distinction of *Icriodus brevis* from both *I. eslaensis* and *I. lindensis.* Bultynck (1987, p. 158) remarked upon the basic comparability in morphology of these three forms, but differentiated *I. brevis* based upon the "subdued" morphography of the blade (in lateral view). For *I. eslaensis* the blade comprises 2-4 subdued, small denticles, and an enlarged terminal cusp. In profile, the blade of *I. lindensis* Weddige increases progressively in height towards the anterior terminus.

Icriodus cf. *brevis* Stauffer

Plate 3.4, figs. 7, 8.

cf. 1940 *Icriodus brevis* Stauffer, p.424, Pl. 60, figs. 30, 43, 44, 52.

Description. ≈Biconvex elements; axis straight to slightly arcuate and maximum element width ≈midlength, or slightly anterior of midlength. The posterior terminus is marked by a rounded node. The spindle bears between 5-6 lateral denticulate pairs; nodes subcircular to ovate in outline, longitudinally discrete and closely appressed to the median denticles. This median row comprises elongate, ovate nodes that become increasingly confluent anteriorwards. The denticles at the junction between the blade and spindle are markedly reduced. The blade comprises 2-3 narrow denticles, and constitutes ≈1/3 to 1/4 the total element length. The cusp may appear slightly enlarged.

In lateral view the element axis is straight and the upper surface ≈convex-upwards. The median row may appear obviously elevated above the level of the lateral nodes, and the anterior blade somewhat arcuate in profile. The cusp is displaced below the level of denticulation on the spindle. The cavity outline is rarely preserved intact; the bowl appears most pronounced beneath the junction of the blade and spindle. Remnants of a faint spur and sinus may be discernible.

Occurrence. Exclusive to Sample 86.019.

Remarks. This morphotype differs to *I. brevis*, *sensu stricto* (Stauffer 1940) in displaying a markedly elevated median denticulate row, a distinctly biconvex outline and also subdued denticulation at the blade/spindle junction.

Icriodus ?corniger corniger Wittekindt
Plate 3.1, figs. 5, 10.

? 1966 *Icriodus corniger* Wittekindt, p. 629, Pl. 1, figs. 9-12.
? 1977 *Icriodus corniger corniger* Wittekindt, in Weddige, p. 287-288, Pl. 16-20.
? 1982 *Icriodus corniger corniger* Wittekindt, in Weddige, Pl. 2, fig. 31, 32.
cf. 1985 *Icriodus corniger corniger* Wittekindt, in Austin *et al.*, Pl. 4.2, fig. 7.
? 1985 *Icriodus corniger corniger* Wittekindt, in Bultynck, p. 269, Pl. 6, fig. 6-10.

Description. ≈Biconvex, parallel-sided or concavo-convex in plan outline; element axis straight to slightly incurved. The posterior terminus is rarely preserved. On the spindle the denticulation may appear well defined, comparatively uniform, or becomes increasingly indistinct/irregular towards the posterior tip. The lateral nodes are subcircular to ovate in outline, are longitudinally discrete and may be connected by weak transverse ridges to the median row. The median nodes are small, subcircular in outline and laterally compressed. The spindle constitutes four-fifths of the overall element length. The anterior blade is reduced, irregular or simple in outline and comprises one to three indistinct denticles (which are longitudinally contiguous and usually indistinguishable). The anterior cusp is ill-defined, subdued.

In lateral view, the elements axis is straight; the upper surface planar to convex-upwards. The denticles commonly appear rounded or ridged in profile, and the middle row may project slightly above the level of the lateral nodes. The anterior edge is erect, straight, rarely reclined.

The cavity outline is poorly preserved, with ?faint traces of a spur and associated sinus. The anterior edge is ±oblique or ≈perpendicular to the longitudinal axis of the element.

Occurrence. The Watersmeet section.

Remarks. All representatives of this species were poorly preserved, with the lower surface commonly fragmented or missing. In view of element preservation, these forms are affiliated with the *corniger* group, and believed probable representatives of *Icriodus corniger corniger.* Within the population recovered from north Devon, certain forms recovered resemble *I. corniger rectirostratus* Bultynck (1970), whereas others appear morphologically gradational with *I. corniger retrodepressus* Bultynck (1970). Poor element preservation favoured retention within the concept of *Icriodus corniger corniger* applied herein.

Comparisons. The spindle of *Icriodus c. leptus* Weddige (1977, p. 289) appears somewhat narrower (elongate), and the spindle denticulation more distinct, subalternate.

Icriodus culicellus Bultynck
Plate 1, figs. 1-4, 6-9, 12, 14.

1974 *Icriodus culicellus* Bultynck, in Bultynck & Godefroid, guidebook; 1, 35 (nomen nudem).
1976a *Caudicriodus ?culicellus* Bultynck, p. 37-40, Pl. 10, fig. 5, 7-14.
1977 *Icriodus culicellus* (Bultynck) Weddige, p. 291-292, Pl. 3, fig. 46-47.
1982 *Icriodus culicellus* (Bultynck) Weddige, in Weddige, Pl. 2, fig. 34.
non 1987 *Icriodus culicellus* (Bultynck) Weddige, in Smolderen Pl. 1, fig. 3.
Refer to Weddige (1977, p. 291-292) for additional synonymy.

Description. Broad, robust elements; spindle margin biconvex, subtriangular, or parallel-sided. The upper surface appears densely denticulate (crowded); typically comprising 4 to 5 denticle triads that are discrete or with occasional, weak, transverse ridges fusing the lateral with the median nodes. The posterior terminus tends to be pointed, with the spindle margins diverging sharply anteriorwards. Denticles tend to appear isodiametric in plan view; the lateral nodes are commonly aligned or subalternate with the related median node (of the triad). The anterior blade comprises 2-3 denticles; the cusp may be enlarged (two or three times the size of the other blade denticles), and elevated above the level of the spindle.

In lateral view, the element axis is straight, or slightly convex-upwards. The nodes appear rounded to slightly angular, and the median row may seem somewhat depressed. The denticulation tends to increase in height anteriorwards. In profile the cusp is obviously higher and larger. The lower surface may display a weak, subtle spur and sinus.

Occurrence: The Watersmeet Section. The A39 Road section. The Valley of the Rocks.

Remarks. Preservation is highly variable, although the lower surfaces are consistently poorly preserved. In addition, some of the specimens appear tectonically distorted (refer to the figured specimen of Pl. 3.1, fig. 6; extension fibres are discernible anterior of the first triad). Indeed, this distorted specimen bears a resemblance to *Icriodus corniger leptus* (Weddige, 1977).

Comparisons. Weddige & Requadt (1985) define a new subspecies of *I. culicellus*, namely *I. culicellus altus* which resembles some of the specimens recovered in the present study (Bultynck *pers. comm.*). *Icriodus corniger leptus* bears a more elongate, attenuated spindle.

Icriodus cf. *difficilis* Ziegler and Klapper
Plate 3.2, figs. 12-16.; Plate 3.8, 11 (?).

cf. 1976 *Icriodus difficilis* Ziegler & Klapper p.117-118, Pl.1, figs.1-7, 17.
1977 *Icriodus difficilis* Ziegler & Klapper, in Weddige, p.292, Pl.2, fig. 36.
1979 *Icriodus* aff. *difficilis* Ziegler & Klapper, Orchard, Pl.1, fig. 11, 18, 19, 21, 23.
cf. 1985 *Icriodus difficilis* Ziegler & Klapper, in Austin *et al.*, Pl. 4.4, figs. 11, 12.
cf. 1987 *Icriodus difficilis* Ziegler & Klapper, in Bultynck, Pl. 9, fig. 25-26.
? 1988 *Icriodus difficilis* Ziegler & Klapper, in Sparling, p.15, Fig. 18, 5.

Description. Element robust, elongate; spindle broadly biconvex or ≈parallel-sided, bearing more or less well aligned, closely spaced denticles. In upper view the element axis is straight, arcuate, to distinctly sinuous; in general element length is five times element width. The posterior terminus comprises an angular or rounded node. The upper surface usually displays up to six distinct denticle triads, which are transversely aligned, and the denticles crowded but discrete (may be partially contiguous with the median row). The lateral denticles are subcircular to ovate in outline; rounded, pointed or ridged. The median nodes vary from subcircular to laterally compressed, and coalesce longitudinally, extending as an irregular ridge from the ≈posterior to anterior termini. Two to three laterally compressed, enlarged denticles fuse to form the blade; the blade commonly constitutes one fifth of the overall element length, and is usually incomplete. The anteriormost cusp appears distinct, enlarged and ±discrete from the blade denticulation.

In lateral profile, the element axis is straight or convex upwards. On the spindle the median denticulate row may be slightly raised above the level of the lateral nodes, particularly adjacent to the blade. The cusp is commonly elevated above the level of the spindle. The anterior edge of the blade is erect or reclined.

The lower surface may be severely fragmented, asymmetric, and with a distinct to barely discernible spur and sinus. The basal cavity is deepest underlying the anterior blade.

Occurrence: The Lester Slates & Sandstones; *the Rillage Limestone.* The Combe Martin Slates; *the Combe Martin Beach and David's Stone Limestones.*

Remarks. In terms of gross morphology, some specimens attributed to *Icriodus* cf. *difficilis* bear a close resemblance to aberrant adult forms of *Icriodus brevis* Stauffer also recovered from north Devon (note distinctions below).

Comparisons. According to Ziegler & Klapper (1976, p.118), *Icriodus brevis* exhibits a longer blade ("posterior extension" of Ziegler and Klapper, 1976) with fewer lateral row denticles on the platform, which tend to alternate with the median row. *Icriodus arkonensis* Stauffer differs in displaying a laterally expanded platform "anterior" of midlength (reflecting a broadening of the marginal nodes).

Icriodus ?difficilis Ziegler & Klapper
Plate 3.3, fig. 10.

? p 1976 *Icriodus difficilis* Ziegler & Klapper p.117-118, Pl.1, figs.1-7, 17.
? p 1987 *Icriodus difficilis* Ziegler & Klapper, in Bultynck, Pl. 9, figs. 25.

Description. Broad, ≈bilaterally symmetrical spindle; the blade is ill-defined, short and appears to merge with the spindle. The spindle flanks diverge regularly towards the anterior terminus; the maximum element width is located well posterior of midlength. The lateral row denticles appear bulbous, robust, longitudinally discrete, in part may be contiguous with the median row and generally increase in size towards the anterior terminus of the spindle. The median nodes are subcircular, subdued, ±depressed and/or indistinct anteriorly, and are ≈longitudinally discrete. The blade comprises two or three indistinct subordinate nodes, and an enlarged, bulbous cusp.

In lateral view, the lateral row denticles on the spindle are clearly enlarged. A distinct, posteriorly directed spur and associated sinus are discernible on the lower surface. The cavity appears deepest underlying the anterior part of the spindle.

Occurrence. The Combe Martin Slates; *the David's Stone Limestone.*

Comparisons. This form resembles the broad-platformed morphotypes of *Icriodus difficilis* illustrated by Ziegler & Klapper (in Ziegler *et al.*, 1976, Pl. 1, fig. 4, 17), although the spindle and blade denticulation apparent upon *Icriodus ?difficilis* described herein appears somewhat atypical.

Icriodus eslaensis Van Adrichem Boogaert
Plate 3.2, Fig. 9.

1967 *Icriodus eslaensis* Van Adrichem Boogaert, p. 180-181, figs. 9, 10, 12; ?11.
1987 *Icriodus eslaensis* Van Adrichem Boogaert, in Bultynck, p. 158, Fig. 8, a-f.

Description. Slender, biconvex spindle; the upper surface displays distinct, discrete denticulation (comprising 4-5 triads). The nodes appear transversely aligned, and subcircular in outline. The maximum element width is approximately midlength, tapering to a (rarely preserved) pointed, posterior terminus. The blade comprises ovate, longitudinally contiguous, diminutive nodes; the anteriormost "cusp" appears enlarged and slightly discrete from the rest of the blade.

In profile the denticles are by an large angular, and the anterior margin ≈reclined; the cusp is distinct. The cavity outline in lower view is narrow, constricted (?preservational).

Occurrence. The Lester Slates & Sandstones; *the Holey Limestone and the Rillage Limestone.* The Combe Martin Slates; *the David's Stone Limestone.*

Remarks. In general, elements were recovered poorly preserved.

Comparisons. *Icriodus eslaensis* is similar in gross morphology to *I. brevis* Stauffer (1940) and *I. lindensis* Weddige (1977) but is distinguishable from these two species based upon blade morphology; the blade of *I. eslaensis* comprises relatively small denticles adjacent to the spindle, but with an enlarged, markedly higher and wider cusp anteriormost (refer to Bultynck 1987, p. 158).

Icriodus ?fusiformis Carls & Gandl
Plate 3.4, fig. 9.

? 1969 *Icriodus fusiformis* Carls & Gandl, p. 186, Pl. 17, figs. 17-19.

Description. Element axis openly sinuous; the spindle is broadly biconvex with an indistinct blade. Maximum spindle width anterior of midlength. The denticulation is highly variable; comprises irregular, ridged lateral denticles, and subrounded to angular median nodes, which may fuse forming indistinct to pronounced transverse ridges. Towards the posterior tip the nodes tend to appear more bulbous, discrete, subcircular and rounded in form; the denticulation becomes increasingly chaotic and diffuse anteriorwards.. The cavity outline is well preserved, and visibly "laterally flared" in both upper and lower view.

In side profile, the denticulation appears comparatively even in height. The anterior edge is slightly oblique. The cavity outline is broad, well defined and laterally expanded; the edges may appear somewhat upwardly flexed.

Occurrence. Sample 86.055.

Remarks. The basal cavity of the figured specimen is obscured by matrix.

Comparisons. This form resembles *I. fusiformis* Carl & Gandl (1969) in displaying a broad, laterally expanded basal cavity, and in the general morphology of the spindle. However, the disposition of the denticles and the outline of the basal cavity of the figured specimen (of the present study) are atypical of this species. The holotype of *I. fusiformis* Carls & Gandl (1969; Pl. 17, fig. 19) displays more regular transverse ridges, and a more asymmetric basal cavity.

Icriodus lindensis Weddige
Plate 3.2, figs.18, 19, 21; Pl. 3.8, fig. 5,

P 1972 *Icriodus eslaensis* assemblage - Bultynck, p. 81, Fig. 14 (A, E, F).
1977 *Icriodus lindensis* Weddige, p. 293-294, Pl.2, figs. 38-39.
? p 1979 *Icriodus latecarinatus* Bultynck, in Orchard, Pl. 1, fig. 14, 20.
1987 *Icriodus lindensis* Weddige, in Bultynck, p.159, Pl.4, figs. 17-22.

Description. Spindle ≈biconvex; in upper view the axis is straight, rarely curved. The blade constitutes ≈third the overall element length. The posterior tip appears rounded, rarely angular; the element flanks diverge progressively anteriorwards, accommodating distinct, generally discrete and subcircular nodes. The median row comprises ovate denticles that are longitudinally contiguous, and occasionally fused by weak bridges to the lateral pairing. Maximum element width is anterior of midlength. In plan view the blade appears straight to slightly arcuate, and comprises between one to three small denticles which tend to increase in size towards the (anteriormost) cusp. This cusp appears enlarged, distinct (typically twice the dimensions of all other nodes) and somewhat isolated from the other blade denticles.

In lateral view the denticles on the spindle appear pointed to subrounded, and in general lie below the level of the blade. In profile the denticles appear to increase in height from the posterior terminus to the anterior tip, and culminate in the enlarged cusp. The anterior margin of the blade is usually erect, rarely reclined. The spindle flanks may appear constricted towards their lower surface, marked by a longitudinal furrow.

The lower surface is poorly preserved, appears asymmetric in outline with a spur and sinus barely perceptible.

Occurrence: The Lester Slates & Sandstones; *The Rillage and Holey Limestones.* The Combe Martin Slates; *the Jenny Start Limestone.*

Remarks. Weddige (1977, p.293) commented that the denticles on the blade of *Icriodus lindensis* may be equal in height, but the cusp is strongly "pointed" (reclined). According to Bultynck (1987, p. 159), the blade denticulation increases regularly in height. The specimens recovered from north Devon displayed a variety of spindle morphology, but were still within the species concept as defined by Weddige (1977) and subsequently reiterated by Bultynck (1987). As noted earlier, in the present study gradational forms with *I. brevis* were identified.

Comparisons. *Icriodus lindensis* bears a superficial resemblance to *I. culicellus* and *I. werneri,* in displaying a pronounced and elevated cusp. However, the spindle morphologies of both *I. culicellus* and *I. werneri* differ in appearing more subquadrate, robust, and with crowded denticulation. For *Icriodus werneri* the median denticulation on the spindle may appear subdued. *Icriodus lindensis* differs to *I. brevis* and *I. eslaensis* in the dimensions and disposition of the cusp. The denticulation on the blade of *Icriodus lindensis* increases regularly in height above the level of the spindle (culminating anteriorly in a pronounced cusp).

Icriodus obesus Bultynck
Plate 3.3, fig. 6.

1972 *Icriodus* n. sp. a assemblage Bultynck, p. 82, figs. 16, A-E.
1979 *Icriodus* aff. *I. subterminus* Youngquist, in Brice *et al.,* p. 334, Pl. 27, figs. 28, 29, 32.
1987 *Icriodus obesus* Bultynck, p. 160, Pl. 6, figs. 15-20.

Description. Spindle robust, broad and biconvex; maximum element width approximately midlength. The spindle bears distinct but somewhat subdued denticulation; the anterior blade appears ill-defined. The posterior terminus may comprise rounded to angular nodes. The spindle denticulation comprises four to six pairs of rounded, transversely ovate lateral-row denticles, well aligned and partially contiguous (through weak bridges) with the median nodes. The lateral denticles are equal or slightly larger in size than the median nodes, being longitudinally discrete, circular to subcircular in outline and squat. The median row nodes are morphologically similar. The blade usually comprises two to three indistinct denticles, which are reduced in size and may form a sharp-crested ridge, commonly displaced below the level of the spindle denticulation.

In lateral view the upper surface is straight to convex-upwards. The cusp is usually ill-defined and merged with the blade, or slightly isolated from other blade nodes. The anterior edge of the cusp is straight.

In lower view the cavity outline may appear symmetrical, or with a remnant spur and sinus developed. The bowl is usually positioned below the anterior portion of the spindle.

Occurrence. The Wild Pear Slates. The Lester Slates & Sandstones; *the Rillage Limestone.*

Remarks. The laterally expansive, flared basal cavity so obvious in the illustrations of Bultynck (1987) was not preserved on the specimens recovered from north Devon.

Comparisons. The denticulation on the spindle of *Icriodus subterminus* Youngquist (1947) appears more discrete and the cusp seemingly elevated and enlarged. *I. amabilis* Bultynck & Hollard (1980) is similar but the median row denticles tend to become elevated towards the blade. The expanded basal cavity (bowl) of *I. amabilis* is also displaced slightly more to the anterior.

Icriodus aff. *obesus* Bultynck

Plate 3.4, figs. 5, 6.

aff. 1987 *Icriodus obesus* Bultynck, p. 160, Pl. 6, figs. 15-20.

Description. Broadly biconvex elements; axis straight to openly sigmoidal. The spindle and blade are distinct, easily separable (the spindle constitutes two-thirds to three-quarters the overall element length). Maximum element width is variably located, but generally anterior of midlength. The spindle bears distinct denticulation, comprising six to seven enlarged, bulbous, robust and rounded lateral denticle pairs (subcircular to ovate in outline). These nodes are longitudinally discrete, although may be fused by weak transverse ridges to the median row, and tend to increase in size towards the anterior terminus. The median row comprises well rounded nodes which only tend to coalesce longitudinally on the anterior part of the spindle. The blade is readily distinguishable, and comprises between three and five identifiable but laterally contiguous nodes. The blade is broad and robust in plan view, with the anteriormost denticle seemingly subdued.

In lateral view, the upper surface appears comparatively linear, with the blade depressed somewhat below the level of the spindle. In profile the nodes appear rounded, rarely angular. The element flanks are high, and may appear constricted towards the lower margin. In general the anterior edge of the blade appears straight, occasionally slightly reclined.

The basal cavity is poorly preserved, ≈asymmetrical, but the remnants suggest a markedly flared, laterally expanded cavity. A ≈weak spur and sinus may be discernible.

Occurrence. The Lester Slates & Sandstones; *the Rillage Limestone.* The Combe Martin Slates; *the David's Stone Limestone.*

Remarks. This form is differentiated from *Icriodus obesus, sensu stricto,* Bultynck (1987) primarily due to the pronounced development of the blade. Bultynck (1987, p.160) remarked that the "posterior" extension is short, broad and comprises 2-3 denticles. For *Icriodus* aff. *obesus* (herein) the blade tends to appear more elongate. *Icriodus arkonensis* lacks such discrete nodes on the upper surface, displaying instead well defined transverse ridges.

Icriodus obliquimarginatus (Bischoff & Ziegler 1957) Weddige
Plate 3.3, figs. 1-5.

1957 *Icriodus obliquimarginatus* Bischoff & Ziegler, p. 62-63, Pl. 6, fig. 14.
p 1970 *Icriodus regularicrescens* Bultynck, p. 111, Pl. 8, fig. 2, 4, 7, 8.
1970 *Icriodus obliquimarginatus* Bischoff & Ziegler, in Bultynck, p.109, Pl. 8, figs. 1, 3, 5.
1972 *Icriodus regularicrescens* assemblage Bultynck, p. 80-81, fig. 12, A-C.
1977 *Icriodus obliquimarginatus* (Bischoff & Ziegler) Weddige, p. 294-295, Pl. 2, fig. 33-35.
1985 *Icriodus obliquimarginatus* (Bischoff & Ziegler) Weddige, in Austin *et al.,* Pl. 4.3, figs. 16, 17. (from Orchard, 1978a, Pl. 107, figs. 13,14).
1987 *Icriodus obliquimarginatus* (Bischoff & Ziegler) Weddige, in Bultynck, p. 160, Pl.4, fig. 7-10, 12-16.
non 1988 *Icriodus obliquimarginatus* (Bischoff & Ziegler) Weddige, in Sparling p.14, Fig.17, 12.

Description. In upper view, the element axis appears rectilinear, rarely arcuate. The element flanks are subparallel and usually of considerable depth; the element length is usually seven times greater than the maximum element width. In plan the spindle appears laterally-compressed, triangular in outline, narrow and typically constitutes ≤½ the overall element length. When preserved, the posterior terminus is commonly angular, being defined by an erect, pointed denticle; the spindle flanks tend to be subparallel or only slightly divergent. The upper surface of the spindle displays highly irregular, discrete, pointed denticles (2-4 triads); these nodes are morphologically variable, with rare symmetry in the disposition of the lateral/median nodes (the lateral nodes may be laterally opposed). The median denticles tend to be longitudinally contiguous, ovate, and transversely discrete. In plan these denticles are subtriangular rarely rounded in basal outline, and tend to increase in size towards the anterior blade. The blade comprises up to 10 partially or completely fused, ≈distinguishable, laterally compressed (ovate) denticles. The cusp is usually enlarged, set slightly apart from the main blade, and located anteriormost.

In lateral view, the platform appears comparatively shallow (in height), and rarely equal to the maximum height of the blade. In profile, the denticulation on the spindle commonly appears uniform, or with the median row slightly elevated above the level of the lateral nodes. The blade morphology is highly variable; the median row denticles may increase in height immediately anterior of the spindle, reaching a maximum height midlength but then decreasing towards the anterior terminus. Overall the upper surface of the blade in side profile may appear convex-upwards to linear. Conversely the blade denticulation may increase progressively in height, with the anteriormost cups the highest and most enlarged denticle. The anterior margin of the blade varies from markedly reclined to straight.

Only traces of the basal cavity outline are preserved on the lower surface. The cavity is commonly best preserved below the spindle, but only slightly laterally expanded below. A shallow basal groove underlies the blade.

Occurrence. The Lester Slates & Sandstones; *the Rillage and Holey Limestones.* The Combe Martin Slates; *The Combe Martin Beach and David's Stone Limestones.*

Remarks. The initial description and associated illustrations of Bischoff & Ziegler (1957) are vague. Specimens identified as *Icriodus obliquimarginatus* in the present study were in accordance with the emended diagnosis of Weddige (1977), and display a comparable range in spindle/blade morphology.

Virtually all specimens of *Icriodus obliquimarginatus* recovered from north Devon were incomplete, with the basal cavity particularly prone to fragmentation. A striking feature of these specimens was the elongate, narrow blade, which bears a superficial resemblance to the anterior free-blades of a number of polygnathid and spathognathodid elements.

Comparisons. The proportions of the blade to spindle in *Icriodus obliquimarginatus* and the morphology of the blade itself differentiates this form from *Icriodus regularicrescens* Bultynck. For *I. regularicrescens* the spindle denticulation usually appears coarser, denser and constitutes a far greater percentage of the total element length than is apparent upon *Icriodus obliquimarginatus.* The maximum element width of *I. regularicrescens* is commonly anterior of midlength.

Icriodus ?platyobliquimarginatus Bultynck
Plate 3.3, fig. 7.

p ? 1970 *Icriodus obliquimarginatus* Bischoff & Ziegler, in Bultynck p. 109-110, Pl. 8, figs. 1, 5.
? 1972 *Icriodus* aff. *obliquimarginatus* assemblage Bultynck, p. 81, figs. 13, C, D.
? 1987 *Icriodus platyobliquimarginatus* Bultynck, p.160-161, Pl. 5, figs. 1-9.

Description. Spindle broad, robust; axis straight and generally biconvex to triangular in outline, and typically constitutes over half the total element length. Maximum element width midlength, or at the junction between the spindle and the blade. The spindle denticles appear longitudinally discrete, and commonly transversely fused. 3-5 ridged, angular lateral-denticle pairings may be fused by faint or pronounced bridges with the median nodes. The median denticles tend to appear laterally compressed, smaller and more rounded in morphology, and may coalesce longitudinally to form an irregular ridge that extends from anterior to posterior terminus. The triads are ≈well aligned. The anterior blade may comprise between four to five contiguous, ≈barely distinguishable nodes. The basal cavity may be distinct in upper view.

In profile, both the spindle surface and the blade appear broadly linear to convex-upwards.

On the spindle, the median row may be slightly elevated above the level of the lateral nodes. Conversely the blade denticulation tends to fall below the level of the spindle, and is deepest at the anterior margin (which is straight to strongly reclined in lateral profile).

The cavity appears ≈asymmetric, and broadly expanded midlength (or towards the anterior terminus) of the element. Rarely preserved intact.

Occurrence. The Lester Slates & Sandstones; *the Holey Limestone.* The Combe Martin Slates; *the David's Stone Limestone.* The Orchard Collection.

Remarks. Specimens are rarely recovered complete. The gross morphology of the blade and spindle combined are comparable to *Icriodus platyobliquimarginatus* Bultynck, although poor element preservation and the slightly atypical profile of the blade questions a definitive assignment.

Icriodus cf. *regularicrescens* Bultynck.
Plate 3.3, fig. 8; Plate 3.8, fig. 8 (?).

cf. 1970 *Icriodus regularicrescens* Bultynck, p. 111-112, Pl. VII, fig. 1-7.
cf. 1977 *Icriodus regularicrescens* Bultynck, in Weddige, p. 295-296, Pl. 2, fig. 30-32.
1985 *Icriodus regularicrescens* Bultynck, in Austin *et al.*, Pl. 4.2, fig. 18.
cf. 1985 *Icriodus regularicrescens* Bultynck, in Bultynck, Pl. 6, 15.
cf. 1987 *Icriodus regularicrescens* Bultynck, in Bultynck, Pl. 4, fig. 1-3, 11.

Description. In plan view the element is elongate, relatively slender and arcuate. The margins taper to a distinct point anteriorly and posteriorly, being marked at both extremities by an angular, pointed node. Maximum element width is posterior of midlength. The upper surface bears pronounced, distinct and generally discrete denticles; encompass up to five paired, peg-like and subtriangular in outline lateral denticles, which obviously decrease in size towards the anterior blade. The median nodes appear laterally compressed (ovate) longitudinally contiguous, and subalternate with the lateral nodes. The median denticles may increase in size towards the anterior terminus of the element. Very occasionally, weak transverse bridges join the lateral and median denticulate rows, although triads are in general longitudinally discrete. The blade is ill-defined, short and comprises up to three, discrete, ovate to subcircular denticles which are commonly smaller than the spindle nodes (constitutes less than one third of the total element length).

In lateral view, the elements axis is straight to convex-upwards. The denticulation appears subrounded, rarely angular, and the median row denticles are usually enlarged/elevated above the lateral nodes.

The cavity is poorly preserved, fragmented with a marginally expansive "remnant" bowl located towards the anterior blade, and with a simple basal groove underlying the posterior spindle.

Occurrence: The Lester Slates & Sandstones; *the Rillage and Holey Limestones.*

Remarks. Specimens accord with the original circumscription of *regularicrescens* Bultynck (1970), in displaying the characteristic reduction in lateral denticulation and platform width towards the anterior margin. However, the overall morphology of the spindle and the size/disposition of the denticles is atypical of this species.

Icriodus retrodepressus Bultynck
Plate 3.1, figs. 15, 16.

1970 *Icriodus corniger retrodepressus* Bultynck, p. 110, Pl. 30, figs. 1-6.
1977 *Icriodus corniger retrodepressus* Bultynck, in Weddige, p.290-291, Pl. 1, figs. 10-12.
1982 *Icriodus corniger retrodepressus* Bultynck, in Weddige, Pl. 2, fig. 26, 27.
1985 *Icriodus retrodepressus* Bultynck, in Austin *et al.*, Pl. 4.2, fig. 1.
1985 *Icriodus retrodepressus* Bultynck, in Bultynck, Pl. 6, fig. 14.
1985 *Icriodus retrodepressus* Bultynck, in Feist, Schönlaub, and Bultynck, Pl. 3, figs. 10-13.
1987 *Icriodus corniger corniger* Wittekindt, in Smolderen Pl. 1, fig. 1.
? 1987 *Icriodus retrodepressus* Bultynck, in Smolderen Pl. 1, figs. 7-9.

Description. Element ≈biconvex to pyriform in shape; longitudinal axis straight to slightly arcuate. The posterior terminus is ≈pointed, and the maximum element width located ≈midlength. The spindle bears up to five distinct, discrete, robust lateral-denticle pairs, being subcircular (rarely ridged) in outline and profile, and by and large laterally opposed. The median denticulate row varies in morphology along its length, comprising relatively enlarged, rounded nodes towards the posterior terminus, becoming increasingly subdued and indistinct anteriorly. Towards the junction of the spindle and blade the median nodes appear so reduced that they may seem situated within a "depression". The anterior blade is short, and commonly comprises one, rarely two squat nodes; the anteriormost cusp tends to be broad, enlarged, and rounded.

In lateral profile the element is straight, rarely arcuate, and the denticulation appears rounded to subangular. The lateral nodes are obviously enlarged and elevated above the median row. The anterior margin of the blade tends to be oblique, rarely erect. The element flanks may appear constricted below the spindle (resembling a longitudinal furrow), with remnants of a basal cavity "flange" discernible.

In lower view, the cavity is rarely complete; appears symmetrical, corroded or with ?remnants of a weak spur and sinus.

Occurrence. The Watersmeet section.

Remarks. Despite poor preservation, the identity of these specimens was confirmed by Bultynck (*pers. comm.*), and are referred (unambiguously) to *Icriodus retrodepressus* Bultynck (1970). Identification of this species relies principally upon the suppression and reduction in size of the median row denticles in the anterior part of the spindle.

Icriodus cf. *werneri*, Weddige

Plate 3.1, fig. 13; Pl. 3.7, fig. 3 (?).

cf. 1977 *Icriodus werneri* Weddige, p. 298-299, Pl. 3, figs. 40-43.

cf. 1982 *Icriodus werneri* Weddige, in Weddige, Pl. 2, fig. 35.

1985 *Icriodus werneri* Weddige, in Feist, Schönlaub, and Bultynck, Pl. 3, figs. 16, 17.

non 1987 *Icriodus werneri* Weddige, in Smolderen, Pl. 1, figs. 4, 5.

Description. Element pyriform in outline; spindle triangular and usually constitutes over 3/4 the overall element length. The posterior tip comprises a pointed denticle, from which the spindle flanks gradually diverge. The upper surface displays distinct denticulation, comprising between three and six lateral nodes: are transversely ridged, discrete, and laterally opposed. The median denticles are only well defined within the anterior portion of the spindle; being subcircular in basal outline, discrete and generally smaller than the lateral nodes. Towards the posterior terminus, the triads generally coalesce forming transverse ridges. The blade comprises between one to three longitudinally fused nodes, of which the anteriormost cusp is ≈distinct (may be slightly broader than the other blade denticles).

In lateral profile, the element axis is straight to convex upwards. The lateral nodes may appear pointed and somewhat raised above the median row denticles; the anterior cusp may not always appear obviously elevated above the level of the spindle. The anterior edge of the blade appears erect or gently inclined.

The preserved cavity outline may be ≈symmetrical, with a trace of a weak spur and sinus.

Occurrence. The Watersmeet section.

Remarks. A greater variability in blade/cusp morphology was noted within the population referred to *Icriodus* cf. *werneri*. Indeed, the cusp was not always enlarged, or elevated above the level of the spindle. The preservation in this species population was highly variable.

Comparisons. *Icriodus culicellus* and *I. subterminus* Youngquist (1947) are comparable, in displaying a similarly pronounced and elevated anterior cusp. However the spindle of *I. culicellus* appears more bilaterally symmetrical (parallel-sided) and more densely denticulate; the cusp is also more enlarged. *I. subterminus* displays a somewhat broader, more robust and squat spindle.

Icriodus sp. A.

Plate 3.1, fig. 11

Description. Biconvex, straight element, tapering gradually to subrounded (rarely angular) anterior and posterior terminations. The spindle constitutes ≈four-fifths the overall element length; the upper surface displays distinct, discrete, pointed (rarely subrounded) and subcircular (in basal outline) lateral row denticles. These vary from three to five pairings, and generally appear laterally opposed. The median denticles are somewhat smaller, depressed and subalternate with the bilaterally paired marginal nodes. The anterior blade is short, and comprises between two and three denticles (commonly in line with or below the level of the spindle denticulation). The penultimate denticle may be the enlarged cusp.

In lateral view, the slight suppression of the median row is distinct, and the anterior edge erect to slightly reclined. Denticles are clearly discrete, angular and peg-like.

Faint to discernible traces of a weak spur and sinus are evident in the basal cavity outline. The bowl is most expansive below the anterior spindle and blade, but resembles a groove towards the posterior terminus.

Occurrence. The Watersmeet section.

Comparisons. *Icriodus werneri* Weddige (1977) differs in overall blade and spindle morphology. The denticulation of *I. culicellus* appears far more concentrate, whereas the spindle of *I. retrodepressus* is markedly enlarged and substantially broader. *Icriodus* sp. A may represent a juvenile growth stage of *I. retrodepressus*.

Icriodus sp. B
Plate 3.3, fig. 9.

Description. When complete, spindle ≈biconvex to subtriangular: axis straight. The blade appears elongate and readily distinguishable from the spindle. Three to five triads are noted on the upper surface of the spindle; the lateral denticles are bilaterally opposed, bulbous, rounded and subcircular to ovate in outline. These elements are longitudinally discrete, but may form pronounced ridges with the median nodes. The median row denticles appear somewhat smaller, laterally compressed and form a longitudinal ridge, extending anteriorly beyond the spindle to form the blade. This blade comprises ?three ill-defined denticles. The blade constitutes less than one third of the restored element length.

In lateral profile, the upper surface of the spindle appears flattened; the blade is clearly elevated above the level of the spindle. The anteriormost cusp appears enlarged, and the anterior margin slightly inclined.

The cavity is poorly preserved, with probable traces of a weak spur and sinus.

Occurrence. The Lester Slates & Sandstones; *the Holey Limestone.*

Comparisons. The enlarged cusp is reminiscent of *Icriodus culicellus*, although the spindle denticulation is atypical of this species.

Icriodus sp. C
Plate 3.3, figs. 11, 12.

Description. Elements broad, pyriform to ≈biconvex in outline; axis straight to slightly arcuate. The spindle is elongate-triangular in form and the anterior blade ill-defined, bulbous and may be virtually indistinguishable from the spindle. Maximum element width anterior of midlength. The upper surface displays distinct denticulation, with between five and seven rounded, ≈ovate lateral nodes; commonly increase in size towards the anterior of the spindle, being most enlarged at the point of maximum element width. The lateral nodes may be partially fused to the median row by weak transverse bridges. The median denticles tend to be subcircular in outline, and longitudinally discrete over the posterior part of the spindle (fuse progressively anteriorwards). The triads are well aligned upon the main body of the spindle, although appear disrupted and increasingly irregular towards the posterior terminus. Immediately posterior of the blade the spindle denticulation may be markedly reduced and subdued (the spindle at this point may also appear somewhat constricted). The blade is commonly ill-defined, occasionally distinct, elongate and extends anteriorly as a rounded or angular ridge; comprises up to three denticles. The cusp may be enlarged. The flanks of the blade are laterally expansive, robust and of reasonable depth.

In lateral profile, the spindle and blade may collectively appear wedge-shaped, being of substantial height. The upper surface is straight; the cusp enlarged and erect. In profile the spindle denticles appear rounded and ≈equidimensional.

The cavity is deep, symmetrical, incomplete (with probable remnants of a flange).

Occurrence. The Lester Slates & Sandstones; *the Holey Limestone.* The Combe Martin Slates; *the Combe Martin Beach Limestone.*

Comparisons. The spindle outline of *Icriodus obesus* Bultynck is more obviously biconvex and displays a less pronounced anterior blade. *Icriodus excavatus* Weddige (1984) may exhibit a median depression over the "anterior" part of the spindle. Some of the specimens of *Icriodus excavatus* Weddige illustrated by Bultynck (1987; Pl. 6, figs. 21-25) are very similar in morphology, differing merely in the more slender and in part elongate (attenuated) nature to the blade.

Icriodus sp. D
Plate 3.3, fig. 13.

Description. ≈Biconvex element; axis slightly arcuate. The spindle displays distinct, subcircular and generally discrete denticulation, comprising five lateral-pairs which increase in size progressively towards the anterior terminus. These nodes generally appear enlarged relative to the median denticles, and may also be joined by weak, diffuse, transverse bridges with this median denticulate row (over the anterior part of the spindle). The denticles tend to diverge laterally upwards from the surface of the spindle. The blade constitutes approximately 1/3 the overall element length, appearing longitudinally ridged and comprising up to ?4 indistinct denticles. The blade flanks are straight and moderately broad.

In lateral view, the element axis appears straight, and the upper surface flat; the spindle flanks are ≈constricted towards the basal cavity. The anterior edge of the blade appears inclined in its upper part. The cavity is poorly preserved, with a faint trace of a weak spur and sinus.

Occurrence. Sample 86.014.

Remarks. A combination of the spindle/blade outline, coupled with the disposition and form of the denticulation appears somewhat unique to this morphotype.

Icriodus sp. E
Plate 3.4, figs. 2, 3, 4.

Description. Element axis straight to openly sinuous; spindle ≈elongate subtriangular in outline and usually constitutes in excess of 4/5 the overall element length. The posterior terminus is pointed to subrounded, and the spindle flanks diverge gradually towards the anterior margin; maximum element width at the ≈junction between the spindle and blade. Between four and seven lateral nodes adorn the spindle, appearing robust, angular, subcircular to ovate in outline, as well as transversely ridged. These lateral denticles are commonly discrete from the median row. The median nodes are generally well aligned with the lateral pairs, are laterally compressed, reduced and longitudinally confluent (rarely discrete). The blade appears to be simple and ill-defined; comprises either one or two nodes and a pronounced anteriormost cusp. The cusp is enlarged, distinct and may be slightly isolated from the other denticles of the blade.

In lateral profile, the element axis is straight and the upper surface convex-upwards. In general the lateral denticles appear elevated above the median row. The anteriormost cusp is distinct; the anterior edge markedly inclined.

The basal cavity outline may appear laterally flared, and displays a distinct or remnant trace of a posteriorly directed spur and sinus. The cavity is deepest below the cusp.

Occurrence. The Combe Martin Slates; *the David's Stone Limestone.* The Kentisbury Slates; *sample K53.*

Comparisons. The denticulation of *Icriodus* sp. E appears similar to that displayed by specimens identified as *Icriodus werneri* Weddige by Feist *et al.* (1985; Pl. 3, fig. 16, 17). The marked triangularity in spindle outline, the peg-like denticulation, and the slight isolation of the cusp from the rest of the element distinguishes *Icriodus* sp. E from other form species described herein.

Icriodus sp. F
Plate 3.4, fig. 10.

Description. Broadly biconvex element in outline; axis straight and the posterior tip pointed to subrounded. The spindle constitutes two-thirds the overall element length. The denticulation on the spindle appears differentiated, with the posterior portion displaying a subdued, transversely contiguous ridged sculpture. The remainder of the spindle appears ornamented with between three and four pairs of discrete, robust, lateral denticles: ≈subcircular, bulbous or ridged in form. The median row denticles are subdued, laterally compressed (ovate) or subcircular in outline, and in general appear longitudinally contiguous. The anterior third of the element extends beyond the spindle as a robust, ridged blade; four "nodes" may be differentiated on this broadened blade (on distinguishable by subtle constrictions along the blade). The cusp may appear slightly enlarged, elevated and pointed, or conversely subdued and indistinguishable.

In lateral profile the element axis is straight, and the differential development of the spindle denticulation obvious. The anterior edge appears erect to slightly reclined. The cavity outline is poorly preserved, displaying traces of what originally may have been a pronounced spur and sinus.

Occurrence. The Lester Slates & Sandstones; *the Rillage Limestone.*

Comparisons. Weddige (1977) illustrates a number of form species which appear similar in morphology to the upper surface of *Icriodus* sp. F. *Icriodus* sp. E of Weddige (1977; Pl. 2, figs. 23-25) and *Icriodus ancestralis* (Weddige, 1977 *partim*; fig. 4) in part bear a comparable configuration in denticulation, but the overall spindle and/or blade morphology is clearly different in both cases.

Icriodus sp. G
Plate 3.4, figs. 11, 12.

Description. In upper view the element axis appears broadly arcuate to openly sigmoidal (rarely linear), and the sides ≈parallel. The posterior terminus is commonly rounded, rarely angular. The upper surface displays a distinct, regular and generally subrounded denticulation, comprising between six and nine (commonly 7-8) bilaterally opposed lateral nodes. These nodes appear ≈subcircular in basal outline, bulbous, and are longitudinally discrete: may be joined to the median row by weak to pronounced bridges. The median denticulate row is equal to or slightly smaller in size than these lateral denticles: appear more distinctly circular in outline, and are commonly displaced slightly to the posterior (the three nodal rows are longitudinally discrete, but tend to be laterally compressed). The blade is virtually indistinguishable; the anterior part of the element may lack discernible denticulation. Upon some specimens the remnants of an anterior, deflected processes may be discernible.

In side profile the element appears considerably high. The element flanks are planar, straight, and do not diverge into a broad, flared cavity. The anterior edge appears reclined, and both posterior and anterior termini rounded in form.

The cavity is deep, narrow, with the remnants of a confined, ?lateral flange located ≈midlength.

Occurrence. The Lester Slates & Sandstones; *the Holey Limestone.* The Combe Martin Slates; *the David's Stone Limestone.*

Comparisons. *Icriodus latericrescens latericrescens* Branson & Mehl (1938) displays a distinct, well defined lateral process.

Sadler (1973a) studied the Lower Devonian stratigraphy of the Roseland Peninsula (south Cornwall) and representatives of the conodont faunas recovered from this area are illustrated by Austin *et al.* (1985; Pl. 4.1). Of these elements, *Icriodus* sp. G (the present study) resembles in part the spindles of *Icriodus huddlei curvicauda* Carls & Gandl (fig. 5, Pl. 4.1 of Austin *et al.*, 1985), *I. huddlei huddlei* Klapper & Ziegler (fig.6, Pl. 4.1 of Austin *et al.,* 1985) and *I. huddlei ?celtibericus* Carls & Gandl (fig. 7, Pl. 4.1 in Austin *et al.*, 1985). Unfortunately any further comparison is futile as no lateral processes (key to the speciation of these form taxa) were preserved on specimens recovered from north Devon. The resemblance of *Icriodus* sp. G with these forms suggests the possible reworking of Lower Devonian conodonts.

Carls & Gandl (1969) defined a plexus of narrow platformed icriodid elements encompassing *Icriodus angustoides*. Weyant *et al.* (1988) subsequently describe and illustrate variants of this species from the Lower Devonian of Sevilla Province (Spain), which appear broadly comparable in form to *Icriodus* sp. G. However, the cavity of *I. angustoides* appears somewhat laterally expanded and the denticulation markedly ridged, as well as decreasing in size away from the midpoint of the spindle.

3.2.4 The *Polygnathus* plexus.

3.2.4a. *Introduction.*

Polygnathus is the nominate genus for the Family Polygnathidae, which collectively are widely favoured as zonal indices in the correlation of late Lower, Middle and Upper Devonian strata. Amongst others, Bultynck (1970), Telford (1975) and Chatterton (1979) have postulated potential evolutionary trends within this plexus. Weddige (1977) detailed extensive phylogenetic lineages for Emsian through to Givetian polygnathids, based largely upon relationships interpreted from faunas recovered from the type Eifel region, and based upon evolutionary lineages earlier proposed by Klapper & Johnson (1975). Weddige (1977) compiled a phylogenetic "tree" with *serotinus, linguiformis, robusticostus, trigonicus* and *costatus* lineages, descending from *Polygnathus dehiscens* stock. Subsequently, Weddige & Ziegler (1979) readdressed the earlier findings of Weddige (1977) and remarked that the genus probably originated from spathognathodid elements in the middle part of the Lower Devonian; conceivably from forms such as *Eognathodus* or *Polygnathus pireneae* Boersma (Note: the ancestral polygnathid species, *Polygnathus dehiscens*, displays an enlarged spathognathodid basal cavity). Weddige & Ziegler (1979) remarked that with the progressive development of this plexus through the Devonian, species tended to develop a constricted basal cavity (resembling a basal "pit"), accompanied by a far greater diversity in upper surface platform morphology.

According to Klapper and Philip (1971, 1972), *Polygnathus* is characteristic of Type 1 apparatuses, that comprises the following elements:- P = polygnathan, O_1 = ozarkodinan, N = neoprioniodontan or synprioniodontan, A_1 = hindeodellan, A_2 = angulodontan or plectospathodontan, A_3 = diplodellan or hibardellan. Therefore Klapper & Philip (1971, 1972) proposed the *Polygnathus* apparatus to be seximembrate, comprising both platform and multidenticulate ramiform elements. Several authors have subsequently proposed that seven element-types were the normal complement to the multielement apparatus of this genus (*inter alia*, Chatterton 1974; von Bitter 1976; Nicoll 1977, 1985; Sparling 1981). In particular Nicoll (1985) listed 15 individual elements (of 7 element-types) within the apparatuses of *Ozarkodina brevis* Bischoff & Ziegler (1957) and *Polygnathus xylus xylus* Stauffer (1940), namely:- M (2), Sa (1), Sc (4), Sb (2), Sd (2), Pb (2), and Pa (2).

Recently, Aldridge *et al.* (1987, p. 63-75) evaluated the limited number of recurrent patterns displayed by bedding-plane assemblages of Carboniferous polygnathacean apparatuses. Based upon the septimembrate configuration of *Gnathodus bilineatus* Roundy, they interpreted the architecture of such assemblages as indicating an initial arrangement of elements about a dorso-ventral plane of symmetry. Within this arrangement, ramiform elements are located at the anterior and set at a steep angle to the long axis of the animal, followed posteriorly by Pb and Pa elements (lying vertically and near normal to the long axis of the animal).

Unfortunately, the polygnathid recovery from north Devon was poor; confined to the Ilfracombe Slates and far exceeded in diversity and abundance by the associated icriodid fauna. No polygnathids were recovered from the Lynton Formation. Only the Pa pectiniform elements are described in any detail below.

3.2.4b *Descriptive systematics*. The format of the following systematics is in accordance with the approach outlined within the "Treatise" (Robison, 1981), in preference to that of Sweet (1988). PHYLUM/CLASS : Conodonta, Eichenberg 1930; ORDER : Conodontophorida, Eichenberg 1930; Superfamily : Polygnathacea Bassler, 1925.

Family : Polygnathidae Bassler, 1925.

Genus *Polygnathus* Hinde, 1879.

Type species. *Polygnathus dubius* Hinde, 1879.

Polygnathus cf. *decorosus* Stauffer

Plate 3.5, figs. 8, 10, 14, 15, 17.

cf. 1938 *Polygnathus decorosus* Stauffer, p.438, Pl. 53, figs. 1, 5, 6, 10, 11, 15, 16, 20, 30.

p 1970 *Polygnathus decorosus* Stauffer, in Kirchgasser, p. 347-348, Pl. 64, figs. 2-3, 5, ?6, 8 (only).

cf. 1970 *Polygnathus decorosus* Stauffer, in Seddon, p. 738-739, Pl. 12, figs. 17-19.

cf. 1970 *Polygnathus decorosus* Stauffer, in Klapper, Philip and Jackson, p.652-654, Pl. 3, figs.1-6

cf. 1981 *Polygnathus decorosus* Stauffer, in Huddle assisted by Repetski, B29, Pl. 17, figs. 13-15.

Description. Narrow platformed polygnathid. Platform ≈lanceolate or with a more rounded posterior terminus. The blade is distinct, and equal to or less than the platform length. In upper view the element axis is straight or slightly arcuate; the platform appears narrow, constricted (rarely broadened) and the posterior terminus attenuate, subrounded to angular in form. The adcarinal grooves tend to shallow posteriorly. The anterior trough margins are ill-defined and short (constitute less than 1/5 the platform length), appearing ≈bilaterally symmetrical and lacking ornament. The geniculation points are ≈laterally opposed: the anterior trough margins tend to join the blade at approximately the same point. The carina comprises ≈discrete, enlarged, subcircular to ovate, rounded nodes. The posterior platform margins display a distinctive ornamentation, predominantly of nodes, which on occasion are elongate perpendicular to the element axis forming short ridges. This sculpture is usually concentrated on the middle platform, becoming increasingly diffuse and indistinct posteriorly. The adcarinal grooves generally lack ornament, although occasionally very rare, discrete, subcircular nodes may be indiscriminately scattered towards the carina. The blade is straight to slightly arcuate in plan and appears ≈thickened, robust.

In lateral profile the anterior trough margins are moderately inclined; the blade axis is ≈straight, linear and the denticulation increases progressively in size/height towards the anterior (the blade denticulation may be erect or slightly inclined towards the posterior terminus). In profile, the platform appears ≈convex-upwards; the cavity approximately underlies the junction between the anterior trough margins and the platform proper. In lower view the platform may appear lachrymiform in outline, with a narrow basal groove commonly extending from the anterior to posterior terminus.

Occurrence. The Kentisbury Slates; K53.

Remarks. Compared with the specimens illustrated as *Polygnathus decorosus* Stauffer (1938) by Klapper *et al.* (1970; Pl. 3, fig. 1-6) and Seddon (1970; Pl. 12, fig. 17-19), the faunas recovered from north Devon are clearly not *P. decorosus*, *sensu stricto*, although certain specimens (Pl. 3.5, fig. 8, 10 & 17) do display the more typical lanceolate, attenuated platform outline (which characterises this species). A number of illustrations of *P. xylus xylus* in the literature appear similar to forms attributed herein to *P.* cf. *decorosus*, in displaying more pronounced ornament on the platform margins, and in the platform appearing more lanceolate in outline (*e.g.* refer to the P-element of Uyeno 1978, Pl. 4, figs. 1-3; Nicoll 1985, Fig. 2(J,I), & Fig. 4,(B)). Indeed, within the narrow-platform polygnathid fauna recovered from sample K53, a selected few specimens display platform morphology more reminiscent of *P. xylus xylus* (Plate 3.5, figs. 14 & 15 - displaying a more rounded posterior margin). These transitional forms display a somewhat broader, more robust and comparatively shorter platform, with the margins exhibiting a more subdued and subtle ornament. However, these forms were considered atypical of *P. xylus xylus* and more closely affiliated with *P. decorosus.*

The apparent variation in denticle height on the specimen figured herein on Plate 3.5, fig.10(b) is largely due to blade distortion. Although partially concealed by matrix, figure 14a (Plate 3.5) shows the typical blade dimensions, with the denticulation ≈increasing in height towards the anterior terminus.

Comparisons. As remarked in Klapper *et al.* (1970) *Polygnathus decorosus* has been confused with *Polygnathus xylus xylus* Stauffer (1938). According to Klapper *et al.* (1970, p. 653) *P. decorosus* displays a sagittate platform outline and distinct marginal nodes, as opposed to the broader, parallel-sided platform margins of *P. xylus xylus* (bearing a more subtle ornament, if at all present). Furthermore, the deep adcarinal grooves noted on the anterior platform of *P. decorosus* tend to shallow posteriorly.

Within the literature there has also been some confusion in differentiating *Polygnathus decorosus* from *P. ovatinodosus* Ziegler & Klapper (in Ziegler *et al.*, 1976; refer to synonymy therein). *P. decorosus* differs to *P. ovatinodosus* in displaying a less dense, coarsely nodose platform ornament; the platform also appears more attenuate, narrow, and lacking a rostrum. The platform of *Polygnathus dubius* Hinde is broader, asymmetric and displays rostral ridges. *P. strongi* Stauffer is a *nomen dubium* (refer to Ziegler *et al.*, 1976). *Polygnathus ansatus* displays a distinctly asymmetric platform outline, induced through the unequal outward-bowing of the anterior trough margins. *Polygnathus pollocki* Druce (1976) is comparable in form, but the platform appears distinctly lanceolate, displaying shallow adcarinal grooves, ill-defined anterior trough margins, and a suppressed, more subtle platform ornament. *Polygnathus angusticostatus* Wittekindt in Weddige (1977, *partim*, Pl. 6, fig. 104) resembles some of the specimens attributed to *P.* cf. *decorosus* herein (*e.g.* fig. 17, Pl. 3.5), but the former exhibits a broader, more coarsely ornamented platform midlength.

Subsequent to the first description of *Polygnathus linguiformis* Hinde (1879, p.367), various forms have been assigned both at subspecies and morphotype level to this group or "complex". This group embraces rather elongate polygnathids, that display relatively broad platforms and a variably developed, ornamented posterior "tongue" (refer to Bultynck 1970, p. 126, footnote 1). The basal cavity (pit) is fairly small and is commonly displaced towards the anterior of the platform. Morphological variability within this species is now believed far greater than originally circumscribed by Hinde (1879), with Bultynck (1970) subsequently defining three morphotypes (namely *Polygnathus linguiformis linguiformis*, *alpha*, *beta* and *gamma* morphotypes). To discriminate subtle variants within this species, Bultynck (1970) cited disparities in the development of the posterior "tongue", as well as variation in the architecture of the anterior platform. Ziegler & Klapper (1976) later defined four additional morphotypes (*delta*, *epsilon*, *eta* and *zeta*).

Polygnathus linguiformis linguiformis Hinde, *gamma* morphotype Bultynck

Plate 3.6, figs. 1-4.

1879 *Polygnathus linguiformis* Hinde, p. 367, Pl. 17, fig. 15.

1970 *Polygnathus linguiformis linguiformis* Hinde *gamma* forma nova, Bultynck, pp. 126-127, Pl. 11, figs. 1-3, 6; pl.12, fig. 2, 3, 5.

1976 *Polygnathus linguiformis linguiformis* Hinde *gamma* morphotype Bultynck, in Ziegler & Klapper, p. 122-123, Pl. 4, fig. 9, 13.

1977 *Polygnathus linguiformis linguiformis* Hinde, in Weddige, p. 315-316, Pl. 5, figs. 80-82.

1978a *Polygnathus linguiformis linguiformis* Hinde , in Orchard p. 948, Pl. 110., figs. 18, 22, 24, 27; Pl. 114, figs. 24, 27, 28, 31, 33-37.

1978 *Polygnathus linguiformis linguiformis* Hinde *gamma* morphotype Bultynck, in Johnson & Klapper, Pl. 1, fig. 12.

1979 *Polygnathus linguiformis linguiformis* Hinde (= *gamma* morphotype Bultynck), in Orchard, Pl. 1, fig. 27.

1983 *Polygnathus linguiformis linguiformis* Hinde *gamma* morphotype Bultynck, in Sparling, p. 858, Fig. 11 (E-G); Fig. 13 (U, V, AC).

1988 *Polygnathus linguiformis linguiformis* Hinde, in Sparling, Fig.15 (10, 12); Fig.17 (14); Fig. 18 (15).

For additional synonymy refer to Ziegler *et al.*, (1976, p. 122).

Description. Broad platformed polygnathid; the platform may constitute over four-fifths of the overall element length. When preserved, the free blade appears comparatively high, bearing ≈distinct denticulation. The carina is pronounced in the anterior part of the blade, becoming increasingly diffuse posteriorly (appears incipient or absent upon the tongue): the carina is displaced towards the inner element margin. The adcarinal grooves shallow posteriorly and appear markedly asymmetric in profile; deeper, narrower towards the inner margin, and appearing more open/subdued on the outer expansive part of the blade. Midlength the inner and outer platform margins are subparallel, converging to a rounded posterior terminus; margins appear undulose or distinctly serrated. The upper surface displays a number of ≈irregular, transverse ridges coupled with rare and isolated, ovate to subcircular nodes. These ridges tend to taper towards the carina. The flat tongue constitutes less than one third of the total platform length (defined by a ≈pronounced inward and downward deflection of the outer platform margin). When the tongue is preserved in its entirety, the degree of deflection may be variable, as is the regularity of taper and angularity of the terminus. The carina terminates at or near to the first complete transverse ridge of the tongue. Posteriorly, the outer edge of the platform sweeps round in a crescent, meeting the inner margin. The junction between the platform & tongue may be angular or rounded.

In lateral view, the outer platform margin usually appears slightly elevated above the level of the rest of the platform. The downward deflection of the tongue varies from slight to pronounced, and the platform margin ornamentation similarly variable. In lower view, a diminutive, ovate basal pit may be discernible, extending antero-posteriorly as a fine basal groove that effectively bisects the element.

Occurrence. The Combe Martin Slates; *the Combe Martin Beach and David's Stone Limestones.*

Remarks. Ziegler & Klapper (1976, p. 122-124) considered the *gamma* morphotype of Bultynck (1970) to be identical to the holotype of *Polygnathus linguiformis* Hinde (1879). This was corroborated by Orchard (1978a, p. 948) who dropped the morphotype designation of Bultynck (1970). To save confusion with other morphotypes of *P. linguiformis linguiformis* Group, the usage of the *gamma* terminology is maintained in the present study.

Element preservation was variable. Surfaces may appear etched, lacking discernible ornament and the blade/platform tongue fragmented. On the occasional specimen, the posterior tongue appeared markedly elongate, (as apparent upon the figured specimen of Pl. 3.6, fig. 3). This is considered tectonically induced, and not a primary attribute. However, such accentuation of the tongue morphography does resemble the specimens identified by Orchard (1978a, Pl. 110, figs. 9, 10, 28, 30) as *Polygnathus linguiformis* Hinde, ?*delta* morphotype Ziegler & Klapper.

Comparisons. The *delta, eta* and *zeta* morphotypes of *Polygnathus linguiformis linguiformis* lack a prominent tongue, and also display a carina that tends to reach the posterior terminus. In large *epsilon* specimens, somewhat irregular rostral ridges develop.

Ziegler & Klapper (1976) regarded *Polygnathus parawebbi* Chatterton as affiliated to the *Polygnathus linguiformis* group, treating it as subspecies of *Polygnathus linguiformis* (= *Polygnathus linguiformis parawebbi*). Klapper (in Ziegler 1977, p. 477) subsequently returned this form to species status, noting that although this and *P. linguiformis linguiformis* are similar in gross form, *Polygnathus parawebbi* displays incomplete transverse ridges on the posterior tongue (and also a better defined, more complete carina). Furthermore, Klapper perceived the multielement apparatuses of these two species distinct.

The *Polygnathus varcus* Group. Klapper, Philip & Jackson, 1970.

Synonymy.

? 1979 *Polygnathus varcus* Stauffer group, in Orchard, Pl. 1, fig. 12, 15.

Klapper, Philip & Jackson (1970) rationalised *Polygnathus varcus* "type" elements, believing the species concept of *P. varcus* (as it was then defined) to circumscribe a heterogeneous grouping of conodont elements. Consequently, Klapper *et al.* (1970) defined the "*varcus* Group", that embraced Stauffer's *Polygnathus varcus* and *P. xylus* species, in addition to two new forms proposed by them; *P. rhenanus* and *P. timorensis*. Klapper *et al.*, (1970) differentiated species according to: the relative length and breadth of the platform, the degree of platform ornament, the position of the basal cavity and the nature of the anterior platform margins. More recently, appraisals of this plexus have emphasised the need for an awareness of ontogenetic growth stages (Orchard 1978a, p. 950).

Subsequent to Klapper *et al.* (1970), Ziegler & Klapper (in Ziegler *et al.* 1976, p. 125) interpreted *P. rhenanus* to be a junior synonym of *P. timorensis* (the former representing junior growth stages of the latter species). Since then the concept of *P. rhenanus* has been resurrected in its own right, being considered distinct from *P. timorensis* (*e.g.* Bultynck, 1987). Thus this taxon is legitimately recognised in the present study. Ziegler & Klapper (1976) also proposed *P. ansatus* and *P. xylus ensensis*, which are informally included within the *varcus* Group herein, due to their described similarity with *P. timorensis* (refer to Ziegler *et al.*, 1976, p. 120) and *P. xylus xylus* (refer to Ziegler *et al.*, 1976, p. 125-126) respectively.

The adverse preservation of most specimens recovered in the present study often limited precise species identification.

Polygnathus ?ansatus Ziegler & Klapper
Plate 3.5, fig. 11.

? 1976 *Polygnathus ansatus* Ziegler & Klapper, p. 119-120, Pl. 2, figs. 11-26.

? 1985 *Polygnathus ansatus* Ziegler & Klapper, in Austin *et al.*, Pl. 4.4, fig.2.

? p 1987 *Polygnathus hemiansatus* Bultynck, Pl. 8, fig. 6 only.

? p 1987 *Polygnathus ensensis* Ziegler & Klapper, in Bultynck, Pl. 7, figs. 7, 8 (only).

Description. In upper view the element axis is openly arcuate, rarely straight. The platform constitutes just less than one half of the total element length; the outer and inner margins are constricted, preferentially towards the anterior of the platform (≈coincides with the geniculation points). The posterior platform margins are ornamented with discrete nodes or transverse ridges, and the adcarinal troughs relatively deep, unsculptured. The posterior portion of the platform may appear relatively flattened, and laterally expanded. The anterior trough margins lack ornamentation, appearing markedly asymmetric and bowed: the ?outer margin appears relatively reduced, and the ?inner more pronounced. The geniculation points are offset, with the anterior trough margins meeting the blade at approximately the same point. The carina comprises rounded, ovate nodes that are fused longitudinally into an irregular carina.

In side profile, the blade is straight and the platform arched. The denticulation on the blade is distinct, varying from erect to inclined (directed towards the posterior terminus). The anterior trough margins appear gently inclined, and the geniculation points rounded. The basal cavity underlies the junction of the blade and platform.

Occurrence. The Kentisbury Slates; K53.

Remarks. The figured specimen (Pl. 3.5, fig. 11) resembles one of the *Polygnathus ansatus* paratypes of Ziegler & Klapper (1976; no. 39627, Pl. 2, fig. 21), although differs to the holotype in overall platform morphology. Within the polygnathid population recovered from sample K53, forms attributed to *Polygnathus ?ansatus* were noted to intergrade with *P.* cf. *decorosus* (as the anterior platform and trough margins become increasing rectilinear).

In the figured specimen, the ?inner and not the ?outer anterior trough margin appears the more distinctly outwardly bowed.

Comparisons. *Polygnathus timorensis* Klapper, Philip & Jackson (1970) displays a narrower blade, with the outer anterior trough margin meeting the blade slightly anterior of the inner margin (note: Ziegler & Klapper (1976, p. 120) acknowledge that juvenile forms of *P. timorensis* may be virtually indistinguishable from *P. ansatus* Ziegler & Klapper, 1976). *P. xylus xylus* Stauffer (1940) displays parallel platform margins that tend to lack any conspicuous ornament, as well as appearing visibly asymmetric. In common with *P. ansatus*, *P. ovatinodosus* Ziegler & Klapper (1976) displays a coarser, nodose platform ornament, as well as bearing much shallower adcarinal grooves (of interest Ziegler & Klapper (1976, p. 124) suggested that *P. ovatinodosus* was a probable descendant of *P. ansatus*). *Polygnathus hemiansatus* Bultynck (1987) was differentiated from *P. ansatus* upon subtle disparities in anterior trough margin morphology. The figured specimens of *P. ensensis* transitional to *P. timorensis* in Bultynck (1987; Pl. 7, fig. 7, 8) resembles this species described herein, although does appear to display serrated anterior trough margins.

Polygnathus aff. *ansatus, sensu* Bultynck, 1987.
Plate 3.5, fig. 16.

aff. 1976 *Polygnathus ansatus* Ziegler and Klapper, p. 119-120, Pl. 2, figs. 11-26.
1987 *Polygnathus* aff. *ansatus* Ziegler & Klapper, in Bultynck, Pl. 8, fig. 9.

Description. Elongate, narrow-platformed polygnathid; element axis arcuate in plan view. The platform constitutes over two-thirds of the, total preserved element length: the anterior part is constricted, broadening posteriorly (resembling a flattened "palate"), and converging finally to a rounded/subangular posterior terminus. The adcarinal troughs are shallow and subdued posteriorly, deepening anteriorly. The platform margins appear nodose or display weak, transverse/slightly oblique ridges. The anterior trough margins are short, poorly developed and are not distinctly outwardly bowed. The carina is robust, comprising over seven, bulbous, ovate and longitudinally contiguous denticles: the carina projects posteriorly beyond the platform.

In lateral profile the element axis is straight and the anterior platform margins are obviously subdued. The platform margin ornament is indistinct. In lower view, the basal cavity appears elliptical in outline, and approximately ≈underlies the constricted anterior portion of the platform. The lower surface may appear "keeled" in part, and also bearing an indistinct basal groove.

Occurrence. The Kentisbury Slates; K53.

Remarks. Bultynck (1987) recently described and illustrated a form comparable to *Polygnathus ansatus* from the Eifelian/Givetian strata of Morocco and Belgium. This species (*P.* aff. *ansatus*) lacked any distinct development of the anterior trough margins (which appeared comparatively short and ill-defined). Specimens recovered from the Kentisbury Slates resemble this form species of Bultynck (1987).

Comparisons. In the present study, *Polygnathus* aff. *ansatus, sensu* Bultynck (1987) intergrades with *P.* cf. *decorosus* and *P. ?ansatus* described earlier, differing in the overall platform outline and the subdued form to the anterior trough margins. The inner anterior trough margins of *P. hemiansatus* Bultynck (1987) are not outwardly bowed, appearing more rectilinear.

Note: the comparisons listed under *Polygnathus ?ansatus* above.

Polygnathus rhenanus Klapper, Philip & Jackson

Plate 3.5, figs. 1, 2, 5.

1970 *Polygnathus varcus* Stauffer, in Kirchgasser, p. 351-352, Pl. 66, figs. 9-11.

1970 *Polygnathus rhenanus* Klapper, Philip & Jackson, p. 654-655, Pl. 2, figs. 13-15, 19-22.

1980 *Polygnathus rhenanus* Klapper, Philip & Jackson, in Bultynck & Hollard, p. 45, Pl. 6, figs. 15-17.

p 1981 *Polygnathus rhenanus marijae* n. subsp. Huddle, p.1132, Pl. 17, figs. 10-12 (only).

1987 *Polygnathus rhenanus* Klapper, Philip & Jackson, in Bultynck, p. 162, Pl. 7, fig. 13-15.

? 1988 *Polygnathus rhenanus* Klapper, Philip & Jackson, in Sparling p. 15, fig. 18; 11.

Description. Platform markedly asymmetric, short and may constitute less than one quarter of the total element length. Platform margins usually parallel-sided, lacking ornamentation and commonly converge abruptly to a rounded posterior terminus (the carina may project slightly beyond the platform). The geniculation points vary from slightly to markedly offset, and may display a rounded, subdued node. The anterior trough margins appear asymmetric in upper view (the platform having its greatest width at this point), and usually join the blade at approximately the same point, although conversely may be markedly offset. Well defined comparatively deep adcarinal troughs are evident, shallowing slightly towards the posterior terminus. The carina comprises between four and ?six ovate, longitudinally elongate and fused denticles.

In profile the blade appears straight, rarely arcuate, and the platform ≈convex-upwards. If preserved, the blade displays erect or variably orientated, discrete, ≈angular and robust denticles, which may alternate in size and height. In general the denticulation on the platform increases anteriorly: the blade denticulation may appear ≈regular. The platform margins are raised above the level of the carina. In lower view, the basal cavity is positioned at or slightly anterior of the junction between the free blade and the platform. The cavity is ovate to lachrymiform in outline, and extends as a ≈perceptible basal groove postero-anteriorly.

Occurrence. The Lester Slates & Sandstones; *the Rillage Limestone.* The Combe Martin Slates; *the Combe Martin Beach and David's Stone Limestone.*

Remarks. Complete specimens of *P. rhenanus* were rarely recovered. Within this species population, probable juvenile and adult forms were represented. Klapper *et al.* (1970) remark that in general, the geniculation points are opposite: for certain specimens recovered in the present study, these appeared distinctly offset. Furthermore, the anterior trough margins were (occasionally) poorly developed.

As mentioned in the preamble to the *varcus* Group, Ziegler *et al.* (1976) consider *P. rhenanus* to be a junior synonym of *P. timorensis*. Recently however, *P. rhenanus* has been re-affirmed in its own right (Bultynck & Hollard, 1980; Bultynck, 1987), and thus is recognised in the present study. Poorly preserved specimens of *P. rhenanus* and *P. varcus* recovered from north Devon proved difficult to differentiate.

Comparisons. In comparison, *Polygnathus varcus* displays symmetrical and smooth platform margins. According to Bultynck (1987, p. 162), the presence of ornamentation on the platform margins of *Polygnathus rhenanus* is insignificant for the recognition of this species. However, following the original intent of Klapper *et al.* (1970) the lack of platform sculpture (in conjunction with the overall platform morphology) allows distinction of *P. rhenanus* from *P. timorensis*. Furthermore, mature specimens of *P. timorensis* display a more balanced platform : blade ratio, and exhibit a basal cavity located well beneath the anterior platform. The platform of *P. xylus xylus* appears far more symmetrical and broader.

Polygnathus varcus Klapper, Philip & Jackson

Plate 3.5, figs. 3, 4, 6, 7.

1940 *Polygnathus varcus* Stauffer, p.430, Pl. 60, figs. 49, 55.

non 1970 *Polygnathus varcus* Stauffer, in Kirchgasser, p. 351- 352, Pl. 66, figs. 9-11.

1970 *Polygnathus varcus* Stauffer, in Klapper, Philip & Jackson 1970, p. 657-658, Pl. 2, figs. 1-3, 23-25.

1978a *Polygnathus varcus* Stauffer, in Orchard, p. 950, Pl.109, fig. 29.

1985 *Polygnathus varcus* Stauffer, in Austin *et al.*, Pl. 4.4, fig. 4 (taken from Orchard 1978a, Pl. 109, fig. 29).

Refer to Klapper *et al.* (1970, p. 657) for additional synonymy.

Description. Narrow-platformed polygnathids; platform short, ≈bilaterally symmetrical and lacking ornamentation. When preserved, the free blade appears comparatively long (over two-thirds of the total element length), straight or arcuate. In plan view, the geniculation points are usually diametrically opposed, and may bear a diminutive, virtually indistinguishable node. The anterior trough margins appear narrow, short and straight to slightly concave upwards: vary in appearance from ≈shallow to steeply inclined. Adcarinal grooves are pronounced and deep, or may shallow posteriorly. The carina is either formed by the longitudinal fusion of over three (distinguishable) denticles, or resembles a simple, undifferentiated ridge.

In lateral profile, the blade (or remnant of) is straight and the platform appears ≈arched. The denticles on the blade vary in inclination from erect to oblique (reclined towards the posterior), and are of variable size (commonly displaced below the level of the platform). In lower view, the basal cavity is located at, or marginally anterior of, the junction between the free blade and platform. A thin, constricted basal groove may extend antero-posteriorly.

Occurrence. The Combe Martin Slates; *the Combe Martin Beach and David's Stone Limestone.*

Remarks. A comparatively broad concept of *Polygnathus varcus* was applied in the present study. In general specimen preservation was poor. The specimen illustrated in Orchard (1979; Pl. 1, fig. 12, 15) shows questionable *varcus* affinity, and appears so poorly preserved that it can only tentatively be assigned to this group (refer to the earlier synonymy).

Comparisons. *Polygnathus rhenanus* similarly lacks platform ornamentation, but the platform outline is markedly asymmetric (displaying unequally developed, irregular and outwardly bowed anterior trough margins). The platform of *P. timorensis* bears pronounced sculpture, whereas for *P. xylus xylus*, the position of the basal cavity and general platform proportions are distinctly different.

Polygnathus xylus ensensis Ziegler & Klapper
Plate 3.8, fig. 13. "The Orchard Collection".

1976 *Polygnathus xylus ensensis* Ziegler & Klapper, (in Ziegler, Klapper and Johnson) p. 125-127, Pl. 3, figs. 4-7.
p 1977 *Polygnathus xylus ensensis* Ziegler & Klapper, in Weddige, p. 321-322, Pl. 4, figs. 62, 64 (only).
p 1977 *Polygnathus pseudofoliatus* Wittekindt, in Weddige, p. 321-322, Pl. 4, figs. 68 (only).
1985 *Polygnathus xylus ensensis* Ziegler & Klapper, in Austin *et al.*, Pl. 4.3, fig. 12.
1987 *Polygnathus ensensis* Ziegler & Klapper, in Bultynck, p. 161, Pl. 7, figs. 1-6.
1988 *Polygnathus xylus ensensis* Ziegler & Klapper, in Sparling Fig. 17 (8); Fig. 18 (7).

Description. Lanceolate, narrow platform; blade of figured specimen not preserved. The adcarinal grooves on the platform shallow posteriorly; the margins are nodose to faintly ridged, and just posterior of the geniculation points appear distinctly serrated (comprising between three and four angular nodes). The morphology of the anterior trough margins is obscure, appearing somewhat shallow and ≈symmetrical.

In oblique lateral view, the posterior platform margins appear slightly subdued, and the carina increasingly indistinct towards the posterior terminus.

Occurrence. The Orchard Collection; *the Leigh Barton Limestone.*

Remarks. The sinuosity to the axis of the figured specimen reflects tectonic distortion, and is not deemed a primary attribute.

Comparisons. The distinct serration to the anterior platform margins, coupled with the apparent symmetry of the anterior trough margins allow identification. The anterior trough margins of *Polygnathus timorensis* are distinctly asymmetrical and lack such pronounced "serration". *P. rhenanus, P. varcus* and *P. xylus xylus* lack such distinct ornamentation.

Polygnathus xylus xylus Stauffer.
Plate 3.5, fig. 13.
Forms ?transitional to *Polygnathus* cf. *decorosus*; Plate 3.5, fig. 9, 12 (?).

1940 *Polygnathus xylus* Stauffer, p. 430-431, Pl. 60, fig. 54, 66, 72-74.
1970 *Polygnathus xylus* Stauffer, in Klapper, Philip & Jackson, p.659-666, Pl. 1, figs. 4-6, 11; Pl. 2, fig. 4, 5, 7-12, 16-18.
1976 *Polygnathus xylus xylus* Stauffer, in Ziegler *et al.*, p. 125, Pl. 3, fig. 1.
1987 *Polygnathus xylus xylus* Stauffer, in Bultynck, Pl. 8, fig. 22, 27; Pl. 9, fig. 12.
Refer to Klapper *et al.* (1970) and Ziegler *et al.* (1976) for additional synonymy.

Description. Short, squat, and relatively broad narrow-platformed polygnathids. The blade constitutes less than one half of the total element length; element axis straight, and may display an inwardly deflected posterior terminus. The platform margins are subparallel, and converge abruptly to a rounded or subangular posterior terminus: platform margins display fine, subdued nodes or traces of transverse ridges (perpendicular to the carina). The platform appears ≈bilaterally symmetrical: the carina comprises ovate, longitudinally contiguous nodes. The anterior trough margins are ill-defined, short, smooth and conservative in design (*e.g.* are not outwardly bowed), and approximately meet the blade at the same point. In upper view, the blade appears robust and short.

In lateral view, the element is straight, and the anterior trough margins range from relatively steep to moderately inclined. In lower view the basal cavity appears confined, ovate in outline and located ≈posterior of the junction between the platform and blade. A faint basal groove may underlie the entire element lower surface.

Occurrence. The Kentisbury Slates; K53.

Remarks. Part of the polygnathid fauna recovered from sample K53 displayed a morphology transitional between *Polygnathus xylus xylus* and *P.* cf. *decorosus* (as described above). Intermediaries between the two exhibit squat, and broad platforms of the "*xylus*-type", but bear distinct ornamentation on the upper surface. Despite such "sculpture", the non-lanceolate and laterally broader form to these elements was considered more compatible with the diagnosis of *P. xylus xylus*, than with that of *P. decorosus* Stauffer (refer to the remarks made above under *P.* cf. *decorosus*).

Comparisons. *Polygnathus ensensis* displays serrated platform margins. *P. timorensis* similarly bears a distinct platform ornament. *P. varcus* differs in exhibiting a narrower, more attenuate platform. Although Klapper *et al.* (1970, p. 664) acknowledge that the anterior trough margins of *P. xylus* may appear somewhat asymmetric, this asymmetry is not as pronounced as that apparent noted for *P. rhenanus*. *P. eiflius* Bischoff & Ziegler and *P. pseudofoliatus* Wittekindt differ in basic platform design, platform "sculpture", and blade proportions.

3.2.5. Conodont Miscellanea - Pb, ramiform and coniform elements.

This section concludes the systematic description of dissociated conodont elements recovered from the Devonian strata of north Devon. Due to the general paucity in preservation, their low numbers and the uncertain multielement affiliation of many of these non-Pa elements, they are described separate to the above. However, where appropriate, the probable multielement identity is discussed.

Pb pectiniform element, unident.
Plate 3.6, fig. 7.

Description. In lateral view: element arched, cavity distinct and slightly laterally flared. The cusp is distinct, enlarged, and inclined. The blade is fragmented posteriorly and anteriorly: bears up to four isolated, ≈erect, relatively subdued but robust denticles. The basal cavity deep ("cavenous"), ≈ovate in outline, and extends postero-anteriorly as a constricted basal groove. The blade surface appears homogeneous, whereas the denticles and apical cusp are longitudinally striated.

Remarks and comparisons. The figured element has been fractured and resealed (attributable to tectonic deformation - improbable that organically sealed). This accounts for the slight sinuosity in the outline of the basal cavity, and the flexure of the anterior blade. Huddle (1981) illustrates a number of homologous form species referred to *Bryantodus* spp.

coniform element, (?S_2 element).
Plate 3.1, fig. 17.

Description. In lateral view: bilaterally asymmetric element, displaying a slightly inclined posterior edge and broadly crescentic anterior margin, both of which converge to a relatively angular, pointed terminus. The basal cavity may appear slightly laterally expanded, being fragmented and subovate in outline. The element lacks any distinct surface texture.

Remarks and comparison. Very few coniform elements of any description were recovered in this study. The figured specimen represents the best preserved specimen of the total coniform assemblage: a variety of cavity outlines and surface textures were noted, but preservation was very poor.

The S_2 element of the *Icriodus latericrescens* apparatus Klapper & Philip (1971; p. 438, Fig. 8), is morphologically similar. The S_{2a} element of the *Icriodus brevis* apparatus, figured by Uyeno (1978; Pl. 4, fig. 31, 32) is similar, but lacks any pronounced lateral expansion of the cavity.

?polygnathid ramiform elements.
Plate 3.6, figs. 8, 9, 10.

Description. Multidenticulate ramiform elements. Bar straight or ± slightly flexed at either extremity. The upper surface displays a range in denticle size and morphology: the cusp may be indistinguishable to distinct, and the cavity usually ill defined, or represented by a simple, constricted groove.

Remarks and comparisons. As is clear from the figured specimens, preservation of this type of element is decidedly poor, hence the lack of detailed taxonomy. The figured material represents the best ramiforms recovered. The linearity in some of the blades tends to favour a probable Sb, ?Sc or Sd identity, and are herein believed to represent the ramiform elements of a "Type 1" (polygnathid) apparatus (*sensu* Klapper & Philip, 1971). For comparison, refer to the vicarious ramiform elements figured by Orchard (1978a, Pl. 111) or Nicoll (1985, Fig. 1).

The upward deflection of the posterior terminus on the specimen illustrated as fig. 8 of Plate 3.6, is considered a preservational and not primary attribute.

ligonodinan element.
Plate 3.6, fig. 11.

Description. Robust, coarsely denticulate elements. The cusp and denticles are typically broken near to their base. The arched bar lacks bilateral symmetry (in side profile). The anterior process bears up to 3 inclined denticles. The posterior process is commonly not preserved, or comprises a short sparsely denticulate bar. The cusp is distinct and ≈strongly posteriorly reclined: the cavity underlying the cusp is distinct but constricted, with the trace of a basal groove extending postero-anteriorly.

Comparisons. The specimen figured in the present study (Pl. 3.6, fig. 11) resembles the B1 element illustrated by Klapper & Philip (1971, Fig. 13) for the Type 2 apparatus of *Parapolygnathus angusticostatus* (Wittekindt). Nicoll (1977, p. 219) perceived the Sc element of the *Oulodus angulatus* (Hinde, 1879) apparatus to be ligonodinan (*Ligonodina panderi*; refer to Seddon 1970, Pl. 15, fig. 10), which if fragmented, is comparable in form to the above figured specimen. The B1 element of a Type 2 apparatus documented and figured from Mount Wise by Orchard (1978a, Pl. 111, fig. 27) similarly appears similar in basic design. Sparling (1981; Text-fig.4) illustrated the multielement element apparatus of *Prioniodina tortoides*: the specimen of the present study (Pl. 3.6, fig. 11) may represent a poorly preserved ligonodinan element, as illustrated by Sparling (1981; Text-fig. 4, F). Huddle (1981; Pl. 29, figs. 10-12, Pl. 31, fig. 22-24) figures a number of morphologically similar elements as *Lonchodina subsymmetrica* Ulrich & Bassler.

?lonchodinan element.
Plate 3.6, fig. 6, ?12.

Remarks. Robust, coarsely denticulate elements. The two figured specimens illustrate variable degrees of bilateral symmetry: Fig. 6 near symmetrical and Fig. 12 markedly asymmetric. The cusp upon both specimens appears well defined, and the cavity of the specimen in Fig. 6 appears distinct, ovate and located beneath the cusp.

Comparisons. One of the few features common to both figured specimens is the coarse denticulation. The exact identity of the figured material is somewhat problematical. Huddle (1981; Pl. 29, fig. 13-17; Pl. 30, fig. 9) figures a number of specimens as *Trichonodella blanda* (Stauffer) which appear broadly similar in design.

?prioniodinan element.
Plate 3.6, fig. 5.

Description. Mature prioniodinan element. Robust, coarsely denticulate element: only one thick-set bar preserved. The denticulation is discrete, enlarged and somewhat elongate. The cusp is pronounced and underlain by a cavenous basal cavity. The denticles appear erect or variably orientated.

Remarks and comparisons. The figured element is remarkably large, and may represent a ?gerontic adult prioniodinan element. Sparling (1981; Text-fig. 4, D) illustrated a broadly homologous element in the apparatus of *Prioniodina tortoides*, although the bar of his specimen (no. S77P37b, Text-fig.4D) does not appear quite as thick-set as the specimen figured in the present study.

Plates 3.1-3.8.

Conodonts and miscellanea recovered in association are illustrated.

All illustrations are x60 unless otherwise stated. In the plate descriptions information is presented according to the following format; figure number; taxonomic name and designating author, and specimen remarks; specimen orientation; sample number and slide code.

PLATE 3.1

Plate 3.1.

Conodont elements recovered from the Lynton Formation.

All specimens are illustrated at x60 unless otherwise stated.
Sample and slide codes are recorded after each identification.

Fig. 1 *Icriodus culicellus*, (Bultynck) Weddige, 1977; (a) lateral elevation, (b) upper view; LN76.3

Fig. 2 *Icriodus culicellus*, (Bultynck) Weddige, 1977; (a) lateral elevation, (b) upper view; LN73.2

Fig. 3 *Icriodus culicellus*, (Bultynck) Weddige, 1977; (a) oblique lateral view, (b) upper view; LN76.13

Fig. 4 *Icriodus culicellus*, (Bultynck) Weddige, 1977; (a) oblique lateral view, (b) upper view; LN108.2

Fig. 5 *Icriodus ?corniger corniger*, Wittekindt, 1966; upper view; LN109.25

Fig. 6 *Icriodus culicellus*, (Bultynck) Weddige, 1977; spindle tectonically elongate; (a) oblique lateral view, (b) upper view; LN73.11

Fig. 7 *Icriodus culicellus*, (Bultynck) Weddige, 1977; upper view; LN109.26

Fig. 8 *Icriodus culicellus*, (Bultynck) Weddige, 1977; upper view; LN77.3

Fig. 9 *Icriodus culicellus*, (Bultynck) Weddige, 1977; (a) upper view, (b) oblique lateral view; LN73.8

Fig. 10 *Icriodus ?corniger corniger*, Wittekindt, 1966; (a) oblique lateral view, (b) lower surface view, & (c) upper surface view; LN76.11

Fig. 11 *Icriodus* sp. A.; (a) oblique lateral view, (b) upper view; LN73.10

Fig. 12 *Icriodus culicellus*, (Bultynck) Weddige, 1977; upper view; LN73.4

Fig. 13 *Icriodus* cf. *werneri*, Weddige, 1977; upper view; LN109.9

Fig. 14 *Icriodus culicellus*, (Bultynck) Weddige, 1977; (a) upper surface view, (b) oblique lateral view; LN76.4

Fig. 15 *Icriodus retrodepressus*, Bultynck, 1970; (a) oblique lateral view, (b) upper surface view; LN110.40

Fig. 16 *Icriodus retrodepressus*, Bultynck, 1970; upper view; LN109.19

Fig. 17 Coniform element, unidentified ($\approx S_2$ element); lateral elevation; LN108.3

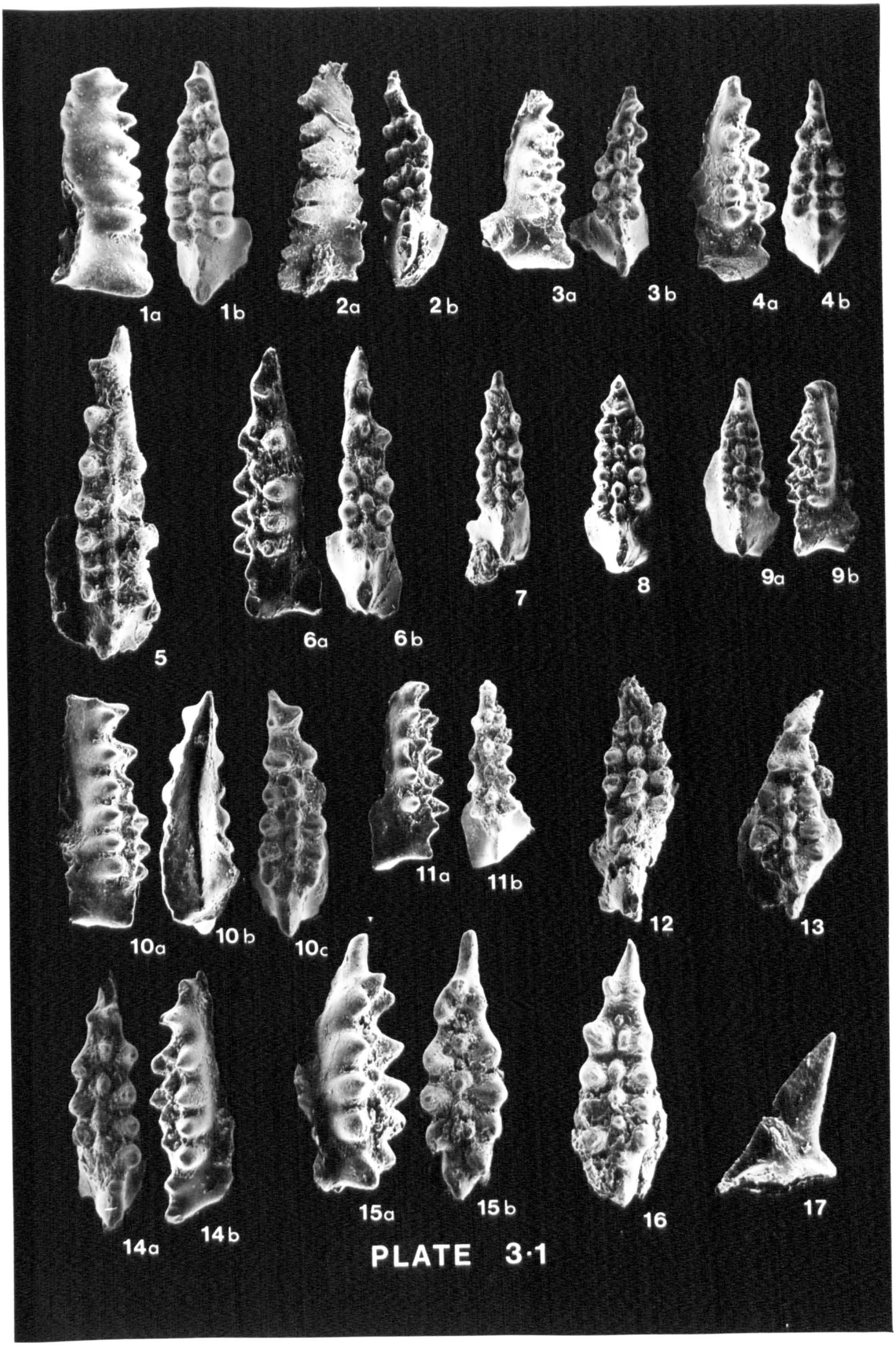

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PLATE 3·1

PLATE 3.2

Plate 3.2.

Icriodus elements recovered from the Ilfracombe Slates.

All specimens are illustrated at x60 unless otherwise stated.
Sample and slide codes are recorded after each identification.

Fig. 1 *Icriodus brevis* Stauffer, 1940; adult morphotype; upper view; L19,13.

Fig. 2 *Icriodus brevis* Stauffer, 1940; adult growth stage; (a) upper surface view, (b) oblique lateral elevation; L16.18

Fig. 3 *Icriodus brevis* Stauffer, 1940; (a) lateral view, (b) upper view; L29.43

Fig. 4 *Icriodus brevis* Stauffer, 1940; (a) upper surface view, (b) slightly oblique lateral view; L29.27

Fig. 5 *Icriodus brevis* Stauffer, 1940; upper view; CM47.9

Fig. 6 *Icriodus brevis* Stauffer, 1940; (a) slightly oblique lateral elevation, (b) upper view; K53.5

Fig. 7 *Icriodus brevis* Stauffer, 1940; upper view; L29.9

Fig. 8 *Icriodus brevis* Stauffer, 1940; ?juvenile; upper view; K53.4

Fig. 9 *Icriodus brevis* Stauffer, 1940; juvenile - comparable to the third triad growth stage of *Icriodus expansus*, *sensu* Nicoll 1983; upper view. Also note the homology with specimens attributed to *Icriodus* cf. *cornutus* Sanneman by Weddige (1984, p. 209, Pl. 4, figs. 76-77); L29.9

Fig. 10 *Icriodus brevis* Stauffer, 1940; juvenile, as for fig.9; upper view; K53.3

Fig. 11 *Icriodus brevis* Stauffer, 1940; upper view; 86.067 .42

Fig. 12 *Icriodus* cf. *difficilis* Ziegler & Klapper, 1976; upper view; 86.067 .47

Fig. 13 *Icriodus* cf. *difficilis* Ziegler & Klapper, 1976; upper view; 86.061 .3

Fig. 14 *Icriodus* cf. *difficilis* Ziegler & Klapper, 1976; (a) upper view, (b) lateral view; CM47.8

Fig. 15 *Icriodus* cf. *difficilis* Ziegler & Klapper, 1976; upper view; L29.39

Fig. 16 *Icriodus* cf. *difficilis* Ziegler & Klapper, 1976; upper view; L29.19

Fig. 17 *Icriodus eslaensis* Van Adrichem Boogaert, 1967; lateral elevation; L28.8

Fig. 18 *Icriodus lindensis* Weddige, 1977; lateral elevation; L29.39

Fig. 19 *Icriodus lindensis* Weddige, 1977; lateral elevation; L29.26

Fig. 20 *Icriodus brevis* Stauffer, 1940; (a) upper view, (b) oblique lateral elevation; K53.2

Fig. 21 *Icriodus lindensis* Weddige, 1977; lateral elevation; L17.20

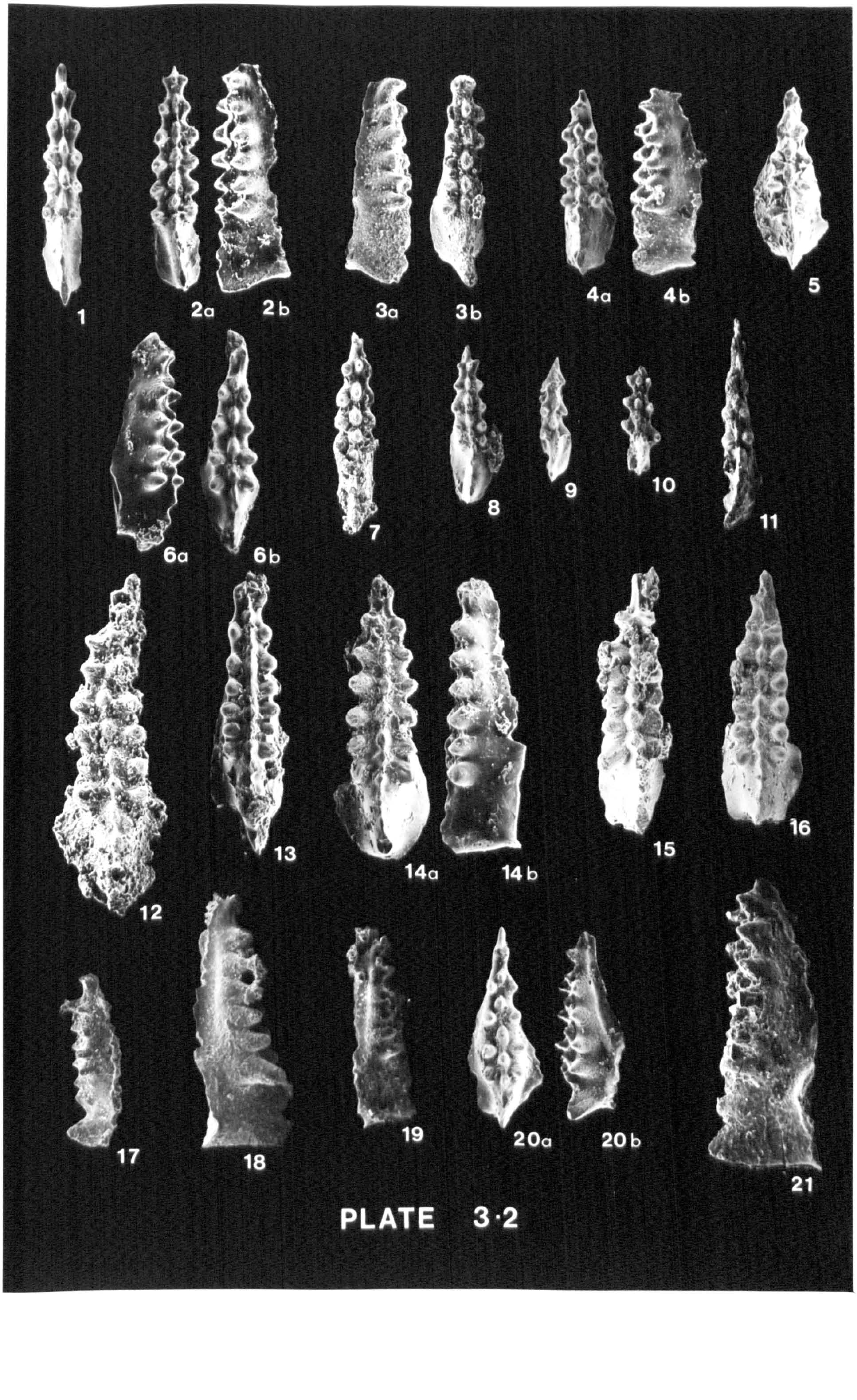

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PLATE 3·2

Plate 3.3.

Icriodus elements recovered from the Ilfracombe Slates.

All specimens are illustrated at x60 unless otherwise stated.
Sample and slide codes are recorded after each identification.

Fig. 1 *Icriodus obliquimarginatus* Bischoff & Ziegler emend. Weddige, 1977; (a) slightly oblique lateral view, (b) upper surface view; 86.067 .27

Fig. 2 *Icriodus obliquimarginatus* Bischoff & Ziegler emend. Weddige, 1977; (a) upper surface view, (b) lateral view; CM51.7

Fig. 3 *Icriodus obliquimarginatus* Bischoff & Ziegler emend. Weddige, 1977; lateral view; CM65.25

Fig. 4 *Icriodus obliquimarginatus* Bischoff & Ziegler emend. Weddige, 1977; lateral view; CM50.9

Fig. 5 *Icriodus obliquimarginatus* Bischoff & Ziegler emend. Weddige, 1977; lateral view; CM49.24

Fig. 6 *Icriodus obesus* Bultynck, 1987; (a) upper surface view, (b) oblique lateral view; WP28.3

Fig. 7 *Icriodus ?platyobliquimarginatus* Bultynck, 1987; upper view; 86.055 .5

Fig. 8 *Icriodus* cf. *regularicrescens* Bultynck, 1970; upper view; L17.10

Fig. 9 *Icriodus* sp. B; oblique lateral view; L16.22

Fig. 10 *Icriodus ?difficilis* Ziegler & Klapper, 1976; (a) oblique lateral view, (b) upper surface view; CM47.5

Fig. 11 *Icriodus* sp. C; (a) upper surface view, (b) oblique lateral view; CM31.6

Fig. 12 *Icriodus* sp. C; (a) oblique lateral view, (b) upper surface view; 86.061 .11

Fig. 13 *Icriodus* sp. D; (a) upper surface view, (b) oblique lateral view; 86.014 .51

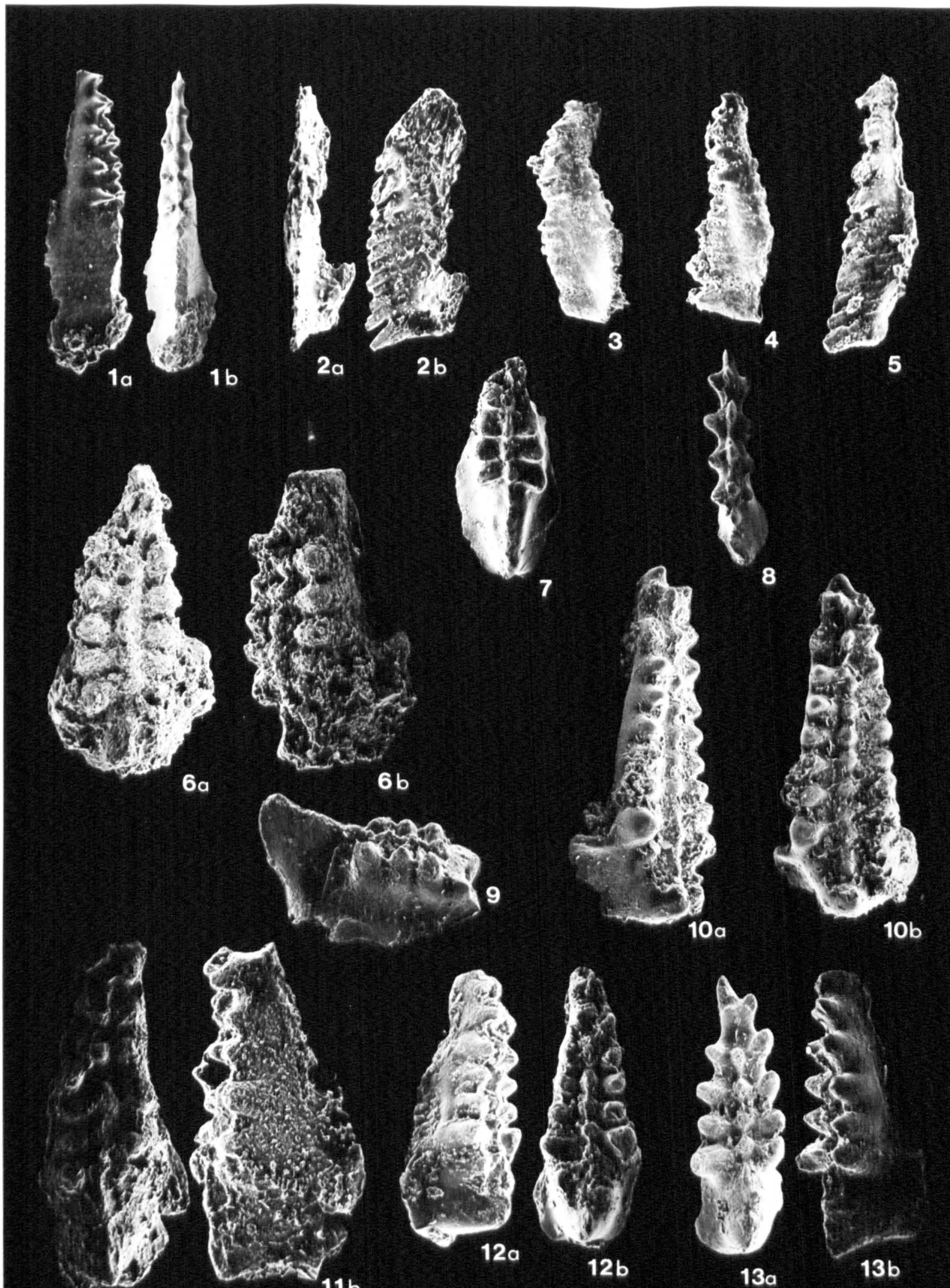


PLATE 3·3

PLATE 3.4

Plate 3.4.

Icriodus elements recovered from the Ilfracombe Slates.

All specimens are illustrated at x60 unless otherwise stated.
Sample and slide codes are recorded after each identification.

Fig. 1 *Icriodus ?arkonensis* Stauffer, 1938; (a) oblique lateral view, (b) upper surface view; 86.067 .26

Fig. 2 *Icriodus* sp. E; upper surface view; CM56.11

Fig. 3 *Icriodus* sp. E; upper surface view; CM56.11

Fig. 4 *Icriodus* sp. E; (a) lower surface view, (b) upper surface view; K53.6

Fig. 5 *Icriodus* aff. *obesus* Bultynck, 1987; (a) oblique lateral view, (b) upper surface view;CM77.3

Fig. 6 *Icriodus* aff. *obesus* Bultynck, 1987; spindle fractured, and distorted; (a) upper surface view, (b) oblique lateral view; CM49.18

Fig. 7 *Icriodus* cf. *brevis* Stauffer, 1940; upper view; 86.019 .21

Fig. 8 *Icriodus* cf. *brevis* Stauffer, 1940; upper view; 86.019 .22

Fig. 9 *Icriodus ?fusiformis* Carls & Gandl, 1969; upper view; 86.055 .22

Fig. 10 *Icriodus* sp. F; upper view; L19.7

Fig. 11 *Icriodus* sp. G; (a) lateral view, (b) upper view; CM59.2 - x40

Fig. 12 *Icriodus* sp. G; (a) oblique lateral view, (b) upper view; L29.3

PLATE 3·4

PLATE 3.5

Plate 3.5.

Narrow-platform polygnathid (Pa) elements,
recovered from the Ilfracombe Slates.

All specimens are illustrated at x60 unless otherwise stated.
Sample and slide codes are recorded after each identification.

Fig. 1 *Polygnathus rhenanus* Klapper, Philip and Jackson, 1970; specimen tectonically deformed; (a) lateral view, (b) upper surface view; CM47.34

Fig. 2 *Polygnathus rhenanus* Klapper, Philip and Jackson, 1970; blade missing; upper surface view; CM58.34

Fig. 3 *Polygnathus varcus* Klapper, Philip and Jackson, 1970; specimen blade distorted; (a) oblique lateral view, (b) upper view; CM47.35

Fig. 4 *Polygnathus varcus* Klapper, Philip and Jackson, 1970; (a) oblique lateral view, (b) upper surface view; CM47.35

Fig. 5 *Polygnathus rhenanus* Klapper, Philip and Jackson, 1970; lateral view; L29.50

Fig. 6 *Polygnathus varcus* Klapper, Philip and Jackson, 1970; (a) upper surface view, (b) lateral view; CM31.18

Fig. 7 *Polygnathus varcus* Klapper, Philip and Jackson, 1970; (a) upper surface view, (b) lateral view; 86.056 .18

Fig. 8 *Polygnathus* cf. *decorosus* Stauffer 1938; blade missing; (a) lateral view of platform, (b) upper view; K53.42

Fig. 9 *Polygnathus xylus xylus* Stauffer 1940, transitional to *P.* cf. *decorosus* Stauffer 1938; (a) lateral view, (b) upper surface view; K53.43

Fig. 10 *Polygnathus* cf. *decorosus* Stauffer 1938; complete specimen; (a) upper surface view, (b) slightly oblique lateral view & (c) lower surface view; K53.44

Fig. 11 *Polygnathus ?ansatus* Ziegler and Klapper 1976; (a) upper surface view, (b) lateral elevation; K53.38.

Fig. 12 *P.* cf. *decorosus* Stauffer 1938, transitional to *Polygnathus xylus xylus* Stauffer 1940; posterior portion of platform missing; upper surface view; K53.39

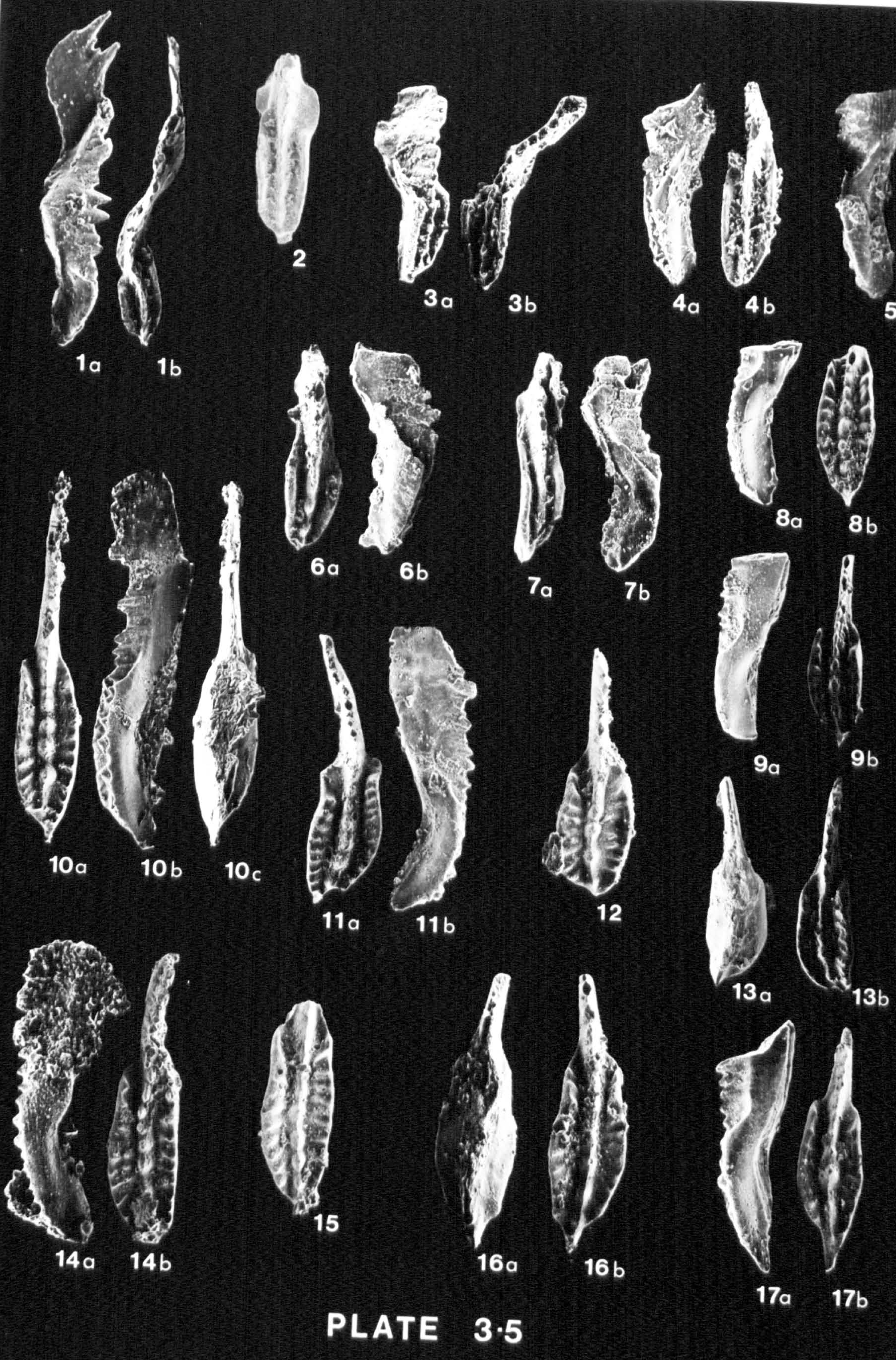
Fig. 13 *Polygnathus xylus xylus* Stauffer 1940; (a) lower surface view, (b) upper surface view; note the platform ornament is markedly subdued relative to forms assigned to *P.* cf. *decorosus*; K53.45

Fig. 14 *Polygnathus* cf. *decorosus* Stauffer 1938; the posterior tip of platform is notably rounded - a feature atypical of *P. decorosus, sensu stricto* (a) lateral view, (b) upper surface view; K53.41

Fig. 15 *Polygnathus* cf. *decorosus* Stauffer 1938; upper view; K53.42

Fig. 16 *Polygnathus* aff. *ansatus* Ziegler & Klapper 1976, *sensu* Bultynck 1987; (a) lower surface view, (b) upper view; K53.45

Fig. 17 *Polygnathus* cf. *decorosus* Stauffer 1938; (a) lateral elevation, (b) upper surface view;K53.40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17b

PLATE 3·5

PLATE 3.6

Plate 3.6.

Polygnathid (Pa) elements and miscellaneous non-Pa elements, recovered from the Ilfracombe Slates.

All specimens are illustrated at x60 unless otherwise stated. Sample and slide codes are recorded after each identification.

Fig. 1 *Polygnathus linguiformis linguiformis* Hinde *gamma* morphotype Bultynck, 1970. x40; (a) upper view, (b) oblique lateral view & (c) lower surface view; CM47.36

Fig. 2 *Polygnathus linguiformis linguiformis* Hinde *gamma* morphotype Bultynck, 1970; upper surface view; CM33.18

Fig. 3 *Polygnathus linguiformis linguiformis* Hinde ?*gamma* morphotype Bultynck, 1970; element incomplete with the posterior tongue ?tectonically elongated; CM49.40

Fig. 4 *Polygnathus linguiformis linguiformis* Hinde *gamma* morphotype Bultynck, 1970; (a) upper surface view, (b) oblique lateral view & (c) lower surface view; CM33.20

Fig. 5 ?gerontic prioniodinan element; lateral view; CM33.36 - x40.

Fig. 6 ?lonchodinan element; lateral view; K53.50

Fig. 7 Pb element. ?bryantodontan element; (a) lateral view, (b) lower surface view; CM47.71

Fig. 8 polygnathid S element, unident; lateral view; CM56.52

Fig. 9 polygnathid S element, unident; lateral view; CM64.34

Fig. 10 polygnathid S element, unident; lateral view; CM47.52

Fig. 11 ligonodinan element; lateral view; K53.51

Fig. 12 ?lonchodinan element; lateral view; CM47.54

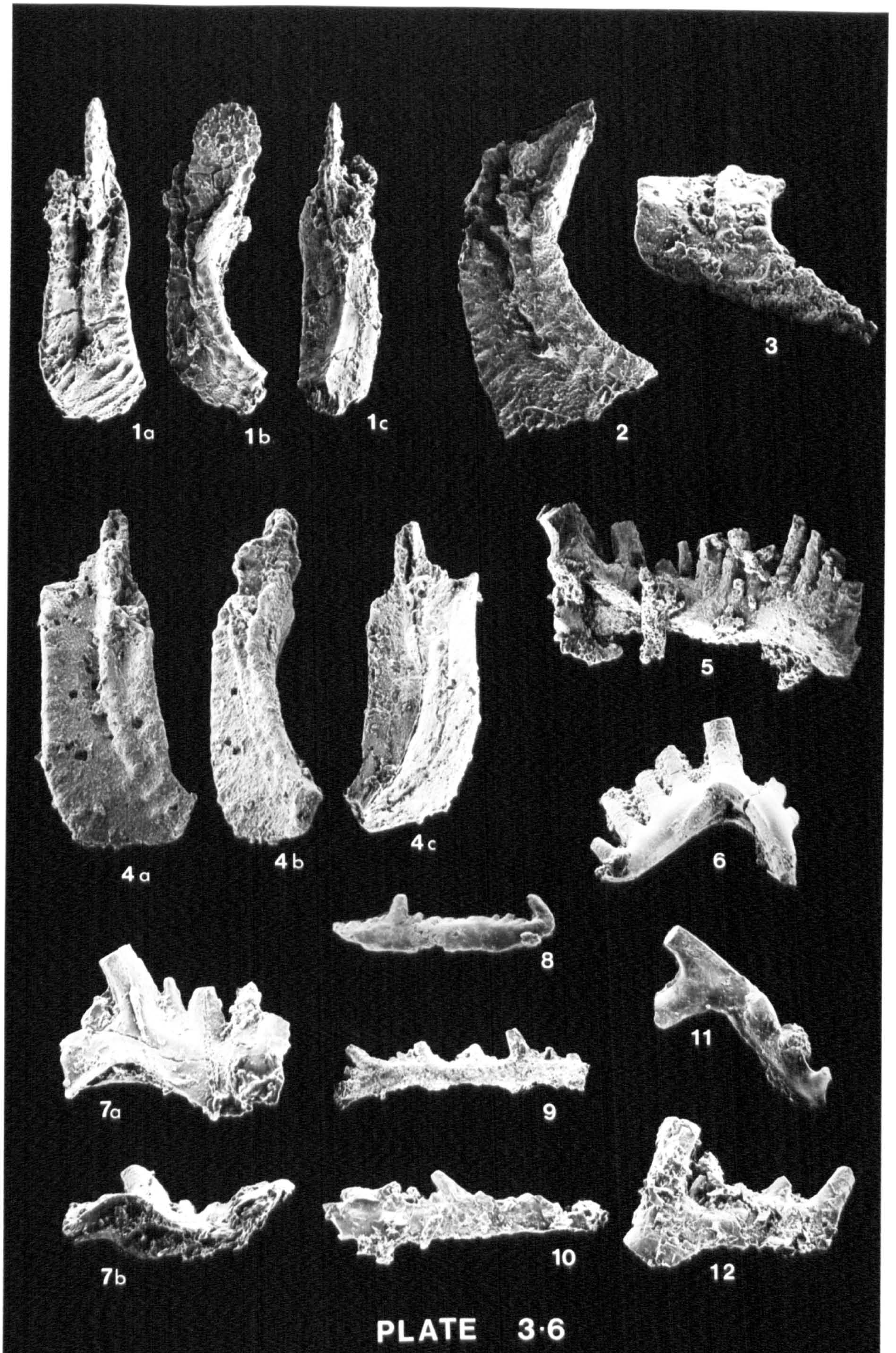


PLATE 3·6

PLATE 3.7

Plate 3.7.

Miscellaneous microfossils and ultrastructural detail of conodont elements, representative of the Ilfracombe Slates.

All specimens are illustrated at x60 unless otherwise stated.
Sample and slide codes are recorded after each description.

Tectonically deformed conodont elements - upper surface views unless, specified.

Fig. 1 Distorted *Icriodus ?brevis*, Stauffer 1940. Spindle extended longitudinally; CM58.8.

Fig. 2 Distorted icriodid, transversely sheared; CM57.2

Fig. 3 Distorted *Icriodus* ? cf. *werneri*, Weddige 1977. Spindle transversely sheared; LN109.27.

Fig. 4 Distorted *Polygnathus rhenanus* Klapper, Philip and Jackson, 1970. Juvenile specimen - blade sinuosity tectonically induced, not primary. Oblique lateral view; CM47.34.

Conodont textures.

Fig. 5 Lower surface view; K53.50 (lateral elevation Pl. 3.6, fig. 6). Enlarged image x300 - concentric growth lamellae discernible.

Fig. 9 Upper surface view of *Icriodus brevis*, CM47.9. Enlarged image x300 depicts diagenetic alteration of the spindle surface; cubic crystal growth between the denticulation.

Miscellanea.

Fig. 6 Tentaculites, unident; L20.57

Fig. 7 Tentaculites, unident; CM65.45

Fig. 8 Tentaculites, unident; L29.57

Fig. 10 Gastropod steinkern; planispiral growth mode; oblique view; L17.45

Fig. 11 Gastropod steinkern; planispiral growth mode; LN78, x40

Fig. 12 Gastropod steinkern; planispiral growth mode; LN74.43

Fig. 13 Gastropod steinkern; helical growth mode; L29.56, x40

Fig. 14 Articulated ostracod carapaces, lateral elevation, unident; L29.62

Fig. 15 Ichthyodont, unident; L29.57

Fig. 16 Ichthyodont, unident; L29.40. Enlarged field of view details surface pseudoreticulation, x350.

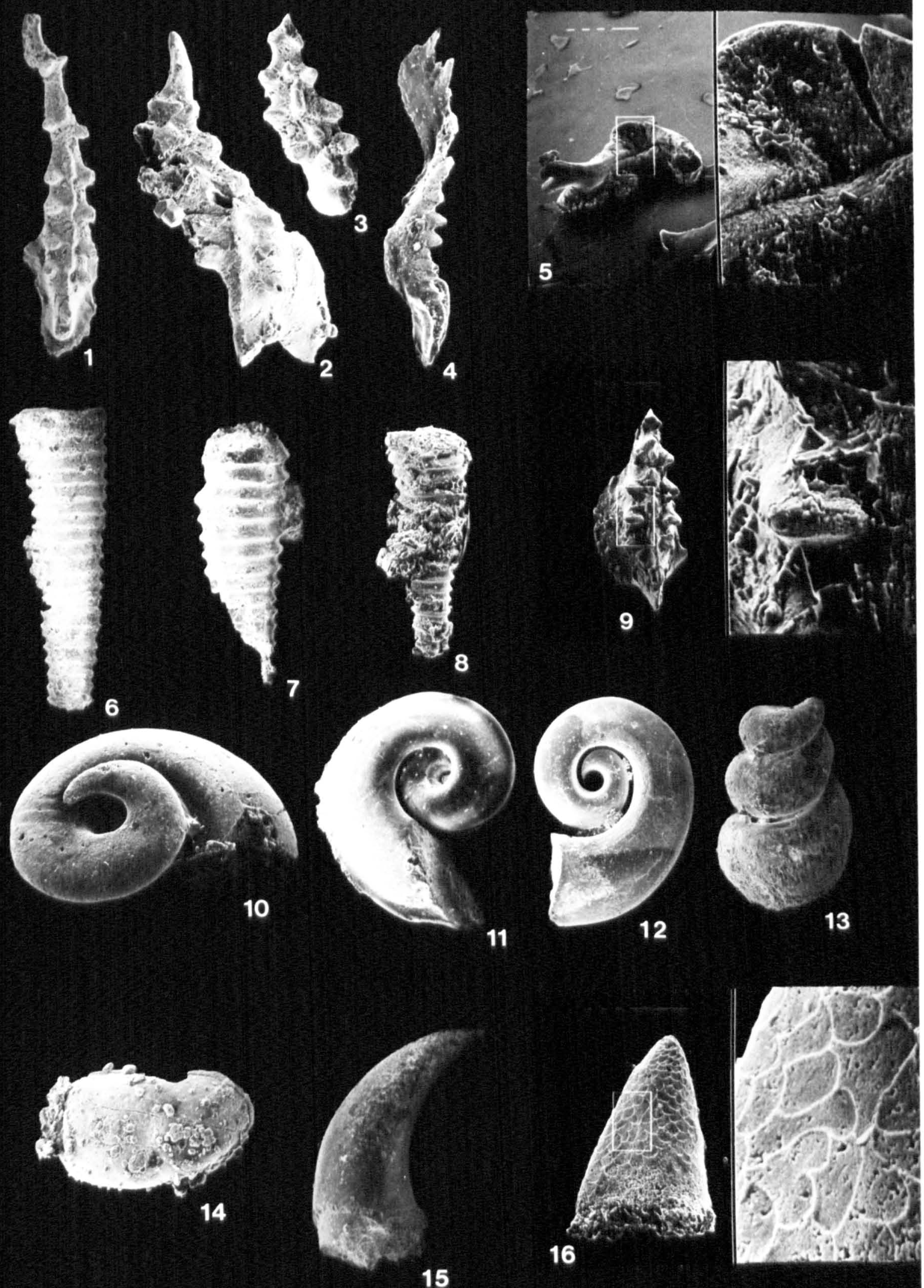


PLATE 3·7

PLATE 3.8

Plate 3.8

The Orchard Collection

Photomicrographs provided by Mike Orchard (*pers.comm.*, 1989) are figured. Identification proved problematical, as it was based exclusively on these illustrations.

Details of specimen magnification and limestone source are provided.

Fig. 1 *Icriodus arkonensis* Stauffer, 1938; oblique upper view; Rodhuish Limestone (lateral equivalent of the Rillage Limestone, *sensu* Webby, 1966a) - locality no. 5, NNE of Hill Farm, south of Withycombe (ST 015408). Refer to Austin *et al.* (1985, p. 114).

Fig. 2 *Icriodus arkonensis* Stauffer, 1938; slightly oblique upper view; Rodhuish Limestone (lateral equivalent of the Rillage Limestone, *sensu* Webby, 1966a) - locality no. 5 as above.

Fig. 3 *Icriodus brevis* Stauffer, 1940; upper view; Rodhuish Limestone (lateral equivalent of the Rillage Limestone, *sensu* Webby, 1966a) - locality no. 5 as above.

Fig. 4 *Icriodus brevis* Stauffer, 1940; upper view; Roadwater Limestone (lateral equivalent of the Jenny Start Limestone, *sensu* Webby, 1966a) - locality no. 1, quarry south of Parsons Lane, NNW of Aisholt (ST 192361). Refer to Austin *et al.* (1985, p. 114).

Fig. 5 *Icriodus lindensis* Weddige, 1977; lateral view; Roadwater Limestone (lateral equivalent of the Jenny Start Limestone, *sensu* Webby, 1966a) - locality no. 7, south of Sandhill Farm, near Withycombe (ST 020405). Refer to Austin *et al.* (1985, p. 114).

Fig. 6 *Icriodus ?brevis* Stauffer, 1940; upper view; Roadwater Limestone (lateral equivalent of the Jenny Start Limestone, *sensu* Webby, 1966a) - locality no. 7, south of Sandhill Farm, near Withycombe (ST 020405). Refer to Austin *et al.*, (1985, p. 114).

Fig. 7 *Icriodus* sp. 1, unident. (*?lindensis*); upper view; Roadwater Limestone (lateral equivalent of the Jenny Start Limestone, *sensu* Webby, 1966a) - locality no. 7, south of Sandhill Farm, near Withycombe (ST 020405). Refer to Austin *et al.*, (1985, p. 114).

Fig. 8 *Icriodus* cf. *regularicrescens* Bultynck, 1970; upper view; Rodhuish Limestone (lateral equivalent of the Rillage Limestone, *sensu* Webby, 1966a) - locality no. 4, quarry NE of Stiles Farm, Rodhuish (ST 013396). Refer to Austin *et al.*, (1985, p. 114).

Fig. 9 *Icriodus* sp. 2, unident; (a) upper view, (b) lateral view; Rodhuish Limestone - locality no. 5 (see above).

Fig. 10 *Icriodus* sp. 3, unident; upper view; Roadwater Limestone - locality no. 1 (see above).

Fig. 11 icriodid element, unident (*?difficilis*); upper view; Lower Aisholt Limestone (lateral equivalent of the Combe Martin Beach Limestone, *sensu* Webby, 1966a) - locality no. 2, quarry ESE of Tudballs Farm (ST 212236). Refer to Austin *et al.*, (1985, p. 114).

Fig. 12 *Icriodus ?brevis* Stauffer, 1940; upper view; Leigh Barton Limestone - locality no. 3, quarry at Badger Copse, east of Cothelstone (ST 189318). Refer to Austin *et al.*, (1985, p. 114). As with fig. 11, element displays extreme corrosion.

Fig. 13 *Polygnathus xylus ensensis* Ziegler & Klapper, 1976; blade missing, but the serrated anterior platform margins evident; platform ?tectonically distorted; oblique lateral view; Leigh Barton Limestone - locality no.3, See above.

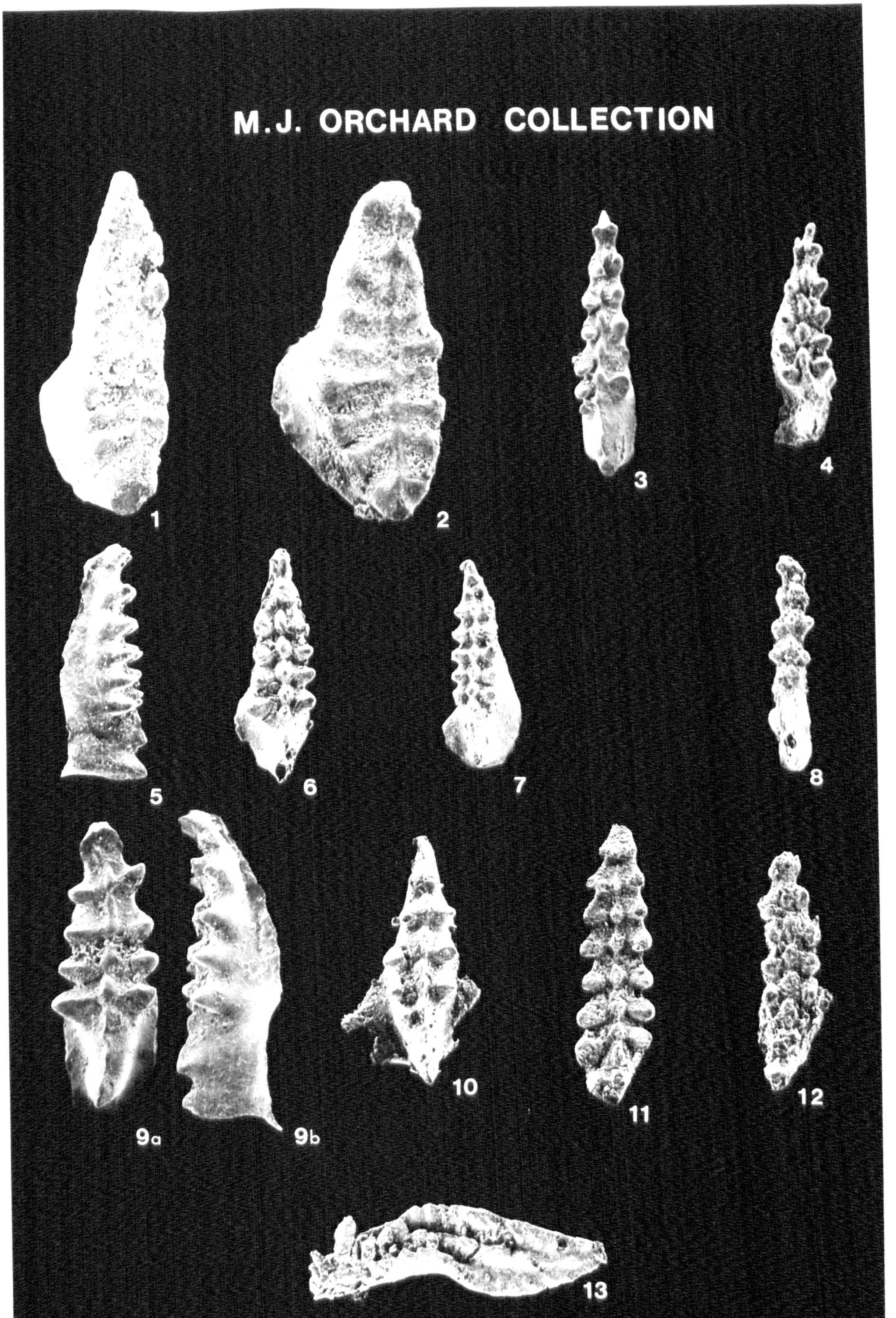


PLATE 3·8

3.3 PALYNOMORPHS.

3.3.1 MIOSPORES.

3.3.1a *Nomenclature and systematic treatment.*

At present there is a divergence of opinion whether or not to sustain a suprageneric classification in the ordering of spore taxonomic data. The grouping of taxa into suprageneric categories is common practice in palynology, and is considered advantageous as it identifies complexes of spores with similar, arbitrarily selected morphological features. A number of hierarchial schemes are currently available (*e.g.* Potonié & Kremp, 1954, 1955, 1956; Dettman, 1963), with modifications to these systems having been proposed by, amongst others, Richardson (1965), Neves & Owens (1966) and Smith & Butterworth (1967). However, despite appearing formal, such suprageneric systems are in fact quite artificial, with no real phenetic or phylogenetic basis. Furthermore, there is no singular, suprageneric approach that is widely recognised or ubiquitously applied.

The many inadequacies and limitations of suprageneric classificatory schemes are widely acknowledged (*e.g* Balme, 1988; p. 115), although numerous workers still advocate the organization of spore systematics according to such methodologies, awaiting the ultimate and optimum palaeobotanically driven scheme. However, many palynologists have expressed objections to such schemes (*e.g.* Schopf 1969, Urban 1971), particularly as such methodologies tend to imply potential botanical affinities for spore genera that are of unknown palaeobotanical affiliation. To counter such criticisms, Peppers (1970), Ravn (1979) and more recently Balme (1988) attempted to organise descriptive systematics according to the format of these suprageneric systems, but without citing the terminology. Unfortunately such an approach appears somewhat random, and may not only confuse those unfamiliar with suprageneric schemes, but furthermore make such work virtually inaccessible.

Many palynologists have attempted to incorporate known or suspected palaeobotanical affinities of spores into their classifications (*e.g.* Romans 1975). Ravn (1986) devised one such scheme for Carboniferous spore taxa, equating genera with major plant groups, and integrating known palaeobotanical affinity with major morphological characteristics. Ravn (1986; p. 20-21) remarked that with minor modifications and the addition of a few other basic categories, such a scheme could be adapted to other parts of the Palaeozoic column. Furthermore, he considered that in view of recent advances in the known palaeobotanical affinities of many Devonian spores (*e.g* Allen 1980; Gensel 1980), an adequate basis was in fact available for the formulation of a rudimentary, palaeobotanically driven classificatory scheme for palynofloras of this age. Such a scheme is still awaited.

McGregor and Camfield (1976) pioneered the departure away from suprageneric classifications, by simply ordering genera alphabetically: in adopting this approach, McGregor & Camfield (1976) still acknowledged the basic principles of suprageneric schemes, but favoured this more utilitarian approach. Ravn (1986) recognised that alphabetical ordering simplifies data presentation, but was critical of its validity, as it tends to obscure potential or real generic relationships, as well as lacking taxonomic stability. However, despite such criticisms the utilitarian, alphabetical ordering of taxa by genera as introduced to Devonian spore systematics by McGregor & Camfield (1976) is favoured and applied below. Such an approach is acknowledged to be temporary, awaiting the formulation of the ultimate, palaeobotanically driven systematic scheme.

The descriptive terminology and nomenclature rationalised by Grebe (1971) on behalf of the

C.I.M.P. is adhered to in the following systematic descriptions, with the supplements of Owens (1971; p. 87, Fig. 4) and Balme (1988; p. 117-118) also utilised: Owens (1971) devised a nomenclature for describing the variation in the morphology of grapnel-shaped termini to spines. The more important morphological features of spores are schematically shown overleaf on Figure 3.3.1.

As mentioned in the introduction to this chapter (Section 3.1), synonymy lists are intended primarily to summarise nomenclatural histories, and if appropriate, indicate previous British records of the taxon concerned. Consequently, for most species described overleaf, the related synonymy citations are brief and do not profess to be comprehensive.

3.3.1b *Estimation of the composition of assemblages.*

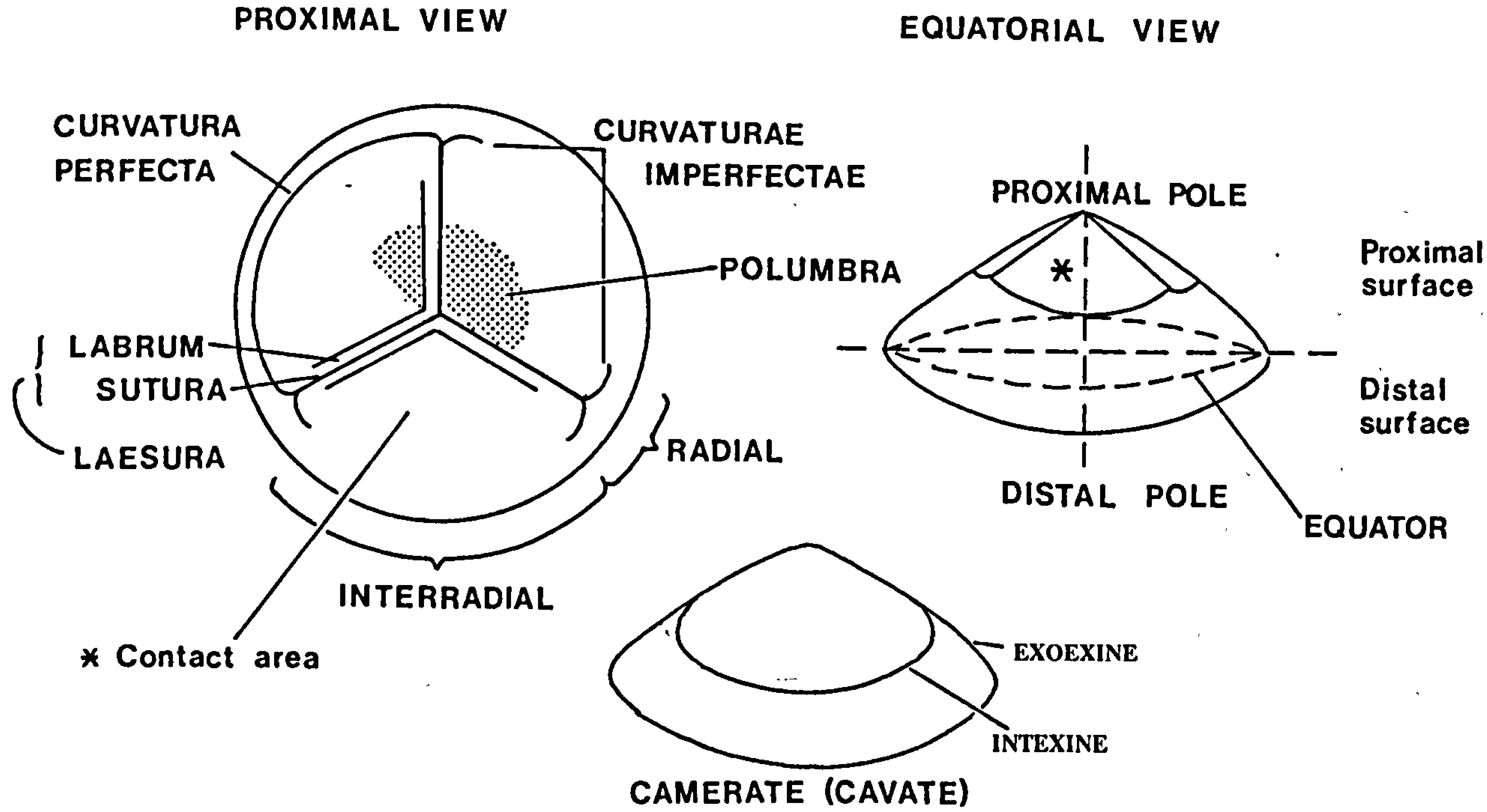
Generalised estimates of the abundance of specific taxa per lithostratigraphic unit are provided below, following in principle the methodology outlined by Balme (1988, p. 119). An approximation of species abundance was noted, and equates to the number of individuals counted within a single strewn mount: a maximum of 20 specimens of each species were counted within two slide preparations of the same sample (Note: typically ≈100g of each sample was processed, and a representative amount of the extracted kerogen oxidised and subsequently analysed). Thus, the typical (generalised) occurrence of each taxon within the major lithostratigraphical units studied is provided (under the heading of *Occurrence*), according to the following criteria:

Very rare: on average one to four specimens recorded per sample.
Rare: five to ten specimens.
Common: ten to twenty specimens.
Abundant: in excess of twenty specimens.
R: occurrence believed reworked.

The temporal distribution of miospore taxa through the studied sequence and related biostratigraphical interpretations are discussed in detail in Chapter 4.

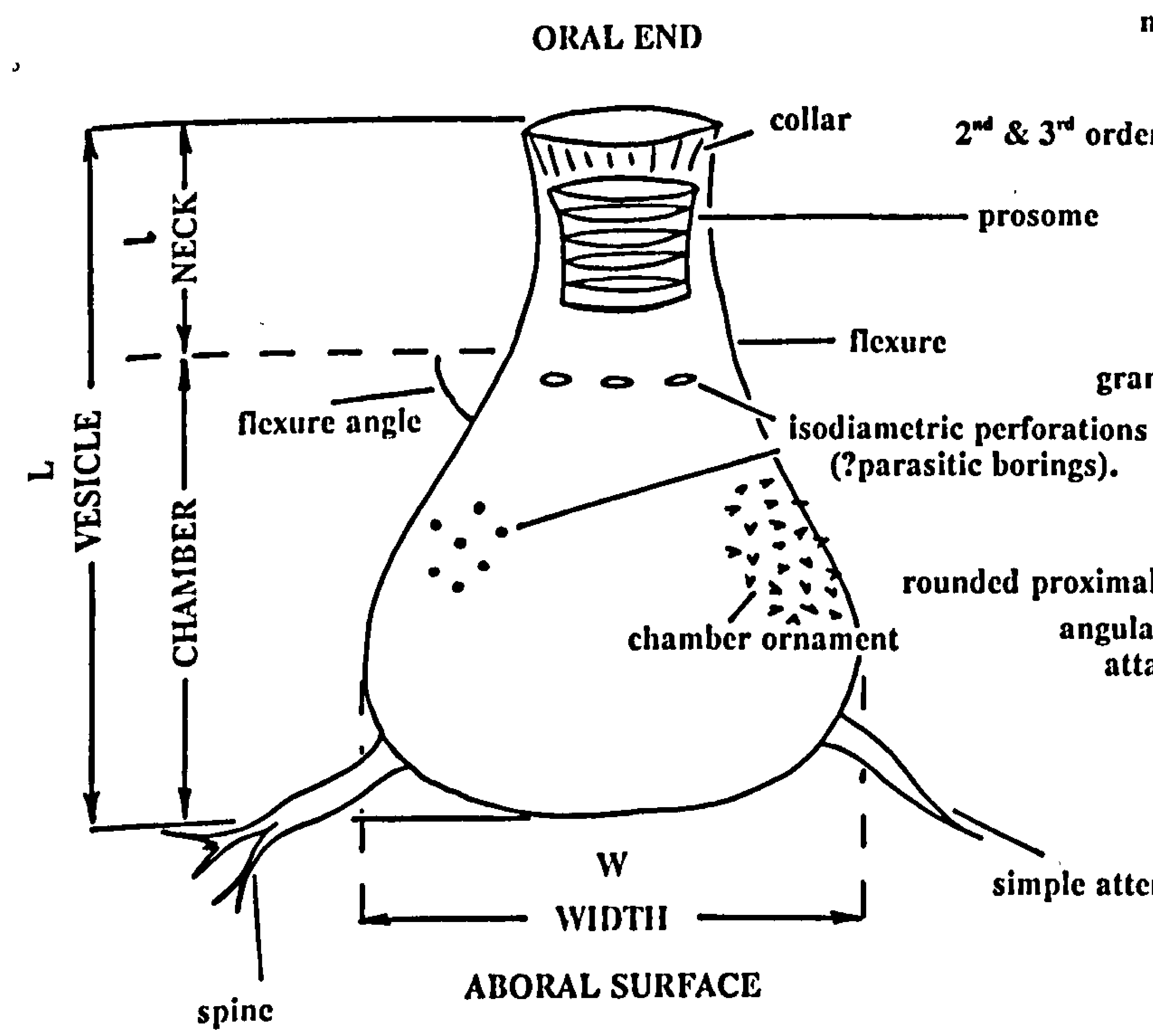
FIGURE 3.3.1 MIOSPORE, ACRITARCH AND CHITINOZOAN ORIENTATION AND MORPHOLOGICAL TERMINOLOGY.

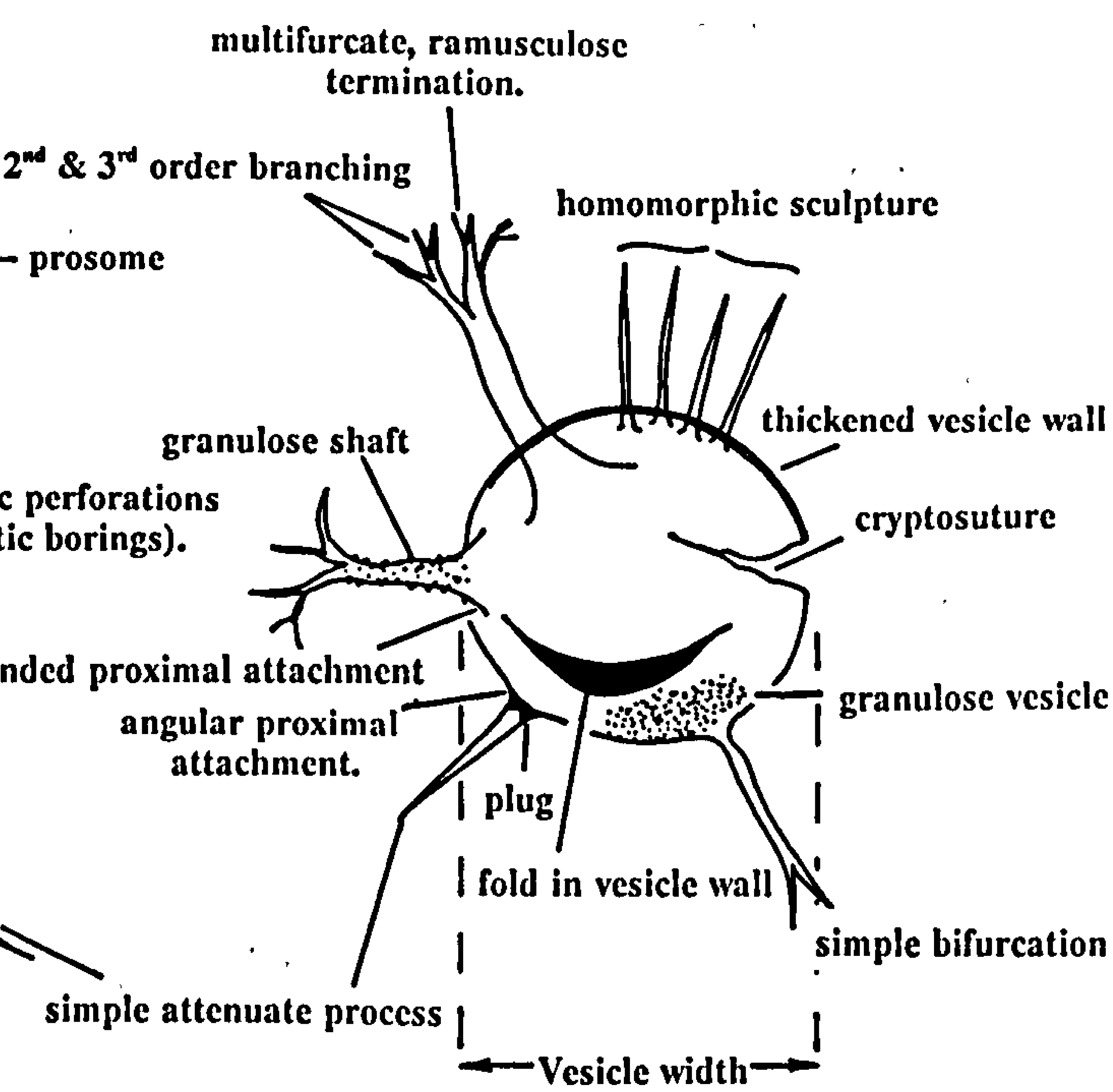
MIOSPORE



CHITINOZOAN

ACRITARCH





after Legault (1973, p.15, Figure 7).

Spherical vesicle, with heteromorphic processes; irregularly disposed.

3.3.1c *Descriptive systematics.*

Genus *Acinosporites* Richardson 1965.

Type species. *Acinosporites acanthomammillatus*, Richardson 1965.

Synonymy.

p 1969 *Biornatisporites* Lele & Streel, p. 97-98.

Discussion.

The genus *Acinosporites* was proposed by Richardson (1965) to circumscribe spores which display a biform murornate ornament: the sculptural elements merge resembling convoluted and anastomosing muri, which (according to Richardson) are in turn surmounted by mammae, biform verrucae, and/or spines and cones. No mention was made by Richardson to basic spore construction or the differential development of haptotypic features. More recently, McGregor & Camfield (1982, p. 11) questioned whether the "primary muri" described by Richardson (1965) were such, or merely represented the basal confluence of the "secondary" verrucate sculpture of Richardson (1965).

In comparison, *Convolutispora* Hoffmeister, Staplin & Malloy (1955) is ornamented by anastomosing ridges that lack any superimposed "secondary" elements. The distinction between *Acinosporites* and *Corystisporites* (Richardson, 1965) can on occasion prove difficult to sustain. The sculptural elements of *Corystisporites* were perceived by Richardson (1965) to be discrete, whereas those of *Acinosporites* are basally contiguous.

According to the definition of Lele & Streel (1969, p.97), the plexus *Biornatisporites* typically displays a reticuloid murornate sculpture, which in turn is surmounted by, or intermixed with, apiculate elements. Lele & Streel (1969) distinguished *Acinosporites* from *Biornatisporites* by the presence of "convolute muri", which characteristically bear "biform" elements. In view of McGregor & Camfield's (1982) re-evaluation of the sculpture of *Acinosporites, Biornatisporites* is herein considered (in part) a junior synonym of *Acinosporites* (Note also the comments made in relation to *Acinosporites crassus*, by Riegel, 1973, p.91). Alternatively, certain species of *Biornatisporites* may more suitably be allocated to either *Dictyotriletes*, *Verrucosisporites* or *Convolutispora*, particularly in view of the more flexible circumscriptions now informally applied for these genera.

The Late Devonian and Carboniferous genus *Cordylosporites* (Playford, 1985, p.144) circumscribes spores that display essentially non-spinose supramural projections, with bacula, pila and/or verrucae developing on the non-reticulate parts of the exine (*i.e.* on the contact areas, or within the lumina).

Acinosporites cf. *acanthomammillatus* Richardson

Plate 3.10, figures 1-3.

cf. 1965 *Acinosporites acanthomammillatus* Richardson, p. 577-578, Pl. 91, figs. 1,2, text-fig. 6.

cf. 1982 *Acinosporites acanthomammillatus* Richardson, in McGregor & Camfield, p. 11, Pl. 1, figs. 1-6, text-fig. 8.

cf. 1988 *Acinosporites acanthomammillatus* Richardson, in Loboziak, Streel & Burjack, Pl.I, fig.12.

cf. 1989 *Acinosporites acanthomammillatus* Richardson, in Loboziak & Streel, Pl. 1, fig. 4.

Description. Miospores, trilete; amb subcircular, oval to convex triangular. Trilete mark distinct to diffuse. The suturae extend 3/4 to 1/1 the spore radius and are commonly obscured by sinuous, flexuous labra, $\leq 6\mu m$ in height and rarely exceed $4\mu m$ in width: the labra taper gradually towards the spore circumference. The contact areas are laevigate to scabrate in texture. Proximo-equatorially and distally the exine displays an ornament, comprising verrucae and squat, biform elements (usually mammae), typically 2-4.5μm in height and basal diameter, although occasionally may range from ≤ 1.75 to $8\mu m$ in size. These elements are rarely discrete, but tend to coalesce at their base forming bulbous, irregular, ±sinuous and anastomosing muri, commonly 6-15μm in length. Most elements are surmounted by a fine cone, grana or "ciliate" spine, ≤ 0.75-1.25μm in length. This ornamentation is comparatively uniform on one individual, although may vary in density from compact, moderately crowded ("pseudoreticulate"), through to notably loose and sparse: typical rugulae/element isolation 0.5-0.75μm, rarely greater than 2.5μm. A faint ?intexinal body may be discriminated, where the exine is partially ruptured and torn.

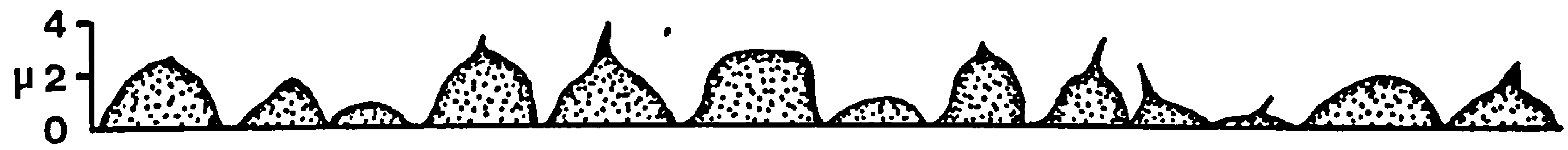


Figure 3.3.2: Sculptural elements of *Acinosporites* cf. *acanthomammillatus*, lateral elevation.

Dimensions: Maximum spore diameter 51-98, mean 71μm (55 specimens). 1 specimen $\approx 171\mu m$ diameter. Diameter of the intexinal body (off-polar compression) 64%, 74% of the total spore diameter (2 specimens measured).

Occurrence. R, S; *common*. LH, WP, L, CM; *very rare*.

Remarks. Richardson (1965, p. 577) perceived the sculpture of the genotype *Acinosporites acanthomammillatus* as comprising ridges, upon which secondary, rounded verrucae were superimposed, and which in turn were surmounted by diminutive spines. As mentioned earlier, McGregor & Camfield (1982, p. 11) interpreted the sculpture somewhat differently, regarding the "secondary" verrucate ornament as the primary form, which were fused at their base resembling "muri". The difference in interpretation is one of emphasis. Based on the population of *A.* cf. *acanthomammillatus* documented from north Devon, the perspective of McGregor & Camfield (1982) is favoured, seeming the more realistic.

Specimens are only tentatively attributed to *Acinosporites acanthomammillatus*, as the size of spores recovered herein is substantially smaller than that range specified by Richardson (1965).

Comparisons. McGregor & Camfield (1982) suggested that *A. acanthomammillatus* may form one end member of a morphologically intergradational spore complex that also encompasses *A. hirsutus* and *A. macrospinosus*: the latter two species display more elongate sculptural elements that clearly project from the spore surface.

Forms of *Corystisporites* exhibit basally discrete, isolated sculptural elements. The ornament of *Dibolisporites variverrucatus* Massa & Moreau-Benoit (1976) is smaller, less laterally expansive and more discrete, lacking distinct murornate elements. Loboziak *et al.* (1988; p. 354, Pl. 1, figs. 4-11) recently proposed the species *Acinosporites eumammillatus*. Although somewhat similar in morphology to that of *A.* cf. *acanthomammillatus* (described herein), *Acinosporites eumammillatus* is $\approx$smaller in size (35-53μm), bears a more discrete, conspicuously mammoid ornamentation.

Acinosporites cf. *apiculatus, sensu* Streel, 1967
Plate 3.10, figure 5-7.

cf. 1964 *Acinosporites apiculatus* Streel,
1967 *Acinosporites* cf. *apiculatus* Streel, B36-37, Pl. III, figs. 38, 39.
non 1985 *Acinosporites* cf. *apiculatus* (Streel), Streel in Paris *et al.*, Pl. 23, fig. 15.

Description. Trilete, acamerate miospores; amb circular, subcircular, to convex-triangular. The trilete mark is distinct to diffuse, simple, straight and extends 1/3 to 3/4 the spore radius. The exine bordering the suturae may in part appear thickened (?labrate), $\leq$1.5μm in total width. The exine is $\leq$1.25μm thick, and the contact areas poorly defined, bearing either a diminutive or $\approx$coarsely scabrate ornament. Elsewhere the exine is $\approx$uniformly covered by a subdued, dense sculpture composed largely of grana, small verrucae and squat coni, all of which commonly display an apical ciliate spine. The ornament varies in width and height, typically from $\leq$0.25μm to 1.25μm and rarely projecting up to 2μm. The sculpture is dense: elements either cluster, or as is more common fuse into barely distinguishable "sinuous", irregular rugulae.

Figure 3.3: Ornamentation of *Acinosporites* cf. *apiculatus*, lateral view.

Dimensions. Maximum spore diameter 47-59μm, mean 54μm (10 specimens measured).

Occurrence. R, S; *common*. H, LH, WP, L, CM; *very rare*.

Remarks. The suturae were usually ruptured and gaping. No internal feature (body) was noted. The extent of the contact areas invariably proved difficult to evaluate.

Comparisons. As defined by (Streel, 1964) *Acinosporites apiculatus* ranges in diameter from 118-150μm. Streel (1967; B36-37) subsequently described a form identical in gross morphology to this species, that differed only in size and the somewhat trivial development of the trilete rays, as well as displaying a differentially smooth proximal surface: *Acinosporites* cf. *apiculatus, sensu* Streel (1967) is 54-65μm in diameter.

A number of finely sculptured species of *Convolutispora* resemble *Acinosporites* cf. *apiculatus* described herein (e.g. *C. ampula* Hoffmeister, Staplin & Malloy, 1955; p.384, Pl.38, fig. 12), but lack the biform murornate sculpture diagnostic of the *Acinosporites* plexus. *Convolutispora porcata* McGregor & Camfield (1982; p. 25-26, Pl. 4, fig. 21) is larger (70-131μm), and displays a marginally coarser, verrucate and "simple" muronate sculpture (ridges 1-3μm wide; verrucae 1-7μm wide).

Acinosporites cf. *crassus* Riegel
Plate 3.10, figures 4, 8.

cf. 1973 *Acinosporites crassus*, Riegel, p. 91, Pl. 13, figs. 11-13.

Description. Trilete, ?acamerate miospores; amb circular to convex-subtriangular. The exine is thick, of uncertain thickness (≤?3μm), and scabrate to finely granulose. The trilete rays are distinct: the suturae are straight to openly arcuate, and partially obscured by robust, ±tightly sinuous labra, ≤2-8μm in total width (usually 3-6.5μm), which usually broaden towards the spore equator. The contact areas are delimited equatorially by pronounced curvaturate ridges: interradially the exine is scabrate, ?thinner than the remainder of the spore wall and appears somewhat depressed. Equatorially the exine thickens quite substantially, resembling an opaque "rim" that is broadest radially: associated with this thickening in the exine is an increase in ornament size. Proximo-equatorially and distally the exine is sculptured with elongate, simple or biform coni and spinae, which may be constricted at their base or mid-length. The sculpture varies in size, from 2.5μm to 4.25μm in length, and ≤0.75-2μm in basal diameter. Elements appear crowded, ≤0.25μm apart (rarely exceed 0.5μm): overall, the ornamentation is extremely dense, with elements either fused at their base, or contiguous along 4/5 of their length. The tips of the sculpture may be simple-rounded, blunted, or as is more typical, surmounted by a fine, hair-like capitate spine. Approximately 150-200 elements project at the equatorial margin.

Figure 3.3.4: Sculptural variation of *Acinosporites* cf. *crassus*, lateral view.

Dimensions. Maximum spore diameter 71-106μm, mean 83μm (15 specimens measured).

Occurrence. CM; *common*. S, LH, L, K; *rare*.

Remarks. *Acinosporites* cf. *crassus* (herein) resembles *Acinosporites crassus, sensu stricto* (Riegel, 1973; Pl. 13, fig. 11) in relation to overall morphology and size, but differs primarily in the nature of the sculpture: the ornament that adorns forms described herein appears more elongate and demonstrably biform than that illustrated by Riegel (1973). In the description, Riegel (1973, p. 91) does, however, quote the sculptural dimensions as 2-3μm wide and only marginally higher. Occasionally forms of *Acinosporites* cf. *crassus* (the present study) were less than 80μm in diameter: Riegel (1973) specifies the size range of this species as 85-108μm.

The opacity of the equatorial region outside of the contact areas is believed to reflect a thickening in the exine, and also a marked change in the type of ornamentation: this darkened "rim" is not interpreted as a patina, as observed for forms of *Cymbosporites* Allen (1965).

Comparisons. The sculpture of *Acinosporites* cf. *crassus* bears a superficial resemblance to that of *Dibolisporites bullatus* and *D. echinaceus*, but differs in its greater density and basal continuity. *Contagisporites optivus* var *vorobjevensis* (Chibrikova) Owens, in Loboziak & Streel (1981; Pl.III, fig.1) appears similar in gross morphology, although the sculpture seems finer and more subdued.

Acinosporites sp. A (described herein) differs in being ≈smaller, with a less visibly robust exine, and a more subdued, ?biform sculpture. *Acinosporites* sp. A and *A.* cf *crassus* are stratigraphically discrete.

Acinosporites lindlarensis Riegel var. *lindlarensis* McGregor & Camfield
Plate 3.10, figures 9-12.

1968 *Acinosporites lindlarensis* Riegel, p. 89, Pl.19, figs. 11-16.
1973 *Geminospora treverica* Riegel, p. 97, Pl. 16, figs. 4-7.
1976 *Acinosporites lindlarensis* Riegel var. *lindlarensis* McGregor & Camfield, p. 6-8, Pl. 5, figs. 2, 3, text-figure 4-6.
1980 *Geminospora libyensis* Moreau-Benoit, p. 44, Pl. 13, fig. 6.
1982 *Acinosporites lindlarensis* Riegel var. *lindlarensis* McGregor & Camfield, in McGregor & Camfield, p. 13, Pl. 1, figs. 9, 10, text-figure 10.
1986 *Acinosporites lindlarensis* Riegel, in Turnau, Pl. VII, figs. 9 ,12, 13.
1988 *Acinosporites lindlarensis* Riegel, in Loboziak, Streel & Burjack, Pl. I, fig. 13.
1989 *Acinosporites lindlarensis* Riegel, in Loboziak & Streel, Pl. II, fig. 5,6.

Description. Trilete, ±camerate, laminate miospores; amb convex-triangular, oval to distinctly circular. The trilete mark is pronounced to barely discernible: the laesurae are straight to openly arcuate and extend 3/4 to 7/8 the spore radius (usually 4/5). The suturae are paralleled by sinuous, ≈membraneous labra, ≤1-3.25μm in total width at the proximal pole and which taper equatorially. The intexine is thin, ≤0.5-0.75μm thick, laevigate and commonly folded: the outline of the intexinal body is concentric with the spore circumference. The two exinal layers are usually closely appressed, rarely separated by as much as 8-12μm. The contact areas are either barely discernible, or conversely distinct, delimited equatorially by faint curvaturate ridges. The exoexine is finely scabrate to markedly granulose, ≤1-1.75μm thick equatorially. The proximo-equatorial and distal regions are ornamented by an assortment of ±bulbous-based, predominantly biform sculptural elements, in association with simple coni, spinae, bacula and verrucae. Elements are discrete, or basally contiguous: up to six elements coalesce. The ornament varies in size, typically ≤1.25-4.75μm in height (very occasionally up to 6μm), ≤1-3.5μm in basal diameter, and elements are ≤0.5-5.25μm apart: the sculpture is distinctly circular to subpolygonal in basal outline, and the largest elements tend to be concentrated preferentially towards the equatorial margin. Subordinate grana and diminutive coni (≤0.5μm in size) may be interspersed amongst these larger elements.

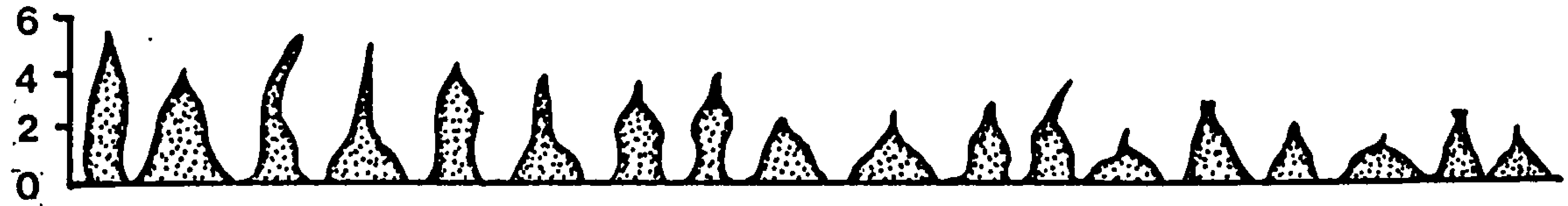


Figure 3.3.5: Sculptural variation on *Acinosporites lindlarensis* var. *lindlarensis*, lateral view.

Dimensions. Maximum exoexinal diameter 52-93μm, mean 71μm (60 measurements). Intexine diameter 40-81μm, mean 63μm; diameter of the central body 68-94% (mean 89%) of the total spore diameter.

Occurrence. LN, H, R, S; *common*. LH, WP, L, CM; *very rare*.

Remarks. McGregor & Camfield (1976, p. 6) considered *Geminospora treverica* (Riegel, 1973) to be a junior synonym of *Acinosporites lindlarensis* var. *lindlarensis*, and discussed in more general terms the assignment of *lindlarensis* to the *Acinosporites* plexus: the ornament may on occasion appear predominantly isolated. Indeed, discrete sculptural elements are a common feature of this species, which question the affiliation of *lindlarensis* with the *Acinosporites* plexus. Hypothetically a more realistic repository for this species may be *Geminospora*, although the exoexine of *lindlarensis* rarely appears preferentially thickened.

The population of *Acinosporites lindlarensis* var. *lindlarensis* documented in the present study marginally overlap in size with the specifications of *A. lindlarensis* var *minor*, as quoted by McGregor & Camfield (1976, p. 8; 32-54μm). Very occasionally the exoexinal layers were ruptured and torn, revealing an unornamented, "simplistic" intexinal body.

Comparisons. The comparatively subdued, often discrete spinose ornamentation, as well as the distinctly camerate construction, distinguishes this taxon from other members of the *Acinosporites* plexus. McGregor & Camfield (1976) differentiate *A. lindlarensis* var. *minor* from *A. lindlarensis* var. *lindlarensis* due to a disparity in size, the former being smaller.

Acinosporites ?macrospinosus Richardson
Plate 3.10, figure 14.

? 1965 *Acinosporites macrospinosus* Richardson, p.578, Pl. 91, figs. 3-6.
? 1970 *Corystisporites hirsutus* Brideaux & Radforth, p. 36, figs. 17, 19.
? 1982 *Acinosporites macrospinosus* Richardson, in McGregor & Camfield, p. 13-14, Pl. 1, figs. 11, 14, 15, 16.

Description. Trilete miospores with a convex triangular to subcircular amb. A faint ?intexinal body may be distinguished from the exoexine. The trilete rays extend 4/5 to 7/8 the spore radius, and are partially or entirely accompanied by thin, flexuous labra, which are most pronounced and thickest at the proximal pole (≤14μm in height), tapering towards the equatorial margin. The proximal surface is ≈scabrate, and lacks pronounced, coarse ornamentation. Distinct processes project equatorially and distally. Sculptural elements are typically 4-9μm in length, occasionally projecting up to 16μm beyond the spore surface. Elements are ≤3-6μm in basal diameter, and either taper to an abrupt, blunted terminus, or an attenuate, acuminate point: these elements may in turn exhibit a delicate, hair-like capitate spine. Processes may display numerous constrictions along their length. Overall, sculptural elements tend to appear closely spaced, and their bases ±contiguous, forming a subdued, "irregular", often ill-defined pseudoreticulate network of low, sinuous ridges: individual processes are typically <2-9μm apart.

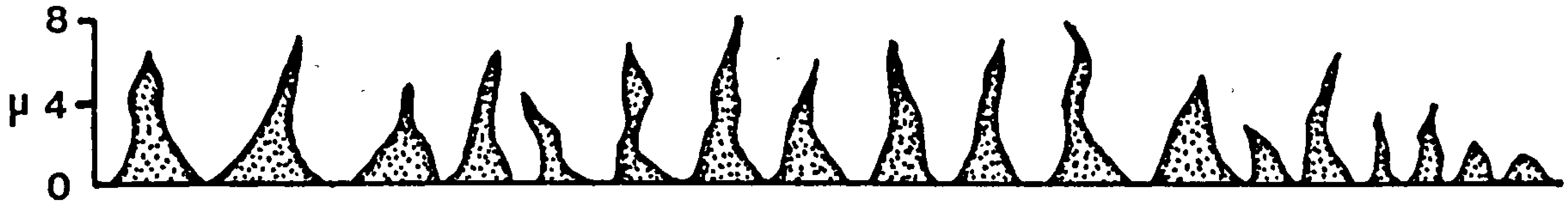


Figure 3.3.6: Sculptural elements of *Acinosporites ?macrospinosus*, lateral elevation.

Dimensions. Maximum spore diameter 71-92μm, mean 83μm (6 specimens measured).

Occurrence. R, S; *rare.*

Remarks. McGregor & Camfield (1982, p. 11-13) proposed a new combination of *Acinosporites hirsutus* (al. *Corystisporites hirsutus* Brideaux & Radforth, 1970). They remarked that *A. hirsutus* displays morphological characteristics intermediate between those of *A. acanthomammillatus* and *A. macrospinosus*. Although forms documented in this study show a strong resemblance to *A. hirsutus, sensu* McGregor & Camfield (1982), the criteria cited by these authors (p. 13) to distinguish this species from the other two is considered too subtle and trivial. Indeed, process size and morphology was noted to be so variable on one individual specimen, that differentiation based upon sculpture alone seems ill-advised. Consequently, the concept of *Acinosporites hirsutus sensu* McGregor & Camfield, may well prove synonymous with *A. macrospinosus*.

Forms of *Acinosporites ?macrospinosus* recorded in the present study are atypical of *A. macrospinosus, sensu stricto* (as defined by Richardson, 1965), differing in sculptural morphology, process continuity, and overall spore dimensions. Subsequently this species is only tentatively identified.

Comparisons. *Acinosporites acanthomammillatus* displays a more subdued, less elongate ornament. Forms of *Corystisporites* spp. (diagnostically) bear discrete sculptural elements.

Acinosporites sp. *A*

Plate 3.10, figures 13, 15, & 16.

Description. Trilete, ?camerate miospores; amb subcircular to ovate. The exine is scabrate to finely granulose, robust, rigid, and typically dense, thus of uncertain thickness (?1.5-2μm). The trilete rays are distinct, the suturae simple or obscured by straight to openly arcuate flexuous labra, ≤1.5-2.5μm in total width. The laesurae extend 2/3 to 4/5 the spore radius: in part, the contact areas may be delimited by ill-defined, ≈invaginated curvaturae imperfectae. The exine over the proximal surface is depressed, thinned and scabrate to finely granulose in texture ("grana" ≤0.75μm in size). The remainder of the exine appears somewhat thickened, opaque, and exhibits a dense sculptural veneer comprising fine, attenuate coni and spinae, with rare bacula and grana: elements ≤2.25μm in height (usually 0.75-1.25μm), ± a ciliate, apical spine/grana. If discernible, the basal outline of the ornament is circular to subpolygonal, and ≤0.75μm in diameter. As well as being fused at their base, adjacent elements may also be contiguous in part, if not entirely, along their length: elements are rarely discrete, separation ≤1.5μm. The density of the ornamentation is such that individual elements are virtually indistinguishable.

Figure 3.3.7: Sculptural variation on *Acinosporites* sp. *A*, lateral view.

Dimensions. Maximum spore diameter 43-67μm, mean 51μm (12 specimens). ?Intexinal body 37-52μm (4 specimens).

Occurrence. LN, H; *rare.*

Remarks. Specimens proved difficult to oxidise adequately, which may be an indication of substantial exine thickness. As with *A.* cf. *crassus,* the opacity of the exine towards the equatorial margin does not constitute a patina: such equatorial darkening is commonly accentuated by the somewhat thinned and depressed appearance of the contact areas.

Comparisons. This spore-type was attributed to *Acinosporites* largely due to the basal continuity of the diminutive sculpture: this morphotype may be differentiated from all other species of *Acinosporites* by the character of the sculpture. Clearly *A. acanthomammillatus* and *A. macrospinosus* bear substantially larger, more pronounced and obvious elements. The closest kindred morphotype, namely *Acinosporites apiculatus,* exhibits a more bulbous, and less crowded, "spinose" sculpture. In principle the morphology of *Acinosporites crassus* is similar, but differs in being larger, displaying clearly defined contact areas and in bearing more robust, enlarged sculptural elements. The circumferential ornament of *Acinosporites ambiguus* Tiwari & Schaarschmidt (1975; p. 26-27, Pl. 12, figs. 2, 3) appears broadly similar. However, according to the diagnosis of *A. ambiguus,* this species is substantially larger in overall diameter (80-100μm), and the sculpture markedly larger, more elongate and significantly, superimposed upon a reticulate infrastructure.

The ornamentation of *Geminospora spinosa* Allen (1965) is more pronounced, larger (3-6μm) and discrete. Within the population of *Acinosporites* sp. A noted herein, a differential thickening of the exinal "walls" was impossible to gauge.

Genus *Anapiculatisporites* Potonié & Kremp, 1954.

Type species. *Anapiculatisporites isselburgensis* Potonié & Kremp, 1954.

Discussion.

McGregor & Camfield (1982, p.14) remark that the taxonomy of simple, spinose spores is in general extremely chaotic, and consequently re-evaluated the *Anapiculatisporites* plexus. They acknowledged the diagnosis of Potonié & Kremp (1954) for *Anapiculatisporites,* but incorporated (albeit temporarily) species which had formerly been assigned to *Acanthotriletes*. The holotype of *Acanthotriletes* is now accepted to be a Cambrian acritarch (note Jansonius in Jansonius & Hills, 1976), and therefore this genus is no longer considered a valid repository for trilete spores. According to Potonié & Kremp (1954), *Anapiculatisporites* differed from *Acanthotriletes* largely due to the rarity of ornamentation that projects at the equator. Following McGregor & Camfield (1982), such a distinction is herein considered trivial, and of minimal taxonomic significance at generic level.

The differentiation of *Apiculatasporites* Potonié & Kremp (1956) from *Apiculatisporis* Potonié & Kremp (1956) proposed by McGregor & Camfield (1982, p. 18) was based upon differences in sculptural size and is applied in the present study. The distinction between *Apiculatisporis* and *Anapiculatisporites* is, however, more ambiguous.

Anapiculatisporites sp. A

Plate 3.11, figures 1 & 2.

Description. Trilete, acamerate miospores with a subcircular to broadly subtriangular amb. The exine is laevigate to finely scabrate, and ≤1.75-2.5μm thick equatorially (rarely ≤1μm). The suturae are distinct, straight, and either simple or very occasionally obscured by "labra", which are ≤0.5-3μm wide at the proximal pole, and ±tapering equatorially. The laesurae extend 2/3 to 4/5 the spore radius, and may be terminated by diffuse or pronounced curvaturae imperfectae, ≤1.5μm wide: if present, such curvaturate ridges commonly coincide interradially with the spore circumference. The contact areas are variably distinct, laevigate to finely scabrate, lacking ornamentation, and may appear slightly depressed. Proximo-equatorially and distally the exine displays a regularly spaced sculpture, comprising squat, broad-based spinae and coni: subordinate verrucae, attenuate spinae and bulbous-based biform elements may be co-occur. The apices of the ornament are generally rounded, blunted, rarely angular-pointed. Elements average ≤1.5-2.75μm in length (rarely exceed 3.5μm) and ≤2-3.5μm in basal diameter: individual elements are typically ≤1.5-4μm apart, rarely exceeding 5μm.

Figure 3.3.8: Sculptural elements of *Anapiculatisporites* sp. A, lateral view.

Dimensions. Maximum spore diameter 36-64μm, mean 52μm (15 specimens measured).

Occurrence. LN, S; *common.* H, R, LH, WP; *very rare.*

Remarks. The occasionally thickened, robust spore margin may in part be a compressional attribute, and is not sufficiently pronounced to merit assignment to *Aneurospora.* The trilete rays are commonly ruptured.

Comparisons. The sculpture apparent on *Anapiculatisporites petilus* Richardson (1965, p. 571) is similar, but appears more slender and elongate, with fewer elements projecting at the equatorial margin. *Dibolisporites eifeliensis* (Lanninger) McGregor (1973) is broadly comparable, but bears a predominance of biform elements that exhibit bifurcate or blunted terminations (conceivably, some specimens affiliated with *Anapiculatisporites* sp. A may represent poorly preserved, degraded forms of *D. eifeliensis*).

The sculpture on *Anapiculatisporites* sp. C of Steemans (1989, p. 95, Pl. 20, fig. 12) is similar in size, but dissimilar in overall morphology.

?*Anapiculatisporites* sp. B
Plate 3.11, fig. 4 & 5.

? 1989 *Anapiculatisporites petilus* Richardson (1965) in Steemans, p. 94, Pl. 20, figs. 5-6; fig. 40.

Description. Trilete, acamerate miospores; amb subcircular to ovate. The exine is uniformly laevigate to finely scabrate, and <1μm thick equatorially. The suturae are straight, indistinct at the proximal pole, and obscured equatorially by thickenings of the exine, ≤3.75μm wide and which taper towards the proximal pole. The contact areas are usually well defined, the exine laevigate, ?thinned and may be delimited equatorially by faint "?curvaturae": the extent and development of these "?curvaturae" is highly variable. Proximo-equatorially and distally the exine bears discrete sculptural elements, that comprise slender spinae, coni and rare bacula. In general these elements are ≤1-2.25μm in height and ≤0.75-1.75μm in basal diameter, and may be surmounted by a ciliate, apical spine. Individual elements are commonly 2.75-5μm apart.

Figure 3.3.9: Sculptural elements of ?*Anapiculatisporites* sp. B, lateral view.

Dimensions. Maximum spore diameter 37-45μm, mean 39μm (12 specimens measured).

Occurrence. LN, H; *rare.*

Remarks. A broad species concept was adopted herein, as the morphology of such forms proved highly variable. Although biform elements form part of the sculpture on such spores, they are not a predominant attribute and thus discounts affiliation with *Dibolisporites.* Curvaturate ridges were similarly not a persistent feature, disfavouring assignment to *Apiculiretusispora* (Note: Streel (1967) does mention that curvaturae need not necessarily be apparent on forms attributed to *Apiculiretusispora*).

Clearly the generic identity of such spores is somewhat problematic, and dependant largely upon which morphological attribute is taken to assume generic importance (*i.e.* ± curvaturae, sculpture or biform elements). For this reason this morphotype is only tentatively assigned to *Anapiculatisporites.*

Comparisons. Streel *et al.* (1981) describes and illustrates *Anapiculatisporites* sp. A from the Lower Devonian of the southern margin of the Dinant synclinorium (exclusive to Assemblage A within the

Oignies & St. Hubert lithostratigraphical units). Illustrations of this species resemble *?Anapiculatisporites* sp. B herein, but the sculpture of *Anapiculatisporites* sp. A *sensu* Streel *et al.* (1981) appears on the whole longer, and the overall spore size range somewhat smaller (26-37µm). Forms attributed by Steemans (1989) to *Anapiculatisporites petilus* are considered not truly representative of this species, being broadly identical in morphology to that of *?Anapiculatisporites* sp. B described herein: the two are questionably placed in synonymy, as the disposition of the ornament that adorns *?Anapiculatisporites* sp. B appears somewhat denser.

The scarcity and diminutive size of the sculpture distinguishes this form from the two other species of *Anapiculatisporites* described herein.

Anapiculatisporites sp. C
Plate 3.11, figure 3.

Description. Trilete, acamerate miospores, with a circular to rounded subtriangular amb: the exine ranges up to 1.75µm thick at the equator. The trilete rays are simple, straight, commonly ruptured, and extend 2/3 to 4/5 the spore radius: faint curvaturae imperfectae may occasionally be noted. The proximal surface is laevigate, lacking pronounced sculpture, and the equatorial and distal regions ornamented with coarse grana and subdued, but robust coni. Sculptural elements are in general ≤1.5µm in height and ≤1-2.5µm in basal diameter: individual elements are ≤1-3µm apart.

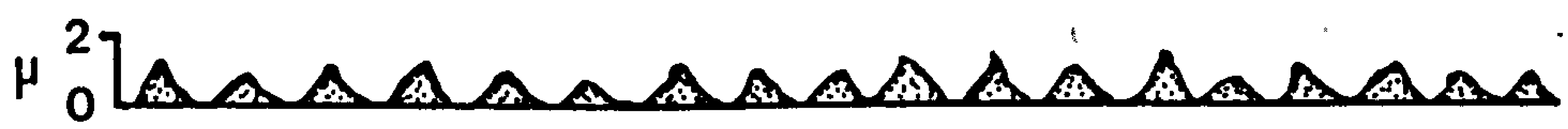


Figure 3.3.10: Sculptural elements of *Anapiculatisporites* sp. C lateral view.

Dimensions. Maximum spore diameter 37-59µm, mean 53µm (10 specimens measured).

Occurrence. LN; *rare.*

Comparisons. *Anapiculatisporites isidori* Pernelle in Streel *et al.* (1981, Pl. 2, fig. 3) is similar in gross morphology, but the sculpture appears more isolated, discrete. *Anapiculatisporites* sp. C is similar in appearance to *A.* sp. A described herein, although the ornamentation is consistently smaller and somewhat denser: morphologically these two species intergrade. *A.* sp. C also intergrades with *Cyclogranisporites* sp. A defined in the present study: the latter taxon may be differentiated by its more subdued, predominantly granulose sculpture.

Genus *Ancyrospora* Richardson emend. Richardson, 1962.

Type species. *Ancyrospora grandispinosa* Richardson, 1960.

Discussion.

As Urban remarked, the plexus *Ancyrospora* currently accommodates an over-proliferation of taxa, and indeed at present the Commission Internationale de Microflore du Paléozoique (C.I.M.P.) is "actively" engaged in rationalising this generic grouping. Aware of C.I.M.P. interest, McGregor and

Camfield (1982, p. 15) were reluctant to re-evaluate many current constituents of *Ancyrospora*, considering such a move to be premature and preempting potential C.I.M.P. findings. However, eight years have lapsed with no emendation forthcoming from the group.

Potonié (1956), Chaloner (1959), McGregor (1960) and Richardson (1962) recognised *Archaeotriletes* (*sensu* Naumova 1953) as a heterogeneous grouping that required radical subdivision. Richardson (1960) consequently defined the genus *Ancyrospora*, and considered bifurcate-tipped sculpture of primary taxonomic significance (more recently the presence of bifurcate sculpture cannot in itself assume generic priority, as many other Devonian spore genera have been recognised to display such biform ornament (exemplified by the reallocation of "?*Ancyrospora magnifica*" (Owens 1971 p. 77-78) to *Grandispora*, by Chi & Hills, 1976). Richardson (1962) later emended and expanded the generic concept of *Ancyrospora*, following a re-interpretation of the construction of the genotype *Ancyrospora grandispinosa*. He considered the exoexine to extend equatorially as a thick, appressed "flange or pseudoflange", and justified a broadening of the original circumscription so as to accommodate a greater diversity in morphology. In contrast to the thin membraneous zona of *Archaeotriletes*, Richardson (1962, p. 177) perceived the flange of *Ancyrospora* to be "thickened", and remarked that *Grandispora* was similar to *Ancyrospora* but differed in being "...smaller and with a more incised margin". In view of Richardson's (1962) re-evaluation of the construction of *Ancyrospora*, and the current perception as to the structure of *Grandispora* (which circumscribes spore that are demonstrably camerate), the two are clearly different, and thus Richardson's original grounds for distinction are inconsequential. Urban (1969, p. 112) later attempted to redefine the *Ancyrospora* plexus as a more natural and stratigraphically useful morphologic group. Realising that some ancyrospores may display multifurcate terminations to their sculpture, Urban was prompted to recommend alternative, more significant characteristics that could be used to unify this complex (*e.g.* exinal stratification). Consequently Urban studied the exinal walls of ancyrospores and noted them to comprise three or four layers, based upon high resolution transmitted light microscopy and scanning electron microscopy. Urban (1969) also remarked that the diagnoses of *Hystricosporites* and *Ancyrospora* are vague, overlapping in certain respects. Furthermore, although such taxa are conspicuous elements of Devonian spore assemblages, Urban considered their biostratigraphical significance limited by such taxonomic ambiguity.

Subsequently, Owens (1971, p. 75) noted the presence of a perisporal membrane in defining *Ancyrospora involucra*, but affiliated such forms with *Ancyrospora* in preference to establishing new monospecific genus. Hills *et al.* (1975) later emended the circumscription of the genus *Ocksisporites* Chaloner, and verified that this plexus should be reserved for megaspores bearing proximal and distal "fluke-tipped echinate" ornamentation. Chi & Hills (1976, p. 764-765) subsequently noted the presence of a lightened, triangular area of exine in the proximal polar region of some ancyrospores, formed by the folding back of the exinal layers. However, they did not propose any formal emendation to the concept of the genus. Contemporaneously Playford (1976, p. 32) discussed at length the relationship between ancyrospores and morphologically comparable forms which exhibit bifurcate-tipped sculpture. He noted, as had Richardson (1962, p. 176), that the genus *Hystricosporites* McGregor (1960) differs primarily in construction, being "azonate". *Nikitinsporites* was likewise distinguished by virtue of its azonate structure.

In recent years questions have been raised as to the applicability of Urban's (1969) emended concept of *Ancyrospora.* Although providing remarkable insight into ultrastructural detail, Higgs & Scott (1982, p. 93) remarked that Urban's re-evaluation did not markedly improve upon the emended generic circumscription proposed by Richardson (1962). McGregor & Camfield (1982, p. 14) likewise commented that the emendation of Urban (1969) was "too detailed and restrictive". The present study concurs with these recent observations, as Urban 's (1969) diagnosis of *Ancyrospora* is considered impractical, relying too heavily upon the integration of an S.E.M. to taxonomic studies.

The nomenclature devised by Owens (1971) to describe variation in bifurcate-tip morphology is applied below.

Ancyrospora ancyrea (Eisenack) Richardson cf. var. *brevispinosa* Richardson
Plate 3.11, figs. 6-8.

cf. 1962 *Ancyrospora ancyrea* var. *brevispinosa* Richardson, p. 179-180, Pl. 25, fig. 8, text-fig. 9A.
cf. 1980 *Ancyrospora ancyrea* var. *brevispinosa* Richardson, in Loboziak & Streel, Pl. IV, fig. 6.
? 1982 *Ancyrospora ancyrea* var. *brevispinosa* Richardson, in McGregor & Camfield, p. 15-16, Pl.2, fig. 7, text-figure 15.
1982 *Ancyrospora ancyrea* cf. var. *brevispinosa* Richardson, in Marshall & Allen, p. 298, 300, Pl. 33, figs. 4, 5.

Description. Trilete miospores; amb subcircular to convex triangular. The trilete mark is variably distinct: the suturae are usually straight to openly arcuate, and may be paralleled by flexuous labra, individually ≤3.5μm high and wide at the proximal pole. The laesurae extend 1/2 to 7/8 the central body radius. The central body is distinct, ≤2.5μm thick equatorially and scabrate to finely granulose in texture: the exoexine only marginally extends beyond the central body outline, at most 7-11μm, and appears scabrate to shagreenate in texture. The thickness of the exoexine is uncertain, ≤?1-3μm. The proximal surface lacks pronounced ornamentation, and the exine may display intense, convolute folds or "wrinkles", which appear arranged about the trilete rays. Equatorially and distally the exoexine exhibits distinct, in general discrete and subdued coni, broad-based spinae, and very rare, elongate verrucae and bacula: these elements are ≤2-6μm in height, (commonly 3-4μm), ≤5.5μm in basal diameter, and taper to a simple or distinctly bifurcate terminus. Such distal bifurcations are ≤1-2μm wide, and simple triangular to slightly laterally extended in morphology. Two to five adjacent elements may coalesce at their base, forming short, irregular rugulae, concentric about the distal pole: the majority of elements are, however, discrete, ≤4-12μm apart.

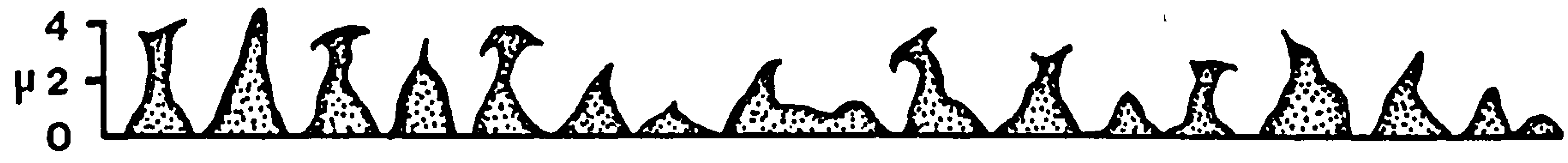


Figure 3.3.11: Sculptural elements of *Ancyrospora ancyrea* cf. var. *brevispinosa*, lateral elevation.

Dimensions. Overall spore diameter; 51-88μm, mean 64μm (25 specimens).

Occurrence. L, CM, K; *common.*

Remarks. Marshall & Allen (1982) record a complex of *Ancyrospora ancyrea* cf. var. *brevispinosa* Richardson from Fair Isle, Shetland, that range in maximum diameter from 39μm to 95μm. Specimens recovered from north Devon are more comparable in size to the species population of Marshall & Allen, than with the dimensions quoted by Richardson (1962, p. 179, 185) for material documented from other localities within the Orcadian Basin (according to Richardson, the dimensions of *A. ancyrea* var. *brevispinosa* range between 75μm and 106μm.

For the population recorded in the present study, the suturae were occasionally ruptured at the proximal pole, and bifurcate terminations were only rarely preserved.

Comparisons. Richardson (1962) defined three variants of the *Ancyrospora ancyrea* complex, namely var. *ancyrea*, var. *brevispinosa*, and var. *spinobaculata*. The three are differentiated primarily upon differences in sculptural morphology, as well as flange dimensions (*i.e.* lateral extent). Although *A. ancyrea* var. *brevispinosa* is similar in general appearance and overall construction to that of *A. ancyrea* var. *ancyrea*, Richardson (1962, p. 179) distinguished the former subspecies by virtue of its smaller and more discrete sculpture, and the closely fitting "outer membrane", which in polar view is only slightly extended in the equatorial plane.

Ancyrospora cf. *eurypterota* Riegel
Plate 3.11, fig. 9.

cf. 1973 *Ancyrospora eurypterota* Riegel p.100, Pl. 17, fig. 1-5.

Description. Trilete, zonate-?camerate miospores; amb subcircular to ovate. The suturae are straight to openly sinuous, and bordered or obscured by thickened labra, ≤7μm in width and height at the proximal pole, which may taper towards the equatorial margin: the trilete rays extend 7/8 to the full spore radius. The "central body" is commonly opaque, of uncertain thickness (≤?2μm), laevigate to slightly granulose in texture and conformable in outline with the spore circumference. The exoexine is laevigate to finely scabrate, and may appear irregularly thickened equatorially (≤3.5μm wide, ≈?limbate), extending in the equatorial plane as a broad "flange", ≤16-27μm wide: this "flange" appears comparatively rigid, and of ≈uniform width about the central body. The exoexine displays rare folds, ≤3.25μm thick and radial about the distal pole. The distal surface exhibits a diminutive sculpture, comprising very fine spinae and/or broad based coni, that either appear simple-attenuate, or conversely bear a distinct bifurcation: this ornament rarely projects at the equatorial margin. Well preserved elements average ≤2-4μm in height, and ≤2.5μm in basal diameter, are discrete and well spaced: typically ≤3-11μm apart. The shafts of individual elements either appear constricted below the bifurcate terminus, or conversely are straight, parallel-sided. The tip is laterally-extended or triangular-extended in morphology.

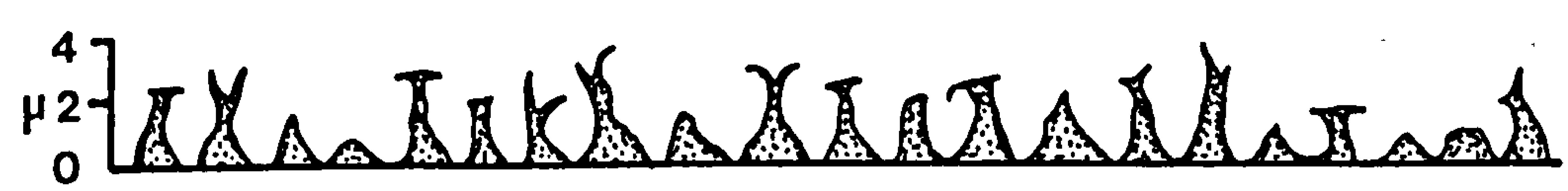


Figure 3.3.12: Sculptural elements of *Ancyrospora* cf. *eurypterota*, lateral view.

Dimensions. Overall diameter, 87-108μm; "central body", 48-70μm.

Occurrence. LN; rare.

Remarks. The bifurcate terminations to the sculpture may appear so subtle, or are so rarely preserved, that certain specimens superficially resemble *Grandispora protea* (Note: in the top right of the figured specimen a small bifurcate-tipped element is indicated). Indeed, certain specimens of *Ancyrospora* cf. *eurypterota* recorded in the present study seemed camerate in construction.

Comparisons. Specimens of recovered from north Devon resemble the holotype illustration of *Ancyrospora eurypterota*, figured by Riegel (1973; Pl. 17, figs. 3, 4): the ornament tends to lack the predominance of distinct bulbous shafts, so apparent on the other specimen figured by Riegel (1973; Pl. 17, figs. 2, 4). *Ancyrospora eurypterota* was, however, only tentatively identified, largely because of the slight disparity in sculptural morphology (smaller and seemingly sparser in distribution), as well as the smaller size range noted herein (87-108μm of the present study, *vs.* 154-252μm of Riegel, 1973).

Ancyrospora eurypterota Riegel (1973) differs to all other members of the *Ancyrospora* plexus in the size and disposition of the sculpture. *Calyptosporites microspinosus* Tiwari & Schaarschmidt (1975, p. 45) is demonstrably camerate in construction.

Ancyrospora langii (Taugourdeau-Lantz) Allen
Plate 3.11, fig. 10.

1960 *Archaeotriletes langi* Taugourdeau-Lantz, p. 145, Pl. 3, fig. 33, 34, and 39.
1965 *Ancyrospora langii* (Taugourdeau-Lantz) Allen, p. 743, Pl. 106, figs. 5-7.
1971 *Ancyrospora langi* (Taugourdeau-lantz) Allen, in Taugourdeau-Lantz, p.46, Pl. VII, fig.9-11, 13, 14.
? 1972 *Ancyrospora* cf.*Hymenozonotriletes incisus* Naumova, in Mortimer & Chaloner, p. 39, Pl. VII, figs. 8-10.
1980 *Ancyrospora langii* (Taugourdeau-lantz) Allen, in Loboziak & Streel, Pl. IV, fig. 4.
1981 *Ancyrospora langii* (Taugourdeau-lantz) Allen, in Loboziak & Streel, Pl. IV, fig. 2.
1988 *Ancyrospora langii* (Taugourdeau-lantz) Allen, in Balme, p. 145, Pl. 11, fig. 7, 9 (not fig.8 as incorrectly quoted in the text)
1988 *Ancyrospora langii* (Taugourdeau-lantz) Allen, in Loboziak, Streel & Burjack, Pl. 1, fig.4.
1989 *Ancyrospora langii* (Taugourdeau-lantz) Allen, in Loboziak & Streel, Pl. VIII, fig. 2.

Description. Trilete miospores; amb triangular to convex triangular, with a $\pm$markedly dentate equatorial margin. Equatorially the exoexine is typically $\leq$2-3.75μm in thickness. The laesurae extend 4/5 to the full spore radius: the suturae are straight to openly sinuous, and commonly obscured by thickened labra, $\leq$8μm high and wide at the proximal pole. The intexine is $\approx$conformable in outline with the exoexine, or somewhat more rounded, $\pm$distinct, $\leq$?2.25μm in thickness and laevigate to finely granulose. The exoexine projects laterally in the equatorial plane as a $\pm$broad flange, $\leq$8-

24μm wide, appearing ≈scabrate, finely granulose or shagreenate in texture. The proximal surface lacks pronounced sculpture, with the equatorial and distal regions regularly covered by distinct, discrete processes, that range from <8μm to 21μm in length: processes taper gradually from a broad base, 5-11μm in diameter, to a constricted distal terminus (≤1-2.5μm wide). 18-28 elements project at the equatorial margin, and are ≤3-11μm apart. The process terminations are commonly simple, blunted (the majority fragmented and lacking bifurcate terminations). When preserved, the bifurcate-tips are simple-triangular to slightly laterally extended in morphology - the termini are laevigate.

Figure 3.3.13: Sculptural elements of *Ancyrospora langii*, lateral view.

Dimensions. Maximum exoexinal diameter (excluding sculpture), 78-114μm, mean 97μm (8 specimens measured).

Occurrence. K, M; *common.*

Remarks. Forms attributed herein to the *Ancyrospora langii* resemble the holotype designated and figured by Taugourdeau-Lantz (1960, Pl. 3, fig. 33), in displaying relatively "short" processes. Taugourdeau-Lantz (1960; Pl. 3, fig 34) does illustrate a form with notably more elongate sculptural elements: forms identified and illustrated as *A. langii* by Loboziak & Streel (1980, 1981, 1989) and Loboziak *et al.* (1988) resemble this latter, coarsely sculptured variant of *A. langii,* as do the sketches of sculptural elements provided by Moreau-Benoit (1980; Pl. 15, fig. 3).

Representatives of *A. langii* documented herein are (in part) slightly smaller than those forms described by Taugourdeau-Lantz (1960) from the Boulonnais, France: Taugourdeau-Lantz specifies the size range as 105-(118)-130μm. The morphology of the distal surface was usually difficult to resolve on specimens recovered in the present study, being obscured by the thickened exine and the inability to adequately oxidise such material.

Comparisons. The population of *Ancyrospora langii* recorded from north Devon intergrade with forms of *Ancyrospora simplex* noted herein: the former species is differentiated by its denser, predominantly shorter sculpture projecting at the equatorial margin. *A. langii* differs to the various subspecies of *Ancyrospora ancyrea* in displaying a more rigid, "thicker" equatorial flange, a ≈triangular amb in polar view, and in bearing more robust sculptural elements.

Ancyrospora cf. *loganii* McGregor

Plate 3.12, fig. 3.

cf. 1973 *Ancyrospora loganii* McGregor, p. 65, Pl. 9, figs. 6, 7, 10-12.

non 1980 *Ancyrospora loganii* McGregor, in Loboziak & Streel, Pl. IV, fig. 5.

Description. Trilete, zonate-?camerate miospores; amb subtriangular to subovate. The exoexine is scabrate or granulose in texture, rarely shagreenate, and ≤1.75-3.5μm thick equatorially. The central body commonly appears optically dense, robust and rigid: thickness uncertain, ≤?2-4μm. When discernible the trilete rays extend 3/4 to 4/5 the central body diameter: the suturae are straight and commonly obscured by thickened labra, ≤8μm in width and height. The exoexine extends laterally in the equatorial plane as a fairly uniform, ≈rigid "flange", 11-23μm in width. The distal surface displays discrete, conspicuous processes, ≤2-11μm in length (usually 3-6μm): this ornament rarely projects at the equatorial margin, and may appear slightly denser, more concentrated over the distal pole. The sculpture comprises robust, squat spinae and coni, ≤2.5-4μm in basal diameter, and tapering distally. If preserved the terminations display subtle bifurcations, which appear extended-triangular, simple-triangular or laterally-extended in morphology, and ≤2.75μm in width: the processes may be constricted just below the bifurcate terminus, or mid-length of the shaft. Sculptural elements are variably isolated, ranging from well spaced on the flange (≈6-11μm), to dense over the distal pole (elements ≤2-7μm apart). Two or three elements may coalesce at their base, forming irregular "cristae".

Figure 3.3.14: Sculptural elements of *Ancyrospora* cf. *loganii,* lateral view.

Dimensions. Overall exoexinal diameter 89-126μm, mean 103μm (15 specimens).

Occurrence. LN, H; *rare.*

Remarks. The specimen identified as *Ancyrospora loganii* McGregor by Loboziak & Streel (1980) appears bizonate in construction, and thus this identification is questioned.

The central body of specimens recovered from north Devon often proved difficult to oxidise, remaining opaque, and thus obscuring haptotypic characteristics. The exoexine on these forms is compressionally thickened, and in general appears turbid and degraded. Many specimens of *Ancyrospora* cf. *loganii* recovered from north Devon appeared "camerate" in construction.

Care was taken to differentiate forms of *A.* cf. *loganii* that lacked bifurcate-tipped sculptural elements, from those of *Grandispora douglastownense* and coarsely sculptured representatives of *Grandispora protea.*

Comparisons. *Ancyrospora loganii* McGregor is only tentatively identified herein, as forms recovered from north Devon are smaller in overall size (89-126μm, the present work, *vs.* 113-278μm of McGregor, 1973) and display a markedly smaller sculpture: McGregor (1973, p. 65) does however state that ornament length rarely exceeds 10μm.

This form differs to most species of *Ancyrospora* by virtue of its comparatively short, robust ornamentation, and laterally expansive flange. Both *Ancyrospora ancyrea* var. *brevispinosa* Richardson and *A. ancyrea* var. *anyrea* display less robust, more flexuous sculptural elements, and a more membraneous, confined flange. The sculptural elements of *A. eurypterota* are smaller, and the flange better defined - more laterally expansive. *A. kedoae* (Riegel) Turnau (1974; p. 152-153) and *A. nettersheimensis* Riegel (1973; p. 100-101) display prominent, ±elongate, conate-spinose sculpture, terminated distally by subtle bifurcate tips. *Grandispora eximia* (Allen) McGregor & Camfield (1982) is camerate in construction, and exhibits a more varied sculpture (bifurcate terminations are the rarity).

Ancyrospora simplex (Guennel) Urban

Plate 3.11, figs. 12-14.

1963 *Ancyrospora simplex* Guennel, p.257, fig. 13.

1969 *Ancyrospora simplex* (Guennel) Urban, p. 112-113.

1971 *Ancyrospora melvillensis* Owens, p.72-73, Pl. XXIII, fig. 5,6.

1971 *Ancyrospora simplex* (Guennel) in Taugourdeau-Lantz, p. 40, Pl. VIII, fig. 1.

1972 *Grandispora* aff. *Archaeozonotriletes naumovii* Kedo in Mortimer & Chaloner, p. 11-12, Pl. 1, fig. 7.

1974 ?*Ancyrospora* sp. in Clayton & Graham, p. 582, Pl. IV, fig. 6.

1977 *Ancyrospora* cf. *simplex* Guennel in Owens, Downie & Reynolds, Pl. 2, fig. 11.

1981 *Ancyrospora simplex* Guennel in Loboziak & Streel, Pl. IV, fig. 6.

Description. Trilete, miospores; amb convex to rounded-triangular, or distinctly triangular. The intexine is comparatively thin, ≤?1.5μm thick, rarely distinguishable. The laesurae extend <3/4 to 7/8 the spore radius. The suturae are distinct, straight and may be paralleled by thin, flexuous, highly convoluted labra, which are ≤6μm high at the proximal pole and taper in width and height towards the equatorial margin: conversely the labra may appear somewhat subdued, robust and rigid. The exine over the proximal pole is thinned, and the trilete rays commonly ruptured. The exoexine extends equatorially as a robust, commonly opaque flange, broadly incised and of comparatively uniform width: typically ≤15μm in lateral extent. The exoexine is coarsely scabrate, ?microfoveolate or shagreenate in texture, with the equatorial and distal regions displaying discrete, well defined processes, 8-26μm in (complete) length (usually fragmented, 12-20μm). These sculptural elements are ≤11μm wide at their base, and are either parallel-sided, or taper to a constricted terminus, which is ≤1-3.5μm wide (rarely 6μm). Two or three elements may coalesce, either at their base or along the length of the shafts. 9-14 processes visibly project at the equatorial margin, being ≈regularly spaced, ≤8-22μm apart (usually 12-15μm). The shafts of the sculpture display a texture comparable to the rest of the exoexine (*i.e* scabrate-shagreenate). When preserved, the bifurcate terminations are laevigate, and triangular, extended-triangular or expanded extended-triangular in morphology: such termini constitute less than one fifth the total process length. Occasionally, terminations may appear weakly serrated (a ?preservational characteristic), and the shafts tend to be constricted just below the bifurcation.

Figure 3.3.15: Variation in process morphology of *Ancyrospora simplex*, lateral elevation.

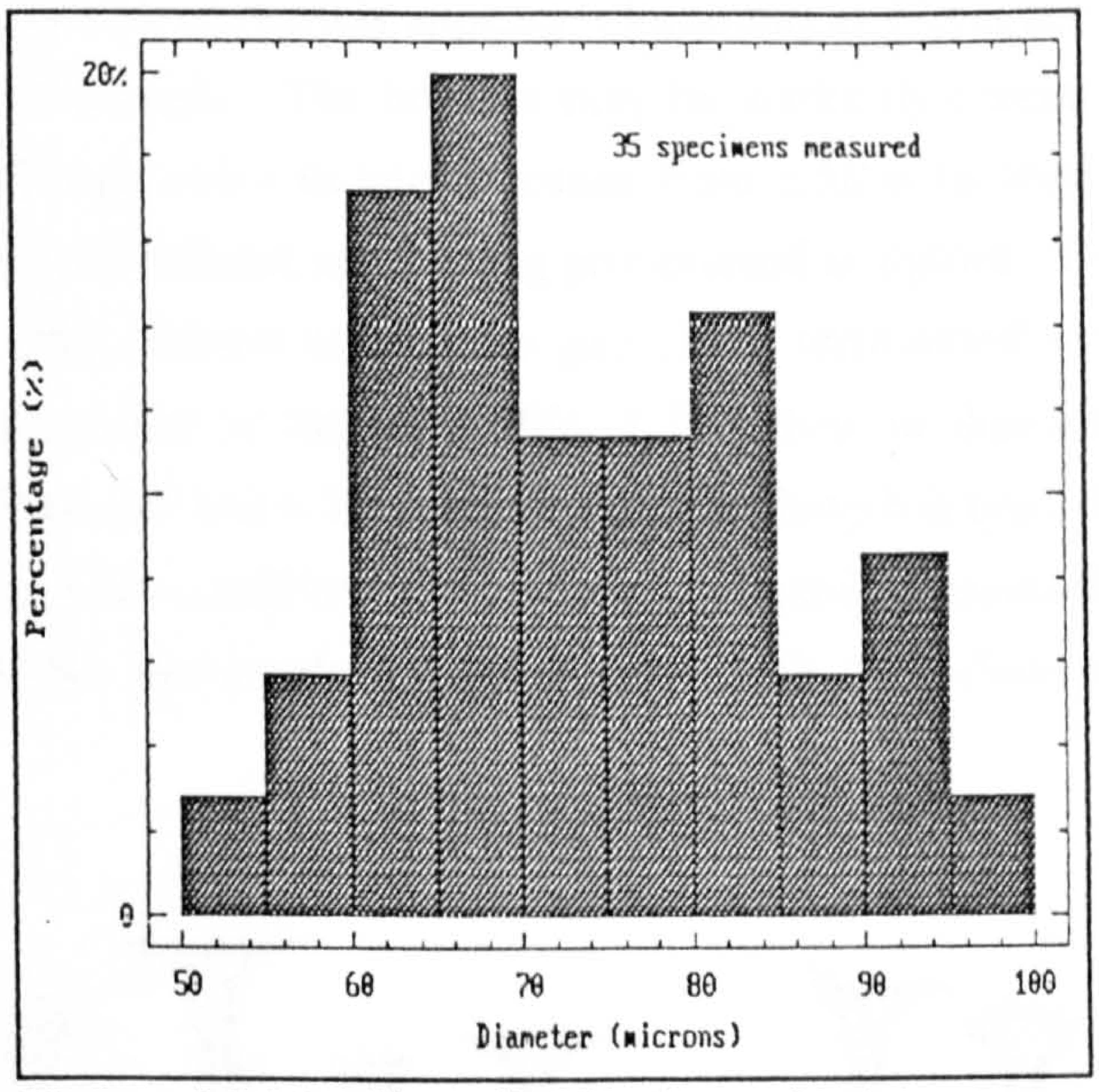


Figure 3.3.16: Size distribution of *Ancyrospora simplex* (Guennel) Urban (1969).

Dimensions. Maximum spore diameter 53-98μm, mean 74μm (based upon 35 specimens). Intexine ≈31-78μm, mean 52μm (based upon 6 measurements).

Occurrence. K, M; *common.*

Remarks. Despite quite extreme oxidation, most specimens documented herein displayed bifurcate termini to their processes, unlike the form described and figured by Guennel (1963). The variably stratified exine of *A. simplex* detailed by Urban (1969) was not readily differentiated in the present study.

Comparisons. As remarked earlier forms of *A.simplex* documented from north Devon intergrade morphologically with *A.langii* Allen (1965): *A. langii* differs in displaying a less elongate, denser sculpture. Owens (1971) proposed six new species of *Ancyrospora,* of which *Ancyrospora melvillensis* is herein considered a junior synonym of *A. simplex* Guennel. According to Owens (1971, p. 73), these two species are comparable, but the processes of *A. simplex* lack bifurcate terminations: *A. melvillensis* displays a differentially developed ornament between the equatorial and distal regions. In view of the work of Urban (1971) and also the findings of the present study, such criteria do not justify maintaining these two species as discrete: *A. simplex* assumes taxonomic priority. The size range noted for *A. simplex* in the present study (51-102μm) is somewhat broader than that specified for *Ancyrospora melvillensis* (92.4-115.5μm, after Owens, 1971).

Ancyrospora furcula Owens (1971, p. 71-72) is similar in size (72.6-105μm) and overall morphology, but the ornament is predominantly multifurcate-tipped, and an "apical prominence", *sensu* Owens (labra), may be present, ≤30μm high. *A. involucra* Owens (1971, p. 74-75) is similar in size (82.5-118.8μm) and gross morphology, but displays a thin perisporal membrane and multifurcate terminations to the sculptural elements. *A. pulchra* Owens (1971, p. 75-77) is larger, and exhibits ±multifurcate-tipped elements that range up to 70μm in length.

?*Ancyrospora* sp. A

Plate 3.11, fig. 11; plate 3.12, fig. 1.

Description. Trilete, zonate-?camerate spores with a rounded subtriangular, subcircular to irregular subcircular amb. The exoexine appears two-layered: the outer layer resembles a diaphanous membrane, ±closely appressed to an inner, more rigid exinal layer, the latter being ≤2μm thick. The laesurae are usually distinct, the suturae straight and extending 3/4 to the full intexinal body radius. Labra are commonly distinct, ≤12μm in size at the proximal pole and tapering equatorially. The intexine may appear diffuse, and ill-defined, whereas the two-fold "exoexine" is distinct and laevigate, finely granulose or shagreenate (rare) in texture. The exoexine may be laterally ±extended in the ≈equatorial plane, resembling a distinct zona, or conversely appears voluminous and irregularly distorted (homologous to a loosely fitting pseudosaccus). The intexine may be markedly eccentric relative to the outline of the exoexine. The flange varies in lateral extent from ≤5μm to 26μm, typically 8-12μm. The contact areas are usually well defined, and lacking pronounced sculpture. The equatorial and distal regions bear discrete, well defined and coarse processes, terminated with bifurcate tips. The process shafts are planoconcave in lateral profile, 1.25-3.5μm in diameter (midlength), and rise from a broad, expansive base ≤8-14μm in diameter: process length is typically 14-32μm. The bifurcate terminations are ≤12μm wide, and laterally-extended, reflexed, occasionally triangular in morphology. Processes are discrete, commonly ≤7-24μm apart, with 9-17 elements projecting at the equatorial margin.

Figure 3.3.17: Sculptural elements of ?*Ancyrospora* sp. A, lateral view.

Dimensions. Maximum overall spore diameter 62-105μm, mean 79μm (10 specimens measured)

Occurrence. LN, H; *common.*

Remarks. Forms assigned to ?*Ancyrospora* sp. A are unified by a three-layered exine structure, although representatives of this species were noted to display a variety of constructions and a diversity in sculptural morphology. This species is only tentatively assigned to *Ancyrospora* because of such exinal stratification (Note: Owens, 1971, recognised three exinal layers for *Ancyrospora involucra*), and more significantly, because the "zona" is occasionally less well defined, and indeed may resemble a voluminous pseudosaccus. As an illustration, the figured specimen of Pl. 3.12, fig. 1 appears zonate in construction (albeit with a thin "perinous" third layer), whereas the specimen figured on Pl. 3.10, fig. 11 appears demonstrably pseudosaccate. *Hystricosporites* may be a potential repository, although likewise a three-layered exinal structure is atypical of this genus.

Comparisons. This species is unique by virtue of its three-layered wall construction. *Ancyrospora involucra* Owens (1971) is noted to possess a third perinous layer, but this species is slightly larger and the sculpture multifurcate-tipped. *Ancyrospora ancyrea* var.*brevispinosa* and *A. ancyrea* var. *spinobaculata* display a shorter and more robust/stout sculpture respectively. *Ancyrospora ancyrea* var. *ancyrea* bears similarly sized sculptural elements, but lacks this persistent, third, diaphanous layer, and is ≈larger (82-169μm).

Ancyrospora sp. B

Plate 3.12, fig. 2.

Description. Trilete, zonate-?camerate miospores; amb irregular, subcircular to rounded triangular. The equatorial margin appears comparatively rounded, unmodified, and the exoexine variably thickened, ≤1-3μm thick: ?limbate. The suturae are usually indistinct and confined to the central body, although exinal folds may perpetuate the trilete mark to the equatorial margin. Occasional, but generally rare traces of labra may be resolved at the proximal pole, ≤8-16μm in height. The contact areas are ill-defined. The central body is usually concentric with the outline of the exoexine, appearing robust, unsculptured and opaque, ≤?2μm thick. The exoexine is scabrate to finely shagreenate in texture, and extends equatorially as a rigid zona that may display radial (?compressional) folds: both proximal and distal surfaces may display such radial folds, ≤0.5-5μm wide. Distally such exinal "folds" tend to resemble a pseudoreticulum, interconnecting the bases of otherwise discrete processes: the "lumina" of this imperfect reticulum are ≤6μm in diameter. The distal surface is also sculptured with irregular, morphologically variable, broad-based spines, ≤5-11μm in length and tapering either to a fine acuminate tip, or a simple-extended or laterally-extended bifurcation: the tip rarely exceeds 2.25μm in width. Two to five elements may coalesce at their base, and collectively such sculptural elements are arranged in "rows" concentric about the distal pole.

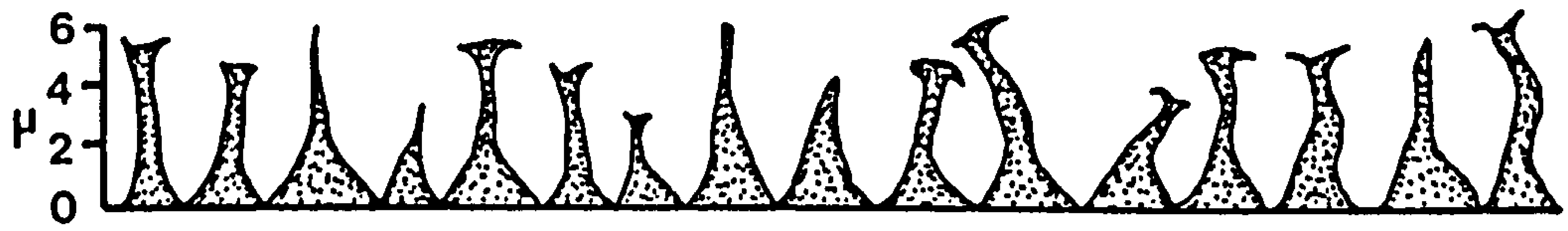


Figure 3.3.18: Sculptural variation on *Ancyrospora* sp. B, lateral view.

Dimensions. Maximum exoexinal diameter 64-87μm, mean 77μm (10 specimens)

Occurrence. L, CM; *common.*

Remarks. The figured specimen is typical of this species population, in displaying an opaque central body, which thus obscures both haptotypic and distal polar features. For the specimen figured herein, traces of the distal pseudoreticulum may be discernible propagating onto the equatorial flange.

For forms recovered herein, the ornament often lacks bifurcate terminations, appearing corroded and attenuated to a fine point.

Comparisons. The distal, imperfect reticulum distinguishes this morphotype from previously described species of *Ancyrospora*. The Eifelian taxon, *Calyptosporites reticulatus* Tiwari & Schaarschmidt (1975; p. 45-46, Pl. 27, figs. 2-4; Pl. 28, fig. 1; text-fig. 35) is similar in merely displaying a distal reticulum, but no mention is made in the diagnosis of this species to bifurcate terminations. The size range specified by Tiwari & Schaarschmidt for *Calyptosporites reticulatus* is larger (90-130μm).

Genus *Aneurospora* Streel emend. Richardson, Streel, Hassan & Steemans, 1982.
Type species. *Aneurospora goensis* Streel, 1964.

Discussion.

Streel (1964) proposed the genus *Aneurospora* to circumscribe comparatively simple, sculptured, acamerate miospores that display an equatorial crassitude. Lele & Streel (1969) later referred to the darker, "thickened" equatorial margin of such spores as "banded curvaturae", and were unsure whether such a feature reflected a true crassitude, or simply a denser, more rigid part of the exine. Also that year, Richardson & Lister (1969, p. 230) believed Streel (1967, p. 47) had transferred the genotype of *Aneurospora,* namely *A. goensis* Streel (1964), to *Geminospora.* Thus Richardson & Lister felt justified in proposing the genus *Streelispora,* which was established to accommodate those species which remained within (what these workers now perceived to be) the obsolete genus *Aneurospora.* However Streel (1972) rejected this supposition, and in the years that followed the status of *Aneurospora* and *Streelispora* became increasingly confused. In 1982, Richardson, Steel, Hassan & Steemans finally clarified the status of both *Aneurospora* and *Streelispora,* and indeed regarded these two genera as discrete. The emended diagnosis of *Streelispora* thus allows for a 2/?3 layered exine, which displays contact areas characterised by tangential or radial folds in the outer, thin exoexinal layer: an ≈equatorial crassitude and distal sculpture are distinct. Conversely, *Aneurospora* is redefined simply to accommodate equatorially "crassitudinous" miospores that display a distal sculpture.

In comparison, the *Synorisporites* complex of Richardson & Lister (1969) circumscribes simple, crassitudinous miospores, that display a distal sculpture comprising verrucae &/or muri. *Breconisporites* Richardson *et al.* (1982) is a bizonate miospore, whereas the genus *Ambitisporites* Hoffmeister (1959) is similar in construction, but the exine appears laevigate, unsculptured (refer to the discussion herein under *Stenozonotriletes* regarding the validity of the genus *Ambitisporites*).

Aneurospora greggsii (McGregor) Streel.
Plate 3.12, figs. 4, 5.

1964 *Retusotriletes greggsii* McGregor, p. 8-10, Pl. I, figs. 1-12.
p 1974 *Aneurospora greggsii* (McGregor) Streel in Becker, Bless, Streel & Thorez, p. 24, Pl. 16, figs. 7, 8, 9, 12, 13, 14, 15(?) (only).
? 1980 *Aneurospora greggsii* (McGregor) Streel in Loboziak & Streel, Pl. II, fig. 6.
? 1982 *Aneurospora greggsii* (McGregor) Streel, in Marshall & Allen, p. 285, Pl. 31, fig. 1.
1986 *Aneurospora greggsii* (McGregor) Streel, in Turnau, Pl. IX, fig. 9.

Description. Trilete, acamerate, ?laminate miospores; amb subcircular, convex-triangular. The exine thickness is uncertain proximo-distally (≤?1-2.25μm). The trilete rays extend 4/5 to 7/8 the spore radius: the suturae are straight, and may be partially obscured by labra, ≤2.25μm in total thickness. Equatorially, the laesurae are joined by curvaturae perfectae, which may be slightly invaginated. The contact areas are laevigate to finely scabrate, over which the exine appears ≈thinned, depressed. The proximo-equatorial and distal regions display a distinct but diminutive sculpture, comprising broad-based coni, coarse grana and subdued mammae, typically ≤0.5-1.75μm in width and height (rarely exceed 2.25μm). Elements are either ≤0.25-2μm apart, discrete, or very occasionally two to seven adjacent elements may cluster or fuse into irregular, "beaded" rugulae, ≤4.5μm long. Spores exhibit a darkened, rigid equatorial "rim", of variable width: this feature may thin inter-radially and varies between 2-7μm in width.

Figure 3.3.19: Sculptural elements of *Aneurospora greggsii,* lateral elevation.

Dimensions. Maximum spore diameter, 54-76μm, mean 62μm (10 specimens measured).

Occurrence. M; *common.*

Remarks. The opaque equatorial "band" described above is distinct and of generic significance: the slightly greater radial extent of this band may be due to invaginated curvaturae. Some specimens also appear to display a faint trace of an intexinal "body", which occasionally caused problems in satisfactorily differentiating this complex from poorly preserved, partially oxidised specimens of *Geminospora lemurata.*

Note: In re-evaluating the *Aneurospora* plexus, Richardson *et al.* (1982, p. 141) do not qualify the validity of *Aneurospora greggsii.*

Comparisons. *Aneurospora goensis* Streel (1964) is smaller in size (30-60μm) than that specified by McGregor (1964) for *Aneurospora* (al. *Retusotriletes*) *greggsii* (the latter being 60-113μm in diameter). *Aneurospora greggsii* also displays a relatively coarse sculpture in comparison to the finer, more granulose ornament that adorns *A. goensis.*

Genus *Apiculatisporis* Potonié & Kremp 1956.

Type species. *Apiculatisporites aculeatus* Ibrahim, 1933.

Discussion.

McGregor & Camfield (1982, p. 18) discuss the current ambiguity in differentiating between *Apiculatisporis* and *Apiculatasporites.* Consequently they distinguish these two genera based upon the predominant height of the sculpture: *Apiculatasporites* displays elements that range from 0.5μm to 1.5μm in length, with those (on average) greater than 1.5μm referrable to *Apiculatisporis.* These arbitrary constraints on ornament size were adopted in the present study.

Apiculatisporis sp.

Plate 3.12, fig. 6.

Description. Trilete, acamerate miospores. The exine appears comparatively robust equatorially,

≤2.25μm thick: the exine is rarely distorted inter-radially by concentric compressional folds. The trilete rays are straight, and extend 4/5 to the full spore radius. The suturae may be simple, but more commonly are obscured by "thickenings" to the exine, ≤2.25μm in height and width, and which taper slightly towards the equatorial margin. The laesurae may occasionally be terminated equatorially by curvaturae imperfectae. The proximal surface lacks sculpture, and appears laevigate to scabrate in texture. The equatorial and distal surfaces display a comparatively uniform, dense, attenuate spinose/conate sculpture: most elements are ≤2μm in height (average 1-1.75μm, and rarely exceed 2.25μ). Individual elements are ≤0.5-2.75μm apart.

Figure 3.3.20: Sculptural elements of *Apiculatisporis* sp., lateral view.

Dimensions. Maximum spore diameter 39-58μm, mean 51μm (20 specimens measured).

Occurrence. WP; *common.* R, S, LH, L; *rare.*

Remarks. Forms attributed to the above taxon display a sculpture that typically exceeds 1.5μm in height: thus, according to the arbitrary size constraints defined by McGregor & Camfield (1982), is more appropriately affiliated with *Apiculatisporis* than with *Apiculatasporites.*

Due to the limited biostratigraphical utility of these spores, speciation is not attempted.

Comparisons. Due to its basic spore architecture and simple sculptural morphology, this form may be compared with numerous established species. Therefore, restricting comparisons to the misopore assemblages recovered from north Devon: this form superficially resembles *Crassispora catenata* Higgs (1975), but lacks distinct, irregular rugulae interspersed amongst the fine apiculate elements. *Apiculatisporis* sp. also differs to *Cyclogranisporites* sp. A and *Cyclogranisporites* sp. B (of this study), in displaying more "elevated" apiculose sculptural elements (the sculpture of the latter two species comprises more subdued, coarse grana and diminutive verrucae).

Genus *Apiculiretusispora* Streel 1964 emend. Streel 1967.

Type species. *Apiculiretusispora brandtii* Streel 1964.

Discussion.

Streel (1964) proposed the genus *Apiculiretusispora* for simple, acamerate, curvaturate miospores, that display a fine apiculate sculpture. Streel considered the presence of curvaturae and a reduction in ornamentation over the contact areas as characteristic of the genus, and thus allowing distinction from comparable genera that display an apiculose sculpture, *e.g Cyclogranisporites* & *Planisporites*. Coincidentally Streel (1964) emended the generic concept *Retusotriletes,* re-defining this plexus so as to circumscribe unsculptured, laevigate miospores. However, Streel (1965) subsequently concurred with Richardson, noting that the presence or absence of curvaturae was not key in the recognition of *Apiculiretusispora* and therefore was insignificant in the generic diagnosis of this genus: *Anapiculatisporites* was considered a possible synonym, although Streel preferred a synonymy with

Dibolisporites, thus emphasising the composite nature of the sculpture on *Apiculiretusispora*.

Streel (1967, p. 32) later expanded the original circumscription of *Apiculiretusispora* to allow for the presence or absence of curvaturate ridges, as well as a greater diversity in sculpture (encompassing grana, spinae & biform elements). However, Streel (1967) did impose a size constraint of $\leq 1\mu$ on the sculpture. In discussing "*Apiculiretusispora*" *microconus* (Richardson) Streel, Richardson & Lister (1969) concurred with Streel (1967), remarking upon the difficulty in recognising curvaturae, if such features are either inherently indistinct, or coincidental with the spore equatorial margin.

Owens (1971, p. 15-16; in proposing the species *Apiculiretusispora granulata*) and subsequently McGregor (1973, p. 26-29; in describing *Apiculiretusispora brandtii* & *A. gaspiensis* from east Gaspé, Canada), make the first reference to an "intexinal body" (inner layer) for forms of *Apiculiretusispora*, observing variable degrees of "wall" separation. Furthermore, McGregor (1973, p. 28) supports the emendation of this plexus by Streel (1967), and considers the affiliation of non-curvaturate forms with *Apiculiretusispora* as perfectly legitimate. In discussing *Apiculiretusispora gaspiensis*, McGregor (1973) draws a comparison with *Geminospora svalbardiae*, but differentiated the two due to differential wall thickness (*Geminospora* displays a preferentially thickened exoexine).

Tiwari & Schaarschmidt (1975 p. 19, 21) partially synonymise *Apiculiretusispora* Streel (1967) with *Dibolisporites*, regarding the emendation of Streel (1967) as circumscribing too great a diversity in ornament. Chi & Hills (1976, p. 697) commented on the morphological similarity between *Apiculiretusispora* and finely sculptured *Verruciretusispora*, although they acknowledge the latter to display a predominance of verrucae, or verrucae surmounted with small, capitate, mammae, coni or spinae.

Apiculiretusispora brandtii Streel

Plate 3.12, figs. 7-10; *cf.* plate 3.13, fig. 7.

1964 *Apiculiretusispora brandtii* Streel, p. 8-10, Pl. 1, 6-10, fig.2.

1978a *Apiculiretusispora brandtii* Streel, in Richardson & Rasul, p. 434, 436, Pl. 2, fig. 3.

p 1982 *Apiculatasporites microconus* (Richardson) McGregor & Camfield, p. 19, Pl. 3, fig. 10; text-figure 23.

Description. Trilete, acamerate miospores; amb subcircular, oval to subtriangular. The exine is ≤ 1.25-$2.5\mu m$ thick (thickness often uncertain): the exine may appear membraneous, finely scabrate and invariably folded. The trilete rays extend 1/3 to 7/8 the spore radius (usually 3/4). The suturae are straight, rarely openly arcuate, simple, or paralleled by subdued, restricted "labra", ≤ 1-$3\mu m$ in total width at the proximal pole. The laesurae are joined equatorially by curvaturate ridges, $\pm$perfectae, which either appear pronounced, thickened, $\leq 1.75\mu m$ in total width, or conversely are barely discernible. The contact areas appear thinned, and are typically finely scabrate, or may display diminutive grana and bacula, $\leq 0.5\mu m$ in size. A concave-triangular, $\pm$diffuse polumbra usually extends across the proximal pole, and may parallel in part the trilete rays: $\pm$distinct and confined to the contact areas. Proximo-equatorially and distally, the exine displays a comparatively $\approx$regular, uniform sculpture, comprising diminutive spinae, coni and grana: biform elements are rare. Sculptural elements are typically ≤0.5-1.25μm in height (rarely exceed 1.5μm), ≤0.25-0.75μm in basal diameter and discrete, ≤0.25-2.75μm apart. Very occasionally two or three elements may coalesce.

Figure 3.3.21: Ornamentation of *Apiculiretusispora brandtii*, lateral view.

Dimensions. Maximum spore diameter 54-89μm, mean 69μm (25 specimens measured)

Occurrence LN, H; *common*

Remarks. The concept *Apiculiretusispora brandtii* applied in the present study strictly follows the original definition of Streel (1964). In his description and illustrations Streel (1964) allows for "thickened laesurae" (refer to the holotype figured by Streel, 1964; Pl. I, fig. 7). Thus considerable variation in laesurae morphology was recognised for this species, encompassing both simple (non-labrate) and demonstrably "labrate" forms. Ornament dimensions were also noted to occasionally exceed the arbitrary size constraint of ≤1μm imposed by Streel (1967): this disparity did not justify differentiation.

Some specimens affiliated with *Apiculiretusispora brandtii* in the present study display a morphology reminiscent of *Apiculatasporites microconus* (Richardson) McGregor & Camfield (1982): refer to the specimen figured herein on Plate 3.13, fig. 7. The differences between these two species appear arbitrary and ill-defined. Realistically, *"Apiculatisporis" microconus* Richardson (1965; size 100-160μm) may simply be an oversized variant of *Apiculiretusispora brandtii* Streel (1964; size 60-101μm), displaying a slightly sparser sculpture. For such aberrant forms (which may be affiliated with *A. microconus*), the presence of a diffuse apical polumbra, their small size (<100μm) and simple construction resembles the paratypes of *Apiculiretusispora brandtii* figured by Streel (1964; Pl. I, figs. 8, 9): such aberrant forms of *A.brandtii* (transitional in morphology with *Apiculatasporites microconus*) were exclusive to sample LN52 of the Lynton Formation.

As the morphology of *Apiculiretusispora brandtii* and *Apiculatasporites microconus* is very similar, those forms of *A. microconus* (arbitrarily) ≤100μm in spore diameter are tentatively placed in synonymy with *Apiculiretusispora brandtii*.

Comparisons. *Apiculiretusispora arenorugosa* McGregor (1973, p. 27) is slightly larger than *A. brandtii* in size (79-124μm), but displays an equally fine sculpture (according to McGregor, 1973: ≤0.25-1μm in height), as well as an intexinal body: McGregor (1973, p. 26) notes an occasional intexine for *A. brandtii*. Clearly these two circumscriptions are very similar, although according to McGregor (1973) *Apiculiretusispora arenorugosa* lacks a polumbra. *Apiculiretusispora densiconata* Tiwari & Schaarschmidt (1975 p.20) is similar in overall size, but the sculpture on this species is notably dense, and ≈coarser: *Apiculiretusispora densiconata* may display well developed curvaturate ridges. *Apiculatasporites microconus* (Richardson) McGregor & Camfield (1982) is non-curvaturate, lacking a polumbra but displaying a comparable, diminutive conate sculpture (≤1μmin size). The ornament on this form may also appear sparser and the exine markedly folded.

Apiculiretusispora cf. *densiconata* Tiwari & Schaarschmidt
Plate 3.12, figs. 13, 14.

cf. 1975 *Apiculiretusispora densiconata* Tiwari & Schaarschmidt, p. 20, Pl. 4, fig. 7; Pl. 5, figs. 1,2.
cf. 1982 *Apiculiretusispora densiconata* Tiwari & Schaarschmidt, in McGregor & Camfield, p. 19-20, Pl. 3, fig. 9, text-figure 25.

Description. Trilete, acamerate miospores with subcircular to distinctly circular amb. Suturae distinct, straight or tightly sinuous at the proximal pole, and obscured by well developed, robust labra, ≤0.75-4.75μm in total width & height. The laesurae extend 2/3 to 4/5 the spore radius, and are of uniform width, or may marginally thicken towards the equatorial margin. The contact areas are usually delimited by distinct curvaturae perfectae, and appear scabrate to finely granulose in texture: the exine over the proximal pole may appear marginally thinned and depressed. The curvaturae are thickest radially (<5μm wide) and may appear slightly invaginated: inter-radially these ridges are either prominent or diffuse, ±coinciding with the spore margin. The contact areas are further accentuated by the juxtaposition in sculpture across the curvaturae ±perfectae. Proximo-equatorially and distally the exine is ≤1-2.25μm thick, appears comparatively rigid, and displays a very dense, granulate, baculate and conate sculpture, ≤0.5-2.5μm in width and height (usually 1-1.75μm): biform elements rarely co-occur (comprising coni/spinae surmounted by a fine, ciliate capitate spine). In plan view elements are circular to subpolygonal in basal outline, and may appear so closely spaced that the exine seems pseudoreticulate: elements are typically ≤0.25-0.75μm apart, rarely greater than 1.5μm.

Figure 3.3.22: Sculptural elements of *Apiculiretusispora* cf. *densiconata*, lateral view.

Dimensions. Maximum spore diameter 54-76μm, mean 64μm (25 specimens measured).

Occurrence. LN; *common.*

Remarks. The above population differs to *Apiculiretusispora densiconata sensu stricto,* in being smaller in size (according to Tiwari & Schaarschmidt, 1975; 75-90μm), and in displaying more pronounced curvaturate ridges.

Comparisons. *Apiculiretusispora granulata* (Owens, 1971) is similar in gross morphology, but is thicker walled, displays a thin, folded intexinal body and is distinctly curvaturate. *Apiculiretusispora brandtii* Streel (1964), and *Apiculatasporites microconus* (Richardson) McGregor & Camfield (1982) differ in the disposition and dimensions of the ornamentation (smaller, sparser), and the character of the contact areas (polumbrate, ill-defined).

Apiculiretusispora leberidos McGregor & Camfield
Plate 3.12, figs. 11, 12.

1982 *Apiculiretusispora leberidos* McGregor & Camfield, p. 20, Pl. 3, figs. 8, 11, 12.

Description. Trilete, acamerate miospores; amb subcircular to convex-subtriangular. The suturae are simple, straight, and extend 1/2 to 2/3 the spore radius: faint traces of the laesurae may propagate the trilete rays almost to the equatorial margin. At the spore circumference the laesurae merge with ±distinct curvaturate ridges. The proximal surface lacks pronounced ornamentation: the exine generally appears laevigate to finely scabrate, and is ≤1.25-1.5μm thick equatorially. The (?proximo)-equatorial and distal regions display a distinct but "patchy" (incomplete) sculptural cover, comprising fine grana and coni, with rare spinae. The ornament typically ranges in size from ≤0.25μm to 0.75μm (rarely exceeds 1.25μm). Where apparent the sculptural elements vary from appearing closely packed to loosely spaced, generally ≤0.25-2.5μm. Up to 45% of the distal hemisphere typically lacks any form of sculpture.

Sculptural variation of *Apiculiretusispora leberidos*, as illustrated for *Apiculiretusispora brandtii.*

Dimensions. Maximum spore diameter 48-59μm, mean 57μm (5 specimens measured).

Occurrence. LN; *rare.*

Remarks. Conceivably, the irregular sculptural "veneer" may be due to poor preservation, although it is considered unlikely that such forms were preferentially corroded: this patchy cover is thus interpreted as primary. The population of this species recovered from north Devon is slightly larger in overall diameter than those described by McGregor & Camfield (1982; 30-50μm) from the Canadian Arctic.

Comparisons. *A. leberidos* differs to all other species of *Apiculiretusispora* by virtue of its patchy, uneven, sculptural cover.

Apiculiretusispora magnifica Tiwari & Schaarschmidt
Plate 3.13, figs. 1, 2.

1975 *Apiculiretusispora magnifica* Tiwari & Schaarschmidt, p.20, Pl. 4, fig. 5,6; Pl. 5, fig. 3.

Description. Trilete, acamerate miospores; amb oval to subcircular. The suturae are distinct, straight (rarely openly arcuate) and obscured by pronounced labra, ≤2-4.5μm in total width. The laesurae extend 2/3 to 4/5 the spore radius, and appear comparatively uniform in width along their length. The laesurae are joined equatorially by either faint or distinct ±invaginated curvaturae perfectae (≤2.5μm thick). The contact areas appear slightly thinned and depressed, lacking distinct sculpture and ranging from laevigate to sparsely scabrate in texture. The extent of the contact areas is further delineated by a juxtaposition in sculpture across the curvaturate ridges. Proximo-equatorially and distally the exine is ≤1-3μm thick, and evenly sculptured with irregular, squat or slender coni, & attenuate spinae: sculptural elements are typically ≤0.5μm to 2μm in height (rarely up to 2.75μm), and 0.25-1.5μm in basal diameter. The sculpture may either appear sparse or moderately dense: elements range from ≤0.5 to 5μm apart.

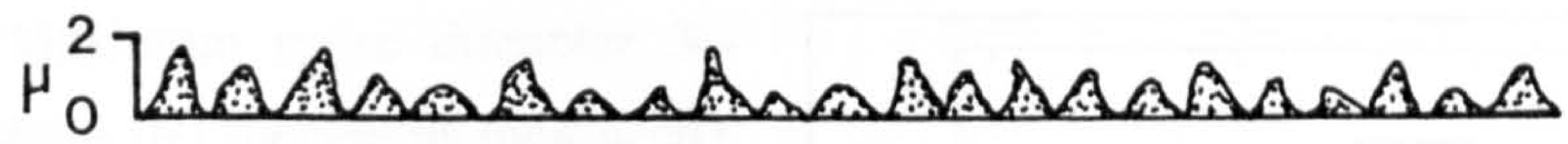


Figure 3.3.23: Sculptural elements of *Apiculiretusispora magnifica,* lateral view.

Dimensions. Maximum spore diameter 76-120μm, mean 92μm (35 specimens measured).

Occurrence. LN, H, S; *common.* R, LH; *rare.*

Comparisons. The population of *A. brandtii* described herein is ≈similar in size, but displays a finer, smaller sculpture, and lacks such well developed labra. *A. brandtii* also displays a polumbra. *Apiculiretusispora nitida* is markedly smaller, whereas *A. gaspiensis* McGregor (1973) and *A. granulata* Owens (1971) display a stratified exine. *Dibolisporites bullatus* (Allen) Richardson displays a coarser, demonstrably biform sculpture.

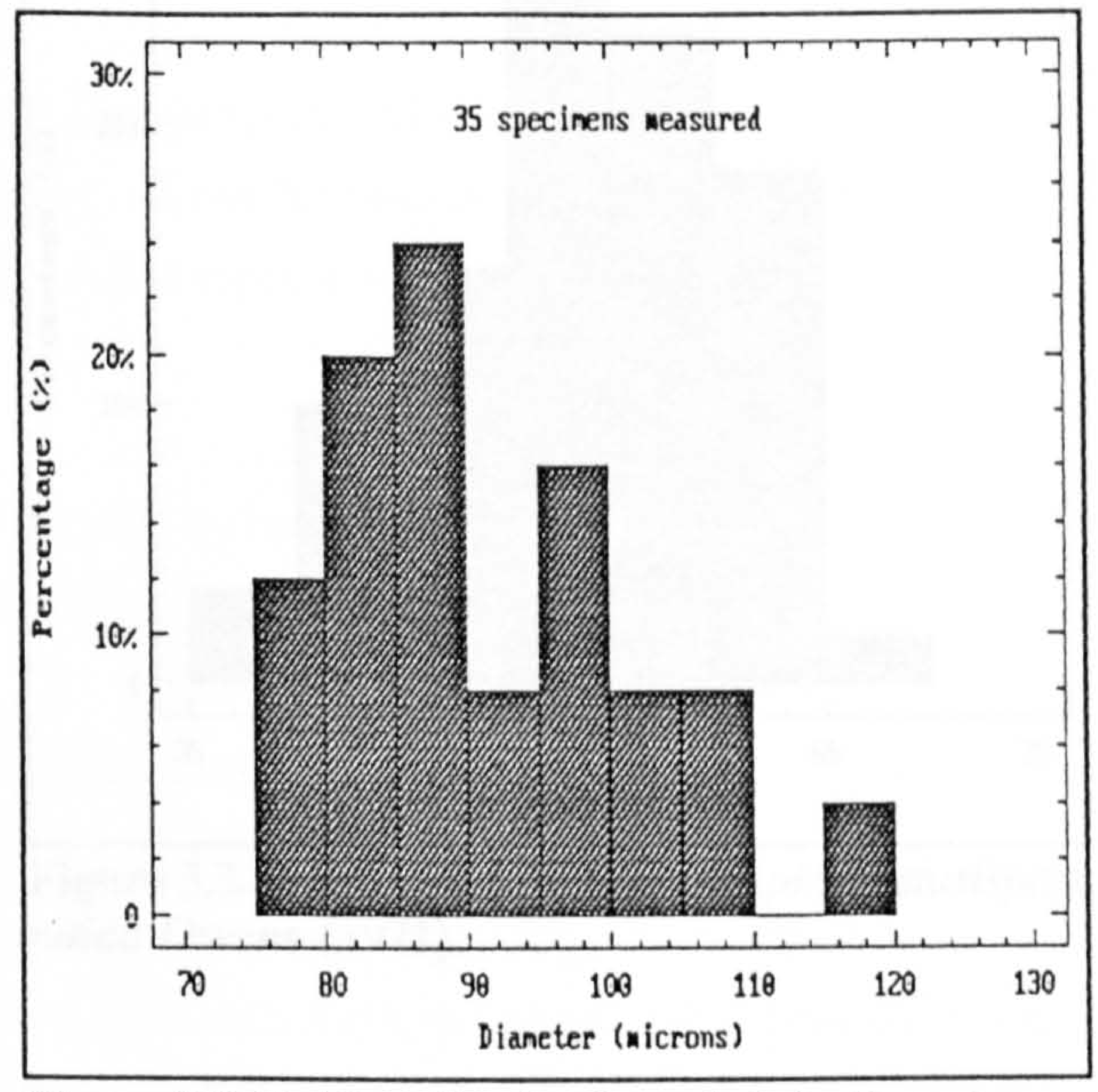


Figure 3.3.24: Size distribution of *Apiculiretusispora magnifica* Tiwari & Schaarschmidt (1975).

Apiculiretusispora nitida Owens.

Plate 3.13, fig. figs. 3-6.

1971 *Apiculiretusispora nitida* Owens, p. 17-18, Pl. III, fig. 9-11.

Description. Trilete, acamerate miospores; amb circular, subcircular to convex-triangular. The exine is laevigate to faintly scabrate and ≤0.75-1.75μm thick. The trilete mark is distinct: the suturae are straight, extending 1/2 to 7/8 the spore radius (usually 3/4) and frequently accompanied by distinct labra, which are ≤2.5-3μm in total width and height at the proximal pole (taper towards the equatorial margin). The contact areas are laevigate to scabrate and the exine commonly appears thin and depressed: may exhibit a faint, incomplete, concave-triangular polumbra. The laesurae are connected equatorially by ±invaginated curvaturae: these curvaturate ridges are faint to pronounced in morphology, and usually ≤1-1.5μm in width (rarely ≤2μm). Proximo-equatorially and distally the exine displays a sculpture comprising predominantly of discrete coni, squat bacula, grana, with rare spinae: elements are typically ≤0.5-1.25μm in height and basal diameter, rarely exceeding 1.5-2μm. Overall the sculpture appears comparatively dense, ranging from ≤0.5μm to 1.75μm apart. Very occasionally two to four elements may coalesce at their base.

Figure 3.3.25: Sculptural elements of *Apiculiretusispora nitida*, lateral view.

Dimensions. Maximum spore diameter 36-67μm, mean 54μm (60 specimens measured).

Occurrence. LN, H, R, S, WP; *common*. LH, L; *rare*.

Remarks. A broad concept of *A. nitida* was applied herein as sculptural morphology and density was variable, although still conforming in principle to the original circumscription of this species by Owens (1971).

Note: Plate 3.13, fig. 6 (herein) figures an over-oxidised specimen, for which the exine appears markedly thin and the ornament predominantly granulose. This form resembles *Apiculiretusispora* sp. A, *sensu* Richardson & Ioannides (1973; p. 274, Pl. 2, fig. 3)

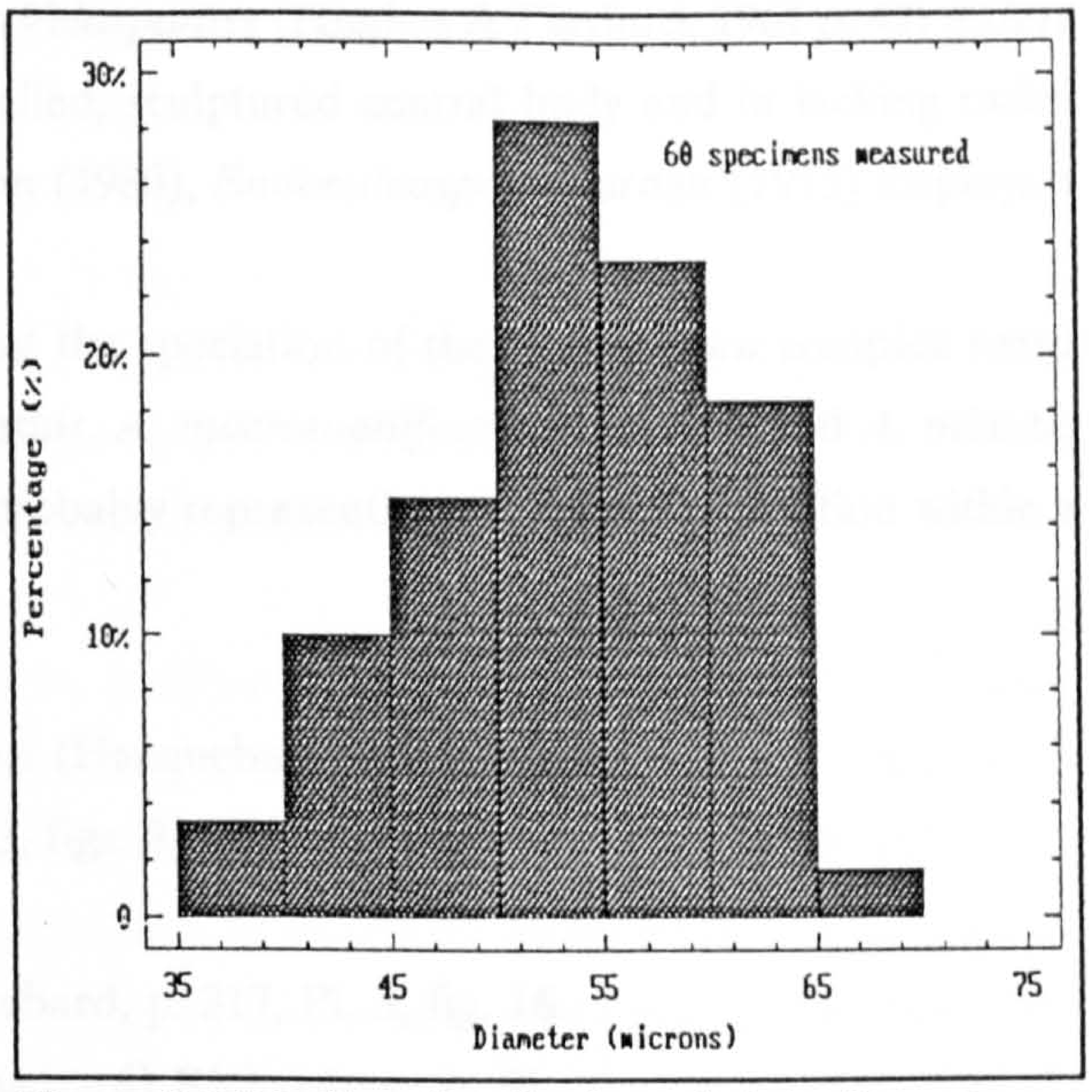


Figure 3.3.26: Size distribution of *Apiculiretusispora nitida* Owens (1971).

In common with the observations of Owens (1971), representatives of this species were often noted in off-polar compression and the exine frequently distorted, displaying numerous compressional folds.

Comparison. The small size, and simple ornamentation of *A. nitida* distinguishes this taxon from most other species of *Apiculiretusispora. Apiculiretusispora microconus* Richardson & Lister (1969; p. 219-220, Pl. 37, figs. 15, 16) is markedly smaller (13-24μm), and the ornament barely discernible, whereas *A. spicula* Richardson & Lister (1969; p. 220, Pl. 38, figs 3, 4) is only slightly smaller in size relative to *A. nitida* (30-46μm & 26-66μm respectively) but is sculptured by more elongate, prominent and slender attenuate spines and cones (0.5-2μm in size), as well as bearing radial murornate folds ($<1\mu$m wide). *A. synorea* Richardson & Lister (1969; p. 221, Pl. 38, figs. 5, 6) is smaller (26-43μm), displays distinctly invaginated curvaturae and bears $\approx$isodiametric cones, 0.5-1.5μm in size. *A. granulata* Owens (1971; p. 15-16, Pl. III, figs. 2, 3, 6, 8) is larger and may display a distinct intexine.

Genus *Auroraspora* Hoffmeister, Staplin & Malloy, 1955.

Type species. *Auroraspora solisorta* Hoffmeister, Staplin & Malloy, 1955.

Discussion.

There is still some confusion as to the validity of *Auroraspora* Hoffmeister, Staplin & Malloy and its relationship with *Endosporites* Wilson & Coe (1940): according to Hoffmeister, Staplin &

Malloy (1955, p. 381) the intexine and exoexine of *Endosporites* are ≈equal in thickness. These two genera circumscribe essentially laevigate, camerate spores, and as Richardson (1960, p. 49) remarked, are seemingly differentiated upon the presence or absence of a limbus: *Auroraspora* is non-limbate, whereas conversely *Endosporites* is limbate.

Grandispora Hoffmeister, Staplin & Malloy emend. McGregor (1973) is similar in construction but ornamented. The Lower Carboniferous genus *Velosporites* (Hughes & Playford, 1961 p. 42) differs to *Auroraspora* in displaying a relatively thick-walled, sculptured central body and in lacking radial folds on the bladder. According to Van der Zwan (1980), *Endoculeospora* Turnau (1975) displays a granulose exine.

Marshall & Allen (1982, p.290-291) contest the speciation of the *Auroraspora* complex *sensu* Richardson (1960, 1965): namely *A. micromanifestus*, *A. macromanifestus*, *A. aurora* and *A. minuta*, interpreting these species of dispersed spore as probably representing ontogenetic variation within a common parent plant sporangium.

Auroraspora micromanifestus (Hacquebard) Richardson.
Plate 3.13, figs. 8, 12.

1957 *Auroraspora micromanifestus* Hacquebard, p. 317, Pl. 3, fig. 16.
1960 *Auroraspora micromanifestus* (Hacquebard) Richardson, p. 51.
1965 *Auroraspora micromanifestus* (Hacquebard) Richardson, p. 586, Pl. 93, fig. 1.
1980 *Auroraspora micromanifestus* (Hacquebard) Richardson, in Loboziak & Streel, Pl.IV, fig.1.
1982 *Auroraspora micromanifestus* (Hacquebard) Richardson, in Marshall & Allen, p. 291, Pl. 31, fig. 11.

Description. Trilete, camerate miospores; amb broadly convex-triangular to subcircular (radials well rounded to subangular in form). The laesurae are distinct to barely perceptible, extending ≤1/2 to the full spore radius, and may be paralleled in part by distinct labra, ≤9μm in maximum width and height at the proximal pole: the labra taper towards to equatorial margin. The outline of the intexinal body is either conformable with the spore circumference, or may appear slightly more rounded. Both exoexine and intexine are laevigate to very finely scabrate, with the intexinal body appearing somewhat optically dense, and ≤1.75μm thick. The thickness of the exoexine is uncertain («?1μm): occasionally may appear partially limbate. The two layers are commonly distorted ±independently, displaying concentric and/or radial folds.

Dimensions. Maximum spore diameter 79-106μm, mean 96μm; maximum intexinal diameter 49-64μm (10 specimens measured).

Occurrence. LN, H, S; *common*. LH; *rare*.

Comparisons. According to the size specifications of Richardson (1960), *Auroraspora macromanifestus* is larger (102-254μm). *A. aurora* Richardson (1960, p. 51-52) is larger than *A. micromanifestus*, and is in fact more comparable in size (120-201μm) and morphology to that of *A. macromanifestus*: *A.*

aurora is differentiated somewhat tenuously from *A. macromanifestus* according to the roundness of the amb, the predominance of exinal "wrinkles" and the greater variability in the form of the trilete mark (refer to Richardson, 1960; p. 51-52). *A. minuta* Richardson (1965, p. 586-587) is comparable in size, but displays a somewhat enlarged, poorly attached intexinal body relative to the exoexine.

Auroraspora cf. *torquata* Higgs.
Plate 3.13, fig. 9.

cf. 1975 *Auroraspora torquata* Higgs, p. 398, Pl. 4, figs. 1-3.
cf. 1988 *Auroraspora torquata* Higgs, in Higgs, Clayton & Keegan, p. 69, Pl. 10, figs. 3-4.
cf. 1988 *Auroraspora torquata* Higgs, in McGregor & McCutcheon, Pl. 3, fig. 13.
? 1989 *Auroraspora torquata* Higgs, in Richardson & Ahmed, Pl. 1, fig. 3.

Description. Trilete, camerate-?zonate miospores; amb convex-triangular to broadly subcircular. The suturae are variably indistinct to perceptible, simple, straight, or tightly sinuous towards the proximal pole, and extend 1/2 to the full radius of the intexinal body. The exine parallel to the suturae may appear thinned, up to ≤2.25μm in total width, or conversely the suturae may be partially obscured by irregular labra, ≤0.75μm wide. The exoexine thickness is problematic, «?0.75μm, but clearly extends in the equatorial plane as a robust, well defined flange. The exoexine appears ±faintly granulose (grana ≤0.5μm individually in diameter): grana may appear ordered, arranged into sub-radial "rugulae", and which tend to parallel the intense radial folds that distort the "flange". The intexine is distinct, ?laevigate and irregular subcircular to convex-triangular in outline: the precise thickness of the intexine is uncertain, although this feature is very obvious, optically dense: peripheral intexinal folds "thicken" the central body, ≤4-7.5μm in total width.

Dimensions. Maximum overall diameter, 56-84μm, mean 69μm; maximum "intexinal body" diameter, 39-62μm mean 45μm (7 specimens).

Occurrence. M; *rare.*

Remarks. The preservation of the specimen figured herein is typical of forms recovered from north Devon, with the exoexine ("?zona") fragmented and torn equatorially, and hence appears "ragged". The "textured", granulose exine is within the circumscription of *A. torquata* as originally defined by Higgs (1975, p. 398).

Comparisons. The population of *Auroraspora torquata* described by Higgs (1975) is larger (80-(123)-143μm in diameter), and displays a more complete flange, which also lacks the intense, subtle, radial plications so apparent on forms documented herein.

This species differs to all other forms of *Auroraspora* in displaying such a uniform, "(?)compressionally" thickened intexinal body, and also in bearing a subtle exinal texture (granulate).

Genus *Baculatisporites* Thomson & Pflug, 1953.

Type species. *Baculatisporites primarius* (Wolff) Thomson & Pflug, 1953.

?*Baculatisporites* sp.

Plate 3.13, figs. 10, 13, 14.

Description. Trilete, acamerate miospores, with a subcircular to sub-elliptical amb. Laesurae distinct to diffuse: the suturae are simple, and commonly extend 1/2 to 4/5 the spore radius, being partially or entirely paralleled by darkened (?thickened) exine (≤5.25μm in total width at the proximal pole, tapering gradually towards the equatorial margin). The contact areas are either ill-defined or distinct, and may be delineated by a reduction in the sculpture, coupled with a slight thinning and depression of the exine over the polar region. The exine may be distorted by concentric folds, which develop preferentially towards the equatorial margin. Wall thickness is often problematic, occasionally discernible (≤1.25μm thick), and the exine scabrate to coarsely granulose in texture. The proximo-equatorial and distal regions display a predominantly baculate sculpture, with an assortment of secondary elements noted (including verrucae, coni and very rare spinae): elements are ≤0.75-3.25μm in height and ≤0.5-2μm in basal diameter. The subsidiary, ±hemispherical, smooth verrucae, coarse grana and truncated coni are ≤2.5-4μm in basal diameter: clavate elements are rare, ≤0.25-1μm wide at their base, expanding distally to a bulbous terminus, ≤2μm wide. Most elements are greater in height than width. In plan view, the sculptural elements are subcircular or subpolygonal in outline: two to four elements occasionally coalesce, defining highly irregular "rugulae", ≤5μm in total length. Elements are isolated, discrete, although may appear crowded, and typically range from ≤0.25μm to 1.5μm in isolation (rarely exceed 2.5μm). The sculpture on the contact areas is similar in morphology but reduced, and occasionally may consist solely of grana.

Figure 3.3.27: Sculptural variation on ?*Baculatisporites* sp., lateral elevation.

Dimensions. Maximum spore diameter 46-67μm, mean 58μm.

Occurrence. LH, L; *common*. WP, CM; *rare*.

Remarks. There is some question as to the generic identity of this spore type. Although elongate, baculate, sculptural elements predominate, the considerable variability and somewhat coarse form to some of the sculptural elements suggests a plausible affiliation with *Raistrickia* Schopf, Wilson & Bentall emend. Potonié & Kremp (1954). However, the predominance of subdued, rounded and diminutive bacula assumes generic priority. The Carboniferous genus *Schopfites* Kosanke (1950) circumscribes spores that display a patchy ornament, differentiated between the two hemispheres, and also may incorporate a thin intexinal body (*sensu* Clayton 1971).

A broad species concept was applied above, allowing for a considerable diversity in sculpture morphology and disposition. Such diversity is represented by the specimens figured herein, ranging from finely sculptured variants (Pl. 3.13, figs. 13, 14) to coarser forms (Pl. 3.13, fig. 10):

intergradational forms were noted.

Comparisons. *?Baculatisporites* sp. bears a superficial resemblance to a number of Late Devonian/Early Carboniferous species of *Raistrickia.* The sculpture of *Raistrickia condylosa* Higgs (1975), *R. cornyognes* Sullivan (1968) and *R. variabilis* Dolby & Neves (1970) is far more pronounced, elongate and slender (the latter two also display weakly multifurcate tips, *sensu* Higgs *et al.,* 1988). The sculpture of *R. clavata* Hacquebard emend. Playford (1964) is more robust, rounded and clavate in form.

Baculatisporites semilucensis (Naumova) McGregor & Camfield (1982, p. 21-22) is similar, but displays a smaller, regular, and generally more discrete ornament. The morphology of *?Baculatisporites* sp. intergrades with that of coarsely sculptured forms of *Verrucosisporites tumulentus,* and conversely with representatives of *V. scurrus* that display a fine, diminutive ornament: these latter two taxa tend to display a broader, more verrucate sculpture.

?Baculatisporites sp. differs to the (?)*Raistrickia* complex defined herein, in lacking bifurcate, serrated, or biform terminations to the sculptural elements.

Genus *Brochotriletes* Naumova 1939 ex Naumova 1953.

Type species. *Brochotriletes foveolatus* Naumova, 1953.

Brochotriletes ?foveolatus Naumova

Plate 3.13, fig. 11.

? 1953 *Brochotriletes foveolatus* var. *minor* Naumova, p. 58, Pl. VII, fig 23.
? 1953 *Brochotriletes foveolatus* var. *major* Naumova, p. 59, Pl. VII, fig. 24.
1973 *Brochotriletes ?foveolatus* Naumova, in McGregor, p. 39, Pl. 4, figs. 20, 23, 24.
p 1989 *Brochotriletes ?foveolatus* Naumova, in Steemans, p. 108-109, Pl. 24, fig. 13 (only).

Description. Trilete, acamerate miospores; amb subcircular to convex-triangular. The exine is laevigate to finely scabrate, and equatorially ≤?2.25μm thick. The trilete mark is indistinct to pronounced, extending the ≈full spore radius and bordered by subtle labra, ≤2.25μm in total width and height. The distal surface displays distinct foveolae, which are circular to subovate in outline, and ≤1-2.75μm in diameter. In general the foveolae appear perforate.

Dimensions. Maximum diameter 31-47μm, mean 37μm (3 specimens).

Occurrence LN; *?R.*

Remarks. McGregor (1973) records such miospores of similar size and overall morphology from the Emsian to early Eifelian York River and Battery Point Formations, Eastern Gaspé, Canada (the "Lower Assemblage"). McGregor's population differs, however, in the nature of the foveolation, noted as imperforate.

Despite the compatibility in age between the occurrence of *Brochotriletes ?foveolatus* in north

Devon (within the Lynton Formation) and its presence in the sediments of eastern Gaspé, Canada (McGregor, 1973), the low numbers of this species and its exclusive recovery from one sample (LN98) suggested reworking.

Comparisons. *Perforosporites* sp. in Allen (1965) is substantially larger (116-117μm), thicker walled and displays simple laesurae. *Brochotriletes robustus* (Scott & Rouse) McGregor (1973, p. 40) and *B. bellatulus* Steemans (1989, p. 108) display a distinct, ≈spinose sculpture between the foveolae. *Brochotriletes rarus* (Arkhangelskaya 1978) and *Brochotriletes sanpetrensis* (Rodriguez, 1978) display finer, smaller foveolae.

Genus *Calamospora* Schopf, Wilson & Bentall, 1944.

Type Species. *Calamospora hartungiana*, Schopf, Wilson & Bentall, 1944.

Discussion.

According to Schopf *et al.* (1944, p. 49-50) the exine of forms affiliated with the genus *Calamospora* is laevigate, although diminutive grana or rugulae were allowed within the circumscription. Pronounced secondary folding of the exine was taken to be of generic significance: no restriction was imposed on spore outline.

In comparing *Calamospora*, Potonié (1958, p. 17) considered *Phyllothecotriletes* Luber (1955) as more rigid and smaller. Staplin (1960, p. 8) confirmed this thicker wall feature, that lacked both major and/or minor folds. Smith & Butterworth (1967, p. 130-131) also acknowledged this distinction, based upon differences in exine thickness, and also commented that *Punctatisporites* (unlike *Calamospora*) does not exhibit distinct contact areas, but does however display longer laesurae. McGregor (1973, p. 26) noted that calamospores may display a polumbra, and furthermore speculated that certain species of *Calamospora* may in fact be the detached intexinal bodies of *Apiculiretusispora brandtii.*

The megaspore *Laevigatisporites* is appreciably larger (3000 μm), possessing a thick, generally unfolded exine and circular amb. Lachkar (1975, p. 5) remarked upon the potential ambiguity between *Laevigatisporites* and *Calamospora,* restricting the latter genus to thin walled, folded miospores.

(Also note the discussion in McGregor & Camfield, 1982, p. 22).

Calamospora cf. *nigrata* (Naumova) Allen

Plate 3.13, figs. 15-18.

cf. 1953 *Leiotriletes nigratus* Naumova, p.23, Pl. I, fig. 9; Pl. V, figs. 5, 6.
cf. 1958 *Leiotriletes nigratus* Ishchenko, p. 35, Pl. I, fig. 5. (non Naumova, 1953).
cf. 1965 *Calamospora nigrata* (Naumova) Allen, p. 693.
p 1988 *Calamospora nigrata* (Naumova) Allen, in Higgs, Clayton & Keegan, p. 50.

Description. Trilete acamerate miospores; amb circular, subcircular to rounded-subtriangular.

Laesurae ±distinct, simple, and straight (rarely arcuate), extending 1/6 to 2/3 the spore radius. The exine is typically ≤0.25-0.75μm thick equatorially (rarely exceeds 1.25μm), and homogeneous, laevigate, or very finely scabrate in appearance (±turbid): a diffuse or well defined, irregular to distinctly convex-triangular/subcircular polumbra extends over the proximal pole. The polumbra may appear "zoned", comprising an inner lightened area, encircled by an opaque rim, or conversely is ≈comparatively even, homogeneous and dense: covers ≤5-25% of the proximal surface. This polumbra may either be confined to the apical region, or parallels the suturae. Both proximal and distal surfaces are folded and wrinkled irregularly. Such folds are either concentric or radial about the proximal and distal poles, and are of variable width, ≤3.5μm-6μm wide, and usually 10-40μm in length (dependant upon overall spore size). The exine may be distorted by less than three to nine folds.

Dimensions. Maximum spore diameter 42-67μm, mean 55μm (140 measurements).

Occurrence. LN, H, S, WP, CM; *common.* R, LH, L, K; *rare.*

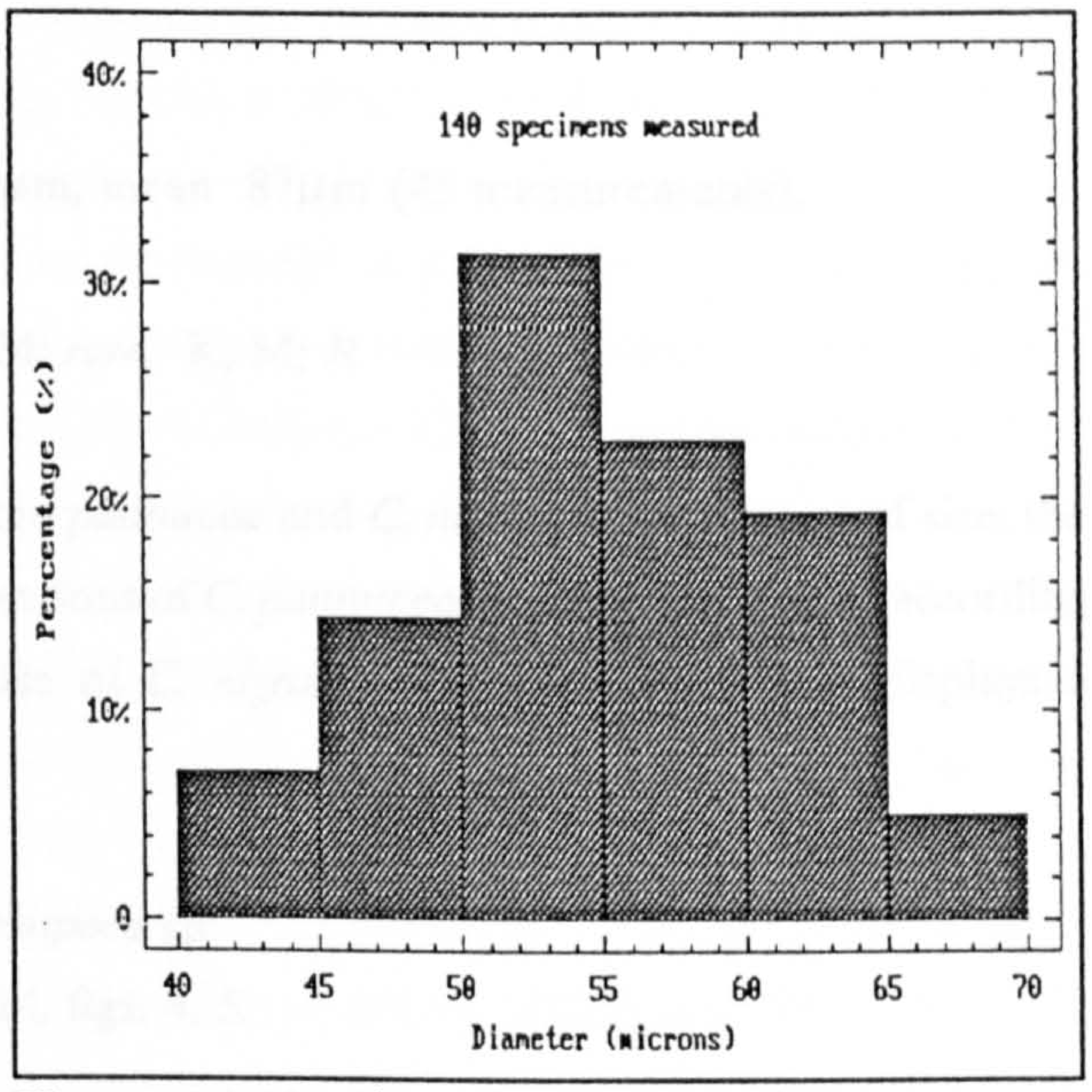


Figure 3.2.28: Size distribution of *Calamospora* cf.*nigrata* (Naumova) Allen (1965).

Remarks. A number of species of *Leiotriletes* were proposed by Naumova (1953). The form of *Calamospora* described above compares closely with *Leiotriletes nigratus* Naumova (1953; in particular the specimen figured on Pl. V, fig. 6). Naumova (1953) quotes the dimensions of *Leiotriletes nigratus* as 60-70μm. Allen (1965) subsequently proposed a new combination of *nigratus,* and specified the size range of *Calamospora nigrata* to be 60-80μm. The population recovered from north Devon are somewhat smaller than both these size specifications. However, in a study of the Tournaisian palynology of Ireland, Higgs *et al.* (1988, p. 50) quote the dimensions of *C. nigrata* as 54-91μm.

Recently McGregor & Camfield (1982, p. 22) remarked upon the difficulty in satisfactorily distinguishing between *Calamospora atava* and *C. nigrata* (Naumova) Allen. In the present study however, and following what is believed to have been the original intention of Naumova (1953), the degree and morphology of exinal folding was used to distinguish between these two species (note comparisons below).

Comparisons. *Calamospora microrugosa* (Ibrahim) Schopf, Wilson & Bentall (1944, p. 52) lacks a distinct polumbra. With reference to the line drawings of Naumova, *Calamospora nigrata* differs to *Calamospora* (al. *Leiotriletes*) *atava* (Naumova) McGregor (1964) in displaying an intensely plicated exine: *C. atava* bears few exinal folds, which are in general confined to the equatorial margin (note also remarks in Allen 1965, p. 693). *Calamospora pannucea* Richardson (1965) is as ≈intensely folded, but is ≈larger and lacks an apical darkening.

Calamospora pannucea Richardson.
Plate 3.14, figs. 1-2.

1965 *Calamospora pannucea* Richardson, p. 563, Pl. 88, fig. 3.

Description. Trilete, acamerate miospores; amb subcircular to subovate. The exine is laevigate to finely scabrate and ≤0.25-0.75μm thick. The suturae are usually indistinct, straight to slightly arcuate, and extend 1/5 to 2/3 the spore radius. The contact areas are ill-defined and commonly delineated by a subtle thinning in the exine, coupled with an apparent absence of exinal folds. Elsewhere the exine is intensely distorted, bearing numerous concentric and/or radial folds: ten to twenty-two folds are usually discernible.

Dimensions. Maximum spore diameter 66-103μm, mean 87μm (45 measurements).

Occurrence. LN, S, WP; *common.* H, LH, L, CM; *rare.* K, M; *R*

Comparisons. The disparity between *Calamospora pannucea* and *C. nigrata* is mainly one of size: the former species is larger, although the size specifications of *C. pannucea,* namely 62-146μm (according to Richardson, 1965), clearly overlap with those of *C. nigrata*. *Calamospora nigrata* displays a prominent, obvious polumbra.

?*Calamospora* sp.
Plate 3.14, figs. 4, 5.

Description. Trilete, acamerate miospores; amb circular to subcircular. The exine apears robust, ≤1-2.25μm in thickness and laevigate, scabrate or finely granulose in texture: turbid in appearance. The trilete rays are indistinct, ?arcuate and thickened, extending 1/4-2/3 the spore radius. The exine may appear comparatively undistorted, robust, although commonly displays 3-7 irregular, radial or concentric curvilinear folds.

Dimensions. 41-93μm, mean 54μm (15 specimens measured).

Occurrence. S, WP, L, M; *common.* LN, H, LH, CM, K; *rare.*

Remarks. This morphotype is only tentatively affiliated with *Calamospora*: the robust and thickened exine is more typical of *Punctatisporites*, although this latter genus is commonly perceived as lacking distinct exinal folds.
Note: The average spore diameter of ?*Calamospora* sp. seemingly increases within progressively younger Devonian strata of north Devon, *i.e.* specimens recovered from the Morte Slates are morphologically identical to forms isolated from the Lynton Formation, but the mean size of the

population notably larger.

Comparisons. This form differs to all established species of *Calamospora* by virtue of its indistinct trilete mark, robust, thickened exine, and coarse, curvilinear exinal folds.

Genus *Camptozonotriletes* Staplin, 1960.

Type species. *Camptozonotriletes vermiculatus* Staplin, 1960.

Camptozonotriletes mcgregorii Ravn & Benson.

Plate 3.14, fig. 3.

1968 ?*Hymenozonotriletes commutatus* Naumova, in Lanninger, p. 144, Pl. 24, fig. 16.

? 1976 *Camptozonotriletes aliquantus* Allen, in Massa & Moreau-Benoit, Pl. 2, fig. 1.

1988 *Camptozonotriletes mcgregorii* Ravn & Benson, p. 186, 188 Pl. 4, figs. 15, 16, 18, 19.

Description. Trilete zonate miospores; amb convex-triangular to subcircular. The exine appears homogeneously scabrate or finely granulose in texture, rarely laevigate. The laesurae are commonly indistinct: when discernible extend 2/3 to 3/4 the spore radius. The suturae are usually straight, simple and ruptured, with the exine parallel to the suturae commonly "thickened", opaque. A thin, comparatively broad zona extends in the equatorial plane: the inner margin of the zona resembles a thickened "rim", 3-5.5μm wide. The zona displays radial "thickenings" ($\approx$muri) and the intervening exine appears "vacuolate": these vacuoles are ovate to subcircular in outline, $\leq$2-6μm in diameter. Overall the zona appears irregularly perforate. The equatorial margin is $\leq$2-3.25μm thick, and the radial "muri" 0.5-1.25μm wide. $\leq$7-16 simple muri traverse the zona per inter-radial. The zona varies in lateral extent between $\leq$9μm and 15μm, and occasionally may appear slightly broader radially. The "central body" is laevigate, commonly opaque, and unfolded.

Dimensions. Maximum spore diameter 42-70μm, mean 56μm; "central body" dimensions 26-45μm, mean 37μm; the central body constitutes 60-73% of the total spore diameter (4 specimens measured).

Occurrence. LN; *rare.*

Remarks. On poorly preserved specimens, the slightly thinned, vacuolate exine on the zona may be ruptured or missing. *C. aliquantus* Allen in Massa & Moreau-Benoit (1976) seemingly lacks a distal polar pseudoreticulate sculpture.

Comparisons. *Camptozonotriletes mcgregorii* Ravn & Benson is similar in construction to *Camptozonotriletes aliquantus* (Allen 1965, p. 720), but the latter species displays an imperfect reticulate sculpture over the distal pole, which comprises high, narrow muri. *C. aliquantus* also displays a somewhat narrower zona relative to the overall diameter of the central body, and according to Allen (1965) may exhibit major compressional folds: the intexine often appears distorted, independent of the exoexine. In comparison *C. mcgregorii* appears comparatively rigid.

Camptozonotriletes asaminthus Allen (1965, p. 719-720) is larger (80-108μ), and displays a distal ornament comprising low verrucae and rare cones. *Camptozonotriletes caperatus* McGregor (1973, p.52) is zonate-camerate, larger (ranging up to 123μm in diameter) and displays a distal verrucose-vermiculate sculpture. *Camptozonotriletes* sp. *sensu* McGregor (1973, p. 53) is similar in morphology to that of *C. caperatus* McGregor (1973), but differs in possessing a coarse pilate ornament.

Genus *Chelinospora* Allen emend. McGregor & Camfield, 1976.

Type species. *Chelinospora concinna*, Allen, 1965.

Discussion.

Allen (1965, p. 728) proposed the genus *Chelinospora* to circumscribe acavate, patinate miospores that display a distal reticulate or foveo-reticulate sculpture: the sculpture is diagnostic of this plexus. McGregor & Camfield (1976, p. 14) emended the generic diagnosis of *Chelinospora* Allen, allowing for forms that display a distally foveolate or convolute-ridged sculpture. Little importance was attached to the nature of haptotypic characteristics (*i.e.* the distinctiveness or length of the trilete rays, the type of proximal ornament, or the proximal exine thickness).

In comparison *Archaeozonotriletes* and *Tholisporites* are similarly patinate, but levigate, unsculptured (Note: the concept and validity of *Tholisporites* is discussed later in this chapter). *Cymbosporites* Allen (1965, p. 725) displays a variable but discrete sculpture, comprising cones, spines and granules.

?*Chelinospora concinna*, Allen

Plate 3.14, fig. 6.

? 1965 *Chelinospora concinna* Allen, p.728-729, Pl. 101, figs. 12-20.
non 1981 *Chelinospora concinna* Allen, in Loboziak & Streel, Pl. II, fig. 16.
? 1982 *Chelinospora concinna* Allen, in Marshall & Allen, p. 289, Pl. 30, fig. 9.
? 1988 *Chelinospora concinna* Allen, in Loboziak, Streel & Burjack, Pl. II, fig. 3.

Description. Miospores, trilete; amb circular to subcircular. The laesurae are usually indistinct, straight, extending 2/3 to 3/4 the spore radius, and either appear simple, or are paralleled by thin labra ≤1.75μm in total thickness. Overall, the exine appears homogeneously laevigate or finely granulose in texture, occasionally coarse-granulose or displaying diminutive verrucae. The contact areas are ill-defined, and the exine over the proximal pole ?thinned and delimited by a juxtaposition in sculpture. The equatorial and distal regions display an imperfect, rarely complete reticulum: individual muri are straight or openly sinuous in plan view, ±thin, flexuous, ≤1-2.75μm wide, and rarely exceed 6μm in height. The distal extremities of these muri are undulose, rounded, or serrated. Muri inter-relate, defining irregular, polygonal lumina, ≤7-16μm in diameter. Equatorially and ?distally the exine appears optically dense and ≈thickened ≤3-9.75μm wide.

Figure 3.3.29: Sculptural elements of ?*Chelinospora concinna,* lateral elevation.

Dimensions. Spore diameter 44-57μm, mean 49μm (excluding the reticulate sculpture: 6 specimens measured).

Occurrence. K; rare.

Remarks. Specimens recovered from north Devon are only tentatively assigned to *Chelinospora concinna,* as they differ to the holotype figured by Allen (1965, Pl. 101, figs. 12, 13). The lumina noted for ?*Chelinospora concinna* (herein) are usually incomplete, ill-defined, and the patina seemingly not as well developed (≤3-9.75μm broad, this study, *vs.* 5-32μm specified by Allen, 1965). However, Allen (1965) does mention and illustrate unusual, aberrant forms of *Chelinospora concinna,* which display a "corroded" patina (refer to Pl. 101, figs. 19, 20 of Allen, 1965). These forms approximate in morphology to those recovered from north Devon, and thus the sculptural elements depicted by Figure 3.3.29 (above) are considered the probable "etched" remnants of a reticulum that once adorned the patina.

Comparisons. *Chelinospora concinna* differs to most other species assigned to this plexus, in displaying a distal reticulate sculpture. Specimens attributed to ?*Chelinospora concinna* (of the present study) accord favourably with the description of *Chelinospora ligurata* Allen (1965, p. 729), in displaying elevated muri (for *C. ligurata* specified as 2-7μm) that form an indistinct reticulum, as well as exhibiting a thinner patina (for *C. ligurata* quoted as 10-21μm thick, including murornate sculpture). However, the sculpture of *Chelinospora ligurata* appears larger, far denser and (subjectively) more irregular in morphology (note specimens figured by Allen, 1965; Pl. 102, figs. 1-7).

Genus *Convolutispora* Hoffmeister, Staplin & Malloy, 1955.

Type species. *Convolutispora florida* Hoffmeister, Staplin & Malloy, 1955.

Discussion.

According to Smith & Butterworth (1967), and taken from Hoffmeister *et al.* (1955), the genus *Convolutispora* circumscribes acamerate, azonate spores that display a dense, ±complete, convoluted pseudoreticulate sculpture, which comprises anastomosing rugulae. *Rugulatisporites* Thomson & Pflug (1953) displays a comparable morphology to *Convolutispora,* but this term is usually applied to post-Palaeozoic forms (note comments in Playford (1962) and McGregor (1964; p. 4-5; 1973, p.49). *Camptotriletes* Naumova emend. Potonié & Kremp (1954) is an allied form, but displays an irregular, sparser murornate ornament that includes cristate elements. *Verrucosisporites* (Ibrahim) Smith (1971) circumscribes spores that bear a predominance of discrete, essentially verrucate sculptural elements *Convolutitriletes* Hamid (1974) is distinguished (somewhat tenuously) by its differentially sculptured exine.

Playford & Satterthwait (1985, p.133) recognised the problem of describing and communicating the density of rugulate sculpture on forms of *Convolutispora*, and thus proposed the *Rugulae Index* (RgI) to quantify the degree of such "convolution": the RgI is determined by counting the number of individual rugula that intersect a line bisecting the distal hemisphere of a spore. This index has been calculated for each species recorded from north Devon.

Convolutispora cf. *caperata* Wicander & Playford
Plate 3.14, figs. 7, 8.

cf. 1985 *Convolutispora caperata* Wicander & Playford, p. 122, Pl. 8, figs. 6-9.

Description. Trilete, acamerate miospores; amb circular, subcircular rarely convex triangular. The margin appears weakly corrugate, and the exine 2-3.75μm thick equatorially. The laesurae are indistinct or pronounced, and simple, straight, or openly arcuate, extending 1/3 to 4/5 the spore radius: the suturae are occasionally bordered by thin, narrow labra, $\leq$0.75-3.25μm in total width, which may taper towards the equatorial margin. The exine is comprehensively covered by rugulae, with an occasional (but often difficult to identify) reduction in ornament over the proximal pole: the contact areas are very occasionally laevigate, unsculptured. The muri are smooth, and convoluted, appearing closely spaced (dense), but generally discrete, $\leq$0.25-1.25μm apart (rarely greater than 1μm). In section these elements are broadly conical, their crests rounded, rarely subangular. The rugulae are tight to openly sinuous, anastomosing, bifurcating or simple: the muri are $\leq$1.5-4μm in basal width and typically $\leq$2.5μm in height.

RgI = 13-17.

Figure 3.3.30: Transverse-sectional view of the rugulae on *Convolutispora* cf. *caperata*.

Dimensions. Maximum spore diameter 48-57μm, mean 54μm (8 specimens measured).

Occurrence. CM, K; *rare.*

Remarks. *Convolutispora caperata* described by Wicander & Playford (1985) from the upper Frasnian Lime Creek Formation (Iowa) differs from those forms recovered from north Devon, in displaying a thicker exine (specified as 4-8μm) and somewhat shorter laesurae.

Comparison. The rugulae of *Convolutispora cerebra* Butterworth & Williams (1958) appear more dense and subdued. *C. usitata* Playford (1962, p. 595, Pl. 82, figs. 7, 8; refer also to Mortimer & Chaloner, 1972, Pl. VI, fig. 12) is larger, thicker walled and displays more distinct, coarser (4-10μm wide) and "bulbous" rugulation. *C. jugosa* Smith & Butterworth (1967) is similar in gross morphology, but larger (84-119μm) and bears a coarser murornate sculpture. The muri of *C. disparalis* Allen (1965; p. 704, Pl. 96, figs. 9-13) range from 2-5μm in height, and are more irregular, displaying undulose crests. *C. tegula* Allen (1965; Pl. 705, Pl. 97, figs. 4-8) displays a similarly dense, rugulate sculpture, but the muri are shorter and more irregular (polygonal) in form. The sculpture of *C. cerebra* Butterworth & Williams (1958) in Richardson (1965, p. 576-577; Pl. 90, fig. 6 only) appears somewhat more diffuse, whereas *C.* cf. *cerebra* in Avchimovitch *et al.* (1988, Pl. 2, fig. 8) is broadly comparable, but the sculpture differs in appearing denser, and comprising less identifiable, discrete, convolute ridges.

Convolutispora sp. A described in the present study differs in displaying a coarser, more open murornate sculpture.

Convolutispora cf. *subtilis* Owens.
Plate 3.14, fig. 11.

cf. 1971 *Convolutispora subtilis* Owens, p. 35, Pl. IX, figs. 3-6.
? 1981 *Convolutispora* sp., Higgs & Russell, p. 27, Pl. 2, figs. 3, 4, 8.

Description. Trilete acamerate miospores; amb circular to subcircular. The exine is thin, membraneous and uniformly ≤1.75μm thick. The suturae are commonly indistinct, straight to openly arcuate and extend 1/3 to 2/3 the spore radius. Thin, diffuse labra may parallel the suturae, which rarely exceed 2μm in total width. The exine is comprehensively sculptured with low, narrow, and dense rugulae, that are sinuous in form and may appear simple, bifurcating or anastomosing. These convolute ridges are typically 1-1.75μm in width and height (rarely exceed 2μm), appearing rounded, smooth in profile and generally ≤0.5-0.75μm apart. Individual muri commonly range in length from ≤4μm to 11μm: due to the density of this sculpture, the exine appears to display a fine network of narrow-channels and foveolae. There may be a subtle reduction in ornament adjacent to the trilete mark.

RgI = 23-29.

Figure 3.3.31: Cross-section through the sculptural elements of *Convolutispora* cf. *subtilis*.

Dimensions. Maximum spore diameter 46-63μm, mean 52μm (10 specimens measured).

Occurrence. M; *rare.*

Remarks. Owens (1971) described *Convolutispora subtilis* from the Devonian Griper Bay Formation (Arctic Archipelago, Canada), and remarked that the labra on this species may appear thickened, individually 2-7μm wide. Representatives recovered from the Morte Slates in the present study display far thinner labra (if at all present). *Convolutispora* sp. of Higgs & Russell (1981) is similar, but displays a marginally coarser murornate sculpture, with isolated verrucae occasionally noted.

Comparisons. *Convolutispora ampula* Hoffmeister, Staplin & Malloy (1955; p. 384, Pl. 38, fig. 12) is very similar in overall spore diameter and sculptural dimensions, but circumscribes Carboniferous (Mississipian) spores: forms of *C. ampula* Hoffmeister *et al.*, in Smith & Butterworth (1967; p. 183-

184, Pl 9, figs. 1, 2) and Playford & Satterthwait (1985; p. 134, Pl. 1, fig. 1) display are far more intense, finer, ?granulose sculpture. *C. fromensis* Balme & Hassell (1962; p. 8, Pl. 1, figs. 14-16) is comparable, but displays a slightly coarser sculpture (ridges 2-4μm wide). *C. paraverrucata* McGregor (1964; p. 17, Pl. 2, figs. 9-11) described from the Yahatinda (Ghost River) Formation in Alberta, displays a somewhat coarser (albeit dense), verrucose and rugulose ornament (elements range up to 4μm in height). *C. porcata* McGregor & Camfield (1982; p. 25-26, Pl. 4, fig. 21) is larger (up to 131μm) and bears an ornament comprising verrucae and ridges (the former 1-7μm wide).

Acinosporites apiculatus Streel (1964) is broadly similar in overall appearance, but is larger, and the sculpture comprises a network of muri surmounted by subordinate apiculate elements. Clayton & Graham (1974) defined *Dictyotriletes craticulus* based upon material from the Sherkin Formation of Southwest County Cork (Ireland). This species is comparable in morphology, being sculptured by a fine, murornate ornament (rugulae 1-1.5μm high & 1-2μm wide), but differs in the ordered, reticulate arrangement of these muri.

Convolutispora sp. A.
Plate 3.14, figs. 9, 10

Description. Trilete, acamerate miospores with a convex-triangular to circular amb. The exine is ≤1.5μm to ?4.75μm in thickness. The suturae are ±distinct, straight, and extend 1/4 to 2/3 the spore radius: diffuse labra may partially or entirely parallel the suturae, but rarely exceed 1μm in width. The extent of the contact areas is uncertain, although appearing to display a marked reduction in ornament. Proximo-equatorially and distally the exine displays a robust, coarse but loose murornate sculpture, comprising openly-convolute muri, ≤2.5-5.25μm in width and ≤2μm in height. These elements are generally rounded, less commonly angular in section, and are simple, or anastomose, but rarely simply bifurcate. Collectively, the muri may be arranged in rows, concentric about the distal pole: individual muri are ≤1-3μm apart, overall appearing well spaced, discrete.

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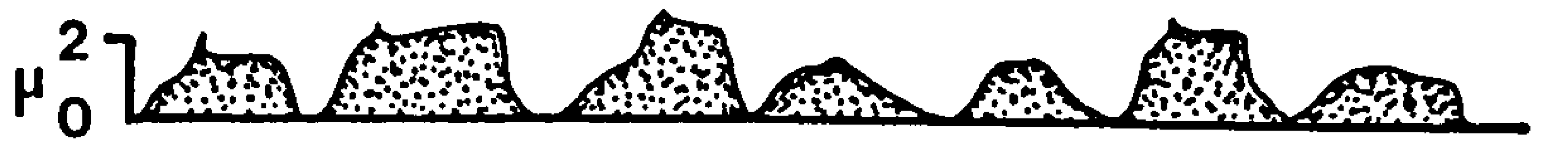

Figure 3.3.32: Cross-section through the murornate sculpture of *Convolutispora* sp. A.

Dimensions. Maximum spore diameter 44-59μm, mean 48μm (10 specimens measured).

Occurrence. M; *rare.*

Comparisons. The robust, coarse and spaced sculpture of *Convolutispora* sp. A (of the present study) merits it distinct from all previously described species of this plexus. *C. florida* Hoffmeister, Staplin & Malloy (1955; p. 384, Pl. 38, fig. 5, 6) is similar in size (39-50μm) but the murornate sculpture appears more irregular. *C. mellita* Hoffmeister, Staplin & Malloy (1955; p. 384-385, Pl. 38, fig. 10) is larger (60-85μm) and displays a far more comprehensive sculptural cover. *C. tessellata* Hoffmeister, Staplin & Malloy (1955; p. 385, Pl. 38, fig. 9) bears a slightly coarser, denser ornament, and ranges in overall spore size up to 86μm. The sculpture of *C. vermiformis* (Hughes & Playford, 1961; p. 30, Pl. 1, figs. 2-4) is coarser and sparser. *C. mimerensis* (Vigran) Allen (1965; p. 704-705, Pl. 97, figs. 1-3) appears very similar in overall morphology, and is only arbitrarily differentiated due to the presence of an imperfect reticulum (lumina ≤7μm wide). *C. amplecta* (Luder) Jachowicz, in Van Veen (1981; Pl. II, figs. 2, 5) bears an open, more widely spaced and irregular murornate sculpture.

Genus *Corystisporites* Richardson 1965.

Type species.*Corystisporites multispinosus* Richardson, 1965.

Discussion.

Richardson (1965) distinguished *Corystisporites* from other genera due to its azonate construction, a pronounced elevation of the labra (resembling a gula), and the basal isolation of the ornament. However, problems have arisen in differentiating *Corystisporites* Richardson from certain species of *Acinosporites* Richardson, particularly when preservation is poor (Note: comments in McGregor & Camfield, 1982, p. 10): these two genera are distinguished upon whether sculptural elements are isolated or basally contiguous.

In common with McGregor & Camfield (1982) there was some degree of uncertainty in the present study as to whether sculptural elements were basally discrete or contiguous. This was largely due to specimen opacity. Consequently the genus *Corystisporites* is only tentatively identified.

?*Corystisporites collaris* Tiwari & Schaarschmidt

Plate 3.14, figs. 13-15, 17.

? 1975 *Corystisporites collaris* Tiwari & Schaarschmidt, p. 28, Pl. 6, figs. 2-5, text-fig. 18.

1982 ?*Corystisporites collaris* Tiwari & Schaarschmidt, in McGregor & Camfield p. 26-27, Pl. 4, figs. 30-32, text-fig. 33.

Description. Trilete miospores: amb convex-triangular to subcircular. When discernible, the suturae are straight to openly arcuate, extending ≈4/5 the spore radius and obscured by labra, which are ≤7μm thick at the proximal pole. The exine is laevigate, scabrate, rarely finely granulose in texture. Distal surface morphology is usually problematic due to specimen opacity, but the sculpture seemingly discrete. Sculptural elements project at the spore circumference, and comprise broad-based, elongate coni, spinae and rare bacula, which appear simple-attenuate, blunted, or with a delicate capitate spine: elements commonly display a bulbous "collar-like" bulge, ≤3-5.25μm in diameter, which develops preferentially towards the element terminus. These elements are broad based (on average ≤9μm), and the shafts parallel-sided or gradually tapering, straight and/or flexed, and the terminations of variable morphology. Elements are typically ≤7-18μm long (rarely exceed 20μm), and appear ≈thin, membraneous and laevigate: the terminations seemingly appear more solid and opaque. The sculpture is variably dense and ±regular at the spore circumference, although appears predominantly discrete: only very occasionally are 2-6 elements basally confluent. Equatorially the fusion of this sculpture may define an irregular, ±narrow, and thin (diaphanous) "flange", which only rarely exceeds 12μm in lateral extent. Elements are ≤2-11.25μm apart (commonly ≤6μm).

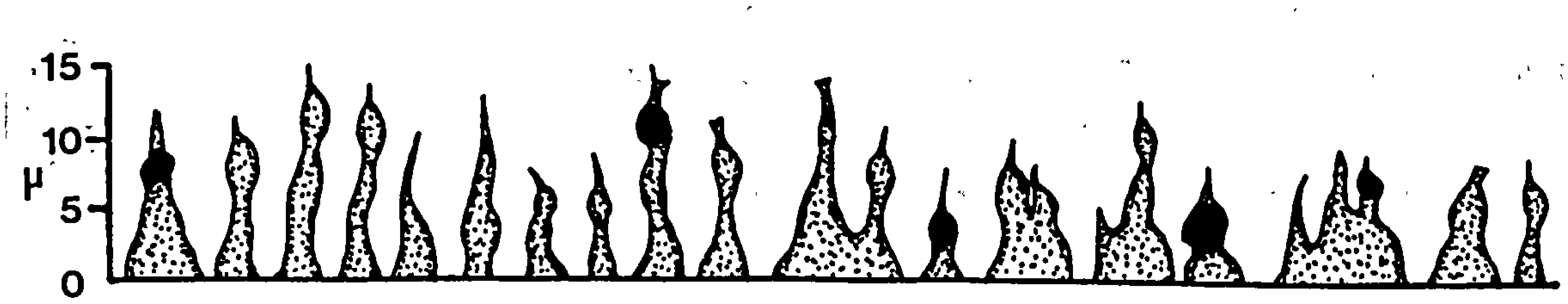

Figure 3.3.33: Sculptural elements of ?*Corystisporites collaris*, lateral view.

Dimensions: Maximum overall diameter 46-72μm, mean 61μm (10 specimens measured).

Occurrence. CM, K; *common.*

Remarks. Tiwari & Schaarschmidt (1975, p. 28) remark that the most striking and taxonomically significant characteristic of this species is the "collar-like" structure to some of the spines. McGregor & Camfield (1982) subsequently question the validity of defining a species based largely upon such sculptural morphology, as other taxa are noted to display similar sculptural elements.

Specimens proved very difficult to oxidised, thus limiting full assessment of both haptotypic and distal characteristics. Consequently the nature and disposition of the equatorial ornament was presumed to be representative of the distal sculpture. The transparency of the ornament and equatorial "flange" suggests that these features may be hollow, in contrast to the darkened, more robust and therefore interpreted as solid terminations.

Comparisons. *Corystisporites multispinosus* Richardson (1965, p. 570) displays larger sculptural elements that lack "collar-like" bulges. The sculpture on species of *Acinosporites* Richardson (1965) is basally contiguous.

McGregor & Camfield (1982) observed a number of specimens that displayed only a few "collared" elements, but considered such specimens were justifiably assigned to the broad circumscription of ?*Corystisporites collaris* as recognised and applied by them. In the present study, problems were encountered in differentiating representatives of ?*Corystisporites collaris* (with few "collared" elements) from ?*Corystisporites* sp. A: the predominant element type of ?*Corystisporites* sp.A lacks "collared" growths, and furthermore the ornament appears more uniform and somewhat smaller in size.

?*Corystisporites* sp. A.
Plate 3.14, figs. 12, 16, 18.

Description. Trilete miospores, with an irregular, subcircular to convex-triangular amb. Exine thickness uncertain, ≤?4μm. When visible, the suturae are variably distinct, straight, and obscured by labra, ≤3-8μm in width and height: the trilete rays extend 4/5 to 7/8 the spore radius. The contact areas are ill-defined, ?bordered by curvaturate ridges, and scabrate to finely granulose in texture. The equatorial margin displays a predominance of discrete, squat, biform elements, in association with bulbous coni and spinae. These elements are straight to distinctly flexed, typically ≤6-10μm in length (rarely exceed 12μm), and ≤3-8μm in basal diameter: element shafts appear transparent, and the termini opaque, solid. Biform elements comprise squat laterally expansive coni, spinae and verrucae, surmounted by a "±solid" spine, mammae, or simple bifurcation. Two to five elements may be partially fused at their base, and which equatorially may extend laterally resembling an irregular "flange". Over the distal pole, the elements may appear marginally denser, and possibly linked by subdued muri, ≤3μm wide and typically ≤15μm in length. However, in general the sculptural elements are discrete, but closely spaced, ≤0.5-8μm apart, and may appear "crowded" at the equatorial margin.

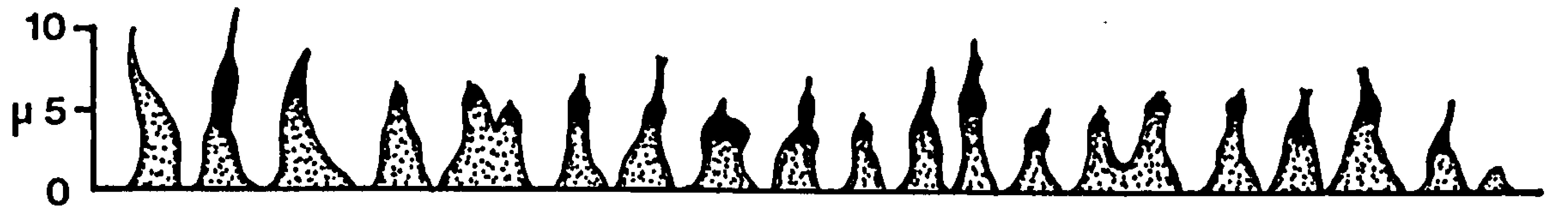

Figure 3.3.34: Sculptural elements of ?*Corystisporites* sp. A, lateral view.

Dimensions. Maximum overall diameter (exclusive of sculpture) 45-91μm, mean 66μm (30 specimens measured).

Occurrence. CM, K; *common*. WP, L; *rare*.

Remarks. As with ?*Corystisporites collaris*, haptotypic and distal characteristics proved difficult to resolve due to the opacity of the spore body. The subtle increase in sculptural density and basal "continuity" towards the distal pole was considered insufficient to justify affiliation with *Acinosporites*.

Comparisons. *Corystisporites multispinosus* Richardson var. *multispinosus* McGregor & Camfield (1982, p. 27) is similar, but substantially larger (126-172μm), and the ornamentation appears more simplistic. ?*Corystisporites* sp. A differs to the ?*Corystisporites collaris* (herein) due to its more uniform and predominantly smaller-sized sculpture, which lack distinct, bulbous, collar-like terminations.

Genus *Crassispora* (Bharadwaj) Sullivan, 1964.

Type species. *Crassispora kosankei* Potonié & Kremp emend Bharadwaj 1957.

Crassispora catenata Higgs

Plate 3.15, figs. 1-3

? 1974 *Apiculatisporis*, Clayton & Graham, p.571, Pl. 1, fig. 5.
1975 *Crassispora catenata* Higgs, p. 396, Pl. 2, figs. 1-3.
? 1975 *Anapiculatisporites crassisetus* Curry, p. 126-127, Pl. 1, fig. 4-6.
? 1987 *Planisporites scaber* Taugourdeau-Lantz, in Streel & Loboziak, Pl. 1, fig. 4.
1988 *Crassispora catenata* Higgs, in Higgs, Clayton & Keegan, p. 55, Pl. 3, figs. 19-20, 23.

Description. Trilete, acamerate miospores; amb circular to convex-triangular. Suturae are distinct, straight, to openly arcuate, and extend 4/5 to 7/8 the spore radius: labra are rare, ≤1.5μm in total width, and curvaturae imperfectae occasionally noted. The contact areas are ±well defined, and lack pronounced sculpture. The exine is uniformly laevigate to scabrate, and turbid in appearance, ≤2.5μm thick at the spore circumference. A barely perceptible, closely appressed and discontinuous "wall feature" may occasionally be observed. The proximo-equatorial and distal surfaces display a variably spaced, diminutive sculpture, comprising coni, grana and rare spinae: elements typically ≤0.5-1.25μm in width and height (rarely 2μm). These elements are usually rounded to subpolygonal in basal outline, and smooth, rounded, and/or truncated, rarely angular, in lateral profile: elements ≤0.25-3μm apart, with between two to six elements occasionally contiguous and thus defining irregular "beaded"rugulae. Such rugulae rarely exceed 4.75μm in length. Equatorially displaced, concentric, compressional folds are rare.

Figure 3.3.35: Sculptural elements of *Crassispora catenata*, lateral elevation.

Dimensions. Maximum exoexine diameter 34-53μm, mean 47μm (30 specimens).

Occurrence. M; *rare.*

Remarks. The population recorded from north Devon was slightly smaller in size than the specifications of Higgs (1975; p. 396; 45-75μm). Occasionally, sculptural elements also appeared somewhat sparser (*e.g.* refer to the specimen figured herein as *Crassispora* cf. *catenata*; Pl. 3.15, fig.2, herein). Such forms are regarded as slight aberrant representatives of *C. catenata,* and have therefore not been differentiated in Chapter 4 (Note: some specimens also appear to display a slightly more verrucose sculpture: such forms still conform to the diagnosis and sculptural dimensions of this species as defined by Higgs, 1975, p. 396). Occasionally, the exine also appeared thickened, but was not sufficiently broad to merit affiliation with *Cymbosporites* Allen (1965): Higgs (1975, p. 396) describes the exine as ranging in thickness from 1.5μm to 3μm.

Comparisons. Forms that are sculptured with coarse verrucae and rugulae are (in Devonian palynological studies) commonly attributed to the genus *Rugospora* Neves & Owens (1966). The small population of *Rugospora* sp. detailed herein, from the Morte Slates, was thus differentiated from *C. catenata* by a predominance of verrucae over grana. Forms of *Cyclogranisporites* lack rugulae interspersed amongst the grana.

Genus *Cristatisporites* Potonié & Kremp, 1954
emend. Butterworth, Jansonius, Smith & Staplin in Staplin & Jansonius, 1964.

Type species. *Cristatisporites indignabundus* (Loose) Potonié & Kremp, 1954.

Synonymy.

1964 *Asperispora* Staplin & Jansonius, p. 107.

p 1965 *Samarisporites* Richardson, p. 581.

Discussion.

Subsequent to the original proposal of the genus *Cristatisporites* by Potonié & Kremp (1954), Richardson (1960, p. 58-61) defined a small complex of Devonian *Cristatisporites,* namely *C. conannulatus, C. mediconus* and *C. orcadensis.* Butterworth, Jansonius, Smith & Staplin in Staplin & Jansonius (1964, p. 100, 108) later emended the diagnosis of *Cristatisporites* Potonié & Kremp (1954): the original interpretation of this genus being single layered was considered incorrect by Bharadwaj and others, and was subsequently confirmed by Butterworth *et al.,* (in Staplin & Jansonius, 1964). In their emendation of *Cristatisporites,* Butterworth *et al.* (in Staplin & Jansonius, 1964) noted prominent sculpture to be confined to the equatorial margin and distal surface of the exoexine, and remarked that representatives of this genus may also display "a peculiar ring of small setose apiculae" surrounding the central proximal area (and separating it from the zona). The distinction between the proximal and distal sculpture, and the two-layered construction of *Cristatisporites,* formed the basis of the emendation to the generic concept of this spore complex by Butterworth *et al.* (1964). Coincidentally, Butterworth *et al.* (in Staplin & Jansonius, 1964) proposed the genus *Asperispora,* being morphologically similar to *Cristatisporites,* but displaying a uniform psilate to minutely granulose proximal sculpture, distinct sutural ridges and lacking internal foveolation or vacuolation. *Cristatisporites* was also noted to display a proportionally wider zona than *Asperispora* (refer to Butterworth *et al.,* in Staplin & Jansonius, 1964, p. 107, p. 108). Butterworth *et al.,* (in Staplin & Jansonius, 1964) emended and clarified the status of *Cingulizonates* and *Densosporites;* the former circumscribing sculptured bizonate spores and the latter sculptured zonate forms.

Following this emendation, Richardson (1965, p. 581-582) proposed *Samarisporites,* a new genus of Devonian zonate spores. Richardson (1965, p. 581-583) attributed one new taxon, namely *Samarisporites megaformis,* to this newly erected genus, as well as defining new combinations of the three taxa earlier allocated by Richardson (1960) to *Cristatisporites.* The principal disparity between these two genera, cited by Richardson (1965, p. 582), was the presence of sculpture upon the proximal surface of forms affiliated with *Cristatisporites,* and conversely the absence of such elements on forms of *Samarisporites.*

Over the ensuing years *Samarisporites* was widely recognised, with only Playford (1971, p. 40-41) and McGregor (1973, p. 58-59) questioning the validity of this genus. In light of the reappraisal of the densospore complex by Staplin & Jansonius (1964), Playford (1971) advocated the suppression of *Samarisporites,* with a preferred application of *Cristatisporites.* Subsequently, McGregor (1973) suggested that *Samarisporites* (amongst others) was a junior synonym of *Grandispora* Hoffmeister, Staplin & Malloy: this latter synonymy has not been acknowledged, as the two genera concerned are believed quite different in basic construction. McGregor & Camfield (1982, p. 43) later recanted this earlier synonymy of McGregor (1973).

In 1982, McGregor & Camfield (p.29-31) readdressed the Devonian densospore complex. They remarked that within the literature, spores of basically similar construction and morphology have been variously attributed to either *Cristatisporites*, *Asperispora*, *Cingulizonates*, *Samarisporites*, *Hymenozonotriletes* or *Densosporites*. McGregor & Camfield that this complex of spores was in urgent needed of revision, and suggested an immediate rationalisation by disbanding with *Samarisporites* in favour of *Cristatisporites*: these workers also regard the genus *Asperispora* to be a junior synonym of *Cristatisporites*. McGregor & Camfield consider the apparent lack of proximal ornament upon specimens of *Samarisporites* to be an inconsequential and thus trivial morphological disparity with *Cristatisporites*. This appraisal has since been acknowledged by a number of authors, including Byvsheva *et al.* (1985) and Turnau (1986).

In recent publications both *Cristatisporites* and "*Samarisporites*" have been informally applied, without any clarification as to which genus is strictly valid, and therefore assumes nomenclatural priority. Furthermore, there is still little conformity of opinion as to the recognition or basic construction of *Cristatisporites* in Devonian palynology. Recently, Balme (1988, p.137) argued a case for the retention of *Samarisporites*, believing that until the structure of the "zona" is clarified, *Samarisporites* must be maintained distinct from *Cristatisporites*. This prognosis was based upon a detailed assessment of the construction of *Samarisporites triangulatus*, isolated from lower Frasnian strata in the Carnarvon Basin (Australia). Within this population, Balme noted some specimens appeared to be paracavate-(two layered)-zonate.

More recently, Loboziak & Streel (1989, p. 191-192) have further confused the "*Samarisporites*-*Cristatisporites*" debate by proposing two new combinations, namely *Samarisporites* (al. *Perotrilites*, Allen, 1965) *eximius*, and *Samarisporites* (al. *Calyptosporites*, Tiwari & Schaarschmidt, 1975) *angulatus*. An interpreted "distal thickening" of the central area formed the basis of these re-evaluations, which according to Loboziak & Streel (1989) was characteristic (?) of *Samarisporites*.

In the present study, the application of *Cristatisporites, sensu* McGregor & Camfield (1982) is favoured, with the abandonment of *Samarisporites*, as minimal taxonomic significance should be attached to the presence or absence of proximal sculpture. Indeed, the application of *Cristatisporites* is considered the more realistic, as in practice proximal ornamentation may be difficult to discriminate in forms with a strong distal sculpture. Furthermore, any subtle feature, whether proximal or distal, is often difficult to assess on compressed, distorted or translucent specimens, using conventional transmitted light microscopy. Thus, reliance upon such subtle morphological attributes is considered an impractical and unrealistic basis for differentiating genera.

Cristatisporites mediconus (Richardson) McGregor & Camfield
Plate 3.15, fig. 10.

1960 *Cristatisporites mediconus* Richardson, p. 60-61, Pl. 14, fig. 14.
1965 *Samarisporites mediconus* (Richardson) Richardson, p. 583.
1982 *Cristatisporites mediconus* (Richardson) McGregor & Camfield, p. 29.
1982 *Samarisporites mediconus* (Richardson) Richardson, Marshall & Allen, p.288, Pl.31, figs.8,9.

Description. Trilete zonate miospores; amb subcircular to convex triangular. The zona is rigid, comparatively broad (projecting 14-27μm in the equatorial plane) and ≤?1.75μm in thickness. The suturae are indistinct, straight to openly arcuate and commonly obscured by ±pronounced labra: ≤7μm in height and width at the proximal pole. The laesurae are usually confined to central body, although may propagate part way onto the flange: the trilete rays may taper gradually towards the equatorial margin. The intexine may seem (?compressionally) thickened, ≤4μm in width, and is generally conformable with the outline of the zona. The proximal and equatorial regions lack pronounced sculpture. Comparatively coarse, bulbous, verrucae and coni, with rare bacula and spinae, are preferentially concentrated towards or around the distal pole: elements average 2-7.5μm in height, rarely exceeding 6μm in basal diameter. Rare, small verrucate elements (≤4μm in size) adorn the distal surface of the flange, towards the equatorial margin of the zona. The zona may display occasional radial folds, ≤3μm wide.

Figure 3.3.36: Sculptural variation of *Cristatisporites mediconus,* lateral elevation.

Dimensions. Maximum spore diameter 88-109μm, mean 93μm; "central body" 49-73μm, mean 57μm (8 specimens measured).

Occurrence. S, LH; *rare.*

Remarks. Richardson (1960) noted the dimensions of the sculpture on *Cristatisporites mediconus* as 6-18μm in width and 3-6μm in height. The sculpture on the population of *Cristatisporites mediconus* recovered from north Devon was comparable in height, but differed markedly in width (being substantially smaller).

The variation in the lateral width of the zona, as recorded in the present study, was within the specifications noted by Richardson (1960, p.60), *i.e.* 12-27μm. Richardson (1960) also remarked that the ratio of the central body diameter to the overall diameter of the spore was 53-83%; for the specimen figured herein (Pl. 3.15, fig. 10) this parameter is 57%.

Comparisons. According to Richardson (1960, p. 61) *Cristatisporites mediconus* can be distinguished from *C. conannulatus* Richardson (1960) and *C. orcadensis* Richardson (1960) by its large cones and concentration of sculpture towards the distal pole. Only a few, small and pointed cones are apparent around the spore circumference of *Cristatisporites mediconus.* According to Richardson (1960, p. 60) the dimensions of *C. conannulatus* and *C. mediconus* are very similar (99-120μm and 90-135μm respectively), but the sculpture upon the former species is fused into a "ring" around the margin of the central area. Although the disposition of sculpture is similar, *Grandispora* (al. *Samarisporites*) *megaformis* (Richardson) McGregor (1973) is camerate and substantially larger (184-254μm). "*Samarisporites*" *tozeri* Owens (1971; p. 41-42, Pl. XI, figs. 6-10) appears optically bizonate, displaying an even, distal sculptural cover that is not preferentially concentrated over the distal polar region.

Cristatisporites triangulatus Allen

Plate 3.15, figs. 7-9, 11-13, 15.

1965 *Samarisporites triangulatus* Allen, p.716-717, Pl.99, figs. 1-6.
1967 *Samarisporites euglyphus* Taugourdeau-Lantz, p. 52, Pl. 2, figs. 7,8.
1972 *Samarisporites euglyphus* Taugourdeau-Lantz, in Mortimer & Chaloner, p. 7.
1972 *Samarisporites triangulatus* Allen, in Mortimer & Chaloner, p. 7.
1980 *Samarisporites triangulatus* Allen, in Loboziak & Streel, Pl. II, figs. 11, 12.
1981 *Samarisporites triangulatus* Allen, in Higgs & Russell, p.33, Pl.5, figs. 1-4.
1981 *Samarisporites triangulatus* Allen, in Loboziak & Streel p.51, Pl.II, figs. 1.5.
1982 *Cristatisporites euglyphus* (Taugourdeau-Lantz) McGregor & Camfield, p. 29.
1982 *Cristatisporites triangulatus* (Allen) McGregor & Camfield, p. 29.
1985 *Samarisporites triangulatus* Allen, in Paris *et al.,* Pl. 29, figs. 6, 7.
1986 *Cristatisporites triangulatus* (Allen) McGregor & Camfield, in Turnau, Pl. IX, fig. 10.
p 1988 *Samarisporites triangulatus* Allen, in Balme p. 136-137, Pl. 7, figs. 8, ?9 (only).
1988 *Samarisporites triangulatus* Allen, in Loboziak, Streel & Burjack, p. 358, Pl. VII, fig.8,9.
1989 *Samarisporites triangulatus* Allen, in Loboziak & Streel p.192, Pl.IV, figs. 6-8.

For additional synonymy refer to Allen (1982, pp. 157-159).

Description. Trilete zonate miospores; amb distinctly triangular to rounded subtriangular. Radially the flange is well defined and elongate, whereas inter-radially the flange generally appears ill-defined. The central body may appear to "bulge" beyond the flange, and in polar view is clearly discernible at the spore circumference: conversely the zona may be complete and well developed, although still distinctly triangular in outline. The suturae are indistinct, straight (rarely arcuate); bordered by distinct, narrow, smooth, and rigid or diaphanous labra. Such labra commonly appear sinuous, and are ≤1.75μm in individual width. The laesurae extend 4/5 to the full spore diameter (usually 7/8 to 1/1). The contact areas are ±well defined, and laevigate to granulose in texture. The intexine is variably distinct, circular to convex-triangular in outline: in general appears laevigate to finely ?scabrate and of uncertain thickness, ≤?3μm (the inner margin of the intexine is usually diffuse). The characteristics of the intexine may be indistinct, obscured by a pronounced distal exoexinal sculpture. The exoexine always reaches its maximum width radially, extending as a single-layered, thin (≤1.25μm) but rigid, turbid to transparent zona; lacks pronounced sculpture (commonly laevigate), and is ≤6-19μm in lateral (radial) width. This flange is somewhat reduced to absent interradially (≤1-7μm in width), and may display a very rare, simple, conate to spinose sculpture ≤2μm in height. Broad-based irregular coni, attenuate spinae, sinuous rugulae, and/or cristate elements, of variable size and density are concentrated around or towards the distal pole. This sculpture rarely exceeds 3.75μm in height and width: individual elements usually 1.75-2.5μm in dimensions. Rugulae vary in morphology from tightly sinuous to openly flexed, ≤14μm long and surmounted by diminutive spinae/coni ≤0.5μm in height. These elements may form an imperfect reticulum, defining irregular, polygonal lumina, ≤5-8μm in diameter. Very occasionally the sculpture projects inter-radially at the spore circumference, particularly where the zona is poorly developed or absent.

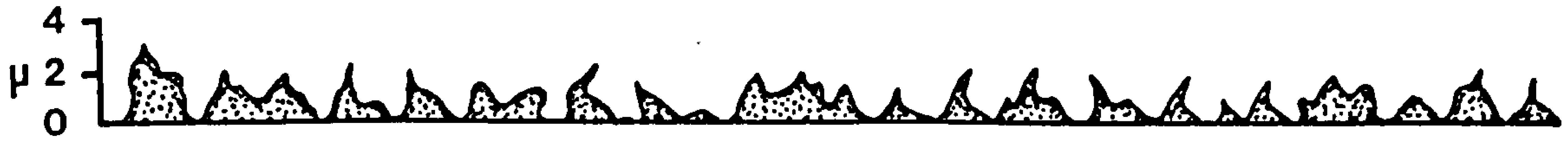

Figure 3.3.37: Sculptural elements of *Cristatisporites triangulatus*, lateral elevation.

Dimensions. Overall spore diameter 41-68μm, mean 58μm (based upon 55 specimens). Intexinal diameter 32-55μm, mean 42μm (based upon 30 measurements).

Occurrence. K, M; *common.* CM; *rare.*

Remarks. Streel (1972, p. 213) regarded *Samarisporites euglyphus* Taugourdeau-Lantz (1967) to be a junior synonym of *Cristatisporites triangulatus* (Allen) McGregor & Camfield (1982), largely because the disparities cited by Taugourdeau-Lantz (1967), namely differences in sculptural morphology and their disposition, are in fact common to both taxa: confirmed by McGregor (1979a, p. 33), Loboziak & Streel (1980, p. 297), Higgs & Russell (1981, p. 33). Higgs & Russell (1981, p. 34) and later Allen (1982, p. 159) remarked upon the morphological gradation between *Cristatisporites triangulatus* (Allen) McGregor & Camfield (1982) and *C. inusitatus* (Allen) McGregor & Camfield (1982): problems of satisfactory differentiation are compounded by the extreme variation in sculptural element morphology exhibited by forms of *C. triangulatus.* In agreement with Clayton & Graham (1974, p. 584), Higgs & Russell (1981) noted that the distal surface of *C. inusitatus* tends to display a more or less near perfect reticulate sculpture, although Allen (1965 p. 716-717) commented that both species may bear an imperfect distal reticulum. Allen (1982) remarked that the zona in well preserved specimens of *C. inusitatus* is more uniform and complete inter-radially. *Cristatisporites inusitatus* tends to be more rounded to convex triangular in outline.

The population of *C. triangulatus* recovered from north Devon rarely exceed 65μm in size, unlike those of Allen (1965; 1982), which range up to 78μm and 88μm respectively. In addition, a considerable diversity in sculptural elements was observed in the present study.

Comparisons. Although somewhat subjective, *Cristatisporites triangulatus* is differentiated from *C. inusitatus* by its more pronounced and distinctly-triangular amb, with a tendency to lack a well defined reticulate sculpture over the distal pole.

?*Cristatisporites* sp. A., (*sensu* Loboziak & Streel, 1981) comb.nov.
Plate 3.15, figs. 14, 16-20.

? 1974 *Samarisporites* sp. cf. *Hymenozonotriletes acanthyrugosus* Chibrikova, in Becker *et al.* Pl.18, Fig.8.

? 1981 *Samarisporites* sp. A., Loboziak & Streel, p.51-51, Pl.II, figs.7-8.

non 1987 *Samarisporites* sp. A., Loboziak & Streel, in Streel & Loboziak, Pl. 1, fig. 7.

? 1988 *Samarisporites* sp. A., Loboziak & Streel, in Loboziak, Streel & Burjack, Pl. VII, fig. 7.

? 1989 *Samarisporites* sp. A., Loboziak & Streel, in Loboziak & Streel , p.192, Pl.IV, Fig. 10.

Description. Trilete zonate miospores; irregular subcircular to convex triangular amb. The spore circumference is strongly dentate or subdued, irregularly serrated: the zona is poorly defined. The central body is well rounded to broadly convex-triangular in outline, and ≤1.5-2.5μm in thickness. The exine is commonly laevigate to finely scabrate, rarely shagreenate. The suturae are straight to openly arcuate, extending 3/4 to the full radius of the central body (rarely propagate onto the "zona"): the suturae may be paralleled by rigid or thin, flexuous labra, ≤2.75μm in total width and usually ≤3μm in height at the proximal pole (rarely up to 7μm). The laesurae may taper towards the equatorial margin. The proximal surface lacks pronounced ornamentation: very occasionally, faint radial striae, and/or a diffuse, ±irregular polumbra extends over 20-30% of the proximal surface. An irregular, transparent to turbid zona extends equatorially. This zona appears thin, "±flexible", and of uncertain thickness, ≤?1-2μm: extends in the equatorial plane beyond the central body, ranging in width from ≤1.5μm to 10μm, typically 4-9μm, and may appear slightly broader radially. Two distinct forms of sculpture are differentiated, adorning the equatorial and distal-polar regions exclusively. Comparatively coarse coni, spinae, bacula and rare mammae project equatorially, ranging between 1.5 to 11μm in length (usually 2-6μm), and ≤1.5-5μm in basal diameter: these elements may be surmounted by a ciliate apical spine, or coarse grana. Between ≈sixteen and forty-three "discrete" elements are discernible at the spore circumference, typically ≤0.25-4.5μm apart (rarely exceeds 6μm). The sculpture over the distal surface appears more uniform and diminutive, comprising squat coni, broad based spinae and biform elements, ≤2μm in width and height. These distal elements are notably discrete, and usually scarce, ≤1-4.25μm in isolation. Very occasionally, two or three elements fuse at their base forming short, ill-defined and irregular "cristae".

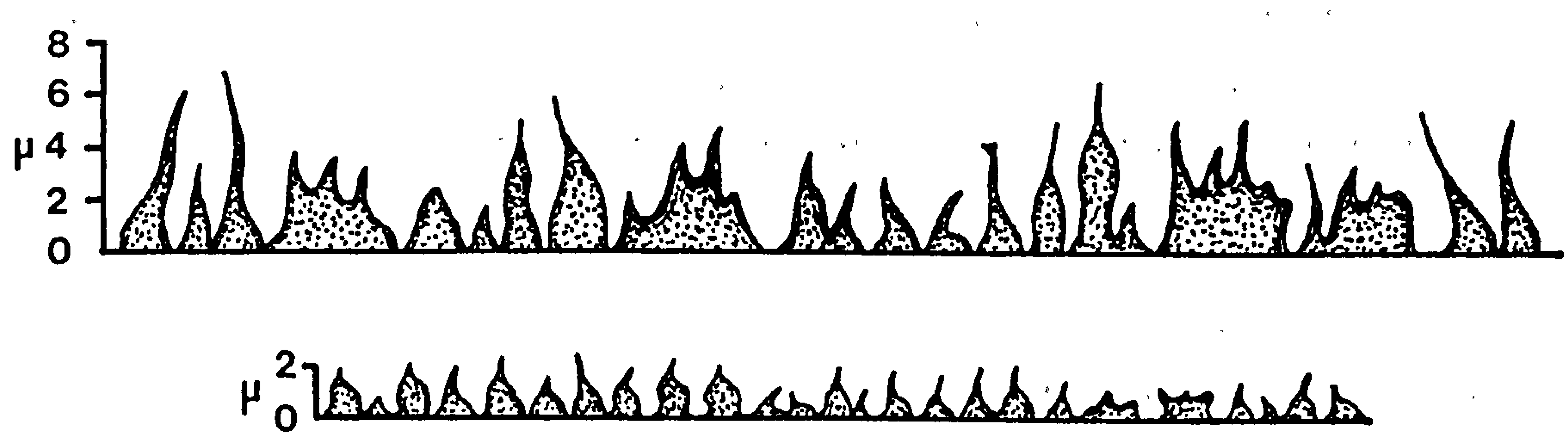

Figure 3.3.38: Sculpture of ?*Cristatisporites* sp A., lateral view; the top row shows a representative selection of those elements that project at the equatorial margin, and the lower row elements that adorn the distal surface.

Dimensions. Overall diameter (including ornament) 41-74μm, mean 54μm. Central body diameter 39-67μm, mean 49μm (based upon 30 specimens).

Occurrence. K; *common.*

Remarks. In view of the synonymy of *Samarisporites* with *Cristatisporites,* a new combination of the species of Loboziak & Streel (1981) is proposed herein. Loboziak & Streel (1981) perceived *Cristatisporites* (al. *Samarisporites*) sp. A. to be a probable gradational morphotype with, or possible derivative of *Cristatisporites triangulatus* (Allen) McGregor & Camfield (1982).

The description and illustrations of *Cristatisporites* (al. *Samarisporites*) sp. A *sensu* Loboziak & Streel (1981), are very similar to forms recovered from north Devon. However, in the present study the sculpture projecting at the equatorial margin is clearly different in morphology to that which adorns the distal surface: such a juxtaposition in ornamentation was not remarked upon by Loboziak & Streel (1981). The distal ornament is notably discrete (only very rarely fuse into short cristae), and thus within the circumscription of the genus *Kraeuselisporites* Leschik emend. Scheuring (1974) - note remarks in McGregor & Camfield (1982, p. 29). However, in view of its probable association with *C. triangulatus*, *C.* sp. A is affiliated with the *Cristatisporites* plexus.

In part, the "zona" appears the product of the basal fusion of the equatorial sculpture.

Comparisons. *Cristatisporites triangulatus* bears the closest resemblance to *Cristatisporites* sp. A: in comparison, the outline of *Cristatisporites triangulatus* is distinctly triangular and tends to lack such pronounced sculpture projecting inter-radially. Furthermore, *C. triangulatus* displays a greater confluence of sculpture over the distal surface.

Genus *Cyclogranisporites* Potonié & Kremp, 1954.

Type species. *Cyclogranisporites leopoldi* (Kremp) Potonié & Kremp, 1954.

Cyclogranisporites sp. A

Plate 3.15, figs. 4, 5.

Description. Trilete, acamerate miospores. Amb circular to convex triangular. The laesurae are ≈indistinct, simple, or "thickened" (≤0.75μm in total) and extend 1/3 to 4/5 the spore radius. The contact areas are poorly defined, often display a slightly subdued ornament and may bear a diffuse, irregular polumbra. The exine is comparatively thin, ≤0.5μm (rarely greater). The exine is coarsely scabrate, or displays a sculpture comprising predominantly discrete, fine grana, in association with very rare, squat bacula, coni and/or spinae. This sculpture is ≤1μm in size (usually 0.25-0.75μm), and ≤1μm in isolation: two to four individual elements may cluster or fuse into short, irregular "beaded" muri. The spore wall commonly bears random, concentric or radial folds, ≤2-12 in number.

Figure 3.3.39: Sculptural elements of *Cyclogranisporites* sp. A, lateral view.

Dimensions. 47-59μm, mean 53μm (15 specimens measured).

Occurrence. LN, H; *rare.*

Remarks. Care was taken to determine whether a subtle granulose texture was a primary or secondary attribute: sculpture upon specimens attributed to above the species concept was considered primary. (?)Tetrads were recorded (refer to Pl. 3.9, fig. 18).

Comparisons. The Carboniferous taxon *Cyclogranisporites aureus* (Loose) Potonié & Kremp (1955) figured in Smith & Butterworth (1967, p. 142-143; Pl. 4, figs. 8, 9) is similar in gross morphology. However, the size of the population recovered from north Devon rarely exceeded 55μm: for *C. aureus* Potonié & Kremp note the size as ranging up to 80μm, Smith & Butterworth similarly up to 99μm). Lanninger (1968) recorded *Cyclogranisporites aureus* (Loose) Potonié & Kremp (1955) within the Emsian Klerfer Schichten, but the figured specimen is poorly preserved, turbid and appears somewhat thicker walled. *Cyclogranisporites plicatus* Allen, (1965, p. 695) is larger in overall diameter (51-82μm), and the laesurae appear somewhat thicker, with curvaturate ridges discernible. The sculpture that adorns species of *Apiculatasporites* Potonié & Kremp (1956) and *Apiculatisporis* Potonié & Kremp (1956) is more spinose, pointed.

?*Cyclogranisporites* sp. B
Plate 3.15, fig. 6.

Description. Trilete, acamerate miospores; amb convex triangular to well rounded. The exine is thickened, ≤2 wide equatorially, with an indistinct, irregular inner margin. The suturae are straight, distinct to diffuse, and extend 4/5 to 7/8 the spore radius, paralleled by a subtle thickening of the exine, ≤3μm in total width. The laesurae may occasionally be terminated equatorially by curvaturae imperfectae. The exine is almost entirely covered by an even, sparse sculpture, comprising coarse grana, small verrucae and occasional coni: average ≤0.75-1.5μm in width and height. Three to five elements may fuse defining irregular rugulae, ≤5μm in overall length. Individual elements are ≤0.5-6μm in isolation. There may be some slight reduction in ornament size over the proximal surface.

Figure 3.3.40: Sculptural elements of ?*Cyclogranisporites* sp. B, lateral view.

Dimensions. 44-56μm, mean 51μm (4 specimens measured).

Occurrence. M; *very rare.*

Remarks. The size of the ornament noted for ?*Cyclogranisporites* sp. B occasionally appeared "coarse", and thus this morphotype may more appropriately be affiliated with the genus *Verrucosisporites*. The exine was also somewhat thicker than perceived typical for *Cyclogranisporites*.

Individual elements were usually discrete, although occasional, short and irregular rugulae may occur. ?*Cyclogranisporites* sp. B is a probable gradational form with, or aberration of, *Rugospora* sp., also recorded from the Morte Slates of north Devon.

Comparisons. This form differs to *Cyclogranisporites* sp. A in displaying a coarser, more verrucate ornament. Lanninger (1968) proposed *Verrucosisporites polygonalis* Lanninger (1968) from the lower Emsian Klerfer Schichten, Eifel (Germany), and noted the sculpture to range in basal diameter from 2μm to 4μm. Overall the sculpture of *V. polygonalis* is notably denser and more uniform.

Rugospora sp. displays greater numbers of rugulae interspersed with coarse grana.

Genus *Cymbosporites* Allen, 1965.

Type species. *Cymbosporites cyathus* Allen, 1965.

Discussion.

Allen (1965, p. 725) distinguishes the genus *Cymbosporites* from other patinate miospores by virtue of its sculpture: *Archaeozonotriletes* (Naumova) Allen (1965) is essentially smooth or punctate, whereas *Tholisporites* Butterworth & Williams (1958) is thickest equatorially, and appears laevigate or displays a diminutive ornament. *Chelinospora* Allen (1965) bears a reticulate/foveoreticulate sculpture and is acavate.

Cliviospora Staplin & Jansonius (1964) is cingulicavate (note the discussion in McGregor, 1973).

?*Cymbosporites* sp.

Plate 3.16. fig. 1.

Description. Trilete, ?patinate miospores with a rounded, convex triangular to subcircular amb. The laesurae are straight, distinct, and extend 3/4 to 4/5 the spore radius. The suturae may be obscured, preferentially towards the spore margin by labra, ≤3.75μm in total width, which taper or become increasingly diffuse towards the proximal pole. The exine appears robust, rigid, and is laevigate to finely scabrate in texture, ?thickened equatorially: ≤2-7μm in width. The contact areas are thin, laevigate, and suppressed, lacking prominent sculpture: delimited by pronounced curvaturae perfectae, ≈2.25μm thick (generally parallel the spore outline). Proximo-equatorial and distal regions bear a regular, distinct and discrete ornamentation, composed predominantly of coni, broad based spinae and rare biform elements: sculpture ≤3.25μm high and ≤2.25μm in basal diameter. The elements are ≤1-3μm apart. In plan, the basal outline of the sculpture apears circular to subpolygonal.

Figure 3.3.41: Sculptural elements of ?*Cymbosporites* sp., lateral elevation.

Dimensions. Maximum spore diameter 51-63μm, mean 56μm (8 specimens measured).

Occurrence. LN; *rare.* LH; *R.*

Remarks. There is some question whether such forms recovered from north Devon are truly patinate in construction, or whether the equatorial "thickening" visible at the equator is the combined effect of a thinned, depressed proximal surface, accentuated by pronounced curvaturate ridges: *Dibolisporites* may be a more appropriate repository.

Comparisons. The illustrations of the holotype of *Cymbosporites cyathus* Allen (1965; Pl. 101, figs. 8, 9), are vaguely reminiscent of the form described above, although the sculpture that adorns *C.*

cyathus is denser and coarser (2-5μm in width and 1-5μm height) - Note: contrary to McGregor & Camfield (1982, p. 32), only *Cymbosporites cyathus* Allen (1965; *partim*, Pl. 101, figs. 10, 11) is regarded herein as synonymous with *Cymbosporites magnificus* (McGregor) McGregor & Camfield (1982). *Cymbosporites catillus* Allen (1965; p. 727, Pl. 100, figs. 11, 12) bears a more diminutive, granulate to verrucate sculpture ($\leq$1.5μm in size). Overall, the sculpture of ?*Cymbosporites opacus* McGregor & Camfield (1982, p. 32-33) and *Cymbosporites* sp. cf. *Retusotriletes tschibrikovii* Mikhailova (in McGregor & Camfield, 1982, p. 33) appears far smaller, being $\leq$2μm in height. *Dibolisporites eifeliensis* Lanninger (1968) resembles ?*Cymbosporites* sp., but differs in displaying a predominance of biform ornament and a less thickened, clearly non-patinate exine.

Genus *Densosporites* Berry emend.

Butterworth, Jansonius, Smith & Staplin, in Staplin & Jansonius, 1964.

Type species. *Densosporites covensis* Berry, 1937.

Discussion.

The construction of Devonian densospores has proved immeasurably difficult to resolve. As with *Cristatisporites,* at present there are available numerous interpretations of densospore structure, with little agreement as to which is truly representative of this plexus. Problems have arisen in applying (and ?corrupting) the concept of a Carboniferous spore complex to Devonian material, which clearly are of different gross morphology. In establishing this genus, it is believed that the initial intent of Berry (1937) was to circumscribe spores with a thickened equatorial walls (thickness approximately 1/3rd the overall spore diameter). Schopf, Wilson & Bentall (1944) subsequently emended the concept of *Densosporites,* allowing for a greater variation in wall thickness: in section, they perceived a compressed densospore to resemble a "dumb-bell", although did note that the exine may extend centrifugally, simulating a flange. Within the re-appraisal of Schopf *et al.* (1944), the exine was acknowledged either to be smooth, or sculptured with apiculate to rugose elements: such ornament was considered either uniform in its distribution, or preferentially developed towards the equatorial margin. In Carboniferous palynology, *Densosporites* (*sensu stricto*) is thus typified by a considerable difference in the thickness of the exine between the proximo-distal and equatorial regions of the spore.

Potonié & Kremp (1954) accepted a strong, massive cingulum as typical of the genus, being wedge-shape in cross section and extending generously over the central body of the spore. However, these workers confused the taxonomy of *Densosporites* by excluding the genotype, *D. covensis,* from their emended circumscription of this plexus: *D. covensis* was instead allocated to a newly erected spore complex, *Anulatisporites* (Note: Smith & Butterworth, 1967, p. 238-239, regard *Anulatisporites* as a superfluous generic category). In contrast, Potonié & Kremp (1954) noted that the equatorial thickening of *Lycospora* to be restricted to the equatorial regions. Bharadwaj & Venkatachala (1962) subsequently constrained the generic concept of *Densosporites* to spores with a triangular to subcircular amb, and a thick cingulum, which was singularly zoned and wedge-shaped: such spores were smooth to faintly granulose. Two years later Butterworth *et al.* (in Staplin & Jansonius, 1964, p. 99, 101-102) emended the diagnosis for *Densosporites,* allowing for the presence of a faint intexinal body, with internal vacuoles or "rods" rare to absent. The sculpture (comprising grana, spines, verrucae and apiculae) on the central distal area may appear differentiated from that of the distal zonal surface. In their study, Butterworth *et al.* (in Staplin & Jansonius, 1964) state quite categorically that the generic concept of *Densosporites* does not circumscribe bizonate spores, but rather should be reserved for spores of homogeneous-zonate construction: this recommended usage has not been applied by Devonian palynologists. In the same paper Butterworth *et al.* (in Staplin & Jansonius (1964, p. 99-100, p. 105) emended the circumscription of *Cingulizonates,* regarding this plexus to accommodate two layered, bizonate spores with minor zonal sculpture.

Recently, McGregor & Camfield (1982, p.33-34) re-addressed the morphology of certain "zonate" Middle Devonian spores, including *Densosporites*. They noted that in Devonian palynological studies, *Densosporites* circumscribes spores that appear optically "pseudo-bizonate": forms exhibit a two fold zona, characterised by an inner, ± complete, darkened zone and a thinner, ≈transparent outer extension. McGregor & Camfield perceived this construction to be in part a compressional attribute, accentuated by the preferential fusion or concentration of sculpture at the outer limits of the contact areas. They confirmed this hypothesis by re-evaluating the microtome sections of *D. devonicus* (Allen, 1965; Pl.98, fig.6). Clearly, McGregor & Camfield's (1982) perspective of Devonian *Densosporites* is different to that typical Carboniferous forms, *sensu* (Berry) emend Butterworth *et al.* (in Staplin & Jansonius, 1964). Furthermore, McGregor & Camfield anticipated the possible establishment of a new genus that would circumscribe such "pseudo-bizonate" forms. In view of the emendation of *Cingulizonates* by Staplin & Jansonius (1964), this genus may well prove to be a far more suitable repository for such "bizonate" Devonian spores, alternative to *Densosporites* which is currently applied.

Until the precise structure of Devonian densospores is clarified, either from high resolution S.E.M. work, further microtome sectioning, or an alternative generic repository proposed, the use of *Densosporites* for Devonian "pseudo-bizonate" spores is sustained, but questioned: the usage of *Densosporites* herein follows that of McGregor & Camfield (1982, p. 33-34).

In the following descriptions the term "annulus" refers to the opaque, thickened, inner portion of the "pseudo-bizona" (*sensu* McGregor & Camfield, 1982, p. 33).

?*Densosporites concinnus* (Owens) McGregor & Camfield
Plate 3.16, figs. 4, 5, 7.

1971 *Samarisporites concinnus* Owens, p.45, Pl. 12, figs. 7-9.
1972 cf. *Hymenozonotriletes inaequus* McGregor, in Mortimer & Chaloner, Pl. IV, fig. 6.
1975 *Densosporites devonicus* Richardson, in Tiwari & Schaarschmidt, p. 31, Pl.14, figs.1-3.
1982 *Densosporites concinnus* (Owens) McGregor & Camfield, p. 34, Pl. 6, figs. 13, 14, 18, 19, text-fig. 46.

Description. Trilete, bizonate miospores, with a subrounded to convex triangular amb. The suturae are straight to openly arcuate, extending 2/3 to 7/8 the spore radius, and commonly paralleled by robust to flexuous labra, ≤7μm in height at the proximal pole. The laesurae either taper towards the equatorial margin, or conversely are thickest at their equatorial extremities. The intexine is rarely distinguishable, commonly closely appressed to the exoexine. The exoexine is laevigate to scabrate, or may bear an even cover of minute, barely discernible grana and spines (individually ≤0.75μm); the exoexine is ?thinner over the proximal surface, and equatorially ≤2.75μm thick. The exoexine is laterally extended, approximately in the equatorial plane, resembling a structured, differentiated "zona". The "zona" comprises two distinct parts: an inner, thickened, robust, and darkened "annulus", (or ring), ≤4-14μm in width (usually obscures the intexine), and a thinner outer flange. The "annulus" may appear discontinuous, and commonly displays a distinct inner margin (rarely diffuse). The outer "flange" appears more transparent, membraneous, and thinner, ≤21μm in lateral extent (usually 5-8μm). The ratio of the inner to outer zona is variable, although the outer zona is commonly smaller. The dimensions of the zona tend to vary considerably upon one individual specimen: the disparity in lateral width usually ±5μm. The equatorial and distal regions of the exoexine display broad based coni and attenuate spinae, with rare verrucae or mammae. In profile the sculpture may either appear rounded, or conversely tapering to a fine, acuminate terminus: in exceptional circumstances the sculpture may display a subtle, minute, bifurcate termination. The ornament tends to be comparatively uniform upon one specimen, with an occasional reduction in element size towards the distal pole. The sculptural elements are ≤2-4.5μm in width and height (rarely up to 8μm), and either markedly crowded or notably discrete, ≤1-9μm apart. The ornamentation tends to concentrate either towards the equator, or over the distal pole.

Figure 3.3.42: Sculptural elements of *?Densosporites concinnus*, lateral elevation.

Dimensions. 53-84μm, mean 64μm (40 specimens measured).

Occurrence. R, S, WP, CM; *common.* LH, L, K; *very rare.*

Remarks. Specimens identified by Tiwari & Schaarschmidt as *Densosporites devonicus* Richardson are similar in size (66-93μm): this size range is more typical of *Densosporites concinnus* (Owens) McGregor & Camfield.

McGregor & Camfield (1982) remark that the "annulus" may be a compressional feature, the result of exine distortion and the distal fusion of sculpture. Within the population of *D. concinnus* recovered from north Devon, the inner, thickened part of the "zona" often appeared incomplete, which favours McGregor & Camfield's interpretation that this "annulus" is in general not a constant, primary attribute.

Comparisons. *Densosporites devonicus* Richardson (1960) is larger in diameter, and displays a more variable, elongate and attenuate sculpture, which may bear subtle bifurcate termini. *"Samarisporites" tozeri* Owens (1971) is similar in sculptural dimensions, but is slightly larger in overall diameter (99-128.7μm), and exhibits a denser, concentrically arranged ornament comprising mammae and verrucae.

Densosporites inaequus (McGregor) McGregor & Camfield (1982, p. 35) is larger, and bears more elongate, predominantly bifurcate-tipped sculptural elements.

?*Densosporites devonicus*, Richardson
Plate 3.16, figs. 2, 3, 6.

1960 *Densosporites devonicus* Richardson, p. 57, Pl. 14, figs. 10, 11; text-fig. 7.
1965 *Densosporites orcadensis* Richardson, p. 580, Pl. 92, figs. 1, 2.
? 1972 cf. *Hymenozonotriletes inaequus* McGregor in Mortimer & Chaloner, p. 28, Pl. IV, fig.6.
non 1975 *Densosporites devonicus* Richardson, in Tiwari & Schaarschmidt, p. 31, Pl. 14, figs. 1-3.
1976 *Densosporites orcadensis* Richardson, in McGregor & Camfield, p. 17, Pl. 6, fig. 3.
1982 *Densosporites devonicus* Richardson, in McGregor & Camfield, p. 34-35, Pl. 6, figs. 20, 21; text-fig. 47.
1982 *Densosporites devonicus* Richardson, in Marshall & Allen, p. 286, Pl. 31, fig. 12.
1989 *Densosporites devonicus* Richardson, in Loboziak & Streel, Pl. IV, figs. 11, 12.

Description. Trilete, zonate miospores with a rounded-subtriangular to convex triangular amb. Dependant upon the dimensions of the sculpture, the equatorial margin of the spore may appear strongly dentate. When discernible, the suturae are distinct, variably straight or openly arcuate: the suturae are commonly obscured by thin, flexuous or robust labra, ≤4-11μm in height and ≤2-7μm wide at the proximal pole, tapering towards the spore circumference. The laesurae extend 3/4 to 7/8 the radius of the spore: commonly confined to within the "annulus", and only very occasionally propagate onto the outer, thinned zona. The contact areas are laevigate to scabrate, and the exine notably thin towards the proximal pole. An intexinal body may be distinguishable, ≤?1.25μm in thickness, laevigate to ?coarsely scabrate and closely appressed to the exoexine. The exoexine extends equatorially as a two-fold zona. The dark, thickened, inner portion to this equatorial extension (annulus) averages 7-19μm in width, rarely exceeding 25μm: the width may vary around the spore margin. Towards the equatorial margin, the exoexine is markedly thinner, flange-like: in comparison this feature is relatively transparent, membraneous, and on occasion may display radial plications. The outer lightened flange varies in width from ≤5μ to 22μm, and is considerably more variable in lateral extent than the inner, darkened "annulus". The proximo-equatorial and distal regions are variously sculptured with broad based coni, spinae, mammae, verrucae and grana. These elements may appear simple-attenuate, or rounded in profile, although are commonly biform: the biform elements usually exhibit ±subtle, diminutive, slightly expanded, extended-triangular or laterally-extended bifurcate termini (rarely exceed 2μm in lateral width). The sculptural elements vary in length from ≤2μm to 11μm (usually 3-8μm), and 1-6μm in basal diameter: are commonly discrete (≤2-8μm apart). The largest elements tend to be concentrated towards the equatorial margin: conversely the flange may lack pronounced sculpture. Two or three (rarely five) adjacent elements may fuse at their base, ≈coincidental with the position of the darkened inner zona). Smaller, subordinate grana, coni and spinae, ≤0.5-1.75μm in size, may be interspersed amongst the coarser sculptural elements.

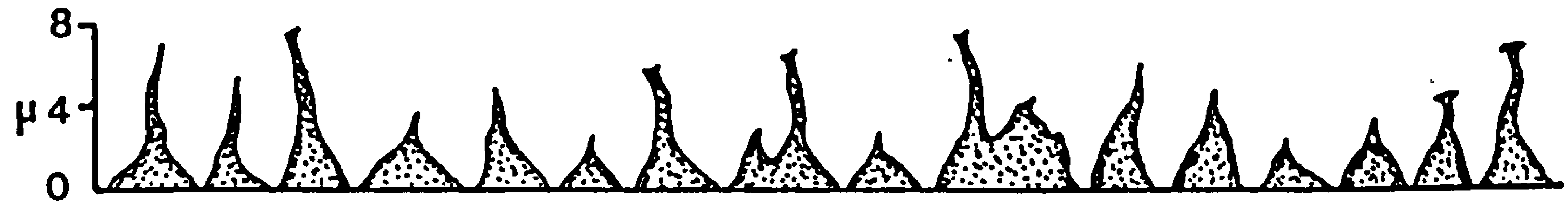

Figure 3.3.43: Sculptural elements of ?*Densosporites devonicus*, lateral view.

Dimensions. Maximum overall spore diameter (excluding sculpture) 91-127µm, 103µm (35 specimens).

Occurrence. S, WP, L; *common*. R, LH; *rare*.

Remarks. Within the population recorded in this study, haptotypic features were usually indeterminate, due to specimen opacity. Representatives of this species were commonly noted in polar compression, and for the vast majority the intexine proved difficult to distinguish (obscured by the optically dense, zonal "annulus"). On any one individual the sculpture proved highly variable in both size and morphology.

Transitional morphotypes between *D. concinnus* and *D. devonicus* were very rare, being intermediate in overall size (≈85-95µm) and sculptural morphology between these two species: such aberrant forms typically display fewer biform elements (*e.g* refer to Pl. 3.16, fig. 3).

Comparisons. *Densosporites concinnus* is smaller, and displays a coarser, more rounded sculpture: generally lacks elongate-attenuate sculptural elements, surmounted by bifurcate termini. The ornamentation of *D. inaequus* appears coarser, more bulbous, and less attenuate.

Genus *Diaphanospora reticulata* Balme & Hassell, emend. Evans, 1970.

Type species. *Diaphanospora riciniata* (Balme & Hassell) Evans, 1970.

Diaphanospora reticulata Guennel
Plate 3.29, fig. 8-12.

1963 *Diaphanospora reticulata* Guennel, p. 258-259, Figs. 17-19.
? 1977 *Apiculiretusispora brandtii* Streel, in Owens, Downie & Reynolds Pl. 2, fig. 11.
1977 *Geminospora* sp. in Owens, Downie & Reynolds, Pl. 2, fig. 8.
1981 ?*Rhabdosporites parvulus* Richardson *sensu* Lele & Streel (1969), in Higgs & Russell, p. 30, Pl. 5, figs. 9-15.
? 1985 *Auroraspora* sp. Wicander & Playford, p.126, Pl. 10, figs. 1A-B, 3A-B.
1986 *Diaphanospora reticulata* Guennel, in Richardson & McGregor, Pl. 17, fig. 11.

Description. Trilete, ?2-3 layered ?zonate-cavate miospores; amb circular, subcircular to rounded triangular. The laesurae are distinct, straight, openly arcuate, to tightly sinuous and extend 1/2 to the full radius of the central body. Thick, robust, occasionally flexuous labra, ≤2-3.75µm in total width and height, may propagate the trilete rays to the spore circumference: commonly taper equatorially, and are simple or terminated equatorially by faint curvaturae imperfectae. The equatorial extremities of the laesurae may appear "splayed", ranging up to 11μm in width. The contact areas are ill-defined or distinct, and are scabrate to finely granulose in appearance. The central body is usually conformable with the spore circumference, ≤2μm in thickness, and scabrate to ?finely granulose in texture; usually folded over the distal surface. The "flange" (exoexine) extends well beyond the central body in the equatorial plane, appearing relatively robust and of comparatively uniform width: individually are ≤4-12μm wide. The flange may appear slightly broader radially, and is occasionally distorted, seemingly "wrapped" around the optically dense central body. The "exoexine" usually appears two layered: the inner layer is laevigate, ≤0.5μm in thickness, and the outer "perinous" membrane perforate, infrapunctate, shagreenate or apiculose. Perforations in this outer perinous layer range from ≤0.25μm to 0.5μm in diameter: the "sculptured" outer membrane projects ≤2.5μm beyond the robust, inner margin of the "exoexine". The density of the "sculpture" generally gives the outer, diaphanous exinal layer an irregular "microreticulate" appearance: "sculptural elements" are ≤0.25-0.5μm apart. In the majority of cases the two outer exinal layers are closely appressed but separable: on a few specimens this "perine" is indistinguishable. The outer layer is often folded, ragged and torn.

Figure 3.3.44: Exinal structure and "sculptural elements" of *Diaphanospora reticulata*, lateral elevation.

Occurrence. M; *common.*

Dimensions. Maximum overall diameter 49-67μm, mean 57μm; maximum central body diameter 40-54μm, mean 47μm. Diameter of central body 75-83% of the total spore diameter.

Remarks. In the above description the exine is differentiated into a central body and "flange". However the exact nature and relationship of these two features is uncertain. The occasional, highly variable centricity of the central body within the "outer layer" tends to suggest a camerate construction. Conversely, the rigidity and morphology of the flange in other specimens (e.g. Pl. 3.29, fig. 11) tends to favour a zonate interpretation. The type species of *Diaphanospora* was described by Balme & Hassell (1962) as displaying a slightly thickened equatorial "zone" to the inner body, which Guennel (1963) subsequently remarked as resembling a cingulum rather than a zona. Guennel (1963) noted that *D. reticulata* may appear saccate-zonate (as noted in the present study). However, despite displaying a construction somewhat dissimilar to the type of *Diaphanospora* Balme & Hassell, Guennel still favoured an allocation to this plexus, in preference to erecting a new monospecific genus.

In some specimens recovered from north Devon, the outer exinal layer was readily differentiated into two distinct "laminae". This feature was not a persistent attribute (*e.g.* note the wall construction of specimen figured on Plate 3.29, fig. 12). Guennel (1963) mentions that *D. reticulata* displays a reticulate to granulose zona, that is covered usually by a tightly fitting, folded or wrinkled "perisporal membrane". Close appression of these outer layers may account for the apparent absence of a third perinous membrane on some specimens: feasibly this may explain the absence of a distinct, third, perinous layer on specimens illustrated by Higgs & Russell (1981) as *?Rhabdosporites parvulus*, and also those of *Apiculiretusispora brandtii, sensu* Owens (1977). Specimens recovered from north Devon rarely displayed as intense exinal folding or wrinkling as illustrated by Guennel (1963; refer to the paratype, Fig. 18, 19 therein).

Auroraspora sp. of Wicander & Playford (1985) is a probable synonym, although these authors regard this form to be pseudosaccate in construction: their figured specimen is conceivably zonate.

Comparisons. *Diaphanospora reticulata* differs from *D. depressa* (Balme & Hassell) emend. Evans (1970), *D. perplexa* (Balme & Hassell) emend. Evans (1970), and *Diaphanospora riciniata* (Balme & Hassell) emend. Evans (1970) primarily in displaying a more equatorially expansive "flange", as well as bearing a pseudoreticulate "perinous layer".

Genus *Dibolisporites* Richardson emend. Playford, 1976.

Type species. *Dibolisporites echinaceus* Richardson, 1965.

Synonymy.

1965 *Bullatisporites* Allen, p. 702-703.

1969 *Umbonatisporites* Hibbert & Lacey p. 423.

1971 *Umbonatisporites* Hibbert & Lacey emend. Clayton, p. 591.

Discussion.

Richardson (1965, p.568) proposed the genus *Dibolisporites,* but failed to clarify the distinction of this plexus from other apiculate and murornate spore complexes. Subsequently Richardson (1969, p. 215) remarked upon the ambiguity between *Dibolisporites* Richardson (1965) and *Bullatisporites* Allen (1965), the former assuming priority (being proposed in January, 1965, whereas *Bullatisporites* was defined in the December of the same year). This was later confirmed by McGregor (1973, p. 30). Tiwari and Schaarschmidt (1975; p. 19, 21) considered *Apiculiretusispora* Streel emend. Streel (1967) in part to be junior synonym of *Dibolisporites*, believing the emendation of Streel (1967) as circumscribing too great a diversity in sculpture. The following year, Playford (1976, p.14-16) provided a more precise and comprehensive emendation of *Dibolisporites,* remarking that biform sculpture was by no means exclusive to this genus, but was however fundamental in its recognition. Simultaneously, Playford formally redefined the term "biform" (further to Richardson, 1969, p. 215), noting that such compound sculpture comprises two distinct forms, and biform does not signify the presence of two (or more) different types of sculpture on a single spore (as has been used).

In emending the generic concept of *Dibolisporites*, Playford (1976) considered the Carboniferous genus *Umbonatisporites* to be a junior synonym, believing there to be little justification for maintaining the two as discrete. In general, Carboniferous workers have been reluctant to adopt Playford's emendation. Recently, Playford & Satterthwait (1986, p. 11) reaffirmed the priority of *Dibolisporites* over *Umbonatisporites*, although Higgs *et al.* (1988, p.61-62) regard the interpretation of Playford (1976) as an over-expansion of the morphologic concept of *Dibolisporites,* retaining *Umbonatisporites* as distinct.

Playford (1976, p. 15) reinforced the generic distinctions noted by Richardson (1965, p. 568).

Although displaying similar sculpture, *Biharisporites* (Potonié 1956) is a megaspore genus, whereas *Acinosporites* (Richardson 1965) exhibits an ornament comprising elongate rugulae/convolute muri which are surmounted by secondary apiculate elements (refer to the re-interpretation of the sculpture of this plexus by McGregor & Camfield 1982, p. 10). Playford (1976) also discussed additional homologies with *Dibolisporites*. *Apiculatasporites* and *Pustulatisporites* do not possess a predominance of biform sculpture, whereas *Kochisporites* (Urban 1971) circumscribes patinate spores that display a "dentate, arcuate rim equatorially". Likewise certain species of *Cymbosporites* Allen (1965) are noted to display biform sculpture, but are patinate in construction (refer to the circumscription and illustrations of the type species of *Cymbosporites cyathus* Allen, 1965; p. 725-726, Pl. 101, figs. 8, 9). A diagnostic feature of the genus *Verruciretusispora* (Owens 1971) are distinct curvaturate ridges, smooth contact areas, and discrete, simple verrucate elements that adorn the exine outside of the contact areas. Owens (1971, p. 22-26) noted however that within the gradational complex of *V. pallida* - *V. magnifica* var. *magnifica* (now *Cymbosporites magnificus*) - *V. grandis*, biform elements may occur (most notable upon *Verruciretusispora grandis* (McGregor) Owens). Subsequently, Playford (1976, p. 15) reviewed the generic concept of *Verruciretusispora,* and believed that this plexus required a more circumspect diagnosis. The subsequent reappraisal of *Verruciretusispora* by Richardson & Rasul (1978a, p. 443-444) unfortunately lacked the clarity Playford (1976) had so desired.

Recently McGregor & Camfield (1982, p. 38) proposed the new combination of *Dibolisporites* (al. *Acanthotriletes*) *uncatus* Naumova (1953): inadvertently this has quite major ramifications to the taxonomy of this plexus. Although the term biform as defined by Playford (1976, p. 14) allows for broad elements (*e.g.* verrucae), the sculpture of *Dibolisporites* has usually (and informally) been perceived to comprise comparatively narrow, subdued and elongate, apiculose elements. Taken literally, the formal (and legitimate, *sensu* Playford, 1976) recognition of coarse, wide, biform bacula and spatula within *Dibolisporites* (as are apparent upon *Dibolisporites uncatus* (Naumova) McGregor & Camfield) suggests that potentially many multifurcate-tipped species of *Raistrickia* may more correctly be circumscribed by *Dibolisporites.* This interpretation has the potential of creating an enormous generic category, analogous to the heterogeneous Russian spore genera *Archaeotriletes, Archaeozonotriletes* or *Hymenozonotriletes* Naumova (1953).

Dibolisporites bullatus (Allen) Richardson, 1969.
Plate 3.16, figs. 11, 14, 15.

1965 *Bullatisporites bullatus* Allen, p. 703, Pl. 96, figs. 5-7.
1973 *Dibolisporites bullatus* (Allen) Richardson, in Riegel, p. 84, Pl. 10, figs. 10-12; Pl. 11, figs. 1, 2.
p 1973 *Dibolisporites echinaceus* (Eisenack) Richardson, in McGregor, p. 29-30.
non 1980 *Bullatisporites bullatus* Allen, in Loboziak & Streel, Pl. I, fig. 11.
p 1986 *Dibolisporites echinaceus* (Eisenack) Richardson, in Turnau Pl. VIII, fig. 1 (only).
1989 *Dibolisporites bullatus* (Allen) Richardson, in Boumendjel, Loboziak, Paris, Steemans, & Streel, Pl.1, fig. 23.

Description. Trilete, acamerate miospores; amb distinctly subcircular to ovate. The exine is laevigate, finely scabrate to granulose, and appears robust, ≤1.25-2.25μm thick at the equatorial margin. The suturae are ±indistinct, straight and extend 2/3 to 3/4 the spore radius: usually obscured by pronounced labra, ≤3.25μm in total width and height. The contact areas are distinct to discernible, and ≈granulose in texture (grana ≤0.75μm in diameter), bordered equatorially by complete or diffuse curvaturate ridges: ≤0.25-4.5μm wide at the terminations of the laesurae, and ±thinning inter-radially. The curvaturae may appear strongly invaginated. The proximo-equatorial and distal regions are ≈uniformly covered with discrete pila, biform bacula and coni, with rare spinae: elements usually surmounted by a distinct, hair-like (ciliate) capitate spine. Overall, element height is ≤2.25μm (usually 0.5-1.75μm), and ≤0.5-1.5μm in basal diameter: these elements may be constricted at their base or midlength, and are usually ≤0.5-4.75μm apart. Minor concentric folds may be confined to the equatorial region.

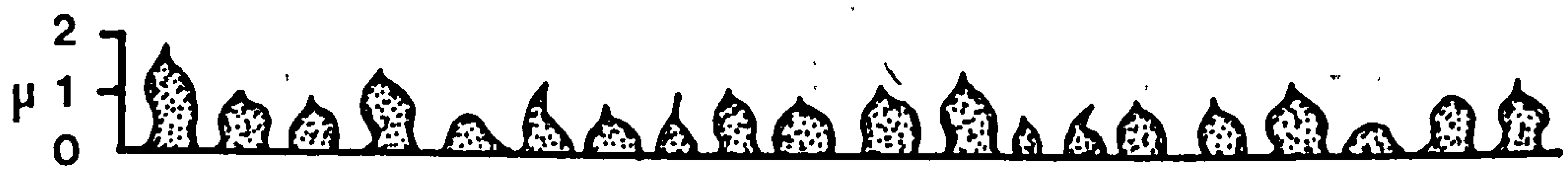

Figure 3.3.45: Sculptural elements of *Dibolisporites bullatus*, lateral view.

Dimensions. Maximum spore diameter 89-117μm, mean 97μm (35 specimens measured).

Occurrence. LN, S; *common.* H, R, LH, WP, L, CM, K; *rare.* K; *R.*

Remarks. McGregor (1973, p. 29) considered *Bullatisporites bullatus* to be a junior synonymy of *Dibolisporites echinaceus*. Although the two are very similar, within the "*D. echinaceus*" population of north Devon *D. bullatus*-types were readily differentiated (see comparisons below). Both have long stratigraphical ranges.

The dimensions of the sculpture noted by Riegel (1973, p. 84; 3-5μm height, 2-3μm width) are somewhat coarser than reported both by Allen (1965; 1-3μm) and the present study (refer to Figure 3.3.45 above).

The figured specimen of *Bullatisporites bullatus* Allen in Loboziak & Streel (1980; p. 289, Pl. I, fig. 11) is too small for *bullatus, sensu stricto* (maximum spore diameter ≈63μm, from the illustration).

Comparisons. *Dibolisporites echinaceus* is morphologically similar but *D. bullatus* may be differentiated due to its large diameter and diminutive, squat sculpture. The sculpture of *D. quebecensis* McGregor (1973) is similar in size but comprises bacula, tubercles or verrucae: *D. quebecensis* is also substantially smaller (28-68μm) than *D. bullatus.*

Dibolisporites echinaceus (Eisenack) Richardson *complex.*

Plate 3.16, figs. 9, 10, 12, 13, 16; Plate 3.17, figs. 1, 8.

1965 *Dibolisporites echinaceus* (Eisenack) Richardson, p.568, Pl. 89, figs 5, 6.

1972 *Dibolisporites echinaceus* (Eisenack) Richardson, in Mortimer & Chaloner, p. 28, Pl. IV, fig. 3.

1973 *Dibolisporites echinaceus* (Eisenack) Richardson, in McGregor, p. 29-30, Pl. 3, figs.8-10, 12 & 13.

1975 *Dibolisporites pseudoreticulatus* Tiwari & Schaarschmidt, p.23, Pl. 9, figs.2, 3.

1975 *Dibolisporites radiatus* Tiwari & Schaarschmidt, p.23, Pl. 9, figs. 4,5; Pl.10, figs. 1, 2.

1975 *Dibolisporites triangulatus* Tiwari & Schaarschmidt, p.21-22, Pl.7, figs.3,4; Pl.8, figs. 1,2.

1975 *Dibolisporites varius* Tiwari & Schaarschmidt, p.22-23, Pl.8, figs.3-5,; Pl.9, fig.1.

1982 *Dibolisporites echinaceus* (Eisenack) Richardson, in McGregor & Camfield, p.37-38, Pl.8, fig.2, text-figure 53.

p 1986 *Dibolisporites echinaceus* (Eisenack) Richardson, in Turnau, Pl. VIII, figs. 3, 5, (only).

Description. Trilete, acamerate miospores; amb convex triangular, circular to ovate in polar compression. Suturae straight to openly flexuous, extending 1/2 to 7/8 the spore radius, and bordered by pronounced, robust labra, ≈1.5-4μm in total width (usually thickened at their equatorial extremity). The contact areas are laevigate, scabrate to finely granulose (grana «1μ in diameter). Faint or distinct, arcuate curvaturae perfectae, ±invaginated, delimit the equatorial extent of the contact areas: these may range up to 4.25μm in thickness. Conversely, some specimens lack any trace of curvaturate ridges, the contact areas simply defined by the juxtaposition between the sculpture on the proximal and equatorial regions of the spore, accentuated by a thinning of the exine over the proximal surface. Equatorially the exine is ≤0.5-1.75μm thick (rarely up to 2.5μm). Proximo-equatorial and distal regions are ≈uniformly sculptured with pila, coni, and spinae, with very rare, broader based verrucose or mammoid elements: most sculptural elements are surmounted either by a fine, delicate and hair-like capitate spine, or a diminutive grana. Typical ornament length ranges from ≤2μm to 5μm (rarely up to 8μm), and 0.75μm to 2.5μm basal width. The sculpture appears comparatively even in its distribution, usually <0.5-2.5μm in isolation. Very occasionally, two to four elements may coalesce at their base.

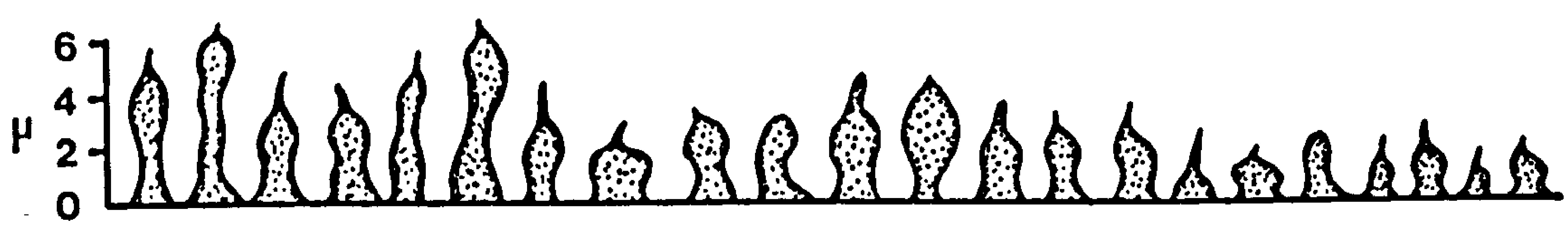

Figure 3.3.46: The sculptural variation of *Dibolisporites echinaceus*, lateral elevation.

Diameter. Maximum miospore diameter 45-87μm, mean 65μm (65 specimens measured).

Occurrence. LN; *abundant.* H, S, WP; *common.* R, LH, L CM, K; *rare.* K; *R.*

Remarks. The concept of *D. echinaceus* applied in the present study was relatively broad, so as to circumscribe the subtle variants defined by Tiwari & Schaarschmidt (1975). The unifying feature of this "complex" is the presence of biform "pila", irrespective of the development of curvaturate ridges or the density/disposition of the sculpture. Richardson (1965; Pl. 89, fig. 5) illustrates an intensely folded specimen, that seemingly lacks prominent curvaturae. However, within the diagnosis of this species he does allow for curvaturate ridges. The size range specified by Richardson (1965) is also substantially larger than that noted herein (92-204μm *vs.* 45-87μm), although McGregor (1973, p. 29-

30) does record specimens as small as 58μm. Furthermore, McGregor (1973) rationalised this species, circumscribing a far greater variation in sculpture and general exinal features.

The population of *D. echinaceus* recorded from north Devon showed marked variability not only in ornament size, or the development of curvaturate ridges, but also in element disposition and density. Initial attempts to consistently distinguish *Dibolisporites echinaceus* Richardson (1965), from *D. pseudoreticulatus* Tiwari & Schaarschmidt (1975, p. 23) *D. radiatus* Tiwari & Schaarschmidt (1975, p. 23), *D. triangulatus* Tiwari & Schaarschmidt (1975, p. 21-22), and *D. varius* Tiwari & Schaarschmidt (1975, p. 22-23), proved in general difficult and impractical. Very rare specimens were occasionally identified, homologous in form to one of these subtle specific varieties of Tiwari & Schaarschmidt (*e.g. D. radiatus* "type", *sensu* Tiwari & Schaarschmidt, 1975; Pl. 3.16, figs. 12, 16 herein). In the present study, such specimens proved so few in numbers, or so sporadic in their distribution through the studied sequence that differentiation was deemed unjustified. Therefore, the somewhat subtle morphological disparities that exist between *Dibolisporites echinaceus* (Richardson, 1965) and the species of *Dibolisporites, sensu* Tiwari & Schaarschmidt (1975) are considered herein trivialities, and thus these four species considered junior synonyms of *D. echinaceus* (which assumes taxonomic priority). This potential synonymy was alluded to by McGregor & Camfield (1982, p. 38).

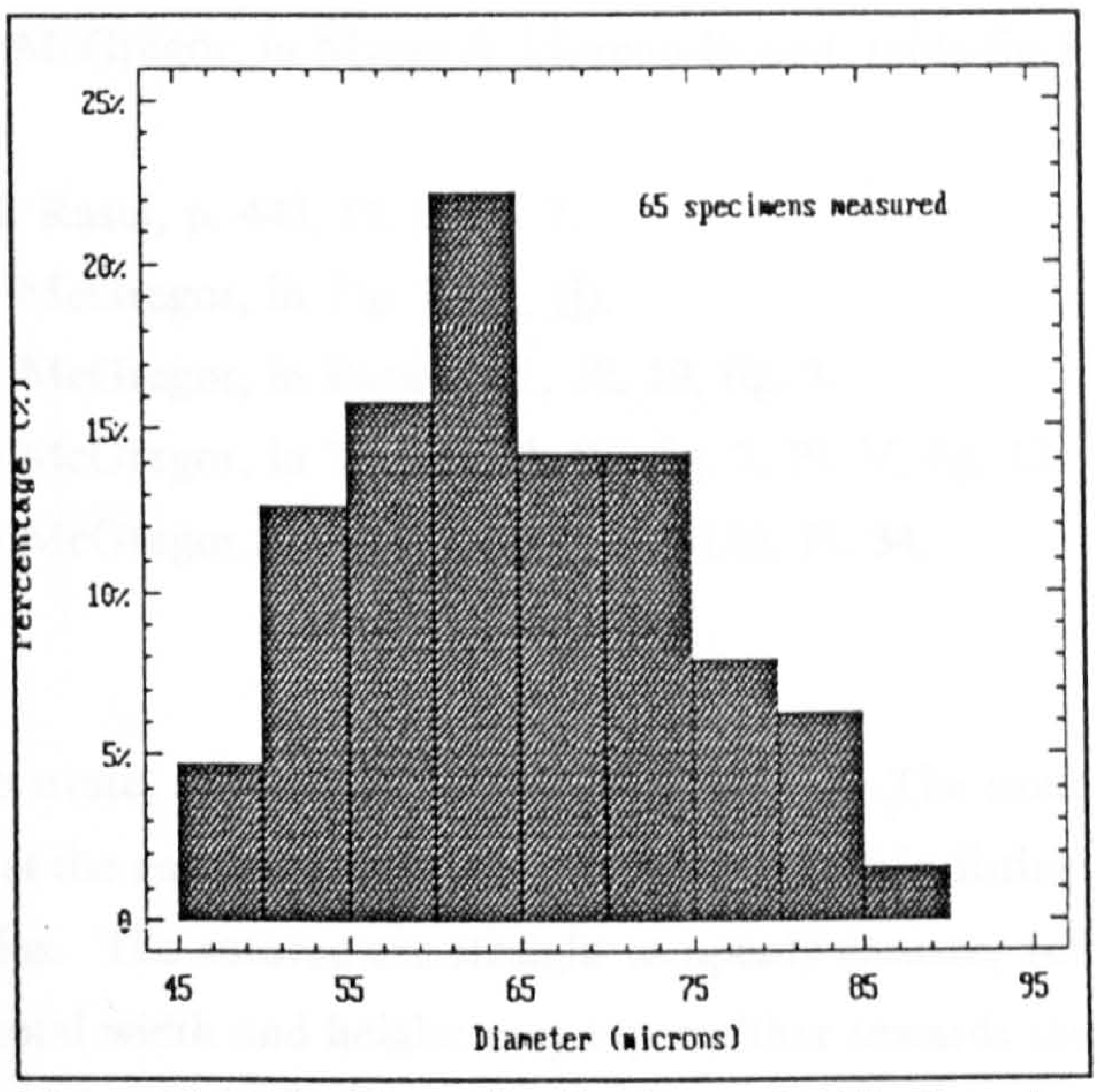

Figure 3.3.47: Size distribution of *Dibolisporites echinaceus* (Eisenack) Richardson (1965).

Comparisons. *Dibolisporites bullatus* is larger in diameter, and displays a consistently smaller sculpture. The sculpture of *D. eifeliensis* Lanninger (1968) and *D. ?eifeliensis* (of the present study) is more conate in form, with blunt or subtle bifurcate termini. *D. variverrucatus* Massa & Moreau-Benoit (1976) exhibits a demonstrably verrucate, biform ornament, and the sculpture of *D.* cf. *quebecensis* (of the present study) is smaller, and less pilate in form. *D. distinctus* (Clayton) Playford (1976) displays a very distinctive sculpture: elements tend to be notably elongate and scarce, with a truncated, blunted terminus, which in turn is surmounted by a delicate capitate spine.

Dibolisporites eifeliensis (Lanninger) McGregor

Plate 3.17, Figs. 2, 3.

1968 *Anapiculatisporites eifeliensis* Lanninger, p. 124, Pl. 22, fig. 11.

p 1972 *Anapiculatisporites* cf. *eifeliensis* Lanninger, in Kemp p. 113, fig. 9.

p 1973 *Dibolisporites eifeliensis* (Lanninger) McGregor, p.31, Pl. 3, figs. 20-22, 26 (only).

1976 *Dibolisporites eifeliensis* (Lanninger) McGregor, in McGregor & Camfield, p. 19, Pl. 4, fig. 21.

non 1976 *Dibolisporites eifeliensis* (Lanninger) McGregor, in Massa & Moreau-Benoit, table-fig.5, Pl. 4, fig. 5.

1978a ?*Dibolisporites* sp. C, Richardson & Rasul, p. 443, Pl. 3, fig. 7.

1982 *Dibolisporites eifeliensis* (Lanninger) McGregor, in Fig. 3, (i), (j).

1985 *Dibolisporites eifeliensis* (Lanninger) McGregor, in Paris *et al.*, Pl. 19, fig. 3.

1986 *Dibolisporites eifeliensis* (Lanninger) McGregor, in Turnau Pl. IV, fig. 2; Pl. V, fig. 13.

1989 *Dibolisporites eifeliensis* (Lanninger) McGregor, in Steemans, p. 127-128, Pl. 34, figs. 15-18.

Description. Trilete, acamerate miospores; amb ovate, subcircular to convex triangular. The exine is laevigate to finely scabrate, and ≤2.5μm thick at the equatorial margin. The trilete mark is distinct to diffuse, and extends 4/5 to 7/8 the spore radius. The suturae are straight to openly arcuate, and usually paralleled in part by labra, ≤3.25μm in total width and height: may taper either towards the equatorial margin, or conversely towards the proximal pole. The contact areas are laevigate to scabrate and may be delineated equatorially by distinct to diffuse curvaturate ridges: ≤1.75μm in maximum width. The proximo-equatorial and distal regions bear a predominance of broad based, biform coni and spinae, in association with simple coni, spinae and "slender" verrucae/bacula. The biform elements comprise a squat conate or spinose base, tapering to a blunted or slightly expanded bifurcate tip. The sculpture commonly ranges between ≤2.25μm and 3.75μm in height (rarely up to 6μm), and 2-2.5μm in basal diameter: the bifurcate terminations are ≤0.25-1.25μm in lateral width. Elements range from ≤1.5μm to 5.5μm in isolation (rarely greater than 6μm). Diminutive grana and rare coni, ≤0.5μm in dimensions, may be interspersed amongst the coarser elements. Compressional, concentric folds may distort the exine equatorially.

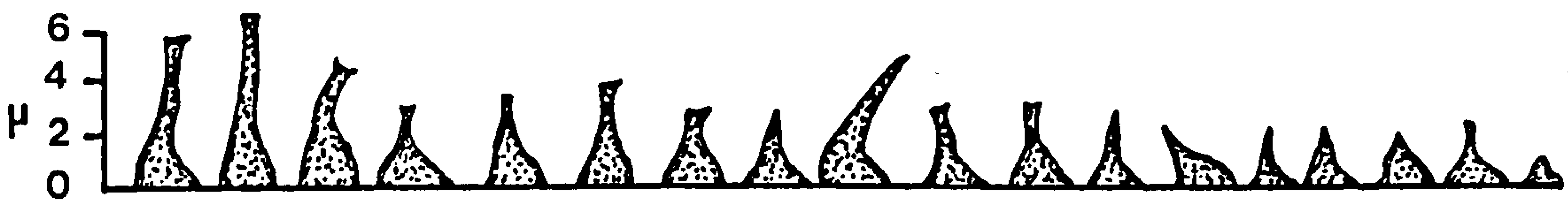

Figure 3.3.48: Sculptural variation upon *Dibolisporites eifeliensis*, lateral view.

Dimensions. Maximum spore diameter 31-63μm, mean 48μm (45 specimens measured).

Occurrence. LN; *abundant.* S; *common.* H, R, LH; *rare.* WP; *R.*

Remarks. McGregor (1973) does not mention the presence of curvaturae in his re-evaluation of *Dibolisporites eifeliensis.* However, the holotype illustration of Lanninger (1968; Pl. 22, fig. 11) clearly displays a proximo-equatorial "feature", interpreted in the present study as curvaturae perfectae. Consequently, specimens recovered from north Devon that display curvaturate ridges are considered more truly representative of *Dibolisporites eifeliensis.* Furthermore, within Lanninger's (1968) original circumscription of *Anapiculatisporites eifeliensis,* reference is made to the presence of tecta. McGregor (1973) later questioned whether in fact such tecta were merely exinal folds. From detailed personal observations, the original interpretation of "labra" as proposed by Lanninger (1968) is preferred. In general, specimens recorded from north Devon also display a sculpture more in keeping with the size specifications quoted by Lanninger (1968; 2-3μm in height), and not as elongate as described by McGregor (1973; 1-6μm in length).

The sculpture that adorns the holotype of *Apiculiretusispora cherata* Richardson & Lister (1969, Pl. 37, fig. 13, 14) is more elongate than *Dibolisporites eifeliensis,* although Richardson & Lister (1969) mention that elements are typically be 3-3.5μm in length. With subsequent re-evaluation, *A. cherata* may well prove homologous with *Dibolisporites eifeliensis* (Lanninger) McGregor (1973).

In the present study, specimens were nearly always documented in proximo-distal orientation. Complete tetrads were common within the Lynton Formation.

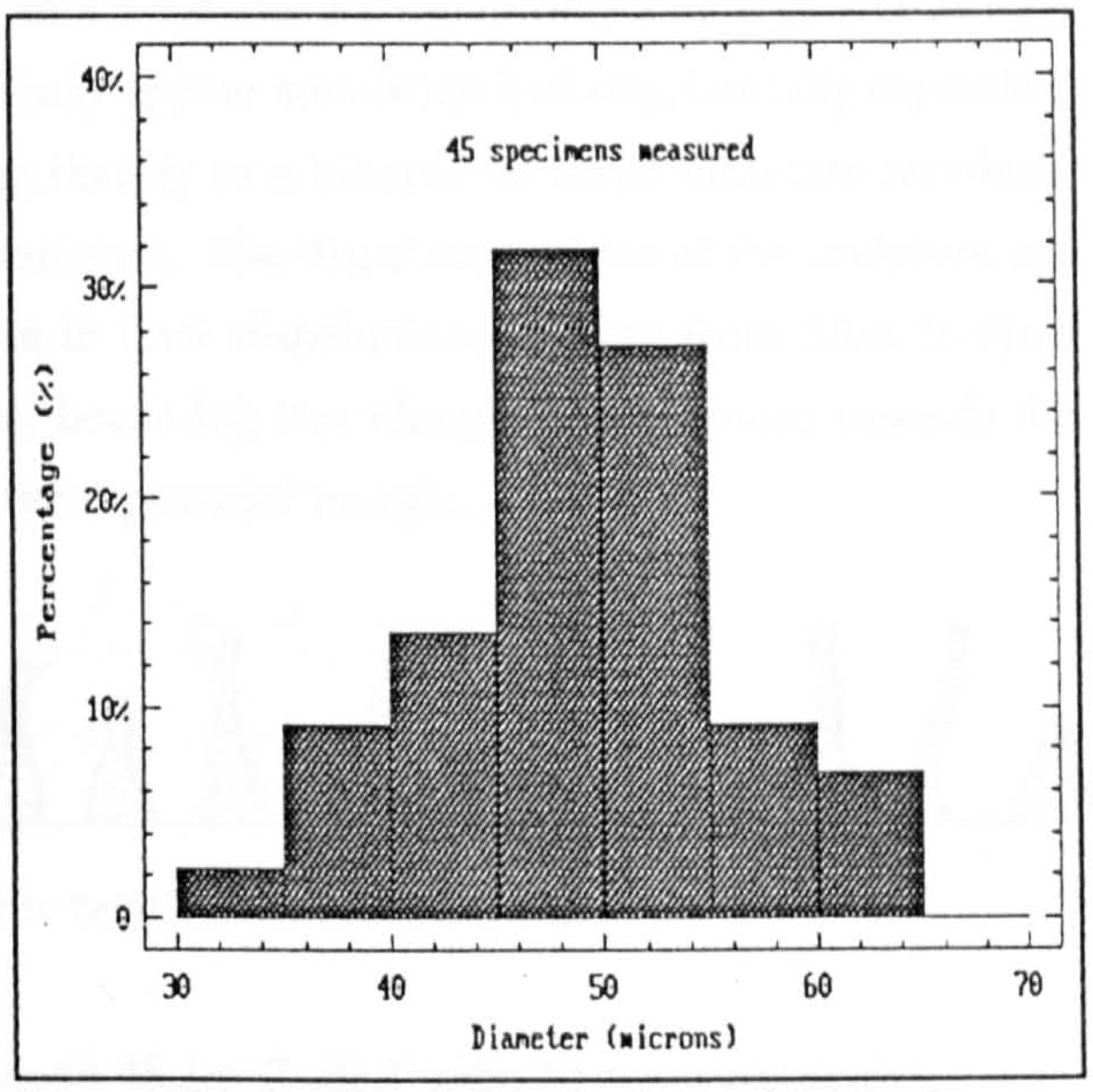

Figure 3.2.49: Size distribution of *Dibolisporites eifeliensis* (Lanninger) McGregor (1973).

Comparisons. *Dibolisporites eifeliensis* (Lanninger) McGregor (1973) differs from *D. ?eifeliensis* (of the present study) in its predominantly smaller, shorter, biform ornament, and the less pronounced, invaginated curvaturae. The ornamentation of *Dibolisporites wetteldorfensis* Lanninger (1968) is smaller and of different morphology. *Dibolisporites quebecensis* McGregor (1973, p. 32) is somewhat similar to *Dibolisporites eifeliensis,* but the sculpture is smaller, seemingly denser and lacks distinct, bifurcate to blunted terminations. McGregor & Camfield (1982, p. 14) compared *Dibolisporites eifeliensis* and *Anapiculatisporites petilus* Richardson (1965). The former species is somewhat thinner-walled (1-2μm thick) and commonly displays biform, blunted or bifurcate-tipped sculpture. (Note McGregor 1973, p. 31, for additional comparisons).

Dibolisporites ?eifeliensis (Lanninger) McGregor.

Plate 3.17, figs. 4-6.

? p 1973 *Dibolisporites eifeliensis* (Lanninger) McGregor, p.31, Pl. 3, figs. 17-19 (only).

Description. Trilete, acamerate miospores; amb broadly subtriangular to distinctly circular in polar view. The exine is laevigate to scabrate and ≤1-2.5μm thick at the equator. The suturae are straight, openly arcuate, and extend 3/4 to 7/8 the spore radius: may be simple or paralleled by labra, ≤2μm in total width. The exine bordering the suturae may also appear markedly thinned, ≤3.5μm in total width, or ruptured. The contact areas are delineated by prominent to perceptible, usually invaginated curvaturate ridges: inter-radially appear coincidental with, or distinct from, the spore circumference. The exine of the contact areas is thinner and "depressed", relative to the remainder of the spore coat. The proximo-equatorial and distal areas display a comparatively regular ornament comprising robust, elongate and discrete tubercles, bacula and/or blunted coni: typically 2.5-5.75μm in length (rarely up to 8μm), and $\leq$1.25-2.25μm in basal diameter. These elements are commonly 1 to 3.5 times as long as basal width. The basal portion of this sculpture may appear somewhat bulbous, laterally expanded, with the "shaft" simple, parallel-sided, or tapering sharply to a blunted or small bifurcate terminus: very rare, simple-attenuate, pointed termini are observed. The distal extremities of the sculpture are commonly $\leq$0.75μm in width. Elements are even in their distribution, ranging from 3μm to 9μm apart (rarely $\leq$2μm): evenly cover the distal pole, becoming less elongate and obvious towards the spore circumference. 14-31 elements project at the equatorial margin.

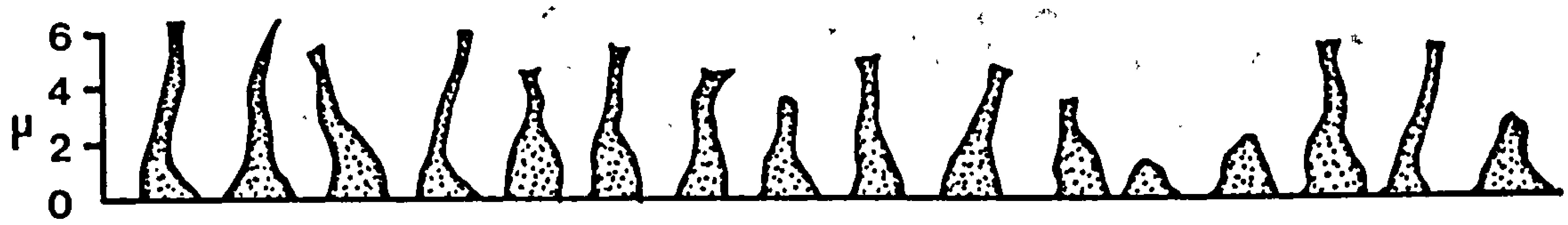

Figure 3.3.50: Sculptural elements of *Dibolisporites ?eifeliensis*, lateral view.

Diameter. Maximum spore diameter 35-63μm, mean 48μm (based upon 55 measurements).

Occurrence. LN; *common.* H; *rare.*

Remarks. Tetrads were common in the Lynton Formation (refer to Pl. 3.9, fig. 17 herein).

Comparisons. The Lower Devonian species *Apiculiretusispora cherata* Richardson & Lister (1969; p.219) compares favourably in overall spore size (30-46μm), and bears comparable, elongate, spinose sculptural elements (1-6μm in length), that appear predominantly blunted. Richardson & Lister (1969) remark that the sutures may be accompanied by labra, 1.5-2.5μm in height. The sculptural elements apparent upon the holotype specimen of *A. cherata* (figured by Richardson & Lister; Pl. 37, fig. 13-14) compare more favourably with the above form than with *Dibolisporites eifeliensis* Lanninger (McGregor) *sensu stricto.* However, *Dibolisporites ?eifeliensis* exhibits pronounced, usually invaginated curvaturae perfectae, and a somewhat sparser sculptural cover. *Dibolisporites eifeliensis* (Lanninger) McGregor (1973) differs in displaying a smaller, less elongate and denser sculpture, as well as less pronounced curvatural ridges. (also refer to the comparisons listed earlier, for *Dibolisporites eifeliensis*).

Dibolisporites cf. *quebecensis* McGregor
Plate 3.17, fig. 7.

cf. 1973 *Dibolisporites quebecensis* McGregor, p.32-33, Pl. 3, figs. 11, 14-16.
1976 *Dibolisporites eifeliensis* (Lanninger) McGregor, in Massa & Moreau-Benoit, table-fig.5, Pl. 4, fig. 5.

Description. Trilete acamerate miospores with a subcircular to convex triangular amb in polar view. The exine is laevigate to finely scabrate and rarely exceeds 1μm in thickness equatorially. The laesurae are distinct, straight, rarely openly arcuate, and extend 4/5 to 7/8 the spore radius; commonly terminated by diffuse curvaturae imperfectae (?perfectae may coincide inter-radially with the spore circumference). The suturae are paralleled by labra, ≤1.25-2.5μm in total width at the proximal pole, which taper slightly towards the equatorial margin. The contact areas lack pronounced sculpture: the exine appear slightly thinned. The proximo-equatorial and distal regions are sculptured with distinct, discrete biform coni, bacula and spinae, which in general are surmounted by a fine capitate, hair-like spine, or simply blunted (bifurcate): simple coarse grana are rare. The ornamentation may display a slightly bulbous base, and are ≤2.25μm in height, ≤1.5μm in basal diameter. Elements are regular, closely packed in their distribution: ≤0.5-1.75μm apart (rarely greater than 2.75μm).

Figure 3.3.51: Sculptural elements of *Dibolisporites* cf. *quebecensis*, lateral view.

Dimensions. Maximum spore diameter 48-59μm, mean 53μm (6 specimens measured).

Remarks. Forms of this morphological type recovered from north Devon differ to *Dibolisporites quebecensis*, *sensu stricto*, in displaying fewer baculate/verrucate elements, and instead a predominance of spinose sculpture. Furthermore, *D.* cf. *quebecensis* (herein) lacks a thickened proximal exine and also displays faint curvaturate ridges.

The diminutive biform elements were often difficult to resolve.

Comparisons. *Dibolisporites* cf. *quebecensis, sensu* McGregor & Camfield (1976) is thicker walled (up to 5μm) and may display ±pronounced curvaturae, 1-2μm in width and height. *D. eifeliensis* and *D. ?eifeliensis* (of the present study) have a propensity for larger, well defined, blunted or bifurcate tipped ornament. *Dibolisporites wetteldorfensis* Lanninger (1968) is slightly smaller in overall diameter (≈45μm). The sculpture of *Dibolisporites wetteldorfensis* Lanninger (1968) *sensu* McGregor (1973, p. 31-32) appears somewhat less bulbous, and comprises more elongate, irregular-spinose elements. *Dibolisporites variegatus* McGregor (1973, p. 33) is larger (61-102μm) and bears irregular, convolute biform verrucae, ≤2.5μm. *Apiculatisporis maculosus* (Knox) Moreau-Benoit (1979, p. 31-32, Pl. 3, fig. 5) is similar in overall morphology, but larger and bears a coarser ornament.

?Cymbosporites sp. (the present study) bears a superficial resemblance to this form, but displays coarser sculpture and appears equatorially ?thickened.

Dibolisporites variverrucatus Massa & Moreau-Benoit
Plate 3.17, figs. 9, 12.

1973 *Verrucosisporites ?polygonalis* Lanninger in McGregor, p. 37-38, Pl. 4, figs. 16,17,19,25,26.
1976 *Dibolisporites variverrucatus* Massa & Moreau-Benoit, table-fig. 5, Pl. 1, fig. 12.
1978a *?Verrucosisporites polygonalis* Lanninger, in Richardson & Rasul, p. 444-445, Pl. 2, fig.9.
1979 *Dibolisporites variverrucatus* Massa & Moreau-Benoit, in Moreau-Benoit, p. 34-35, Pl. 3, fig. 8,; Pl. 14, fig. 1

Description. Trilete acamerate miospores; amb circular to convex-triangular. The exine is ≤3μm thick equatorially, somewhat thinner (≤?1μm) proximally. The suturae are distinct to diffuse, straight and extend 4/5 to the full radius of the spore; obscured by thickened labra, ≤4μm in width, and occasionally terminated by curvaturae imperfectae. The proximo-equatorial and distal surface display an even to dense sculpture that comprises bulbous verrucae, with rare bacula and broad based coni: ≤2.5μm in height and ≤2-3.75μm in basal diameter. These primary elements are surmounted by a diminutive, hair-like (ciliate) capitate spine or grana, ≤0.25-0.75μm in length. Elements are typically ≤0.25-1.5μm apart, rarely exceeding 2μm: the sculpture may appear so dense that the exine seems pseudoreticulate. The contact areas are laevigate, scabrate or granulose, or display a sculpture comparable to remainder of the exine, but is somewhat sparser and smaller.

Figure 3.3.52: Sculptural elements of *Dibolisporites variverrucatus,* lateral view.

Dimensions. 54-67μm, mean 62μm (12 specimens measured).

Occurrence. LN; *rare.* S; *R.*

Remarks. The size specifications and sketches of the sculpture provided by Moreau-Benoit (1979, p. 34-35; 1980, Pl. 14, fig. 1) for *Dibolisporites variverrucatus* are marginally greater (3-4μm height) and more elongate than was noted in the present study. However, the paratype illustration (Moreau-Benoit, 1979; Pl. 3, fig. 8) is identical to the specimens recovered from north Devon. Therefore, any disparity in the dimensions of the sculpture is herein believed to reflect natural variation within this species population.

Comparisons. This species differs from all other forms of *Dibolisporites* by the predominance of verrucate sculpture. *Verrucosisporites polygonalis* is morphologically similar, but lacks biform elements. *Acinosporites acanthomammillatus* Richardson (1965) displays a predominance of verrucate elements, that fuse defining an irregular, murornate sculpture.

Dibolisporites sp. A var. A
Plate 3.17, figs.10, 11, 13, 15.

Description. ?Alete and trilete, acamerate miospores; circular to subcircular amb. The exine is laevigate to finely scabrate, ≤0.5-1.25μm thick equatorially. The suturae are distinct to indistinguishable, straight to irregular along their length, and simple: typically extend 1/2 to 3/4 the spore radius. The "contact areas" lack pronounced sculpture, displaying a ≈diffuse apical polumbra (covering *ca.*15-40% of the proximal surface) and are delineated equatorially by a distinct "rim". This feature (?curvature) is distinctly circular to subcircular in outline, ≤0.5-1.5μm wide, and displays a sharp inner (polar) margin with a diffuse outer (equatorial) edge: the suturae may transect this rim (induced through the ?compressional rupturing and propagation of the trilete rays). Proximo-equatorially and distally the exine bears discrete, slender, parallel-sided coni and spinae, which may either be marginally expanded at their base, or are simple, parallel-sided: display simple attenuate or bifurcate/blunted terminations. These elements are ≤1.25-2.5μm in height, ≤0.5-1.75μm in basal diameter and typically ≤1.5-3.5μm (rarely up to 6μm) in isolation.

Figure 3.3.53: Sculptural elements of *Dibolisporites* sp. A var. A, lateral elevation.

Dimensions. Maximum spore diameter 40-61μm, mean 53μm (20 specimens measured).

Occurrence. S, WP; *common*. LH; *rare*.

Remarks. The suturae are commonly rupture irregularly, and the exine of the "contact areas" may be partially missing: the ornament is also often poorly preserved, with only remnant "stubbles" visible, ≤0.75μm in size. Occasionally, the trilete rays are imperceptible (?alete). Specimens are rarely preserved in off-polar orientation, and the exine is only occasionally distorted by concentric folds.

Two varietal forms of *Dibolisporites* sp. A were distinguished, based somewhat subjectively upon differential haptotypic characteristics. These two forms may simply reflect different growth stages (maturity) of the same species of dispersed spore, reflected by the development of the laesurae and curvaturae.

Comparisons. The predominance of biform sculpture (bifurcate or blunted terminations) confirms affiliation with *Dibolisporites*. *Dibolisporites quebecensis* McGregor (1973) and *D. wetteldorfensis* Lanninger (1968) display markedly different sculpture. *Gneudnaspora* sp. of Balme (1988; p. 125, Pl. 3, fig. 15) is comparable in gross morphology, but is larger (82μm), displays a thicker exine (2-3μm) and lacks such pronounced, demonstrably biform sculpture. The mean size of *Dibolisporites turriculatus* Balme (1988; p. 128, Pl. 5, figs. 10-14) is slightly larger (mean = 71μm), forms displaying distinct laesurae with occasional, incipient curvaturae: the terminations to the sculpture of *D. turriculatus* are spheroidal, ≤1μm in diameter.

Dibolisporites sp. A var. B (of the present study) is similar but displays pronounced laesurae and well defined curvaturae perfectae.

Dibolisporites sp. A var. B

Plate 3.17, figs. 14, 16.

Description. Trilete, acamerate miospores; amb subcircular to convex triangular. The exine is ≤0.75-1.25μm thick, laevigate to finely scabrate and "robust". The suturae are distinct, straight to openly arcuate and extend 4/5 to 7/8 the spore radius: are paralleled by distinct, in part flexuous labra ≤0.5-2.25μm wide at the proximal pole, which thicken equatorially to ≤3.5μm. The contact areas are unsculptured, and are bordered equatorially by distinct, well defined curvaturae perfectae, ≤1-1.75μm thick: may coincide inter-radially with the spore circumference. Proximo-equatorially and distally the exine is evenly sculptured with discrete, slender, attenuate coni or spinae, with rare grana: elements ≤2.5μm in height and ≤1.25μm in basal diameter, and distally may exhibit a blunted, triangular terminus. Sculptural elements are 1.75-4.5μm apart, rarely up to 7μm.

Figure 3.3.54: Sculptural elements of *Dibolisporites* sp. A var. B, lateral elevation.

Dimensions. 41-57μm, mean 52μm (10 specimens measured).

Occurrence. S; *rare.*

Remarks. The laesurae and curvaturae are well developed, and the suturae rarely ruptured.

Comparisons. *Dibolisporites turriculatus* Balme (1988; p. 128, Pl. 5, figs. 10-14) is similar in size (although ranges up to 87μm in diameter), but lacks curvaturate ridges, and bears spheroidal terminations to the ornament. The exine parallel to the laesurae also appears somewhat thinned. *Dibolisporites* sp. A var. A (the present study) is similar but haptotypic features are indistinct.

Refer to *Dibolisporites* sp. A var. A for additional comparisons.

Genus *Dictyotriletes* (Naumova) ex. Potonié & Kremp emend. Ravn, 1986.

Type species. *Dictyotriletes bireticulatus* (Ibrahim) ex. Potonié & Kremp emend. Smith & Butterworth, 1967.

Discussion.

In the past the precise definition of *Dictyotriletes* and its relationship to morphologically similar forms, such as *Corbulispora* Bharadwaj & Venkatachala (1962), and *Reticulatisporites* Ibrahim emend. Potonié & Kremp (1954), has been relatively unclear. Playford & Satterthwait (1985, p. 138) and Ravn (1986, p. 61) critique past and current perceptions of this genus, as well as discussing homologies.

The original intent of Ibrahim (1933) in establishing *Reticulatisporites* was to circumscribe acingulate spores. Neves (1964, p. 1066) considered this plexus to be cingulate in construction: this interpretation was subsequently confirmed by Smith & Butterworth (1967, p. 220). Many subsequent workers (*inter alia*, Potonié, 1966; Playford, 1971; Urban 1971) however view any circumferential feature (darkened rim) as simply an equatorial expression of the reticulate sculpture. Potonié & Kremp (1954) believed that *Reticulatisporites* to be characterised by muri whose height were greater than their width. Peppers (1970), Playford & Satterthwait (1986) and later Ravn (1986) concurred with Potonié & Kremp (1954) in differentiating *Dictyotriletes* from *Reticulatisporites,* based on the relative heights of the sculpture (the former displays subdued sculptural elements, and the latter elevated, strongly projecting muri). Ravn (1986, p. 90) emended the generic diagnosis of *Dictyotriletes,* restricting the concept of this plexus to spores with a reticulum confined to the distal surface.

In comparison, *Corbulispora* Bharadwaj & Venkatachala (1962, p. 24) is similar in construction to *Dictyotriletes,* but differs in possessing strongly lipped laesurae. *Microreticulatisporites* Knox emend. Potonié & Kremp (1954) is applied by Higgs *et al.* (1988, p. 64-65) in the sense of Potonié & Kremp (1954) and not Bharadwaj (1955), circumscribing reticulate-sculptured spores, whose individual lumina are ≤6μm in diameter. *Bascaudaspora* Owens (1983) circumscribes acamerate, cingulate and reticulate spores.

Clearly *Dictyotriletes* forms the intermediate member in the intergradational complex of reticulate-sculptured spores (*Microreticulatisporites-Dictyotriletes-Reticulatisporites*), which are differentiated, albeit subjectively, largely the dimensions of the lumina. In practice, it is less easy to distinguish between these generic categories.

The *Lumina Index* (LmI), a parameter analogous to the *Rugulae Index* (*sensu* Playford & Satterthwait, 1985; refer to the *Convolutispora* complex described therein), was devised to quantify and thus convey the number of lumina apparent upon species of *Dictyotriletes;* this index may also be applied to acritarchs, *e.g Dictyotidium*. This inequality is defined as the number of complete lumina that intersect a line broadly bisecting the distal hemisphere of a palynomorph: excludes incomplete lumina located at the periphery of the specimen.

?*Dictyotriletes* sp. A

Plate 3.17, figs. 17, 18.

p 1989 *Brochotriletes ?foveolatus* Naumova, in Steemans, p. 108-109, Pl.24, fig. 16; Pl.25, ?fig. 2.

Description. Trilete acamerate miospores; amb convex triangular to ovate. The exine is scabrate to finely granulose, and thickened equatorially; ≤4.75μm. The trilete rays are indistinct, simple, and straight or tightly sinuous: the suturae are commonly ruptured and extend 4/5 to 7/8 the spore radius. The proximal surface lacks pronounced sculpture: the exine appears somewhat thinned (≤1μm thick). The distal surface displays a well defined, ≈uniform, regular, and coarse reticulum: muri are ≤2.5μm in height and 2.75-5.25μm in width (rarely narrower). In lateral profile the muri are rounded to subangular. The muri enclose well defined lumina, which in general are imperforate (not a consistent feature), rounded polygonal to subcircular in outline and range in diameter from 3.75μm to 9μm. The muri may project slightly at the equator.

LmI = 4-5.

Dimensions. 54-67μm, mean 58μm (6 specimens measured).

Occurrence. S, LH; ?*R*.

Remarks. The recognition and differentiation of *Brochotriletes* from *Dictyotriletes* is occasionally difficult to resolve: depends largely upon whether the lumina are perforate or imperforate. In the above case, the majority of lumina appear to be imperforate, although this was not always easy to confirm. Indeed, the general morphology of ?*Dictyotriletes* sp. A (herein) resembles a number of forms which in the literature have been attributed to the genus *Brochotriletes* (*e.g* refer to Steemans, 1989). For these reasons uncertainty is expressed as to the generic identity of the above morphotype.

Comparisons. *Dictyotriletes emsiensis* (Allen) McGregor (1973) bears an exine of comparable thickness and muri of similar width, but the sculptural elements are much higher (3-8μm), and individual lumina far greater in diameter (8-20μm). *Dictyotriletes subgranifer* McGregor (1973) displays thinner muri that are "beaded" along their upper edge. *Dictyotriletes ?gorgoneus* Cramer, *sensu* McGregor (1973, p.43) is smaller (14-31μm). The sculptural morphology of *Brochotriletes* sp. A *sensu* McGregor (1973; p. 40-41, Pl. 5, figs. 2, 3) is similar, but this form bears lumina that range up to 19μm in diameter, and ≤6μm in depth: *Brochotriletes* sp. A of McGregor (1973) is also larger in size (60-90μm).

Dictyotriletes sp. B

Plate 3.17, fig. 19.

Description. Trilete, acamerate miospores; amb irregular subcircular to convex triangular. The exine is ≤2μm thick, and laevigate to sparsely granulose. The suturae are ≈distinct, straight to openly arcuate and extend 4/5 to 7/8 the spore radius; are bordered by diffuse labra, ≤2.25μm in total thickness. The proximal surface lacks murornate sculpture, and may display isolated grana which are ≤1.25μm in diameter. The distal surface bears a distinct sculpture that comprises an imperfect reticulum and granulose elements. The lumina are incomplete: the muri ≤1-2.25μm in width and ≤1.5μm in height and conate in profile. The lumina are ≈4-7μm in overall diameter. Sparse grana adorn the exine within these lumina: these subordinate elements are ≤1.75μm in diameter.

LmI = 3-5.

Dimensions. 42-51μm, mean 46μm (4 specimens measured).

Occurrence. K; *very rare.*

Remarks. The exine is compressionally thickened at the spore equator, and may range up to 7.25μm in width. This feature does not represent a "primary" equatorial crassitude, or patina.

Comparisons. *"Reticulatisporites" emsiensis* Allen in Lanninger (1968; Pl. 23, fig. 4) appears somewhat similar in morphology, but the lumina are more regular and complete. *Dictyotriletes subgranifer* McGregor (1973) bears higher muri which display "beaded" extremities. Furthermore, the lumina of *Dictyotriletes subgranifer* McGregor (1973) are broader, ranging up to 15μm in diameter, and notably more "complete".

Genus *Emphanisporites* McGregor, 1961.

Type species. *Emphanisporites rotatus* McGregor, 1961.

Synonymy.

1962 *Radforthia* Winslow, p. 62.

1968 *Emphanizonotriletes* Schultz, p. 30.

refer to McGregor (1973, p. 44) for additional synonymies.

Discussion.

Well defined radial "ribs" on the proximal hemisphere, concentric about the proximal pole, are diagnostic of this plexus (McGregor 1961, p.3). McGregor (1961, 1973) describes these elements as radial "spoke-like" thickened ribs of exine, whereas Allen (1965) refers to them as exinal folds or wrinkles ("muroid folds"). These terms are synonymous, relating to the same morphological attribute.

McGregor (1973, p. 44-45) remarked that some species of *Emphanisporites* display an equatorial thickening, but regarded such "cingulum" development as insignificant in generic differentiation. Consequently, *Emphanizonotriletes* (Schultz 1968, p. 150) was placed in synonymy with *Emphanisporites.*

In contrast to *Costaspora* (Staplin & Jansonius) Staplin (1960), the ribs of *Emphanisporites* extend both radially and inter-radially. McGregor (1973, p. 44) tentatively placed *Radiaspora* (Hoffmeister, Staplin & Malloy) ex. Balme (1962) in synonymy with *Emphanisporites*, although the former was originally conceived for spores that display a distal rather than proximal ribbed-sculpture.

Emphanisporites annulatus McGregor
Plate 3.17, fig. 20; Plate 3.18 figs. 1-8.

1961 *Emphanisporites annulatus* McGregor, p. 3-4, Pl. 1, figs. 5,6.
1963 *Emphanisporites erraticus* McGregor, in Chaloner, p. 103, 105, Fig. 1.
1963 *Emphanisporites rotatus* McGregor, in Chaloner, p. 103, Fig. 2.
1972 *Emphanisporites rotatus* McGregor, in Mortimer & Chaloner, p. 17, Pl. II, fig. 2.
1989a cf. *Radiaspora* Balme in Dean, Fig. 2 (j).
1989a *Emphanisporites annulatus* McGregor, in Dean, Fig. 2 (k).
Refer to McGregor (1973, p. 45) and Steemans (1989, p. 135-136) for additional synonymy.

Description. Trilete acamerate miospores; amb well rounded to convex subtriangular amb. The equatorial margin is smooth to strongly crenulate: the exine is laevigate to scabrate and 1.5μm-4.75μm thick at the equator. The trilete rays are distinct, straight to openly arcuate and extend 3/4 to the full radius of the spore: the suturae may appear simple, but are commonly obscured by pronounced and robust labra, $\leq$0.75-3.25μm in individual width. The proximal surface is sculptured with distinct ribs of variable morphology; typically three to seven (rarely ten) per contact area, which are radial about the proximal pole. Ribs range in width from $\leq$2μm to 4.75μm (rarely 6μm) at the equator, are parallel-sided, or irregular along their length, tapering gradually towards the proximal pole ($\leq$3.25μm in width). These sculptural elements usually become diffuse towards the proximal pole, extending $\approx$1/2 to the full spore radius. The distal surface displays a distinct to diffuse annulate exinal thickening, that may be incomplete and $\approx$eccentric about the distal pole. This annulus ranges in width from $\leq$3μm to 7.5μm, and may be situated $\leq$1/4-1/2 the spore radius from the circumference (rarely merges with the equatorial margin). Faint creases in the distal exine may be discernible, radial about the distal pole, and developed in sympathy with the annulus (preferentially on the equatorial side of this distal feature).

Dimensions. Maximum diameter 34-73μm, mean 48μm (65 specimens measured).

Occurrence. LN; *abundant.* H, S; *common.* R, LH, WP, L; *rare.* CM, K; *R.*

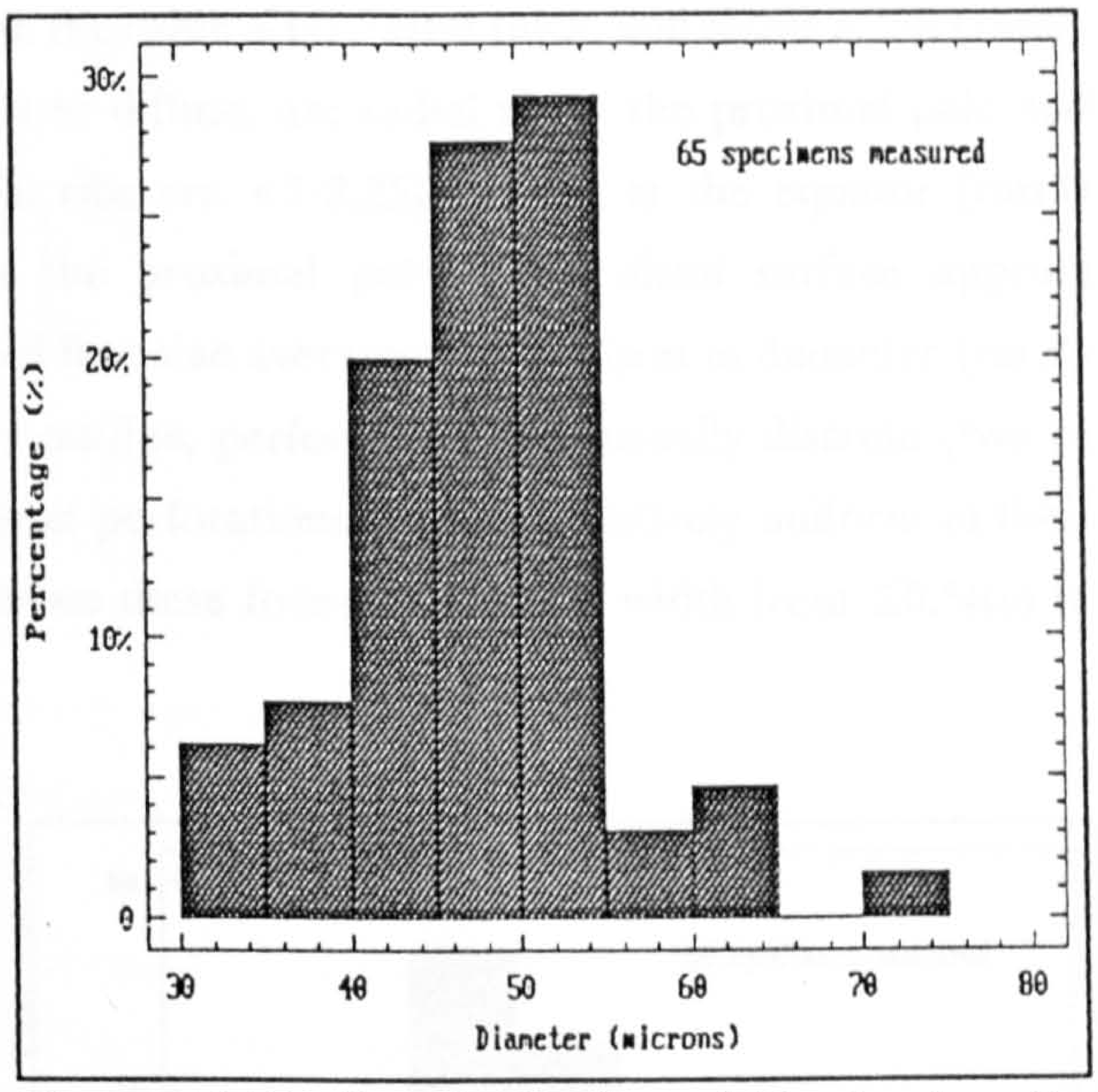

Figure 3.3.55: Size distribution of *Emphanisporites annulatus* McGregor (1961).

Remarks. Occasionally the exine at the equator appeared considerably thickened, resembling a "crassitude". In view of the emendation of McGregor (1973), such a feature is still considered within the circumscription of *Emphanisporites.* Distal creases of the exine are usually indistinct in transmitted light microscopy, but readily discernible under the S.E.M (refer to Pl. 3.18, fig. 7 herein). Dean (1989a, Fig. 2(j,k)) illustrates forms which display a more homogeneous distal surface.

Note: thick walled specimens of *Emphanisporites annulatus* recovered from north Devon and analysed using the S.E.M. were identical in form to those identified by Dean (1989) as cf. *Radiaspora* Balme.

A faint distal annulus may just be resolved upon the degraded specimen of *Emphanisporites rotatus* McGregor, figured by Mortimer & Chaloner (1972).

Comparisons. *Emphanisporites erraticus* McGregor (1961) resembles *E. annulatus*, but differs in the arrangement of the proximal ribbing, as well as displaying a proximal annulus. For *E. erraticus,* the ribbing tends to converge to a point situated well upon each contact face, from both the equatorial margin and proximal polar region, thus resembling a "rosette". *Emphanisporites rotatus* (McGregor) McGregor (1973) is similar in gross morphology, but lacks a distal annulus. *Emphanisporites splendens* Richardson & Ioannides (1979) displays a proximal annulate thickening.

Emphanisporites foveolatus Schultz

Plate 3.18, figs. 10-12.

1968 *Emphanisporites foveolatus* Schultz, p. 21, Pl. 3, figs. 11, 11a.

1968 *Emphanisporites foveolatus* Schultz, in Lanninger, p. 135, Pl. 23. fig. 13.

1968 *Emphanisporites foveolatus* Schultz var. *macrocostatus* Lanninger, p.135-136, Pl. 23, fig.14.

1983 *Emphanisporites foveolatus* Schultz, in Schweitzer Pl. 1, figs. 12, 13.

1986 *Emphanisporites foveolatus* Schultz, in Turnau, Pl. VI, fig. 7.

1989 *Emphanisporites foveolatus* Schultz, in Steemans p. 138, Pl. 38, figs. 1-2.

Description. Trilete acamerate miospores; amb circular to irregular convex triangular. The equatorial margin is smooth to undulose. The suturae are straight to openly arcuate, non-curvaturate, and extend 3/4 to 7/8 the spore radius, appearing either simple or conversely paralleled by exinal "thickenings", ≤1-2.75μm in total width. The exine is laevigate to scabrate, and ≤1-4μm thick equatorially. The proximal surface is imperforate: the exine ≤1-1.75μm thick, and displays 5-8 (rarely 11) ribs per contact area. These ribs are distinct to diffuse, are radial about the proximal pole and extend <1/2 to 2/3 the spore radius: individual ribs are <1-2.25μm thick at the equator (rarely exceed 3μm), parallel-sided or taper towards the proximal pole. The distal surface appears "pseudoreticulate", or densely foveolate: individual foveolae average ≤1.5-3.75μm in diameter (rarely exceed 4μm), appear circular to sub-elliptical in outline, perforate and are usually discrete (two or three adjacent foveolae very rarely merge). These perforations are comparatively uniform in their distribution. The "muri" that isolate and thus define these foveolae range in width from ≤0.5μm to 3.25μm, rarely greater than 4μm.

Dimensions. Maximum spore diameter 38-72μm, mean 49μm (65 specimens measured).

Occurrence. LN; *common.* H; *rare.*

Remarks. The undulose equatorial margin of the spore reflects the encroachment of proximal ribbing and distal foveolation on the spore margin. Occasionally, the foveolae were either noted to be slightly enlarged towards the distal pole, or in very rare cases the foveolation over the polar region appeared markedly reduced (≤0.5μm in diameter). The suturae were very occasionally ruptured and gaping at the proximal pole.

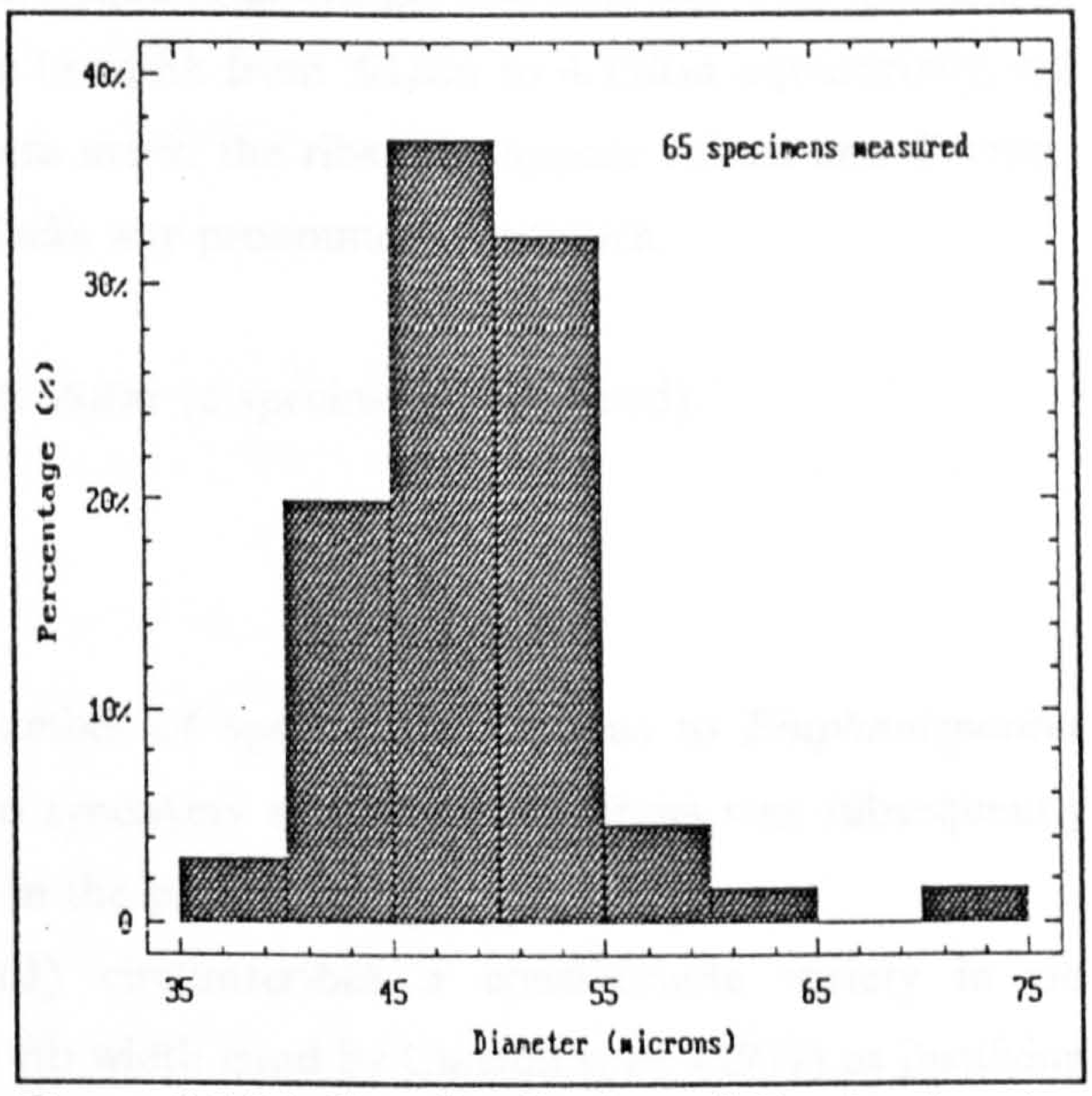

Figure 3.3.56: Size distribution of *Emphanisporites foveolatus* Schultz (1968).

Comparisons. The distal foveolation is unique to this species within the *Emphanisporites* plexus.

Emphanisporites mcgregorii Cramer
Plate 3.18, figs. 14-16.

1961 *Emphanisporites* sp. in McGregor Pl. 1, fig. 12.

p 1962 *Radiaspora* sp. A, Balme, Pl. 1, fig. 12 (only).

1967 *Emphanisporites mcgregorii* Cramer, p. 263, Pl. III, fig. 59.

non 1968 *Emphanisporites macgregori* Schultz, p. 28, Pl. 3, figs. 12, 12a.

1968 *Emphanisporites spinaeformis* Schultz, p. 27, Pl. 3, figs. 10, 10a.

non 1968 *Emphanisporites macgregori* Schultz, in Lanninger p. 136, Pl. 23, figs. 15.

1968 *Emphanisporites spinaeformis* Schultz, in Lanninger, p. 138, Pl. 23, fig. 17.

1969 *Emphanisporites mcgregorii* Cramer, in Cramer, p. 432, Pl. 1, fig. 13.

1976 *Emphanisporites spinaeformis* Schultz,in Massa & Moreau-Benoit, Pl. 2, fig.14, table-fig.5

1977 *Emphanisporites hibernicus* Clayton, Higgs & Keegan p.420, Pl. 1, figs 10-15

1979 *Emphanisporites spinaeformis* Schultz, in Moreau-Benoit p. 56.

1986 *Emphanisporites spinaeformis* Schultz, in Turnau, Pl. VI, fig. 5.

1988 *Emphanisporites rotatus* McGregor, in Loboziak, Streel, & Burjack, Pl. III, fig. 16.

1989 *Emphanisporites mcgregorii* Cramer, in Steemans p. 138, Pl. 38, fig. 3-5.

Refer to Steemans (1989) for additional synonymies.

Description. Trilete acamerate miospores; amb circular, convex triangular to triangular. The exine is laevigate to scabrate, and ≤1.75-4.75μm thick at the equator. The suturae are distinct, straight to openly arcuate, extending 4/5 to the full radius of the spore, and may either be bordered by thickened, robust labra (≤6.25μm in total width), or conversely appear simple, ±ruptured. On the proximal surface 5 to 12 ribs per inter-radial extend from the equatorial margin and intersect with the suturae (producing a "herringbone" pattern). Ribs range in width from ≤1μm to 4.75μm equatorially, are parallel-sided or taper gradually towards the trilete mark: the ribs may appear robust and discrete, or thin, flexuous and dense. The distal surface lacks any pronounced sculpture.

Dimensions. Maximum diameter 51-63μm, mean 56μm (6 specimens measured).

Occurrence. LN; *rare.*

Remarks. Subsequent to Cramer (1967), a number of species homologous to *Emphanisporites mcgregorii* Cramer have been proposed (refer to synonymy above). This plexus was subsequently rationalised by Steemans (1989), and confirmed in the present study.

Emphanisporites rotatus McGregor (1961) circumscribes a considerable variety in rib morphology. Therefore, the subtle difference in rib width cited by Clayton *et al.* (1977) as justifying the differentiation of *E. hibernicus* from *E. spinaeformis* Schultz is regarded herein as trivial. Both *E. spinaeformis* Schultz and *E. hibernicus* Clayton, Higgs & Keegan are thus considered junior synonyms of *E. mcgregorii* Cramer.

Comparisons. The proximal ribs of *E.rotatus* McGregor are radial about the proximal pole, and not orientated towards the laesurae, as apparent upon *E. mcgregorii.*

Emphanisporites pseudoerraticus Schultz

Plate 3.18, figs. 9, 13.

1968 *Emphanisporites pseudoerraticus* Schultz, p.29, Pl. 3, figs. 15, 15a.

1968 *Emphanisporites pseudoerraticus* Schultz, in Lanninger p. 138-139, Pl. 24, fig. 3.

Description. Trilete, acamerate miospores with a subtriangular, elliptical or circular amb in polar compression. The spore circumference is smooth to faintly undulose, with the exine laevigate to scabrate, and ≤2.25-4.75μm thick equatorially. The suturae are straight, ≈distinct, and simple or obscured by labra, ≤2.75μm in total thickness. The laesurae extend 7/8 to the full radius of the spore, and may terminated by curvaturae imperfectae. Inter-radially, 5-8 ribs extend from the equatorial margin, and converge to a single point upon each contact face (located ≤1/2 to 2/3 the spore radius from the proximal pole). The rib arrangement resembles an incomplete "rosette". The ribs are ≤1.5-4.25μm in width at the equator, parallel-sided or tapering to an acuminate point: ribs are discrete, ≤6μm apart at the spore circumference. The distal surface is unmodified, lacking sculpture.

Dimensions. Maximum diameter 47-58μm, mean 49μm (7 specimens measured).

Occurrence. LN, H; *rare.*

Remarks. McGregor (1973) regarded the "cingulate" genus *Emphanizonotriletes,* Schultz (1968) as a junior synonym of *Emphanisporites* McGregor (1961). Some specimens of *E. pseudoerraticus* recovered in the present study appear equatorially "thickened": following McGregor (1973) this is still within the circumscription of *Emphanisporites.*

Comparisons. *Emphanisporites schultzii* McGregor 1973 displays a complete rosette-like rib arrangement on each contact face. *E. erraticus* (Eisenack) McGregor 1961 bears a distal annulus.

Emphanisporites rotatus McGregor
Plate 3.18, figs. 17-21.

1961 *Emphanisporites rotatus* McGregor p.3, Pl.1, figs. 1,2,3,4.
1967 *Emphanisporites* cf. *rotatus* McGregor, in Mortimer, Pl. 1, fig. O.
1973 *Emphanisporites rotatus* McGregor p.46-47, Pl.6, figs. 9-13.
1989a *Emphanisporites rotatus* McGregor in Dean, Fig. 2, a, e, f.
1989a *Emphanisporites* cf. *rotatus* McGregor in Dean, Fig. 2, b.

For a more extensive synonymy refer to McGregor (1973, p.46-47), Balme (1988, p. 131) and Steemans (1989, p. 142).

Description. Trilete, acamerate miospores with a circular to convex triangular amb. The spore circumference is usually smooth, or undulose. The exine is laevigate to finely scabrate and ≤1.75-6.5μm thick at the equator. The suturae are distinct, straight to openly arcuate and extend 3/4 to the full radius of the spore: may appear simple, ruptured or obscured by distinct, robust labra, ≤0.75-4μm in individual thickness. Labra may thicken equatorially (up to 12μm in total width). The proximal surface displays a distinct, ribbed sculpture, with 3-7 ribs (per contact face) radial about the proximal pole. Within this species population, the dimensions and radial extent of the proximal ribbing proved highly variable: in general ≈constant in morphology on one individual specimen. Equatorially, ribs are typically 2.5-5μm in thickness (rarely ≤1.5μm), parallel-sided or tapering gradually towards the proximal pole: extending ≈2/3 to the entire spore radius. The distal hemisphere appears simple, unsculptured.

Dimensions. Maximum diameter 34-71μm, mean 58μm (32 specimens measured).

Occurrence. LN; *abundant.* H, S; *common.* R, LH, WP, L, CM; *rare.* K; *R.*

Remarks. Traditionally, any subtle variation in rib morphology (the most basic of *Emphanisporites* attributes) was considered justifiable grounds for speciation within this complex of simple, unmodified forms of *Emphanisporites.* McGregor (1973) consequently rationalised this plexus, and recognised that a number of taxa were homologous in basic design with that of *E. rotatus*. Thus, a broad concept of *E. rotatus* was recognised and applied in the present study.

Some specimens lack continuous, prominent ribbing over the entire proximal surface (*e.g.* Pl. 3.18, fig. 19 herein): such a feature was still considered to be within the emended circumscription of *E. rotatus.*

Comparisons. The simplistic, proximal, ribbed sculpture, and featureless distal hemisphere distinguishes *E. rotatus* from all other species of *Emphanisporites.*

Emphanisporites schultzii McGregor
Plate 3.18, fig. 22.

1968 *Emphanisporites macgregori* Schultz, p. 28, Pl. 3, figs. 12, 12a.
1968 *Emphanisporites macgregori* Schultz, in Lanninger p. 136, Pl. 23, figs. 15.
1973 *Emphanisporites schultzii* (al. *macgregori*) new name, McGregor, p.48, Pl. 6, fig.14.
1976 *Emphanisporites schultzii* McGregor, in McGregor & Camfield p. 23, Pl. 5, fig. 7.
1989a *Emphanisporites schultzii* McGregor, in Dean, Fig. 2 (c).
1989 *Emphanisporites schultzii* McGregor, in Steemans, p. 142-143, Pl. 39, figs. 7-9.

Description. Trilete, acamerate miospores with a circular to convex triangular amb. The exine is laevigate to finely scabrate, and up to $\leq 4.5\mu m$ thick at the equatorial margin. The suturae are distinct, straight, simple or irregularly labrate ($\leq 1.5\mu m$ in total width). The laesurae extend 4/5 to the full radius of the spore. Each contact area displays a distinct ribbed sculpture, which collectively are arranged resembling a "rosette", centred on a point 1/2 to 1/3 the spore radius from the proximal pole. Each "rosette" is complete, and comprises between 13 to 16 individual, fine ribs, which range from $\leq 1\mu m$ to $2.5\mu m$ in width at the "rosette" periphery, and taper towards the centre. Ribs are of variable length, depending upon the centricity of the rosette upon each contact face. The distal hemisphere lacks sculpture.

Dimensions. Maximum spore diameter 41-53μm, mean 49μm (4 specimens measured).

Occurrence. LN; very rare.

Remarks. The ribbing directed away from the proximal pole towards the centre of the "rosette" may occasionally appear indistinct, and difficult to resolve in transmitted light microscopy.

Comparisons. *Emphanisporites pseudoerraticus* lacks ribbing directed away from the proximal pole:

the ribbed-"rosettes" appear incomplete. *E. erraticus* exhibits a distal annulus.

Emphanisporites sp. A
Plate 3,18, figs. 23, 24.

Description. Trilete, acamerate miospores; amb circular to convex triangular. The exine is ≤2-3.75μm thick equatorially, and laevigate to finely scabrate. The suturae are simple, straight, extending 1/2 to 4/5 the spore radius, and usually ruptured at the proximal pole: the laesurae are commonly terminated equatorially by curvaturae imperfectae. The proximal surface displays discernible to diffuse ribs, 7-9 per contact area, and radial about the proximal pole. These ribs are ≤3.25μm wide, are usually ≤2μm apart and rarely extend to the equatorial margin. The distal surface displays a distinct to diffuse, comparatively uniform annulus, ≤3.5-5.5μm in width. This feature may be slightly eccentric relative to the distal pole.

Dimensions. 49-58μm, mean 54μm (8 specimens measured).

Occurrence S, LH; rare.

Comparisons. *Emphanisporites annulatus* McGregor (1961) and *E. erraticus* (Eisenack) McGregor (1961) bear the greatest resemblance to *Emphanisporites* sp. A (of the present study), in displaying proximal ribbing and a distal annulus. However, for the two former species, the ribbing commonly extends to the equatorial margin. In the case of *E. erraticus* (Eisenack) McGregor (1961), the ribs also resemble "rosettes", centred upon the contact faces. *Emphanisporites splendens* Richardson & Ioannides (1979) displays a proximal annulus, and a more "complete" ribbed sculpture over the proximal surface.

Genus *Geminospora* Balme emend. Owens, 1971.

Type species: *Geminospora lemurata* Balme 1962.

Discussion.

In defining *Geminospora*, Balme (1962, p. 4-5) remarked that the genus circumscribes not only demonstrably camerate spores, but also those with barely discernible intexinal bodies (mesosporoids). Balme also noted that forms attributed to this plexus display an exoexinal sculpture comprising closely packed grana, short cones and infrabacula, as well as a differential thickening to the exoexine; being more appreciable over the distal hemisphere than the proximal surface. Balme (1962) remarked upon the comparability of *Geminospora* with *Archaeozonotriletes* Naumova (1953). Allen (1965, p. 695) subsequently clarified that the disparity in wall thickness between the proximal and distal hemispheres of *Geminospora* was not sufficient to represent a true patina (*e.g.* as with *Cymbosporites*).

Based upon material documented from the Canadian Arctic Archipelago, Owens (1971, p. 59-60) broadened the circumscription of *Geminospora* to accommodate a far greater diversity in exoexinal sculpture. This re-evaluation was prompted largely by the restriction of *Archaeozonotriletes* Naumova (1953) to acavate, patinate spores, following a re-appraisal of the morphology of the genotype, *Archaeozonotriletes variabilis* Naumova (1953), by Allen (1965, p. 721) : Allen in fact followed the proposal of Potonié (1958, p. 28). Owens (1971) considered that a number of Russian species subsequently displaced from the restricted concept of *Archaeozonotriletes* (Naumova) Allen (1965) exhibited the same basic construction as *Geminospora* Balme (1962), merely differing in exoexinal sculpture. Therefore, Owens (1971, p. 59) expanded the concept of *Geminospora* to allow for a wider range in exinal ornament, including grana, coni, verrucae and spinae.

Allen (1980) and McGregor & Camfield (1982, p. 39-40) remarked upon the palaeobotanical significance of geminospores: the latter authors also clarified which practical and realistic criteria allow distinction of *Geminospora* from other "affiliated" camerate genera. McGregor & Camfield (1982) reaffirmed that *Geminospora* differs to *Grandispora* in displaying a comparatively thickened exoexine relative to a thinned intexinal body, and from *Cymbosporites* by the absence of a patina. McGregor & Camfield (1982, p. 41) acknowledged the rather tenuous morphological criteria used in differentiating *Geminospora* from *Rhabdosporites*, and illustrate this point in proposing a new combination of *Geminospora micropaxilla* (Owens) McGregor & Camfield (1982), which was based in part upon the population of *Rhabdosporites micropaxillus* originally described by Owens (1971).

The following year, Playford (1983, p. 311-325) re-evaluated the *Geminospora* plexus, and was critical of Owens (1971) for broadening the concept of this genus to accommodate such considerable variety in exinal sculpture. Playford (1983, p. 312, 315) favoured a more restricted generic concept for *Geminospora*, as he believed was the original intention of Balme (1962). In restating the generic diagnosis Playford (1983) describes the sculpture to comprise short, mostly pointed elements (minute coni and spinae) and/or grana, and considers that a number of forms accommodated within the expanded circumscription of this genus, *sensu* Owens (1971), should be re-allocated to other genera of similar or allied construction. Playford illustrates this point with *Geminospora boleta* Higgs & Russell (1981; p. 31, Pl. 2, figs. 13-16, text-fig. 6B), which he believes may require the establishment of a new (?monospecific) generic repository.

Playford (1983, p. 315) also catalogues practical criteria that allows the distinction of *Geminospora* from other pseudosaccate genera. Playford (1983) applies the concept of *Rhabdosporites* Richardson *sensu* McGregor & Camfield (1982, p. 59), and considers this plexus to display a thin exoexine as well as a predominantly baculate sculpture. Playford lists the salient features of *Grandispora* Hoffmeister, Staplin & Malloy emend. Neves & Owens (1966) as including an intexine and exoexine of comparable thickness, which are more markedly and consistently separated. Furthermore, the exoexine of *Grandispora* does not, in general, tend to overtly thicken equatorially. *Spelaeotriletes* (Neves & Owens 1966) displays a more coarsely and diversely sculptured exoexine, with a discrete and barely discernible intexinal body (note also Playford & Powis 1979, p. 385-388). *Retispora* Staplin (1960) exhibits a reticulate to foveolate-vermiculate exoexine over the distal surface. Playford (1983) reaffirms the distinctions of Lele & Steel (1969, p. 95) and Streel (1972, p. 210) which distinguish *Geminospora* from *Aneurospora* (Streel 1964), the latter plexus being acavate (see also Allen, 1980, p.262; Richardson *et al.* 1982). *Laiphospora* Playford, Wicander & Wood (1983) consists of a two-layered exine, with the disto-equatorial exoexine somewhat membraneous in appearance.

Certain species of *Apiculiretusispora* have been recognised to display an intexinal body (*e.g.* *A. granulata* Owens, 1971; *A. brandtii* Streel, *sensu* McGregor 1973; *A. gaspiensis* McGregor 1973). *Geminospora* differs in basic construction to such variants of *Apiculiretusispora* in being demonstrably camerate, and also in displaying a differential intexine to exoexine wall thickness.

In the present study, the emendation of Owens (1971) is preferred rather than the more recent and restricted reappraisal of *Geminospora* by Playford (1983). The present author believes geminospore construction to be the primary unifying feature, and not, as Playford (1983) appears to advocate, the nature of the exoexinal sculpture: the emendation of Playford imposes unrealistic limitations on the allowed diversity in exoexinal sculpture.

The *Geminospora* population documented from north Devon display typical geminospore construction (*i.e.* thickened exoexine relative to a thinned intexinal body), but exhibit a considerable diversity of exoexinal sculpture, ranging from verrucae (of *G. boleta,* Higgs & Russell, 1981) through predominantly bacula (*G. pilaformis* Loboziak, Streel & Burjack, 1988) to spinae and coni (*G. lemurata* (Balme) Playford, 1983). In view of this variability in sculpture, the emendation of Owens (1971) is considered the more representative and appropriate. Furthermore, the establishment of a new generic category as suggested by Playford (1983, p. 315) to accommodate all forms of "*Geminospora*" that do not strictly accord with the original circumscription of the genus, *sensu* Balme (1962), would only exasperate an already confused and cluttered Devonian systematic scheme.

Unless otherwise specified, the exinal layers are principally attached over the proximal surface.

Geminospora boleta. Higgs and Russell
Plate 3.19, figs. 1-6, 10.

? 1975 *Verrucosisporites rarituberculatus* (Naumova) Curry, p. 126, Pl. 1, fig. 2,3.
1977 *Verruciretusispora* sp., Owens, Downie and Reynolds, Pl. 2 fig. 6.
1981 *Geminospora boleta* Higgs & Russell, p. 31, Pl. 2, figs. 13-16, text-fig. 6B.
1988 *Grandispora tabulata* Loboziak, Streel & Burjack p.357-358, Pl. VI, fig. 9-15.
1988 *Verrucosisporites bullifens* (Taugourdeau-Lantz) Richardson & McGregor in Loboziak, Streel & Burjack Pl. VII, fig. 6.

Description. Trilete, camerate miospores; amb circular to convex-triangular in polar compression. The suturae are distinct, straight and may be bordered by pronounced labra, ≤3μm in total width. The laesurae extend almost to, rarely beyond, the outline of the intexinal body: occasionally are propagated to the spore circumference by folds in the exine, paralleling the trilete rays. The laesurae may be terminated equatorially by faint curvaturate ridges, which usually coincide inter-radially with the spore circumference. The proximal surface lacks pronounced sculpture. The intexinal body is distinct to diffuse (the latter common when the two exinal layers are closely appressed), laevigate, scabrate or finely granulose in texture, ≤0.25-1μm thick equatorially, and typically thinner than the exoexine. The intexine may also appear distorted, displaying concentric compressional folds, independent of the exoexine. The degree of cameration is variable, although the diameter of the intexine is commonly 80-87% of the total spore diameter. The exoexine is ≤2.75μm thick equatorially, robust (rarely membraneous in appearance), and scabrate to finely granulose: exhibits regular, proximo-equatorial and distal sculpture comprising well rounded to subpolygonal verrucae, and very occasional, subdued bacula. In profile these elements are ≈hemispherical, squat and smooth, with flat to 5.5μm in basal diameter (rarely $\leq$2μm or greater than 6μm), and is 0.75-2.25μm in height (average 1-1.5μm). The verrucae are normally discrete, $\leq$0.5-4.5μm apart; usually even in their distribution. Very occasionally, two or three adjacent elements may coalesce. The exoexine between these enlarged verrucae may display subordinate, diminutive grana, which appear subcircular in plan view and $\leq$0.25-0.75μm in basal diameter/height.

Figure 3.3.57: Sculptural elements of *Geminospora boleta*, lateral view.

Dimensions. Maximum exoexine diameter 34-64μm, mean 48μm (70 specimens measured). Diameter of the intexinal body in polar compression, 79-92% of the total spore diameter (27-54μm, mean 41μm).

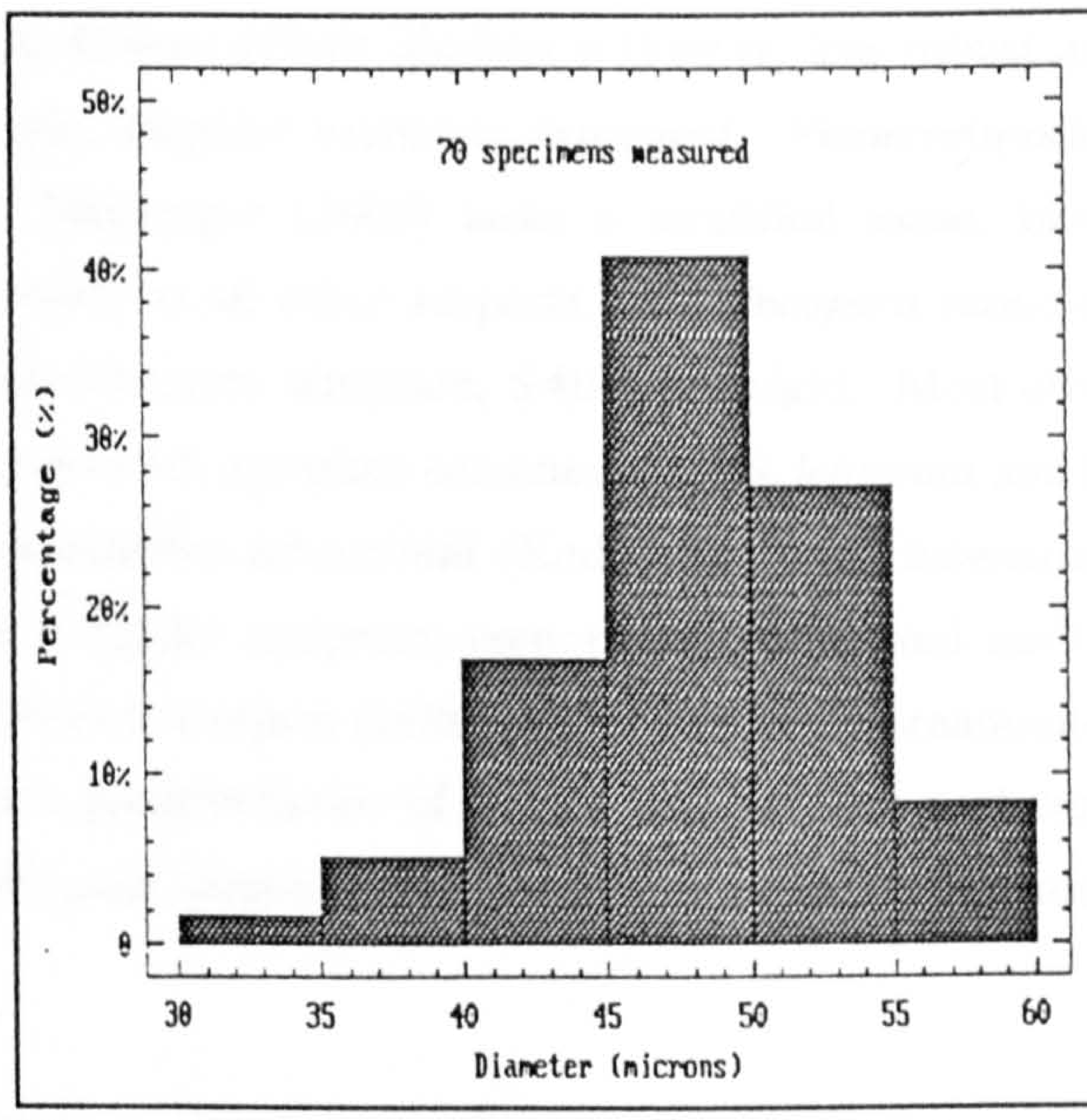

Figure 3.3.58: Size distribution of *Geminospora boleta* Higgs & Russell (1981).

Occurrence. K, M; common.

Remarks. *Geminospora boleta* bears a superficial resemblance to *Verrucosisporites bulliferus*, although the two differ primarily in construction (the former camerate, the latter nonlaminate, acamerate). In the description of *Verrucosisporites bulliferus* (al. *bullatus;* new name after Richardson & McGregor, 1986) Taugourdeau-Lantz (1967) made no reference to exinal stratification. However, difficulties arose in the present when the two exinal layers of forms otherwise referrable to *Geminospora boleta* were not readily distinguishable (*i.e.* specimens did not appear demonstrably camerate, lacking pronounced wall separation: refer to one of the specimens figured herein, Pl. 3.19, fig. 6). For such miospores, either a *Geminospora boleta* or *Verrucosisporites bulliferus* identification would seem equally justifiable. However, in view of the biostratigraphical significance attached to *V. bulliferus,* great care was taken to accurately identify spores of such ambiguous morphology by carefully assessing wall construction. Within the literature these two species appear to have been misidentified, *e.g.* refer to the form illustrated as "*Verrucosisporites bulliferus*" in Loboziak *et al.* (1988; Pl. VII, fig. 6): this form appears to display an "intexinal layer", closely appressed to the exoexine.

The illustrations of *Verrucosisporites rarituberculatus* (Naumova) Curry (1975) appear to show a "wall feature" that may conceivably represent an intexinal body. However, no mention is made by Curry in the text to the presence of an "intexinal layer": with future examination, if the wall construction of *Verrucosisporites rarituberculatus* and *Geminospora boleta* proves the same, *V. rarituberculatus* will assume taxonomic priority.

Loboziak, Streel & Burjack (1988; p. 357-358, Pl. VI, figs. 9-15) recently defined the species *Grandispora tabulata,* based upon specimens recovered from subsurface Frasnian strata of the Parana

Basin, Brasil (referrable to the TCo-IV biozones, *sensu* Streel *et al.*, 1987). Despite acknowledging that the exoexine (≈1μm thick) was thicker than the intexinal body (and therefore more truly representative of the *Geminospora* plexus), Loboziak *et al.* (1988) assigned this species to *Grandispora* and remarked that to their knowledge, the sculpture was unlike any previously defined species of *Grandispora*[1]. The verrucate ornament that adorns *Grandispora tabulata* is marginally smaller (≤2μm high and 0.5-2μm in diameter) than that considered "typical" of *Geminospora boleta*. However, this disparity may simply reflect natural variation in sculpture within the *Geminospora boleta* population, and thus *Grandispora tabulata* is regarded as a junior synonym of *Geminospora boleta*.

Comparisons. *Spelaeotriletes pertriosus* Neves & Owens (1966) displays a thinner, less robust and more retracted intexine, as well as a more chaotic, irregular verrucate ornament. *Verrucosisporites bulliferus* (Taugourdeau-Lantz) Richardson & McGregor (1986) lacks a stratified exine, being acamerate in construction but identical to *G. boleta* in all other respects. *Geminospora verrucosa* Owens (1971, p. 63-64) exhibits a more irregular, verrucate sculpture, ≤4μm in height. Most other species of *Geminospora* display a finer, generally pointed, apiculate ornament (*e.g G. lemurata* and *G. tuberculata* (Kedo) Allen var. *micromata*). *Geminospora tuberculata* (Kedo) Allen var. *tuberculata* McGregor & Camfield (1982) displays a more irregular sculpture, comprising grana, coni and/or mammae. *Geminospora pilaformis* Loboziak, Streel & Burjack (1988) grades into finely ornamented *G. boleta*, although the former species displays a predominance of clavate and baculate sculptural elements, over verrucae. The genus *Rugospora* displays sinuous rugulae interspersed with a verrucate sculpture.

Geminospora lemurata Balme emend. Playford 1983.
Plate 3.19, figs. 7-9, 11-15.

1962 *Geminospora lemurata* Balme, p. 5, Pl. 1, figs. 5-10.
1972 *Geminospora lemurata* Balme, in Mortimer & Chaloner p. 38, Pl. VI, fig. 13.
non 1971 *Geminospora plicata* Owens, p. 64, Pl. XX, figs. 1, 2.
p 1974 *Aneurospora greggsii* (McGregor) Streel in Becker Bless Streel & Thorez, p. 24-25, Pl.16, figs. 6, 7, ?10
1974 *Geminospora plicata* Clayton & Graham, p. 579-580, Pl. 4, figs, 1, 2, 4, 5.
? 1977 *Apiculiretusispora brandtii* Streel, in Owens *et al.*, Pl. 2, fig. 4.
1982 *Geminospora micromanifesta* (Naumova) McGregor & Camfield var. *minor* Naumova, p. 40, Pl. 8, figs. 14, 15, 19-22, text-fig. 57.
1983 *Geminospora lemurata* Balme emend. Playford, p. 311-325, figs. 1-9.
1988 *Geminospora lemurata* Balme, in Balme p. 134-135, Pl. 7, figs. 1, 2.
1988 *Geminospora lemurata* (Balme) Playford, in Loboziak, Streel, & Burjack, Pl.V, figs. 11,12.
p 1989 *Geminospora lemurata* (Balme) Playford, in Loboziak & Streel, Pl.III, figs. 8, 12, 13 (only).
Refer to Playford (1983, p. 318-321) for an additional synonymy and potential synonyms.

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[1] According to Loboziak *et al.* (1988) the inception of "*Grandispora tabulata*" is ≈coincidental with that of *Verrucosisporites bulliferus*.

Description: Trilete (rarely monolete) camerate miospores; amb circular, subcircular to convex triangular. Suturae are straight to openly arcuate, extending 4/5 to 7/8 the total spore diameter, and often accompanied by thin labra, ≤2.25μm in total width. The laesurae taper towards the equatorial margin: the contact areas are laevigate or scabrate, and may be delimited equatorially by faint or pronounced curvaturae perfectae, which are usually distinguishable from the outline of the intexinal body and discrete from the spore circumference. The intexine is thin (≤0.75μm), laevigate to finely scabrate, and may display concentric (rarely radial) compressional folds, ±independent of the exoexine. The exoexine is thickened equatorially and distally, up to 3.75μm. The proximo-equatorial and distal regions display a relatively uniform, dense sculpture that comprises diminutive, broad-based spinae, coni and coarse grana: the sculpture is usually submicron in width and height, rarely exceeds 1.25μm in size. Sculptural elements are typically discrete, ≤0.25-0.5μm apart (rarely exceed 1μm). The exoexine may be distorted, displaying radial and/or concentric compressional folds over the distal surface, ±independant of the intexine. Camera development is variable, although the diameter of the intexinal body is usually ≈75-85% of the total spore diameter.

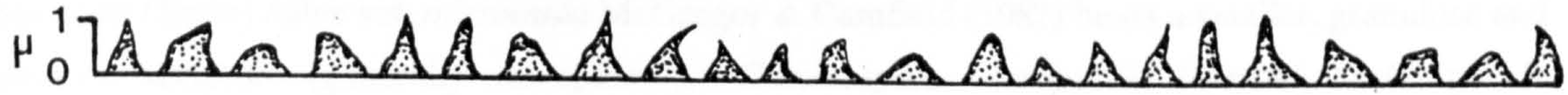


Figure 3.3.59: Sculptural variation of *Geminospora lemurata*, lateral elevation.

Dimensions: Maximum exoexinal diameter 34-75μm, mean 52μm; intexine 29-65μm, mean 44μm (200 measurements). Diameter of the intexinal body in polar view, 58-(80)-92% of the total spore diameter.

Occurrence. L, CM, K, M; *abundant.* WP; *rare-common.*

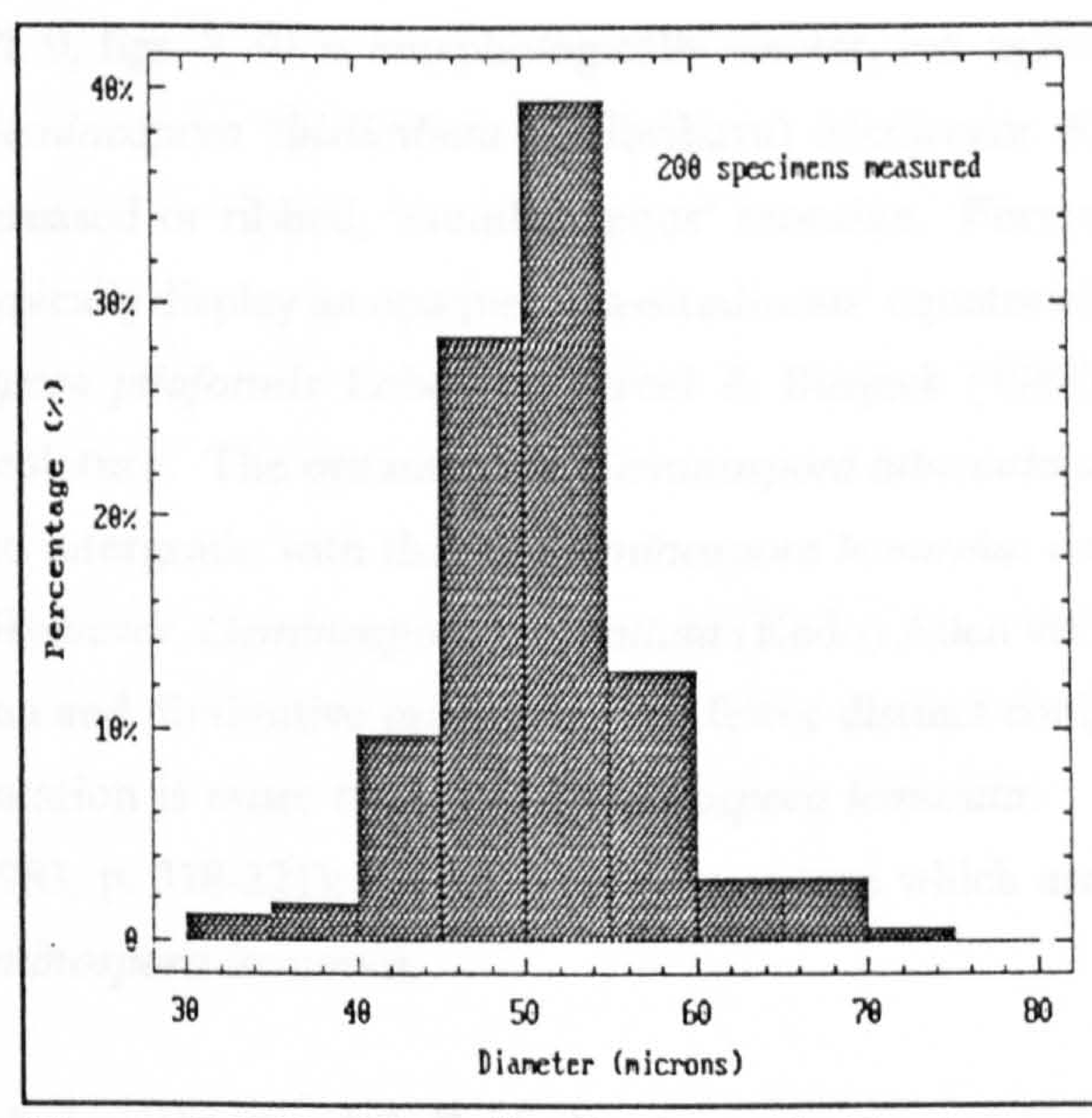


Figure 3.3.60: Size distribution of *Geminospora lemurata* (Balme) emend. Playford (1983).

Remarks. In the present study, the species *Geminospora plicata, sensu* Clayton & Graham (1974) is believed to merely represent forms of *Geminospora lemurata* which display indiscriminate distal compressional folds: such plications differ to the more robust and ?structured folds (of "triradiate" geometry) that develope on forms of *Geminospora plicata, sensu* Owens (1971; p. 64, Pl. XX, figs. 1, 2). *Geminospora micropaxilla* (Owens) McGregor & Camfield (1982) and *Geminospora* sp. *sensu* McGregor & Camfield (1982) differ to *Geminospora lemurata* primarily, and somewhat arbitrarily, in overall spore diameter (both exceed 83μm): Playford (1983, p. 317) quotes the size range of *Geminospora lemurata* to be 32-(52)-76μm. Feasibly, the two former species of McGregor & Camfield (1982) may simply reflect oversized representatives of *Geminospora lemurata.*

The present author concurs with Playford (1983, p. 321) in viewing the rationalisation of *Archaeozonotriletes micromanifestus* var. *minor* Naumova by McGregor & Camfield (1982) as somewhat precipitous. The exact status of this Russian taxon requires clarification, and until such time, the continued application of *Geminospora lemurata* (Balme) Playford (1983) is favoured.

Within the Lester Slates & Sandstones, and the Combe Martin, Kentisbury and Morte Slates, *Geminospora lemurata* (Balme) Playford (1983) was noted within almost every sample, and usually in prolific numbers, in extreme cases accounting for up to 25-30 % of the total palynoflora. Monolete specimens were unique to the Kentisbury Slates. Oblique-equatorial or off-polar compressions were common (?suggesting that the distal thickening of the exine may be appreciable).

Comparisons. The circumscription of *Apiculiretusispora gaspiensis* Owens (1971) is not too dissimilar to that of *Geminospora lemurata:* the latter species does, however, display a differentially thickened exoexine relative to the intexinal body. The exoexine of *Geminospora punctata* Owens (1971, p. 61-62) is densely infrapunctate. *Geminospora boleta* Higgs & Russell (1981) and *G. tuberculata* (Kedo) Allen var. *tuberculata* McGregor & Camfield (1982) display a coarser "verrucate" sculpture. *G. tuberculata* (Kedo) Allen var. *micromata* McGregor & Camfield (1982) bears a smaller, granulose and mammate sculpture (generally non-spinose). *Geminospora micropaxilla* (Owens) McGregor & Camfield (1982, p. 41) is larger in diameter (83-133μm), with a greater intexine/exoexine size ratio relative to *Geminospora lemurata: G. micropaxilla* exhibits a slightly smaller sculpture. *Geminospora* sp. *sensu* McGregor & Camfield (1982; p. 43, Pl. 9, figs. 8, 9) is morphologically similar, but again much larger in spore diameter (83-152μm). *Geminospora ?bislimbata* (Chibrikova) McGregor & Camfield (1982, p. 40) is larger, and displays a creased or ribbed, "membraneous" exoexine. Forms of *Aneurospora* (Streel) Richardson *et al.* (1982) typically display an opaque, "crassitudinous" equatorial margin, and lack an intexinal body. *Geminospora pilaformis* Loboziak, Streel & Burjack (1988) exhibits a coarser, more baculate and/or pilate sculpture. The ornament of *Geminospora tuberculata* (Kedo) Allen var. *micromata* was noted herein to intergrade with that of *Geminospora lemurata*: on occasion the two are virtually indistinguishable. However, *Geminospora tuberculata* (Kedo) Allen var. *micromata* displays a predominance of squat grana and diminutive mammae, with fewer distinct coni, or spinose elements: this latter form of ornamentation is more typical of *Geminospora lemurata.*

Also note the comparisons in Playford (1983, p. 318-321): Playford catalogues taxa which are synonymous or potentially synonymous with *Geminospora lemurata.*

Geminospora pilaformis Loboziak, Streel & Burjack
Plate 3.19, fig. 16.

1988 *Geminospora pilaformis* Loboziak, Streel & Burjack, p. 356-357, Pl. V, figs. 1-9.

Description. Trilete, camerate miospores; amb subcircular to convex triangular. Suturae are straight to openly arcuate, extending 3/4 to 7/8 the intexinal diameter, and are paralleled by robust or slightly flexuous labra: the labra are $\leq 2\mu$m in individual width and height. The laesurae may be terminated equatorially by faint curvaturae imperfectae. The contact areas are laevigate to scabrate: the exine "thins" over the proximal surface and may appear somewhat depressed. The intexine is thin

(≤1.25μm), laevigate, and commonly closely appressed to the exoexine: separation of the two exinal layers may be minimal, such that the camera is barely discernible. The exoexine ranges up to 3.75μm in thickness equatorially and distally, and appears laevigate to coarsely scabrate, rarely sparsely granulose. The proximo-equatorial and distal regions of the exoexine display a highly variable sculpture, that consists predominantly of squat bacula, verrucae and/or clavate elements: ≤2.75μm in width and height (usually 1-1.5μm). The sculptural elements are usually discrete, ≤1-4.5μm apart: two or three elements very occasionally cluster. Between these principal elements, diminutive, subordinate coni, grana, mammae and rare spinae may co-occur, being ≤0.5μm in dimensions. The exinal layers are rarely folded: commonly appear robust and optically translucent.

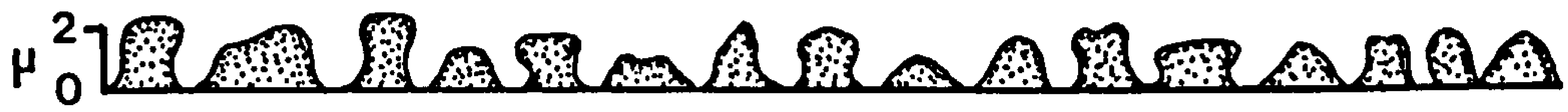


Figure 3.3.61: Sculptural variation of *Geminospora pilaformis*, lateral elevation.

Dimensions. Maximum exoexinal diameter 46-62, mean 54μm. Diameter of intexinal body, 38-54μm, mean 48μm (10 specimens measured).

Occurrence. K; *rare.*

Remarks. This taxon may prove to be the morphological "link" between aberrant forms of the *Geminospora tuberculata* complex and *Geminospora boleta*: the ornament intergrades in morphology from verrucate, through elevated clavate and finally to subdued, laterally expansive "mushroom" in form.

The population recovered from north Devon resemble the holotype illustration of Loboziak, Streel & Burjack (1988; Pl. V, figs. 1, 2) in terms of sculpture.

Comparisons. *G. tuberculata* (Kedo) Allen var. *tuberculata* McGregor & Camfield (1982) display more subdued, irregular elements, comprising verrucae, mammae and coni. *Geminospora boleta* Higgs & Russell (1981) bears a sculpture comprising more rounded, broader verrucae, or "mushroom-shaped" elements.

Refer to *G. lemurata* (herein) for additional comparisons.

Geminospora ?spinosa Allen
Plate 3.19, figs. 17, 18.

? 1965 *Geminospora spinosa* Allen, p. 697, Pl. 94, figs. 17-18.
1971 *Geminospora* sp. A, Owens, p. 64-65, Pl. XX, fig. 3.
? 1972 *Geminospora spinosa* Allen, in Mortimer & Chaloner p. 28, Pl. IV, fig. 5.
? 1988 *Geminospora spinosa* Allen, in Boumendjel, Loboziak, Paris, Steemans & Streel, Pl. 1, fig 20.

Description. Trilete, camerate miospores; amb oval, circular to convex triangular. The outline of the intexinal body is ≈conformable with that of the exoexine, is laevigate to finely scabrate and thin

(≤1.25μm), although may appear compressionally thickened ("?limbate") equatorially (up to 4μm thick). The suturae are straight to openly arcuate, simple or labrate, and extend 4/5 to the full radius of the intexinal body (rarely propagate beyond the intexine). The labra are ≤3.25μm in total width, and the laesurae may be terminated equatorially by indistinct curvaturae imperfectae. The contact areas are laevigate to scabrate in texture, lacking pronounced sculpture, and may occasionally appear somewhat thinned and depressed. The exoexine is laevigate to scabrate, and ≤3.75μm thick over the equatorial and distal regions. The distal surface of the exoexine exhibits discrete, attenuate spinae and rare coni, which form an even but sparse sculptural cover. Elements range in basal diameter from ≤0.5μm to 1.75μm (rarely 2μm), and ≤2.25μm in height: individual elements are 1-4.5μm apart, averaging 2.75μm. This sculpture is subdued, commonly absent proximo-equatorially, rarely projecting at the equatorial margin.

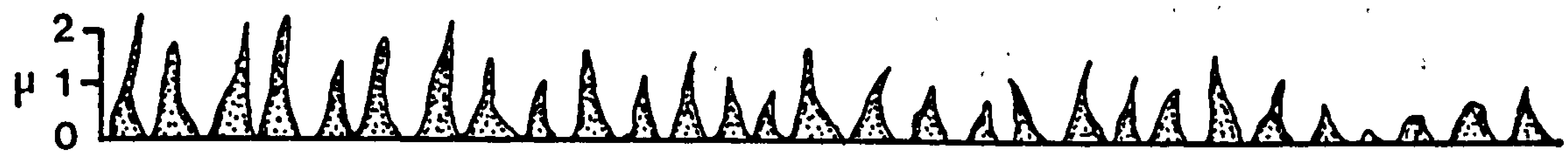


Figure 3.3.62: Sculptural elements of *Geminospora ?spinosa*, lateral view.

Dimensions. Maximum exoexinal diameter 41-65μm, mean 54μm. Intexine, 21-53μm, mean 37μm (20 specimens). Diameter of the intexinal body (in polar view) 40-(68)-86% of the total spore diameter.

Occurrence. M; *rare.*

Remarks. Although conforming in most respects to Allen's (1965) circumscription of *Geminospora spinosa*, specimens recovered from north Devon are only tentatively affiliated with this species. The principal disparity is the relative disposition and size of the sculpture. Allen (1965, p. 697) notes that the spines that adorn *G. spinosa* are 3-6μm in length, and sparse over the proximo-equatorial and distal surfaces. However, the form illustrated by Allen (1965; Pl. 94, figs. 17, 18) displays a somewhat denser sculpture than was apparent upon specimens recovered north Devon.

Geminospora sp. A *sensu* Owens (1971), recorded from the Canadian Arctic Archipelago, displays a comparable but dense "echinate" sculpture, that ranges up to 3μm in height: in the description of this taxon, Owens does not quantify the isolation of individual sculptural elements. Subtle disparities between *Geminospora* sp. A *sensu* Owens and *Geminospora ?spinosa* (of the present study) are considered trivial, and thus the two are placed in synonymy.

Comparisons. *Geminospora lemurata* bears a somewhat shorter, denser and more varied sculpture. *G. pilaformis* displays a predominance of blunted and more rounded baculate elements. The ornament of the *Geminospora tuberculata* (Kedo) Allen "complex" (*sensu* McGregor & Camfield, 1982) appears more granulate, mammate to verrucate in form.

Geminospora tuberculata (Kedo) Allen var. *micromata* McGregor & Camfield
Plate 3.19, fig. 19.

1982 *Geminospora tuberculata* (Kedo) Allen var. *micromata* McGregor & Camfield, p. 41, Pl. 9, fig. 4, 5, text-figure 59.

Description. Trilete camerate miospores; subcircular to convex triangular amb. The suturae are straight to openly arcuate, simple or paralleled by labra ≤1.25μm in individual width, and extend 4/5 to the full radius of the intexinal body: rarely propagate beyond the outline of the intexine. The equatorial terminations of the laesurae are usually simple, rarely delineated by curvaturae imperfectae: the contact areas are either ≈thinned, or are merely noted for their subtle reduction/absence of a pronounced exoexinal sculpture. The intexinal body is laevigate to scabrate, ≤1μm thick, and ±concentric with the spore circumference: the intexine appears robust and rarely folded. The exoexine is ≤1.5-2.75μm thick over the equatorial and distal regions, lacking compressional folds. Proximo-equatorially and distally the exoexine exhibits squat, diminutive mammae, coarse grana and broad-based coni, with rare spinae and bacula: elements typically ≤1-1.75μm in height, ≤1.5μm in basal diameter and ≤0.25-2μm apart. Two to five elements may occasionally cluster, or form irregular, sinuous "beaded" rugulae.

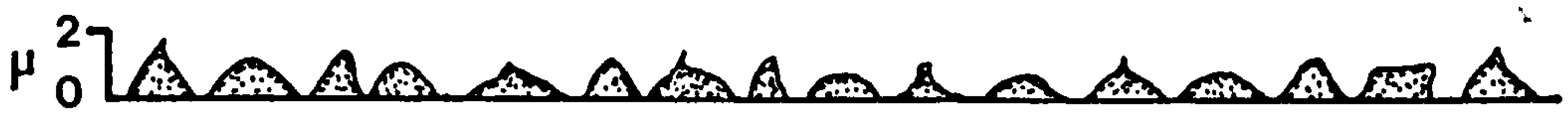


Figure 3.3.63: Sculptural elements of *Geminospora tuberculata* var. *micromata*, lateral view.

Dimensions. 47-68μm, mean 49μm (6 specimens measured). Intexine 36-57μm, mean 44μm. Diameter of the intexinal body 74-91% of the total spore diameter.

Occurrence. M; *very rare.*

Remarks. The size specifications noted by McGregor & Camfield (1982, p. 41; 66-(80)-99μm) are somewhat larger than those recorded for the population recovered from north Devon: herein, this disparity in overall size did not substantiate differentiation. In the present study, sculptural morphology was noted to intergrade with that of *Geminospora lemurata*, and on rare occasions the two spore complexes proved virtually inseparable.

Comparisons. *Geminospora tuberculata* (Kedo) Allen var. *tuberculata* McGregor & Camfield (1982) bears a coarser, but morphologically comparable sculpture. *Geminospora* sp. *sensu* McGregor & Camfield (1982, p.43) is larger (83-152μm), although the sculpture does appear broadly comparable. *Geminospora lemurata* (Balme) Playford (1983) displays a predominantly spinose to conate sculpture. The predominant ornament-type of *Geminospora spinosa* Allen (1965) and *G. pilaformis* Loboziak, Streel & Burjack (1988) comprises larger spinae and pila/bacula respectively.

Geminospora tuberculata (Kedo) Allen var. *tuberculata* McGregor & Camfield
Plate 3.19, figs. 20, 21.

1955 *Archaeozonotriletes tuberculatus* Kedo, p.35, Pl. 5, figs. 6, 7.
non 1965 *Geminospora tuberculata* (Kedo) Allen, p. 696, Pl. 94, figs. 10, 11.
1972 *Geminospora tuberculata* (Kedo) Allen, in Mortimer & Chaloner p. 25, Pl. IV, fig. 8.
? 1976 *Verrucosisporites confertus* Owens, in Massa & Moreau-Benoit, Pl. 5, fig. 4.
1982 *Geminospora tuberculata* (Kedo) Allen var. *tuberculata* McGregor & Camfield, p.41-42, Pl. 9, figs. 6, 7, 10-13, text-figure 60.
1986 *Geminospora tuberculata* (Kedo) Allen, in Turnau, Pl. IX, fig. 5.
p 1989 *Geminospora lemurata* (Balme) Playford, in Loboziak & Streel, Pl. III, figs. 7, 11, 14, 15.

Description. Trilete, camerate miospores with a subcircular to convex triangular amb. The laesurae are simple, straight to openly arcuate, extending 3/4 to the full of the intexinal body: may be paralleled by robust to diffuse labra, $\leq 2\mu m$ in individual width. The exoexine of the contact areas is thin, scabrate to laevigate, or delineated by a marked reduction or absence of pronounced sculptural elements: the contact areas are commonly delimited equatorially by well defined to discernible curvaturae. The intexinal body is usually conformable with the outline of the exoexine, appears thin ($\leq$0.5-1.25μm thick), laevigate and rarely folded. The two exinal layers are attached proximally, with the exoexine $\leq$2.25-3.75μm thick over the equatorial and distal regions. Proximo-equatorially and distally the exoexine is sculptured with coarse grana, squat coni/spinae, and diminutive mammae or verrucae: elements $\leq$1-2.75μm in basal width and height (on average $\approx 2\mu m$). These elements are circular to polygonal in basal outline, and irregular or uniform in their distribution: commonly $\leq$1-4μm apart (rarely 6.5μm). Occasionally two to five elements may fuse into irregular "rugulae" or cluster.

Figure 3.3.64: Sculptural elements of *Geminospora tuberculata* (Kedo) Allen var. *tuberculata* McGregor & Camfield, lateral view.

Dimensions. Maximum overall exoexinal diameter 49-72μm, mean 59μm (10 specimens measured).

Occurrence. CM, K, M; *rare.*

Remarks. The size range of the population of *Geminospora tuberculata* (Kedo) Allen var. *tuberculata* McGregor & Camfield recovered from north Devon is somewhat smaller than that quoted by McGregor & Camfield (1982; 74-(93)-120μm) for material from the Canadian Arctic. However, the overall construction and more importantly the sculpture appear identical.

Comparisons. *Geminospora lemurata* (balme) Playford (1983) displays a more spinose sculpture. *Geminospora tuberculata* (Kedo) Allen var. *micromata* McGregor & Camfield bears morphologically similar but smaller ornament. *Geminospora pilfomis* (Loboziak *et al.*, 1988) differs primarily in displaying a predominantly baculate/pilate sculpture.

Note also the comparisons made earlier under *Geminospora lemurata* (above).

Genus *Grandispora* Hoffmeister, Staplin & Malloy 1955
emend. McGregor 1973.

Type species. *Grandispora spinosa* Hoffmeister, Staplin & Malloy, 1955.

Synonymy.

1957 *Spinozonotriletes* Hacquebard, p. 315.
1962 *Calyptosporites* Richardson, p. 192.
non 1965 *Samarisporites* Richardson, p. 581-582.

Discussion.

Following the proposal of the genus *Grandispora* by Hoffmeister, Staplin & Malloy (1955), Potonié (1960, p.42) suggested that if *Spinozonotriletes* Hacquebard (1957) could be shown to display a central body (*i.e.* was pseudosaccate) then it may well prove to be congeneric with *Grandispora*. Contemporaneously, Richardson (1960, p. 52) defined the genus *Cosmosporites*, which later Richardson (1962, p. 192) renamed *Calyptosporites* (as Nilsson (1958) had earlier applied the terminology *Cosmosporites* to spores from the Lower Lias). Richardson differentiated *Calyptosporites* from *Grandispora* according to its larger size, its markedly subtriangular outline, and the presence on some spores of small bifurcate-tipped spines. Subsequently, Neves & Owens (1966) emended the concept of *Grandispora*, and considered *Spinozonotriletes* as distinct, differentiating the two according to the thickness of the distal exoexine, as well as the rigidity and the lack of compressional folds on the equatorial flange: forms of the *Spinozonotriletes* complex appear far more robust and thicker walled. Furthermore, Neves & Owens (1966) distinguished *Spelaeotriletes* from *Grandispora*, although the differential criteria they cite are in fact not atypical attributes of *Grandispora*. McGregor (1973, p.59) later distinguished *Spelaeotriletes* by virtue of its ornamentation, which is fused laterally into short, irregular ridges.

Playford (1971, p. 45) could not justify maintaining *Calyptosporites* distinct from *Grandispora*, and considered the disparity in size and shape invoked by Richardson (1960, p. 52) to be invalid and trivial, and furthermore an unsound basis for defining a new genus. Playford (1971, p. 45-46) also remarked that no realistic sculptural differences exist between the two complexes, as illustrated by the genotype of *Calyptosporites* (*C. velatus* (Eisenack) Richardson 1962), which in fact displays non-bifurcating coni. Playford agreed with Potonié (1960), who had earlier suggested the potential synonymy of *Spinozonotriletes* within the concept of *Grandispora*. Although Neves & Owens (1966) had maintained that these two genera were distinct, Playford (1971, p. 45) considered microtome sections of certain species of these two complexes as failing to confirm any differential wall thicknesses (refer to the microtome sections illustrated by Dettman & Playford, 1963; Allen, 1965). Playford (1971, p. 46) also remarked on the potential synonymy of *Ibrahimispores* Artüz (1957) with *Grandispora*, although the construction the former genus required clarification.

McGregor (1973, p.58-59) ventured further than Playford (1971) in regarding *Spinozonotriletes*, *Calyptosporites* and *Samarisporites* as junior synonyms of *Grandispora*. Unfortunately, the credibility of this rationalisation was tarnished by McGregor's synonymy of *Samarisporites* with *Grandispora*. According to Richardson (1965, p. 581-582) *Samarisporites* circumscribes zonate spores, homologous in construction with *Cristatisporites*, *sensu* Butterworth *et al.*, (in Staplin & Jansonius, 1964, p. 108). McGregor (1973, p. 58) argued that the construction of *Samarisporites* is often difficult to resolve using conventional light microscopy without recourse to microtome sectioning, and therefore justified the synonymy of this plexus with *Grandispora*. This interpretation is now widely acknowledged to be incorrect: indeed the synonymy of *Samarisporites* and *Grandispora* has been recanted by McGregor & Camfield (1982, p. 43) - see below. Three years later Tiwari & Schaarschmidt (1975, p. 42) also recognised the ambiguity between forms of *Calyptosporites* and *Grandispora*, but judged the two as distinct, based on differential "bladder" and ornament characteristics.

McGregor & Camfield (1982, p. 43) subsequently acknowledged that McGregor (1973) was incorrect in regarding *Samarisporites* as a junior synonym of *Grandispora*, as the two differ fundamentally in basic design. However, McGregor & Camfield (1982) applied the emended generic concept of *Grandispora*, *sensu* McGregor (1973, p. 58), as this allows for a considerable diversity in sculptural morphology, encompassing verrucae, spinae, coni, or biform elements: in comparison, Playford (1971, p. 45) merely circumscribes simple, non-bifurcating spinose and/or conate elements. McGregor & Camfield (1982, p. 43) did not accept the emendation to the diagnosis of *Grandispora* proposed by Neves & Owens (1966), as this required resolution of the extent and location of attachment between the intexine and exoexine: in practice, this may be difficult if not impossible to evaluate (also refer to the discussion in McGregor, 1973, p. 58).

Despite formal emendations to the concept of *Grandispora*, that incorporate forms variously attributed to *Calyptosporites* and *Spinozonotriletes*, all three generic concepts are still widely applied. Indeed, Balme (1988, p. 138) recently argued a relatively strong case for the retention of *Calyptosporites*, regarding the biform sculpture (which he remarked most species of *Calyptosporites* display) to be biologically and biostratigraphically significant, and representative of an important evolutionary phase in plant development through the Devonian Period. Thus, even within a highly artificial taxonomic scheme, Balme perceived the synonymy of *Calyptosporites* with *Grandispora* to be ill-advised.

In part the emended concept of *Grandispora sensu* McGregor (1973) is applied in the present study, as this allows for a far greater range in exoexinal sculpture: usage herein follows the application of McGregor & Camfield (1982).

In comparing *Perotrilites* Couper emend. Evans (1970) with *Grandispora*, McGregor & Camfield (1982, p. 55) consider that in practice the distinctions between these two genera are somewhat ambiguous: the former circumscribes spores with a zonate-camerate construction and a diaphanous exoexine. *Geminospora* (Balme) Owens (1971) displays differentially thickened exinal layers, and *Rhabdosporites* (Richardson) Marshall & Allen (1982) bears an ornament that consists predominantly of minute bacula.

Grandispora cf. *arduinnae* (Riegel) comb.nov.
Plate 3.20, figs. 1, 2.

cf. 1973 *Spinozonotriletes arduinnae* Riegel, p. 97, Pl. 16, fig. 1-3.
cf. 1982 *Spinozonotriletes arduinnae* Riegel, in Riegel, Pl. 1, fig. 10.

Description. Trilete, camerate-?zonate miospores; amb subcircular, broadly convex-triangular to distinctly triangular. The equatorial margin may appear weakly dentate. The suturae are distinct to barely perceptible, simple or labrate, and straight to openly arcuate: extend 3/4 to the full spore radius. The suturae are usually obscured by elevated, flexuous labra, which are ≤4.5-13μm in width and height at the proximal pole, and commonly taper towards the equatorial margin. The terminations of the laesurae may be simple or display curvaturae imperfectae. The contact areas lack pronounced sculpture. The outline of the intexinal body is usually conformable with the spore circumference, or may appear slightly more rounded: the intexine is ≤0.75-1.5μm thick equatorially (rarely up to ≈6μm, "?limbate"), laevigate to scabrate in texture and occasionally folded. The exoexine appears laevigate, scabrate or finely granulose, and is ≤1-2.5μm thick equatorially: the intexine and exoexine commonly show the greatest separation radially. Proximo-equatorially and distally the exoexine bears discrete, subdued, broad-based coni, with rare spinae and mammae: elements typically ≤1-2.25μm in height (up to 4μm on larger specimens), and may either be surmounted by a slender, ciliate, apical spine, or a diminutive grana (these subordinate elements are usually ≤1μm in width and height). The sculpture ranges in basal diameter from ≤2.5 to 6μm: the basal outline of the ornament is usually indeterminate, as the elements are so subdued and appear simply to merge with the exine: do not form a pronounced, positive surficial feature. Elements are generally isolated, 4-9μm apart (rarely dense, ≤2μm in isolation): overall the exine appears very sparsely ornamented.

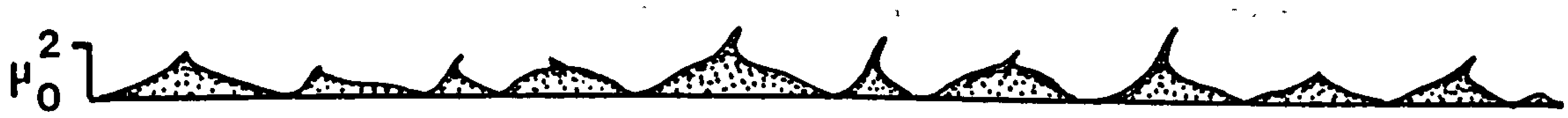


Figure 3.3.65: Sculptural elements of *Grandispora* cf. *arduinnae*, lateral view.

Dimensions. Maximum exoexinal diameter 64-93μm, mean 74μm. Maximum intexinal diameter 43-71μm, mean 54μm. Diameter of intexine 65-83% of total spore diameter.

Occurrence. LN; *common.* H; *rare.* S, LH, WP; *R.*

Remarks. As *Spinozonotriletes* Hacquebard is herein considered a junior synonym of *Grandispora* (refer to the earlier discussion), a new combination of *arduinnae* is proposed herein. Specimens recovered from north Devon differ to the population described by Riegel (1973) from the Eifel (Germany), in being somewhat smaller in overall spore diameter: 64-93μm of the present study *vs.* 86-124μm of Riegel (1973, p. 97).

Occasionally the suturae appear ruptured, or a triangular area of the exine (centred on the proximal pole) demonstrably thinned (refer to the figured specimen on Pl 3.20, fig. 2 herein). The sculpture may be so small that the exoexine appears virtually featureless. For some specimens, the equatorial projection of the exoexine beyond the intexinal body resembled a rigid zona. Occasionally the intexine appeared ?compressionally thickened, or was insufficiently oxidised such that haptotypic features were obscured.

Comparisons. The sparse and subdued sculpture distinguishes this form from most other species of *Grandispora*. *Grandispora echinata* Hacquebard (1957) and *Grandispora tenuispinosa* (Hacquebard) Playford (1971) display a more elongate, echinate sculpture. The amb of *Calyptosporites triangulatus* Higgs (1975) is distinctly triangular, and the ornament more pronounced.

Grandispora diamphida Allen
Plate 3.20, fig. 3-5.

1965 *Grandispora diamphida* Allen, p.733-734, Pl. 103, figs 1-6.
p 1986 *Grandispora diamphida* Allen, in Turnau, p. 345-346, Pl. VIII, fig. 6, 7 (only).

Description. Trilete, camerate-?zonate miospores with a rounded triangular to subcircular amb. The central body is circular to convex-triangular, distinct to diffuse and usually eccentric in its disposition relative to the spore circumference. The intexinal body is laevigate to finely scabrate, robust and ≤1.5μm thick. The exoexine is ≤1.25-3.25μm thick equatorially, appears robust, and usually lacks exinal folds: equatorially the two exinal walls are commonly ≤2-20μm apart. The suturae are straight to openly arcuate, usually distinct, and extend 4/5 to the full radius of the intexinal body: the suturae are commonly obscured by distinct, robust labra, which are ≤5.25μm in total width and up to 8μm high at the proximal pole (≈tapering towards the equatorial margin). The labra tend to propagate the laesurae to the spore circumference. The contact areas lack pronounced sculpture, over which the exine appears somewhat thinned, and laevigate to finely scabrate in texture. The equatorial and distal surfaces display discrete, robust coni, and slender spinae: elements occasionally appear biform, surmounted by a delicate, attenuate, ciliate apical spine - rarely blunted or bifurcate-tipped. The sculptural elements are typically ≤2-7.25μm in height (rarely exceed 9μm), and ≤1.75-4.25μm in basal diameter: elements are either evenly spaced, preferentially concentrated at the spore margin, or conversely crowded over the distal hemisphere: elements are ≤3-11μm apart. Two or three elements may fuse at their base.

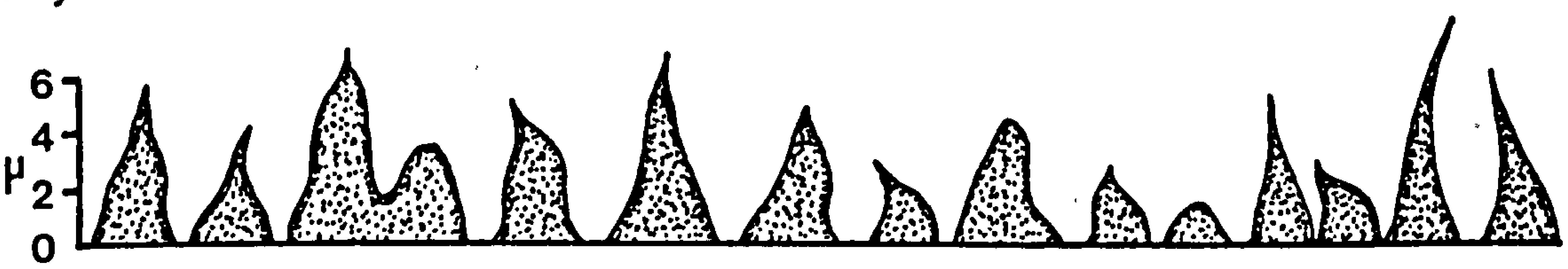


Figure 3.3.66: Sculptural elements of *Grandispora diamphida*, lateral elevation.

Dimensions. Maximum exoexinal diameter (excluding sculpture) 56-102μm, mean 76μm. Central body 34-93μm, mean 56μm (45 specimens measured). Diameter of the intexinal body 60-93% (mean 81%) of the total spore diameter.

Occurrence. LN, *common*. S; *R*.

Remarks. Allen (1965, p. 733) remarked that representatives of *Grandispora diamphida* resembled species of *Calyptosporites* (Richardson 1962), in displaying minute bifurcate terminations on some of the spines, but preferred affiliation with *Grandispora,* based on its smaller size and circular outline. Blunted or bifurcate termini were rarely observed in the present study. Furthermore, considerable variation in ornament size and disposition, as well as haptotypic characteristics was documented for the population of *G. diamphida* detailed herein. Despite this variety, the exinal proportions and gross sculptural morphology are consistent with the diagnosis of Allen (1965), although the range in size is marginally greater than that quoted by Allen (1965; exoexinal diameter 67-90μm).

The specimen figured as *Grandispora ?diamphida* (Pl. 3.20, fig. 5) broadly resembles *Grandispora* (al. *Spinozonotriletes*) *cassideus* (Owens) Chi & Hills (1976, p. 753-754) in the disposition of the sculpture, but differs in the overall spore diameter and dimensions of this ornament (the latter «10μm). The figured specimen was the only one of its kind recovered from north Devon, and as it resembles the figured specimen of *Grandispora diamphida* Allen (1965, Pl. 103, fig. 4), is thus tentatively attributed to this species.

Comparisons. *Spinozonotriletes uncatus* Neves & Owens (1966) differs somewhat arbitrarily from *G. diamphida* in exhibiting a more robust exoexine. *Grandispora douglastownense* McGregor (1973) is larger in overall size (111-195μm) and displays coarser, longer sculptural elements (3-17μm in length). *G. eximia* (Allen) McGregor & Camfield (1982) and *G. ?macrotuberculata* (Arkhangelskaya) McGregor (1973) are approximately similar in style of ornamentation, but are larger in overall spore diameter, and with a somewhat smaller intexinal body relative to the overall exoexinal diameter. G. cornuta Higgs (1975) is similar in size and sculptural organisation, but displays a concentrically folded intexine and seemingly more rigid exoexine.

Grandispora douglastownense McGregor
Plate 3.20, fig. 8.

1973 *Grandispora douglastownense* McGregor, p. 62-63, Pl. 8, figs. 8, 9, 12-14.
1980 *Grandispora douglastownense* McGregor, in Loboziak & Streel, Pl. III, fig. 8.
1989 *Grandispora douglastownense* McGregor, in Loboziak & Streel, Pl.VII, fig.5, Pl.IX, fig.27.

Description. Trilete, camerate miospores; amb subcircular to convex triangular. The intexine is conformable with the outline of the exoexine, or appears more distinctly circular, rounded. The suturae are straight to openly arcuate, rarely simple, extending 7/8 to the full radius of the spore: thin-flexuous, or robust labra may obscure the suturae, $\leq$7μm in height at the proximal pole - taper towards the equatorial margin. The contact areas lack pronounced sculpture. The intexine is laevigate to finely scabrate, $\leq$1.5μm thick equatorially and rarely folded. The exoexine is $\leq$2.75μm thick at the spore circumference, appearing laevigate to coarsely scabrate, and sculptured equatorially and distally with distinct, discrete and coarse coni, spinae and bacula: elements $\leq$11.5μm in height (usually 5-8μm) and $\leq$2-4.75μm in basal diameter. In lateral profile the sculpture may be constricted at one or more places. Elements are variably flexed or conversely rigid-erect, and surmounted by a delicate, ciliate apical spine or grana. Sculptural elements are $\leq$2μm to 14μm apart, commonly $\approx$6μm.

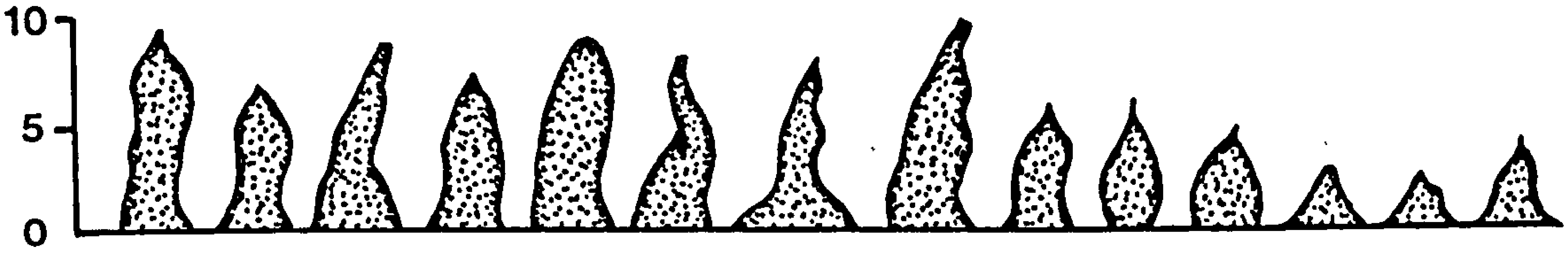


Figure 3.3.67: Sculptural variation of *Grandispora douglastownense*, lateral view.

Dimensions. 97-134μm, mean 109μm. Intexinal body diameter, 55-84μm, mean 67μm (15 specimens measured).

Occurrence. LN, H; *rare.*

Remarks. The sculpture that projects at the equatorial margin may appear uniformly reduced, or indeed absent (refer to the specimen figured herein; Pl. 3.20, fig, 8): despite a superficial homology with *Grandispora variospinosa,* such forms are closer in morphology to the circumscription of *G. douglastownense.* Such an equatorial reduction in ornamentation is probably attributable to poor preservation.

Some specimens recorded from north Devon were marginally smaller in overall size than the specifications quoted by McGregor (1973, 111-195μm). On such forms, average ornament length was typically less than 8μm: McGregor (1973, p. 63) notes that the longest spines are never less than 8μm.

Comparisons. *Grandispora diamphida* Allen (1965) is smaller in overall diameter (67-90μm), with a greater intexine to exoexine ratio. *Calyptosporites pilaspinosus* Lanninger (1968; p. 153, Pl. 26, fig. 1) is noted as ≈110μm in diameter: the holotype illustrated by Lanninger exhibits a sparse sculpture, and a notably retracted central body (≈50μm in size). Until more information is collated about the sculptural morphology of *C. pilaspinosus,* the present study follows McGregor (1973, p. 63) in maintaining *G. douglastownense* as distinct. *Grandispora naumovii* (Kedo) McGregor (1973) displays a coarser, more elongate sculpture, which according to McGregor (1973, p. 62) is 13-68μm in length. *Grandispora cornuta* Higgs (1975) is smaller (45-84μm), and displays a concentrically folded intexine. *Grandispora ?macrotuberculata* (Arkhangelskaya) McGregor (1973) is similar in overall spore size (95-181μm) but displays somewhat shorter, predominantly biform sculpture (≤2-7μm long), that may be concentrated over the distal polar region. *Grandispora eximia* (Allen) McGregor & Camfield (1982) is similar in size but displays somewhat smaller, more irregular and attenuate sculpture.

Grandispora aff. *echinata* Hacquebard.
Plate 3.20, fig. 7.

aff. 1957 *Grandispora echinata* Hacquebard, p. 317, Pl. 3, fig. 17.

Description. Trilete, camerate miospores; amb subcircular to rounded-convex triangular. The exoexine is laevigate, scabrate to finely granulose, ≤2.25μm thick equatorially and rarely folded. The intexine is either conformable with the outline of the exoexine, or appears more distinctly circular.

The intexinal body is laevigate, and barely perceptible, diffuse or distinct, ≤1μm in thickness: may display subtle, concentric compressional folds equatorially. The suturae are distinct to barely discernible, straight and extend 4/5 to the full radius of the intexinal body: the suturae are simple, or ±partially obscured by flexuous labra, ≤7.5μm in width and height, which may taper towards the equatorial margin. The laesurae are very occasionally terminated by curvaturae imperfectae. The equatorial and distal regions display discrete, subdued spinae and coni: elements typically ≤0.5-3.25μm in height, tapering from a slightly expanded base ≤3.5μm in diameter. 12 to 26 elements project at the equatorial margin, and are ≤4-12μm apart over the distal surface.

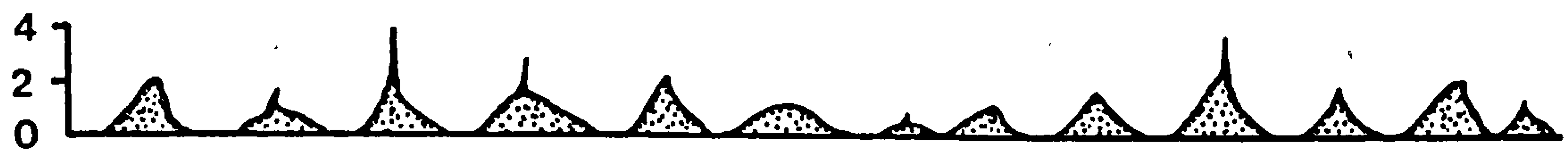


Figure 3.3.68: Sculptural elements of *Grandispora* aff. *echinata*, lateral view.

Occurrence. K, M; *very rare.*

Remarks. The size and sculptural organisation described for *Grandispora echinata* Hacquebard (1957; p. 317) bears the closest resemblance to the above morphotype, although the holotype of *G. echinata* Hacquebard (1957; Pl. 3, fig. 17) differs somewhat qualitatively in the overall disposition and morphology of the sculpture.

The sculpture often appears fragmented, blunted, and the intexinal body faint, virtually indistinguishable.

Comparisons. *Spinozonotriletes uncatus* Hacquebard (1957, p. 316) is larger (82-148μm) and displays coarser sculpture, 4-15μm in length. *Grandispora diamphida* Allen (1965) is similar in overall spore size, and comparable in the occasional scarcity of ornament, but differs primarily in exhibiting coarse, robust sculptural elements (3-10μm in length). *Grandispora tenuispinosa* (Hacquebard) Playford (1971, p. 47) is larger (103-113μm), and displays a longer, more slender sculpture, 4-16μm in length. *Grandispora microseta* (Kedo) Streel (in Becker *et* al., 1974; p. 25, Pl. 18, figs. 13-17) bears somewhat larger, more slender and spinose ornamentation (quoted as ≤5μm in length, by Streel in Becker *et al.,* 1974). *Grandispora cornuta* Higgs (1975) displays independent, concentric and arcuate compressional folds, restricted to the outer edge of the intexinal body, as well as a coarser sculpture (5-16μm in height). *Grandispora* cf. *echinata* Hacquebard in Higgs (1975; p. 399, Pl. 4, fig. 12) differs in displaying a more pronounced, discernible intexinal body and a slightly coarser, spinose sculpture, that are apparently fused at their base.

Grandispora eximia (Allen) McGregor & Camfield
Plate 3.20, figs. 9, 10.

1965 *Perotrilites eximius* Allen, p. 731, Pl. 102, figs. 11-13.
1982 *Grandispora eximia* (Allen) McGregor & Camfield, p. 44, Pl. 10, figs. 2, 6, 7, text-fig. 64.
1989 *Samarisporites eximius* (Allen) Loboziak & Streel, p. 193, Pl. IV, figs.1-4, Pl.IX, figs.5-7.

Description. Trilete camerate miospores; amb circular to convex triangular. The intexine appears enlarged relative to the exoexine, and conformable in outline with the spore circumference. The suturae are distinct, straight or tightly sinuous, and extend 4/5 to the full radius of the spore: appear simple or partially obscured by labra, which are ≤12μm in width and height at the proximal pole, ±tapering towards the equatorial margin. Either these labra or alternatively simple "radial folds" of the exoexine (which parallel the trilete rays) tend to propagate the laesurae almost to the equatorial margin. The intexine is distinct, laevigate to scabrate, and comparatively rigid, robust in appearance; usually ≤2μm thick equatorially. The exoexine ranges up to 4.75μm in thickness (usually ≤1-2.75μm), and appears laevigate, scabrate or sparsely granulose: ornamented equatorially and distally with a diversity of sculptural elements. The sculpture comprises bulbous coni and verrucae, slender, attenuate, spinae and pila, with rare broad-based mammae: most sculptural elements are either terminated by a fine, acuminate, ciliate tip, or conversely (and more rare), display a blunted, ?bifurcate termination. The sculpture ranges in height from ≤2μm to 8.25μm, typically ≤6μm, and ≤4μm in basal diameter. Elements are discrete, ≤2-16μm apart: overall the exoexine appears sparsely sculptured.

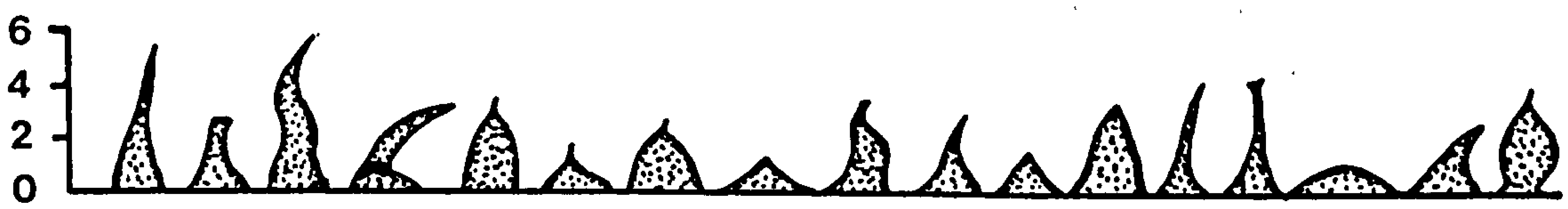


Figure 3.3.69: Sculptural variation on *Grandispora eximia*, lateral view.

Dimensions. 118-167μm, mean 158μm; intexinal body diameter 78-148μm (10 specimens measured). Diameter of the intexine 66-89% of the total spore diameter.

Occurrence. LN; *rare*. S; *R*.

Remarks. Sculptural morphology proved notably diverse, even on single specimens, as well as appearing extremely sparse (*e.g.* refer to Pl. 3.20, fig. 9 herein).

Comparisons. *Grandispora diamphida* Allen (1965) and *G. cornuta* Higgs (1975) are smaller and display a coarser, more regular and robust sculpture. *Grandispora douglastownense* McGregor (1973) and *G. naumovii* (Kedo) McGregor (1973) are similar in size, but display larger sculptural elements. *G. ?macrotuberculata* (Arkhangelskaya) McGregor & Camfield (1976) displays more bulbous, less attenuate and irregular sculptural elements.

Refer also to McGregor & Camfield (1982, p. 44) for additional comparisons.

Grandispora libyensis Moreau-Benoit
Plate 3.20, figs. 6, 11.

1969 *Hymenozonotriletes* sp. no. 2388, no. 2979., Lanzoni and Magloire, Pl VII, fig. 19, Pl.VIII, fig. 1, 4, 5.

1980 *Grandispora libyensis* Moreau-Benoit, p. 33-34, Pl. 11, fig. 2, 3.

1985 *Grandispora libyensis* Moreau-Benoit, in Paris *et al.*, Pl. 24, fig. 7.

1988 *Grandispora libyensis* Moreau-Benoit, in Loboziak, Streel & Burjack, Pl. V, fig. 16.

1988 *Grandispora megaformis* (Richardson) McGregor, in Loboziak, Streel and Burjack, Pl. IV, fig. 1.

? 1988 *Grandispora libyensis* Moreau-Benoit, in Boumendjel, Loboziak, Paris, Steemans, and Streel, Pl. 2, fig. 1.

1989 *Grandispora libyensis* Moreau-Benoit, in Coquel & Latreche, Pl. 2, fig. 13.

1989 *Grandispora libyensis* Moreau-Benoit, in Loboziak & Streel, Pl.VII, fig. 3.; Pl.IX, fig. 25.

1989 *Spinozonotriletes libyensis* (Moreau-Benoit) Coquel & Moreau-Benoit, p. 96, 98, Pl. 3, fig. 5; Pl. 4, fig. 3.

Description. Trilete, camerate miospores; amb convex triangular to distinctly triangular. The intexinal body is usually more rounded-subtriangular to clearly circular in outline, relative to the exoexine. The laesurae are distinct, extending 7/8 to 1/1 the spore radius: the suturae are straight, rarely openly arcuate and occasionally simple, although are typically obscured by ±pronounced, robust or thin-flexuous labra. The labra are ≤11μm wide and high at the proximal pole, tapering to simple terminations at the spore circumference. The intexine is laevigate to coarsely scabrate, ≤?1.5μm thick (optically dense) and very rarely displays concentric folds. The exoexine is laevigate, scabrate to finely granulose, appears rigid and lacks compressional folds. The exoexine displays a comparatively regular, thickened equatorial margin, ≤8.25μm wide: in contrast the exoexine over the polar regions appears comparatively thin, ≤?3μm. The proximal surface lacks pronounced sculptured. The equatorial and distal regions display robust and bulbous coni, attenuate spinae, and a diversity of biform elements including rare mammae. At the equatorial margin, the sculptural elements are ≤8.25μm in height (usually 3-6μm) and ≤4.5μm in basal diameter: elements may be constricted midpoint or towards the element base. Biform elements are the principal type of sculpture, comprising a verrucose, baculate, conate, or spinose base, which in turn are surmounted by a grana or ciliate, capitate spine - rarely blunted or bifurcate-tipped. Usually, the ornament is clearly differentiated between the equatorial and distal regions, being notably finer over the distal surface: ≤3.25μm in width and height.

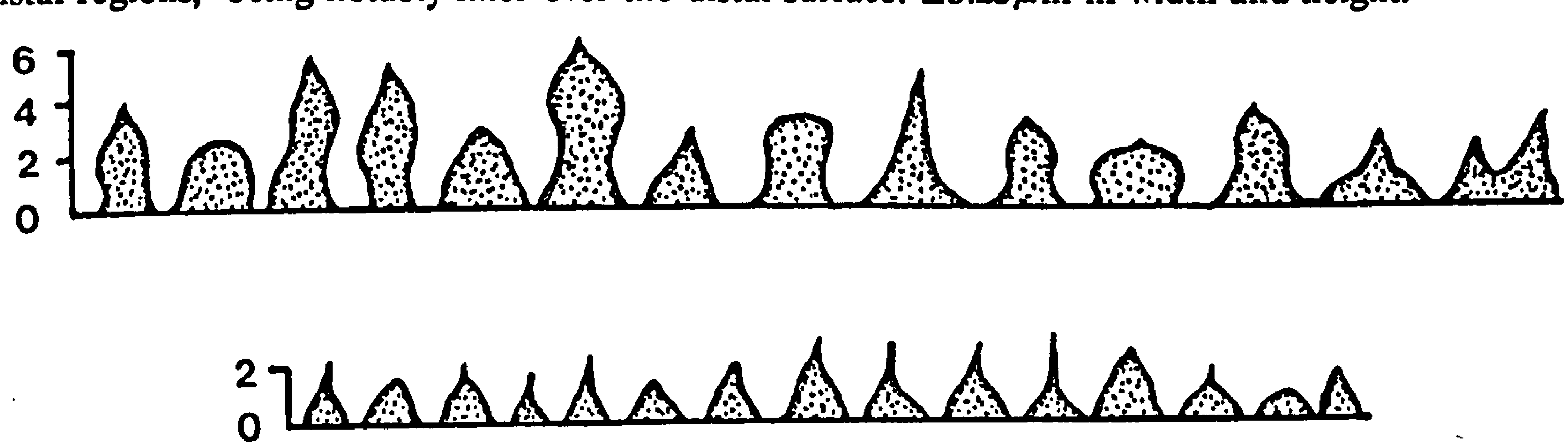


Figure 3.3.70: Sculptural elements of *Grandispora libyensis*, lateral elevation: the top row illustrates the typical sculpture that projects equatorially, whereas the bottom row represents the more usual sculpture that adorns the distal surface.

Dimensions. Exoexine diameter 114-164μm, mean 126μm. Intexinal diameter 61-96μm, mean 86μm (20 specimens measured). Diameter of the intexinal body 48-70% (mean 57%) of the total spore diameter.

Occurrence. S; *common.* H, R, LH, WP, L; *rare.*

Remarks. The recently proposed new combination of *libyensis* by Coquel & Moreau-Benoit, assigns this species to *Spinozonotriletes:* this interpretation is not upheld in the present study (refer to the earlier discussion of the genus).

Specimens of *Grandispora libyensis* were commonly fragmented, rarely recovered complete.

Comparisons. *Grandispora megaformis* (Richardson) McGregor (1973), *G. douglastownense* McGregor (1973) and *G. ?macrotuberculata* (Arkhangelskaya) McGregor (1973) are similar in overall spore diameter and/or sculptural morphology. *Grandispora libyensis* is distinguishable largely by the rigidity and equatorial thickening of the exoexine, and the comparatively even sculptural cover over the distal surface.

Grandispora naumovii (Kedo) McGregor.

Plate 3.21, fig. XX

1955 *Archaeotriletes naumovii* Kedo, Pl. 4, fig. 8.

1965 *?Spinozonotriletes* cf. *naumovii* (Kedo) Richardson, p. 583, Pl. 92, figs. 3-5, text-fig. 7.

1966 *?Spinozonotriletes* cf. *naumovii* (Kedo) Richardson, in McGregor & Owens, Pl.VII, fig.5.

1973 *Grandispora ?naumovii* (Kedo) McGregor, p.61-62, Pl. 9, figs. 1-3.

1982 *Grandispora ?naumovii* (Kedo) McGregor, in Marshall & Allen p. 291-292, Pl. 32, fig. 5.

1986 *Grandispora naumovii* (Kedo) McGregor, in Richardson & McGregor, p. 15, Pl.13, fig.1.

1988 *Grandispora naumovae* (Kedo) McGregor, in Balme, p. 138-139, Pl. 8, figs. 5-7.

non 1989 *Grandispora naumovii* (Kedo) McGregor, in Loboziak & Streel, Pl. VII, fig. 2.

For further suggested synonymies refer to McGregor 1973, p.61.

Description. Trilete camerate miospores, amb circular, subcircular to convex subtriangular. The intexine is ≈concentric with the exoexinal outline. When discernible, the suturae are straight to openly arcuate, being confined to the central body, and extending 3/4 to the full radius of the intexine. The suturae may be bordered either by robust, thickened or conversely flexuous labra, ≤2-7μm in total width and height at the proximal pole (usually ≈3.5-4.75μm), ±tapering equatorially and which may propagate the trilete rays almost to the spore circumference. The terminations of the laesurae are simple, non-curvaturate. The intexine is laevigate to finely scabrate, and commonly opaque (rarely oxidised, ?suggesting a somewhat greater thickness than the exoexine): concentric folds are rare. The exoexine is ≤2.5-4.75μm thick equatorially, seemingly ?limbate (in part): may either display indiscriminant radial and/or concentric folds, or conversely may appear comparatively robust. The exoexine is laevigate, scabrate or shagreenate in appearance, on occasion sparsely granulose in texture (grana ≤1μm; commonly obvious at the junction where the sculptural elements fuse with the exoexine). The proximo-equatorial and distal regions display stout, robust, and elongate spines. These elements are commonly laevigate, parallel-sided, or taper gradually to a fine, acuminate tip from a bulbous, laterally expanded base: processes are rarely blunted (unless fragmented), and may appear constricted towards their base. The sculpture varies in length between ≤5μm and 38μm (usually 15-25μm) and 4-8μm in basal diameter (rarely exceeds 9μm). Subordinate spinae and/or coni (≤3.5μm in height) may be interspersed amongst the coarser elements. The sculptural elements are 2-18μm apart, usually ≈10μm, and appear comparatively even and well spaced over the exoexine. Some specimens display a subtle concentration of ornamentation towards the equatorial margin. Between 16 and 38 coarse processes commonly project at the equatorial margin.

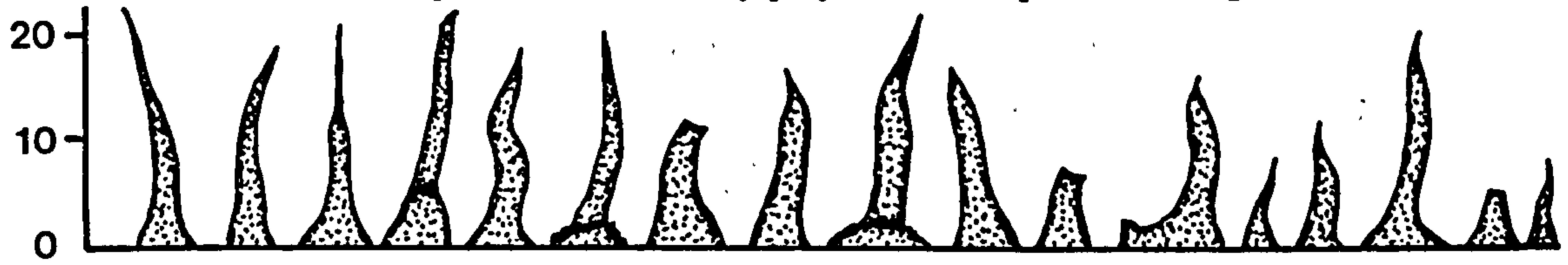


Figure 3.3.71: Sculptural elements of *Grandispora naumovii*, lateral view.

Dimensions. Maximum exoexine diameter 81-142μm, mean 103μm; intexinal body diameter 43-95μm, mean 63μm (35 specimens measured). Diameter of the intexinal body 53-86% (mean 62%) of the total spore diameter.

Occurrence. S, CM; *rare.* LH, WP, L, K; *very rare.*

Remarks. The opacity of the intexine often limited resolution of haptotypic characteristics. Specimens recovered from north Devon were slightly smaller in size than those documented by McGregor (1973) from Eastern Gaspé, Canada.

Comparisons. *Grandispora megaformis* (Richardson) McGregor (1973) displays a more subdued, bulbous sculpture, which is enlarged towards the distal pole. *Grandispora douglastownense* McGregor (1973) is comparable in overall spore dimensions, but as McGregor (1973, p. 63) remarked, consistently displays smaller ornamentation. *Grandispora diamphida* Allen (1965) and *Calyptosporites pilaspinosus* Lanninger (1968) are smaller in overall spore diameter and sculptural dimensions. *Grandispora longa* Chi & Hills (1976) *sensu* McGregor & Camfield (1982, p. 45) differs in displaying a far greater range in sculptural morphology. The sculptural elements of *Grandispora variospinosa* McGregor & Camfield (1982) rarely exceed 12μm in length, and furthermore tend to be concentrated over the distal polar region.

Grandispora protea "complex".

Two distinct morphotypes of *Grandispora protea* were differentiated in the present study. In essence *Grandispora protea* and *G.* cf. *protea* are identical in basic spore construction and also in the gross morphology of the sculptural elements, but were distinguished primarily on disparities in maximum spore diameter (*G.* cf. *protea* is notably smaller). Few specimens were recovered from north Devon intermediate in size between these two populations, thus justifying the differentiation of these two taxa (note remarks made below, under *G.* cf. *protea* below). However, if these two morphotypes prove synonymous, then the size range of *Grandispora protea, sensu stricto,* will have to be altered accordingly.

Grandispora protea (Naumova) Moreau-Benoit.

Plate 3.21, fig. 5.

1953 *Hymenozonotriletes proteus* Naumova, p. 40 Pl. IV, fig. 5.

1965 *Calyptosporites proteus* (Naumova) Allen, p.735, Pl. 103, figs. 10, 11.

1980 *Grandispora protea* (Naumova) Moreau-Benoit, p. 37, Pl. 11, fig. 6.

1982 *Grandispora protea* (Naumova) Moreau-Benoit, in McGregor & Camfield, p. 46-47, Pl. 11, fig. 10; Pl. 12, fig. 1, text-figure 70.

p 1982 *Grandispora protea* (Naumova) Moreau-Benoit, in Marshall & Allen, p.292, Pl.32, figs.3,4.

? 1985 *Calyptosporites proteus* (Kedo) Allen, in Paris *et al.*, Pl. 25, fig. 3.

1988 *Grandispora protea* (Naumova) Moreau-Benoit, in Loboziak, Streel & Burjack, Pl. VI, fig.1.

1989 *Grandispora protea* (Naumova) Moreau-Benoit, in Loboziak & Streel, Pl. VI, figs. 5,6; Pl. IX, figs. 21, 22.

Description. Trilete, camerate miospores; amb oval, circular to convex subtriangular. Intexinal body is usually conformable with the equatorial margin, although on occasion may appear more rounded in outline. The suturae are distinct, straight, openly arcuate or "ragged", and extend 2/3 to in excess of 7/8 the spore radius. The suturae may be simple, although are usually paralleled or indeed obscured by pronounced labra, ≤8μm in width and height at proximal pole: taper towards the equatorial margin. The contact areas are laevigate to scabrate, and lack pronounced sculpture. Both intexine and exoexine are distinct, laevigate to finely scabrate and range between ≤1μm and 3.25μm in thickness equatorially. The equatorial and distal regions display a distinct, discrete and comparatively subdued sculpture, comprising squat coni, verrucae, and biform elements; spinae are rare. The biform elements may comprise mammae or incorporate a conate, verrucate or baculate base, which in turn is surmounted by a either a fine, ciliate (hair-like) attenuate spine, grana or (rare) subtle bifurcation, ≤0.75μm. The sculpture is usually ≤2.25-4.5μm in height (rarely exceeds 6μm), and ≤2.5μm in basal diameter: squat verrucae may range up to 3.5μm in basal width. These elements are even to irregular in their distribution over the exoexine, and are ≤2-11μm apart. In general the ornament appears ≈constant in size and disposition on a single specimen. The two exinal layers may be variably distorted (±independent of one another) by concentric and/or radial folds, or appear "wrinkled".

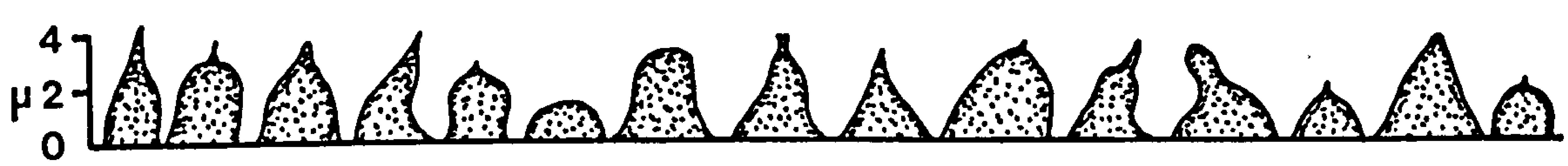


Figure 3.3.72: Sculptural elements of *Grandispora protea*, lateral view.

Dimensions. Maximum spore diameter 103-164μm, mean 118μm; maximum intexinal body diameter 57-95μm, mean 72μm (22 specimens measured). Diameter of the intexinal body 46-72% (mean 62%) of the total spore diameter.

Occurrence. LN, S; *common.* H, R, LH; *rare.*

Remarks. McGregor & Camfield (1982, p. 48) remarked upon the morphological intergradation between *Grandispora protea* (Naumova) Moreau-Benoit and forms of *Grandispora velata* (Eisenack) Playford which display a coarse, enlarged sculpture (for a detailed discussion, refer to the remarks made under *G. velata* herein). Similar observations were noted for the *Grandispora* population detailed from north Devon.

Comparisons. *Hymenozonotriletes Krestovnikovii* Naumova (1953, p. 67, Pl. IX, fig.7) is smaller (diameter 90-100μm) than *Grandispora protea* (Naumova) Moreau-Benoit (1980; 110-170μm in diameter, from Allen, 1965, p.735). Apart from this taxon, very few species of large *Grandispora* display such a fine, but bulbous, diminutive ornament: *G. velata* is the closest affiliated form to *Grandispora protea,* but differs in displaying a finer, more attenuate, and principally spinose sculpture. *Samarisporites* sp. D of Streel (1967) bears a resemblance to *G. protea,* but is interpreted as cingulate in construction, and not pseudosaccate. The ornamentation of *Grandispora eximia* (Allen) McGregor & Camfield (1982) is more variable in form.

For further comparisons refer to *G. protea* in McGregor & Camfield (1982, p. 47), and also *Grandispora* cf. *protea* (herein).

Grandispora cf. *protea.*
Plate 3.21, fig. 4.

cf. 1980 *Grandispora protea* (Naumova) Moreau-Benoit, p. 37, Pl. 11, fig. 6.
p 1982 *Grandispora protea* (Naumova) Moreau-Benoit, in Marshall & Allen, p. 292.

Description. Trilete, camerate miospores; amb oval, circular to (rarely) convex-subtriangular. The intexine is distinct, laevigate to coarsely scabrate, ≤1.5μm in thickness and generally conformable in outline with the equatorial margin. The laesurae are straight, openly arcuate to ragged, extending 2/3 to the full radius of the spore, and very occasionally terminated by curvaturae imperfectae. In general the suturae are simple, although may be paralleled or partially obscured by labra, which are ≤2.5μm in total width and height. The laesurae appear comparatively uniform in width, or may taper towards the spore circumference. The exoexine is typically ≤2.25μm thick equatorially, laevigate to finely scabrate and lacking proximal sculpture. The proximo-equatorial and distal regions are evenly sculptured with simple, bulbous coni, biform coni or rare, squat mammae and spinae: elements are ≤1.75-3.5μm in width and height (rarely exceed 4μm). The biform coni are surmounted by a small, attenuate, ciliate spine, ≤0.5μm in height. Elements are typically ≤1.5-6μm apart, rarely greater than 10μm: overall, the sculpture appears comparatively sparse. The intexine and exoexine may display occasional compressional folds.

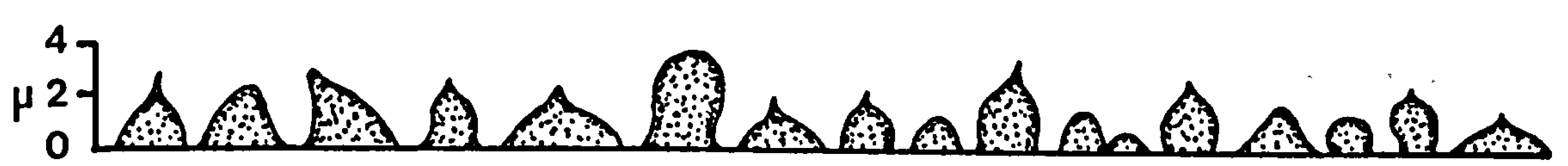


Figure 3.3.73: Sculptural elements of *Grandispora* cf. *protea*, lateral elevation.

Dimensions. Maximum exoexinal diameter 56-89μm, mean 71μm; intexinal diameter 33-61μm, mean

$53\mu m$ (40 specimens measured). Diameter of the intexinal body 52-87% (mean 67%) of the total spore diameter.

Occurrence. LN; *common.* H, S; *rare.*

Remarks. *Grandispora protea*, *sensu stricto*, is an important zonal species: the inception of this taxon delineates the base of the Pro Interval Zone, *sensu* Streel *et al.* (1987). If the circumscription of this taxon were emended to accommodate spores of a much smaller size (as noted for *G.* cf. *protea* herein), then the biostratigraphical utility of this fossil may be impaired. Thus, these two species of *Grandispora protea* are differentiated, primarily due to the disparity in overall spore size: otherwise, the two are acknowledged to be morphologically identical.

Comparisons. The line drawings of *Hymenozonotriletes Krestovnikovii* Naumova (1953; p. 67, Pl. IX, fig. 7 - orthography follows that of Naumova) appears very similar to *Grandispora* cf. *protea*, but according to the size specifications provided by Naumova, is (somewhat arbitrarily) slightly larger in size (90-$100\mu m$). *Grandispora echinata* Hacquebard (1957) displays a more rigid, less voluminous camera. *Grandispora inculta* Allen (1965, p. 734) exhibits a denser, smaller and more subdued conate ornament, $\leq$1-$2\mu m$ in height. *Grandispora tomentosa* Taugourdeau-Lantz (1967) and *Grandispora* sp. E (of the present study) are approximately similar in size, but display a slightly coarser biform sculpture, that comprises long, slender, attenuate spinae, surmounted upon verrucate bases. *Grandispora protea* (Naumova) Moreau-Benoit (1980) is substantially larger in overall spore diameter, but similar in all other respects. *Grandispora rarispinosa* Massa & Moreau-Benoit ex Moreau-Benoit (1980, p. 38) is marginally larger in size (86-$110\mu m$), with a somewhat smaller intexine to exoexine ratio (48-62%) and notably more flexuous labra: the equatorial margin of *G. rarispinosa* is openly dentate, but otherwise the sculpture is comparable in disposition and size to that of *G.* cf. *protea*. *Grandispora* aff. *echinata* (of the present study) is broadly similar, but displays a less pronounced sculpture and a more diffuse intexinal body: the two species are also stratigraphically discrete. *Grandispora* sp. F and *Grandispora* sp. G (of the present study) are similar in size, but display a more diminutive, predominantly spinose, and less bulbous sculpture.

Grandispora saetosa Clayton & Graham
Plate 3.21, fig. 6.

1974 *Grandispora saetosa* Clayton & Graham, p.578, Pl. III, figs. 12-14.
1981 *Grandispora saetosa* Clayton & Graham, in Higgs & Russell, p. 29, Pl. 3, figs. 1-3.

Description. Trilete, camerate miospores; amb subcircular to well rounded. Suturae are distinct to diffuse, straight to openly arcuate, and may be simple or accompanied by thin labra, $\leq 2.25\mu m$ in total width. The laesurae commonly extend 3/4 to the full radius of the intexinal body, or may propagate just beyond the margin of the intexine: are terminated by faint curvaturae imperfectae. The contact areas are ill-defined, scabrate to finely granulose, and lacking pronounced sculpture. The intexine is $\leq 1.5\mu m$ thick, optically dense and may display concentric folds, preferentially developed at the equatorial margin: the intexinal body is commonly eccentric in disposition, relative to the spore circumference. The exoexine appears comparatively thin, membraneous, ≤?1μm equatorially, and ?limbate in part (≤2.5μm). The exoexine is scabrate to finely granulose in texture and densely sculptured proximo-equatorially and distally with small bacula, subordinate coni and pila: elements are ≤1.25-2.25μm in length (rarely exceed 3μm), 0.5-1.25μm in basal diameter, and discrete (typically 0.5-2μm apart). The sculpture usually appears orientated towards the equator, "radiating" away from the distal polar region.

Figure 3.3.74: Sculptural elements of *Grandispora saetosa*, lateral view.

Dimensions. Maximum exoexinal diameter 47-61μm mean 58μm; intexine 32-35μm, mean 33μm (4 specimens measured). Diameter of the intexinal body is 55-69% of the total spore diameter.

Remarks. Attachment of the two exinal layers appears confined to a restricted area over the proximal surface: in accordance with the observations of Clayton & Graham (1974, p. 578). This may explain the common eccentricity of the intexinal body relative to the exoexine outline.

Comparisons. The sculpture on similar, finely sculptured species of *Grandispora* (*e.g. G. echinata* Hacquebard, *G. gracilis* (Kedo) Streel, and *G. inculta* Allen) is not as visibly "orientated" as is apparent on *G. saetosa*. *Geminospora spinosa* Allen (1965, p. 697) is similar in the disposition of the sculpture (being appressed to the exoexine, so as to appear "orientated"), but displays a preferentially thickened exoexine and a coarser, spinose sculpture (elements 3-6μm long).

Grandispora tomentosa Taugourdeau-Lantz.
Plate 3.21, fig. fig. 7.

1967 *Grandispora tomentosa* Taugourdeau-Lantz, p. 53-54, Pl. 1, figs. 7, 8.
? 1971 *Grandispora tomentosa* Taugourdeau-Lantz, in Taugourdeau-Lantz, p. 49, Pl. VIII, fig.9.
? 1972 *Grandispora tomentosa* Taugourdeau-Lantz, in Mortimer & Chaloner, p. 38, Pl.VII, fig.2.
1976 *Grandispora tomentosa* Taugourdeau-Lantz, in McGregor & Camfield, p. 24, Pl. 6, figs. 4, 5, 8.
1976 *Grandispora spinosa* Hoffmeister, Staplin & Malloy, in Massa & Moreau-Benoit, Pl. 5, fig. 5.
1980 *Grandispora tomentosa* Taugourdeau-Lantz, in Loboziak & Streel, Pl. III, figs. 5, 6.
1981 *Grandispora tomentosa* Taugourdeau-Lantz, in Higgs & Russell, p. 29, Pl. 3 figs. 13, 14.
? 1988 *Grandispora tomentosa* Taugourdeau-Lantz, in Loboziak, Streel & Burjack Pl. V, fig. 14.

Description. Trilete, camerate-?zonate miospores; amb subcircular to rounded convex triangular. The suturae are straight to openly arcuate, and obscured by ±thin, flexuous, sinuous labra, ≤4.75μm in width and height. The laesurae extend 3/4 to the full radius of the spore, commonly tapering towards the equatorial margin: may be terminated by curvaturae imperfectae. The intexine is distinct, ≤2μm in thickness, and appears ≈conformable with the outline of the exoexine: the intexine is laevigate to faintly ?scabrate in texture. The exoexine is scabrate to finely granulose, seemingly rigid and robust (rarely folded) and ≤1.5μm thick equatorially. The proximal surface lacks pronounced sculpture: the equatorial and distal regions display a distinct ornament, comprising broad based coni, and/or elongate, attenuate spinae which develop from an enlarged, laterally expansive, verrucose base. Elements are ≤2-6.5μm in height (rarely exceed 8μm) and usually ≤2.75μm in basal diameter: in plan view are subcircular to ovate in basal outline. The sculptural elements are discrete, ≤2-8μm apart, although very occasionally two or three adjacent elements may fuse into irregular and ill-defined, short cristae.

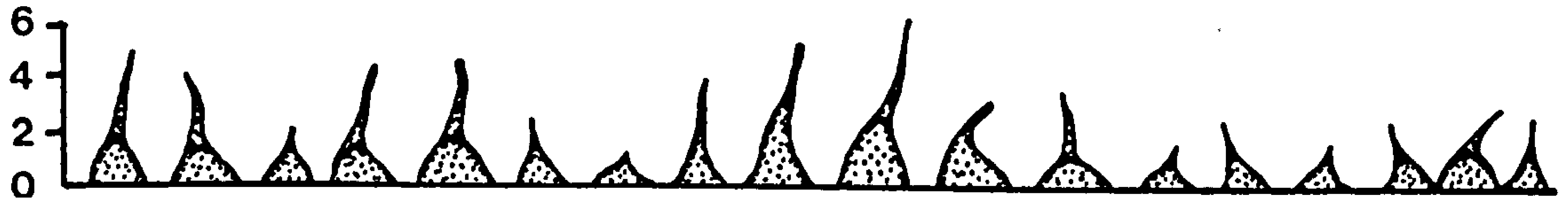


Figure 3.3.75: Sculptural elements of *Grandispora tomentosa*, lateral view.

Dimensions. 57-69μm, mean 64μm; diameter of intexinal body 41-55μm, mean 49μm (6 specimens measured). Diameter of the intexinal body 72-84% of the total spore diameter.

Occurrence. K, M; *very rare.*

Remarks. *Grandispora tomentosa* is a typical constituent of Frasnian assemblages. Taugourdeau-Lantz (1967, 1971) and Loboziak & Streel (1980) record this species from Frasnian strata of the Boulonnais (France). Mortimer & Chaloner (1972) recovered this species from subsurface Frasnian sediments in the Wyboston Borehole, southern England. McGregor & Camfield (1976) subsequently documented *G. tomentosa* from the Middle Devonian of the Moose River Basin, Ontario, Canada. More recently, Higgs & Russell (1981) have recorded this species from the Upper Devonian of County Kerry, Ireland. The recovery of *Grandispora tomentosa* from north Devon accords with earlier reports from Frasnian strata, and qualifies the Frasnian age interpreted for the Kentisbury and Morte Slates of north Devon.

The size specifications of the population of *Grandispora tomentosa* documented herein are more compatible with the measurements quoted by Taugourdeau-Lantz (1967; 55-(72)-90μm), than with those of McGregor & Camfield (1976; 87-(102)-122μm).

Comparisons. Few species resemble *Grandispora tomentosa* in overall spore size and sculptural morphology: Taugourdeau-Lantz (1967, p. 54) compared *G. tomentosa* with *G. echinata*, but considered the two distinct. *Grandispora diamphida* Allen displays a coarser, broader sculpture. *Grandispora* sp. E (of the present study) is larger, displays a thickened (?limbate) equatorial margin and a larger intexine to exoexine ratio.

Grandispora cf. *variospinosa* McGregor & Camfield
Plate 3.21, figs. 8, 9.

cf. 1982 *Grandispora variospinosa* McGregor & Camfield, p. 47-48, Pl. 12, figs. 5, 6, text-fig.73. Refer also to the synonymy of McGregor & Camfield 1982, p. 47.

Description. Trilete, camerate-?zonate miospores; subcircular, subtriangular to broadly convex triangular amb. The intexinal body is conformable with, or more rounded than, the exoexinal amb. The laesurae are distinct: the suturae are either simple, straight to openly arcuate, or obscured by prominent, flexuous labra, ≤4.5μm wide and ≤6.5μm high at the proximal pole. The laesurae extend 2/3 to the full radius of the spore, usually tapering in width towards the equatorial margin, and are simple or terminated by curvaturae imperfectae. The intexine is laevigate to faintly granulose, ≤1-3.75μm thick (?limbate), with a distinct outer edge and a diffuse inner margin. The exoexine is ≤2μm thick, with rare or minor concentric folds preferentially developed towards the equatorial margin. The exoexine projects laterally in the equatorial plane, resembling a rigid, robust "zona": however, is usually demonstrably cavate. The proximal surface lacks pronounced sculpture, whereas the equatorial and distal surfaces display a predominance of biform elements, in association with simple, slender spinae and coni, coupled with squat verrucae and rare mammae. The biform ornament comprises expanded verrucate bases, surmounted by parallel-sided bacula or attenuate spinae, which taper either to an acuminate point, or a blunted terminus: the distal tip may consist of a small cone, grana or hair-like "ciliate" spine. In lateral profile, these elements are usually constricted in at least one or more places along their length. There is a tendency for the longer, most robust elements to be concentrated towards or over the distal pole, becoming increasingly smaller and more isolated towards the equatorial margin. The sculpture ranges up to 9.25μm in length over the distal pole, although is typically 4-6.75μm in length, and 2.25-4.5μm in basal diameter (rarely 5μm). Overall, the sculptural elements are ≈2-6 times as long as wide, and may appear partially confluent at their base. The ornament towards the equatorial margin comprises biform coni, in general ≤2.5μm in width and height. Elements are ≤1-5μm apart over the distal pole, and sparser towards the spore margin: ≈4-10μm.

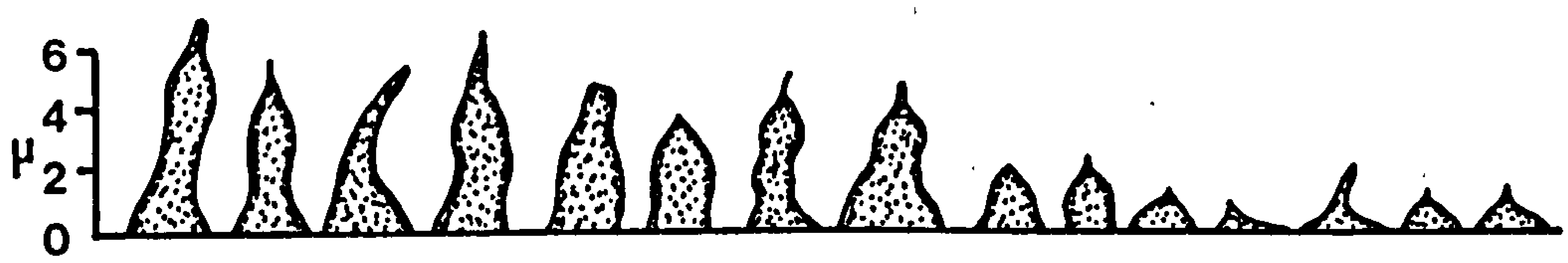


Figure 3.3.76: Sculptural elements of *Grandispora* cf. *variospinosa*, lateral view.

Dimensions. Maximum exoexinal diameter 74-106μm, mean 83μm; maximum intexinal diameter 39-63μm, mean 49μm (12 specimens measured). Diameter of the central body 52-61% of the total spore diameter.

Remarks. This species is only tentatively identified herein: *Grandispora variospinosa sensu stricto* McGregor & Camfield (1982, p. 47-48) is similar in gross morphology, but ≈larger in overall diameter (117-218μm), and displays a coarser ornament (elements ≤20μm in length). The two figured specimens (of the present study; Pl. 3.21, figs. 8, 9) represent two end members attributable to *G.* cf. *variospinosa:* as applied herein, the concept of this species encompasses enlarged variants with a notably sparse distal sculpture (that appear basally contiguous), to somewhat smaller forms which display a markedly denser, more concentrated sculpture over the distal polar region.

All specimens were recorded in polar compression.

Comparisons. *Grandispora megaformis* (Richardson) McGregor (1973) is larger and displays more robust, squat, and less elongate ornament: the sculpture is densely distributed over the distal polar region. *Calyptosporites decorus* Tiwari & Schaarschmidt (1975, p. 43-44) is slightly larger in overall diameter (90-130μm), but differs primarily in the "leathery" texture to the exoexine, and the concentration of sculptural elements around the body margin and over the distal surface (resembling a "ring" of ornament). *Grandispora longa* Chi & Hills (1976) in McGregor & Camfield (1982) is larger (145-286μm) than the complex described in the present study, and exhibits more elongate sculptural elements (≤35μm in length). *Grandispora eximia* (Allen) McGregor & Camfield (1982) is likewise larger (110-205μm) and displays a more even sculptural cover, that comprises more morphologically diverse elements.

Grandispora velata (Eisenack) Playford
Plate 3.22, figs. 1, 3.

1944 *Triletes velatus* Eisenack (pars), p.108, Pl. 1, figs. 1-3.
1960 *Cosmosporites velatus* (Eisenack) Richardson, p. 52, Pl. 14, fig. 4, text-fig. 3.
1962 *Calyptosporites velatus* (Eisenack) Richardson, p.192.
1971 *Grandispora velata* (Richardson) Playford, p.47.
1973 *Grandispora velata* (Richardson) McGregor, p.61, Pl. 8, figs. 10, 11, text-fig. 34.
1982 *Grandispora velata* (Eisenack) Playford, in McGregor & Camfield, p. 48, Pl. 12, fig. 8, text-fig. 74.
1982 *Grandispora velata* (Eisenack) Playford, in Marshall & Allen p. 292, Pl. 32, fig. 2.
? 1988 *Grandispora velata* (Eisenack) Playford, in Marshall, Fig. 3 (10).
non 1989 *Grandispora velata* (Richardson) Loboziak & Streel, p. 190, Pl. VI fig. 7; Pl. IX, fig. 23.

Description. Trilete, camerate miospores; subcircular to broadly convex triangular amb. The intexinal body may be concentric with the exoexinal outline, or appears more rounded. The laesurae extend 4/5 to the full spore radius: the suturae are indistinct, straight to openly arcuate, occasionally simple, but commonly obscured by flexuous, sinuous labra, ≤11μm in total width and height at the proximal pole. The laesurae taper uniformly to the spore circumference. The intexine is laevigate to finely scabrate, ≤2.25μm thick, and rarely distorted with concentric and/or radial compressional folds. The exoexine is laevigate, scabrate (typical) to finely granulose in texture, appearing optically thinner (≤?1.25μm thick) and more membraneous than the intexine: extends laterally in the equatorial plane as a rigid, rarely folded "flange". The proximal surface lacks ornamentation. The distal surface of the exoexine is sculptured predominantly with minute and slender spinae, coupled with subordinate grana, coni & rare biform elements: ornament commonly ≤2.25μm in height (rarely exceeds 3μm) and ≤0.75

in basal width. The majority of the sculptural elements taper to a distinct point, rarely rounded, with biform elements comprising a rounded base, surmounted by a ciliate, apical spine. The sculpture barely projects at the spore margin. Sculptural density is highly variable, ranging from very sparse (individual elements ≤8μm apart), to comparatively dense (≤1-3μm in isolation).

Figure 3.3.77: Sculptural elements of *Grandispora velata*, lateral elevation.

Dimensions. Maximum exoexinal diameter 102-146μm, mean 119μm; diameter of central body 48-86μm, mean 65μm (55 specimens measured). Diameter of the intexinal body 41-69% (mean 59%) of the total spore diameter.

Occurrence. S, WP; *common*. R, LH, L, CM, K; *rare.*

Remarks. McGregor and Camfield (1982, p.47, 48) remarked on the morphological intergradation between *Grandispora velata* and *G. protea*. *Grandispora protea* is perceived to display larger, more rounded and bulbous sculptural elements, whereas *G. velata* bears more pointed, attenuate elements. Forms intergradational between these two complexes were recorded from north Devon.

As with the *Grandispora protea* complex, two variants of *G. velata* are distinguished herein: *G. velata* and *G.* cf. *velata* differed primarily in overall spore diameter, with basic spore construction and sculptural morphology/density virtually identical.

Comparison. Few species of *Grandispora* resemble *G. velata*, that is in being so large but displaying such a sparse, diminutive spinose sculpture. *Grandispora inculta* Allen (1965) and *G. micromata* Tiwari & Schaarschmidt (1975) are both smaller, but display a predominance of conate sculpture. *Grandispora* cf. *velata* (of the present study) is smaller, and consistently displays a sparser ornament, comprising more bulbous spinae and conate elements.

Grandispora cf. *velata* (Eisenack) Playford

Plate 3.21, fig. 10.

cf. 1944 *Triletes velatus* Eisenack (pars), p.108, Pl. 1, figs. 1-3.
cf. 1960 *Cosmosporites velatus* (Eisenack) Richardson, p. 52, Pl. 14, fig. 4, text-fig. 3.
cf. 1962 *Calyptosporites velatus* (Eisenack) Richardson, p.192.
cf. 1971 *Grandispora velata* (Richardson) Playford, p.47.

Description. Trilete camerate-?zonate spores; amb subcircular, ovate, to broadly convex triangular. The suturae are simple indistinct, straight or "ragged", and extend 3/4 to the full radius of the central body: the suturae are only occasionally boarded by thin labra, which individually are ≤1.75μm wide, and ±taper towards the equatorial margin. The labra may propagate the laesurae beyond the intexine, almost to the equatorial margin. The intexine is generally conformable in outline with the exoexinal amb, appears laevigate and ≤1μm thick equatorially. Concentric folds (≤4.25μm wide) commonly develop at the equatorial margin of the intexine: ?limbate. The exoexine extends laterally in the equatorial plane and may appear single layered, resembling a ?zona. The exoexine is laevigate to finely scabrate, thin (thickness usually uncertain, ≤?0.5μm) and sculptured distally with distinct, discrete and subdued ≈bulbous coni, or (typically) attenuate, slender spinae. Sculptural elements are usually ≤1-1.25μm in height (rarely exceed 2μm), ≤1.5μm in basal diameter and evenly distributed, typically 5-11μm apart (rarely ≤3μm, or greater than 15μm in isolation). Elements are barely discernible at the equatorial margin: overall may be so scarce that the distal surface appears unsculptured.

Figure 3.3.78: Sculptural elements of *Grandispora* cf. *velata*, lateral elevation.

Dimensions. Maximum exoexinal diameter 74-92μm, mean 86μm; maximum intexinal diameter 42-58μm, mean 50μm (8 specimens measured). Diameter of the intexinal body 49-64% of the total spore diameter.

Occurrence. LN, H; *very rare.*

Remarks. This form is differentiated from *Grandispora protea*, *Grandispora* cf. *protea*, and *Grandispora velata* (all of the present study), despite some striking morphological similarities with all three species. The sculpture that adorns *Grandispora* cf. *velata* is transitional in morphology between that of *Grandispora protea* and *Grandispora velata, sensu stricto,* comprising both slender subdued "*velata*-type" spinae and more robust, squat "*protea*-type" coni. Indeed, *G.* cf. *velata* (of the present study) resembles the transitional "*protea-velata*" morphotype figured by McGregor & Camfield (1982, Pl. 11, fig.10) from the Canadian Arctic, although this form is larger (≈126μm in diameter) and the sculpture seemingly more robust and bulbous.

In present study, *Grandispora* cf. *velata* has a rare, restricted occurrence, being confined to the upper Lynton Formation and the palyniferous Hollowbrook Formation. *Grandispora velata, sensu stricto* (Eisenack) Playford is a key zonal taxon utilised by both Richardson & McGregor (1986) and Streel *et al.* (1987): the inception of this taxon may verify an early Eifelian age interpretation. The ambiguous, "gradational" morphology exhibited by *Grandispora* cf. *velata* (described herein), merited this tentative identification, particularly in view of the biostratigraphical significance attached to the occurrence of *Grandispora velata, sensu stricto.*

The proximal surface of *Grandispora* cf. *velata* may appear faintly "striated"/folded, with short radial folds preferentially developed at the "junction" between the intexine and exoexine.

Comparisons. *Grandispora protea* is larger and displays a more bulbous, predominantly conate sculpture. *Grandispora velata* is likewise larger, and exhibits a predominance of slender, spinose sculptural elements. The ornamentation of both *Grandispora echinata* Hacquebard (1957) and *Grandispora tenuispinosa* (Hacquebard) Playford (1971) is coarser an more elongate. *Grandispora* *inculta* Allen (1965) is similar in overall spore size (51-86μm), but bears a notably dense conate sculptural cover. (Also refer to the comparisons listed earlier under *Grandispora* cf. *protea*).

Grandispora sp. A.
Plate 3.22, figs. 5, 6.

Description. Trilete, camerate-?zonate miospores; amb subcircular to rounded convex-triangular. The suturae are indistinct, straight and obscured by thickened, robust labra: the labra are $\leq 7\mu$m high and wide at the proximal pole, and taper $\pm$uniformly towards the equatorial margin. The laesurae extend 4/5 to the full radius of the spore, and very occasionally are terminated by curvaturae imperfectae. The intexine is usually diffuse, barely perceptible, and notably thin ($\leq$?0.75μm), appearing ?laevigate and conformable in outline with the equatorial margin. The exoexine is $\leq$0.75-3μm thick equatorially, ?limbate ($\leq$7.5μm thick), and scabrate, finely granulose or shagreenate in texture: turbid in appearance. The proximal surface lacks distinct sculpture, whereas the equatorial and distal surfaces bear a pronounced biform ornament, that comprise mammae, bulbous pila, clava or baculate-conate elements; these are in turn surmounted by a coarse grana or attenuate spine. Elements are typically $\leq$2-7.25μm in length, rarely exceeding 9μm in height, and $\leq$2-4.25μm in basal diameter. The sculpture may be constricted at one or more places along their length, commonly towards the element base or below the expanded tip. One individual may display an immense diversity in sculpture. Elements are comparatively scarce, usually $\leq$6-14μm apart (rarely as much as 28μm). 12-19 elements (average 17) project et the equatorial margin.

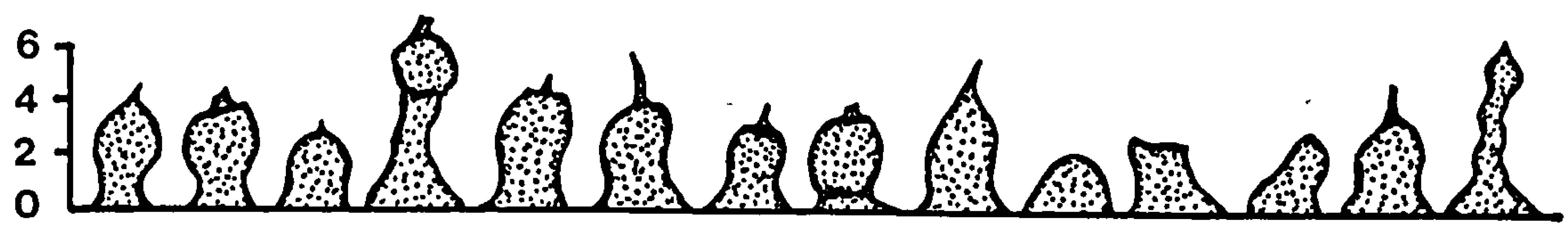


Figure 3.3.79: Sculptural elements of *Grandispora* sp. A, lateral elevation.

Dimensions. 62-79μm, mean 67μm; intexinal body 44-59μm (10 specimens measured). Diameter of the intexinal body 70-82% of the overall spore diameter.

Occurrence. LN; *rare.* R, S, LH, WP, L; very rare.

Comparisons. The combination of a robust exoexine, diffuse intexinal body and an unusual, sparse, biform sculpture distinguishes this form from all previously described species of Grandispora. cf*Archaeozonotriletes laetus*[2] Sergeeva in Richardson & McGregor (1986, Pl. 17, fig. 7) bears the closest resemblance to *Grandispora* sp. A, in exhibiting a similarly turbid, robust exoexine, and a distinct, sparse sculpture. However, the central body of cf*A. laetus* appears more diffuse and enlarged, and the ornament more attenuate-spinose.

[2] This species is "characteristic" of the Frasnian *ovalis-bulliferus* Assemblage Zone *sensu* Richardson & McGregor (1986).

Grandispora sp. B.

Plate 3.22, figs. 2, 4.

Description. Trilete camerate miospores. The laesurae are distinct; the suturae are straight, extending 3/4 to the full radius of the intexinal body. The suturae are partially or entirely obscured by robust, "ragged" labra, ≤4.25μm in total width and height: commonly taper towards the spore circumference and tend to propagate the laesurae to the equatorial margin. The trilete rays are non-curvaturate. The intexinal body is limbate, ranging up to ?2.75μm in thickness equatorially (commonly ≤1μm), appears optically dense and robust, lacking concentric and/or radial folds: the intexine is ≈conformable in outline with the spore circumference. The proximal surface lacks pronounced sculpture. The exoexine is laevigate to coarsely scabrate, ≤2μm thick equatorially and extends in the equatorial plane as a comparatively robust "flange", ≈broader radially. The equatorial and distal surfaces display a distinct to barely perceptible sculpture, comprising broad based coni, spinae and biform elements, with rare mammae and grana: ≤3.75μm in height (commonly ≤1-2.5μm), and ≤2.25μm in basal diameter. Biform elements comprise a broad spinose or conate base, surmounted by a thin capitate spine, grana or diminutive bifurcation. Elements are comparatively even in their distribution over the distal hemisphere, typically ≤2-6μm apart: very occasionally appear ≈sparser and slightly smaller towards the equatorial margin.

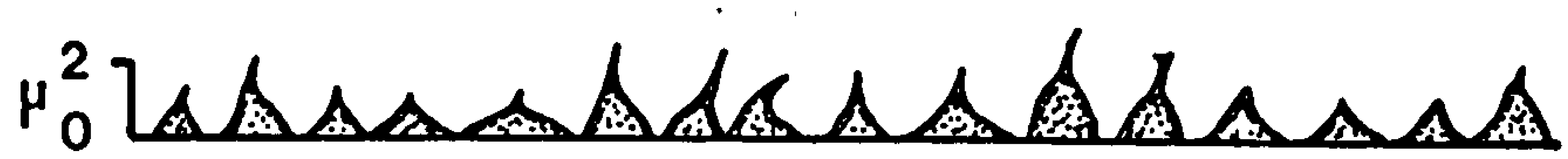


Figure 3.3.80: Sculptural elements of *Grandispora* sp. B, lateral view.

Dimensions. Maximum exoexinal diameter 67-86μm, mean 71μm; intexinal body diameter 47-69μm, mean 56μm. The diameter of the intexinal body 68-81% of the total spore diameter.

Occurrence. LN, H; *very rare.*

Remarks. Although equatorially "thickened" (≤2μm), in comparison to the rigid intexinal body the exoexine appears relatively flimsy, and is commonly fragmented, torn. The suturae are often ruptured.

Comparisons. The line drawings of *Hymenozonotriletes spinulosus* Naumova (1963; p. 63, Pl. VIII, fig. 14) are similar in overall gross morphology, sculpture and disposition of the central body. However, the equatorial margin of this Russian species is notably dentate (more intensely sculptured). Furthermore *Hymenozonotriletes spinulosus* Naumova differs in being marginally larger (100-125μm). *Grandispora echinata* Hacquebard (1957) and *Grandispora tenuispinosa* (Hacquebard) Playford (1971) display a coarser, more elongate sculpture. *Grandispora inculta* Allen (1965) displays a less rigid, more voluminous camera, and a distinctly dense, smaller, conate sculpture. *Grandispora ?macrotuberculata* (Arkhangelskaya) McGregor (1973; p. 59, Pl. 8, figs. 1-5) is larger (95-181μm), with a smaller intexine to exoexine ratio (≈50-66%) and bears a slightly coarser, more bulbous and varied sculpture. *Grandispora riegelii* Loboziak & Streel (1989; p. 190, Pl. V, figs. 1-5, Pl. IX, figs. 10-13) is larger (80-120μm) and exhibits a denser, more varied sculpture. The ornament that adorns *G.*

gabesensis is coarser, more elongate.

Grandispora cf. *velata* (of the present study) displays a sparser, finer and more diminutive sculpture. *Grandispora* sp. D (of the present study) bears a coarser ornament and a more robust, optically dense camera. *Grandispora* sp. E (of the present study) is larger, with a thicker, scabrate and more turbid exoexine, but more significantly displays a substantially enlarged, coarser, spinose sculpture.

Grandispora sp. C

Plate 3.22, fig. 7.

Description. Trilete, camerate miospores; amb broadly subcircular to ovate. The intexinal body is circular to subcircular in outline, and usually appears markedly eccentric in its disposition relative to the exoexinal amb. The laesurae are indistinct: the suturae straight, "ragged", extending 2/3 to 3/4 the total spore radius and occasionally paralleled by subtle, diffuse labra, ≤3μm in total width. The contact areas are ill-defined, lacking pronounced sculpture or curvaturate ridges. The intexinal body is robust, laevigate to finely scabrate and ≤2μm thick equatorially. The exoexine extends as a voluminous camera, and may be indiscriminately distorted by two to four radial/concentric folds: the exoexine is ≤2.75μm thick equatorially, and is laevigate to scabrate in texture. The distal surface displays a varied, distinct to barely perceptible sculpture comprising squat, subdued verrucae, coarse grana and very rare mammae: elements are ≤2μm in height (usually ≤1-1.5μm), and ≤3.75μm in basal diameter. The sculptural elements are rounded, hemispherical in profile, or distally flattened-blunted, and circular to subcircular in basal outline. Elements are usually discrete, ≤1-7μm apart, although very occasionally two or three adjacent elements may cluster or coalesce into irregular cristae. The sculpture may be discernible at the equatorial margin or encroach onto the proximal surface: the ornamentation is usually reduced or absent on the contact areas.

Figure 3.3.81: Sculptural elements of *Grandispora* sp. C, lateral elevation.

Dimensions. maximum exoexinal diameter 96-106μm, mean 101μm; intexinal body 42-59μm, mean 54μm (4 specimens measured). Diameter of the intexinal body 44-57% of the total spore diameter.

Occurrence. R, S; *very rare.*

Comparisons. *Calyptosporites* sp A, of Owens (1971; p. 48, Pl. XIII, fig. 8) is substantially larger (198.4μm x 186.4μm), displaying a slightly larger intexine to exoexine ratio and a markedly coarser sculpture, that comprises predominantly coni: ornament dimensions specified by Owens as 2.5-9.5μm in height and 3-7.5μm in basal diameter. *Grandispora uyenoi* McGregor & Camfield (1982; p. 47, Pl. 12, figs. 3, 7) is similar in size (ranging down to 89μm in diameter), but the intexine to exoexine ratio is greater (60-90%), and the sculpture seemingly more dense and enlarged (2-6μm in height).

In general, species of the Carboniferous genus *Spelaeotriletes* Neves & Owens (1966, p. 342-346) display a more diffuse intexinal body, and a more chaotic, irregular sculpture.

Grandispora sp. D.

Plate 3.22, figs. 8-10.

Description. Trilete, camerate miospores; amb triangular, convex triangular to subcircular. The intexinal body is distinctly triangular to circular in outline. The suturae are indistinct, straight and commonly obscured by robust, openly sinuous labra, ≤3μm in width and height at the proximal pole. The laesurae extend 4/5 to the full spore radius and may taper towards the spore circumference, occasionally terminated by curvaturae imperfectae. The intexine is laevigate, optically dense and ≤1μm thick: very occasionally the intexine bears concentric folds ≤4μm wide, which preferentially distort the equatorial margin. The exoexine is laevigate to coarsely scabrate, ≤2.75μm thick equatorially (?limbate, up to 5μm thick) and lacks compressional folds. The proximo-equatorial and distal regions display a distinct, discrete sculpture, that comprises broad based, flexed spinae, squat coni with rare mammae elements: ≤2-4.25μm in height (rarely exceed 5μm) and ≤2-3μm in basal diameter. The sculptural elements are ≤2-9μm apart (usually ≈6μm). Overall the ornamentation appears comparatively sparse.

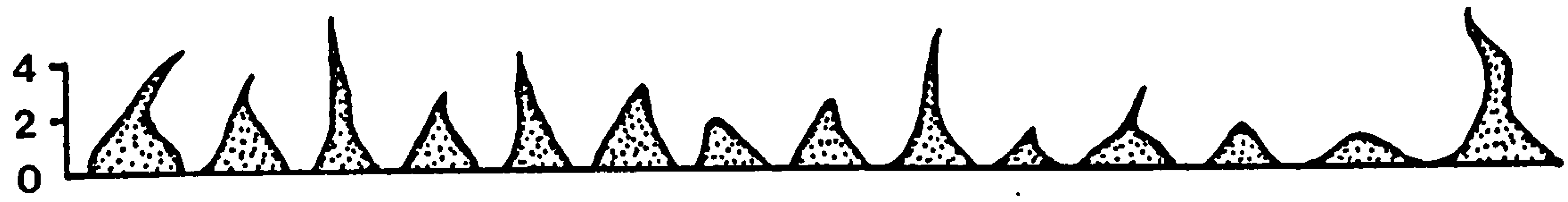


Figure 3.3.82: Sculptural elements of *Grandispora* sp. D, lateral elevation.

Dimensions. Maximum overall diameter 73-92μm, mean 79μm; intexinal body 43-64μm, mean 50μm (8 specimens measured). Diameter of the intexinal body 59-70% of the total spore diameter.

Occurrence. S, WP, L; *rare.* LH; *very rare.* M; *R.*

Remarks. *Hymenozonotriletes praetervisus* Naumova, in Lanninger (1968; p. 146, Pl. 25, fig. 2) and possibly *Grandispora spinosa* Hoffmeister, Staplin & Malloy, in Lanninger (1968; p. 155, Pl. 26, fig. 4) are potential homologies with *Grandispora* sp. D described herein.

Comparisons. A number of representatives of *Grandispora* sp. D recovered in the present study (*e.g.* Pl. 3.22, fig. 9) resemble one of the specimens of *Grandispora gabesensis* (Pl. VI, fig. 4) figured by Loboziak & Streel (1989): the distribution of the sculpture and overall spore construction appear similar. However, the sculpture upon the holotype of *Grandispora gabesensis* in Loboziak & Streel (1989, Pl. VI, fig. 2) is far denser, more crowded.

Grandispora sp. B (of the present study) displays a somewhat similar but smaller sculpture, as well as exhibiting a thinner, less robust pseudosaccus. *Grandispora* sp. E (of the present study) is slightly larger, and displays a thicker exoexine. Furthermore *Grandispora* sp. E bears a coarser, more elongate sculpture.

Grandispora sp. E.

Plate 3.23, figs. 1-3, 6.

Description. Trilete, camerate miospores; amb circular, ovate to convex-subtriangular. The intexinal body is conformable with the exoexinal outline, or more demonstrably rounded. The suturae are indistinct, straight and obscured by pronounced, thickened labra, ≤6.75μm high and wide at the proximal pole. The laesurae extend 7/8 to the full radius of the spore, tapering towards the equatorial margin and occasionally terminated by curvaturae imperfectae. The contact areas lack pronounced, sculpture, and the exine may appear slightly thinned. The intexinal body is optically dense, ≤2-?5μm thick equatorially and scabrate to faintly granulose. The exoexine is robust and rigid, thickness uncertain, (up to ?5μm thick; ?limbate), and finely scabrate to granulose in texture. The equatorial and distal surfaces display an even to dense sculptural cover, comprising coni, and spinae surmounted upon a bulbous, verrucate base: mammae are rare. Elements are ≤2-7.25μm in height (usually 3-6μm), ≤4μm in basal diameter and ≤2-6μm apart. The ornament may either appear slightly denser towards the outline of the intexinal body, or more crowded over the distal pole: two or four elements may fuse into short, imperfect cristae, ≤11μm in length.

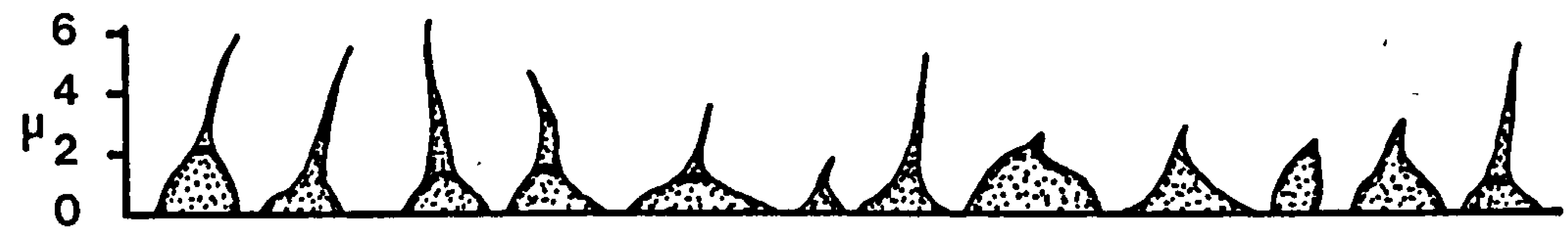


Figure 3.3.83: Sculptural elements of *Grandispora* sp. E, lateral view.

Dimensions. Maximum spore diameter 91-117μm, mean 104μm; intexinal body diameter 49-67μm (11 specimens measured). Diameter of the intexinal body 53-72% of the total spore diameter.

Occurrence. CM, K; *rare.* M; *?R.*

Remarks. The exoexine commonly appears turbid, such that distal surface or haptotypic features are difficult to resolve.

Comparisons. *Hymenozonotriletes melanidus* Naumova (1953; p. 63, Pl. VIII, fig. 15) is similar in size (100-120μm), but from the line drawings appears to display a denser, more even sculptural cover, with cristae adorning the flange. *Grandispora* cf. *melanidus* (Naumova) Taugourdeau-Lantz (1971; p. 49, Pl. X, fig. 8) displays a similar sized sculpture (≤4μm long), but is slightly smaller in overall diameter (75μm), and exhibits a distinctly bulbous/confluent ornament. The exine of *Grandispora* cf. *melanidus* (Naumova) Taugourdeau-Lantz in Higgs & Russell (1981; p. Pl. 4, figs. 3, 6) appears optically dense (?bizonate). *Grandispora diamphida* Allen (1965) is slightly smaller in overall diameter, and displays a less rigid exoexine, sculptured with broader, conate elements. *Grandispora tomentosa* Taugourdeau-Lantz (1967) is smaller, with a larger intexine to exoexine ratio. *Calyptosporites spinosus* Tiwari & Schaarschmidt (1975; p. 43, Pl. 24, fig. 4 - holotype only) is similar in size (although ranges up to 160μm in diameter), but bears a comparatively uniform ornament comprising denser, spinose elements (4-8μm in length). *Grandispora incognita* (Kedo) McGregor & Camfield (1976; p. 23 Pl.

6, figs. 9, 10) displays a denser and considerably larger, more elongate ornament. *Grandispora maxima* (Lanninger) McGregor & Camfield (1976; p. 24, Pl. 7, figs. 6, 8) exhibits coarser sculpture and a less pronounced, more diffuse intexinal body. *Samarisporites* sp. in Loboziak & Streel (1981, Pl. II, fig. 9; size ≈80μm) is more comparable in morphology to *Grandispora* cf. *melanidus* (Naumova) Taugourdeau-Lantz (1971) than *Grandispora* sp. D (herein). *Grandispora riegelii* Loboziak & Streel (1989, p. 190; Pl. V, figs. 1-5; Pl. IX, figs. 10-13) displays a smaller, denser sculpture (1-3μm in size), that consists predominantly of mamillate and biform conical elements. The sculpture of *Grandispora gabesensis* Loboziak & Streel (1989) is denser and appears more uniform.

Grandispora sp. B and *Grandispora* sp. D (of the present study) are slightly smaller in overall diameter, and the exoexinal walls seemingly thinner, less turbid and bearing a finer, more diminutive sculpture.

Grandispora sp. F.
Plate 3.23, figs. 4, 5, 8.

? 1988 *Samarisporites* sp. of Boumendjel, Loboziak, Paris, Steemans, & Streel, Pl. 1, fig. 22.

Description. Trilete, camerate-?zonate miospores; amb ovate, irregular subcircular to angular subtriangular. The intexine is irregular subcircular to rounded triangular in outline. The suturae are indistinct, straight to tightly sinuous and may appear simple, although usually are obscured by robust, or thin-flexuous labra, ≤5.5μm wide and high at the proximal pole. The suturae may appear confined to the central body, although the labra typically propagate the laesurae to the equatorial margin. The contact areas lack pronounced sculpture. The intexine is laevigate, optically dense and ≤?1.5μm thick. In comparison the exoexine appears thinner and more membraneous, being ≤1.25μm thick equatorially and displaying a sparse, diminutive sculpture over the proximo-equatorial and distal regions of the spore. This ornament comprises small, barely discernible, broad based spinae and coni: elements are ≤2μm in basal width and height. The sculptural elements are discrete, ≤4-11μm apart, and may appear so subtle and sparse that the exoexine tends to appear unornamented.

Figure 3.3.84: Sculptural elements of *Grandispora* sp. F, lateral view.

Dimensions. Maximum exoexinal diameter 70-78μm, mean 74μm; intexinal body diameter 44-53μm, mean 51μm (11 specimens measured). Diameter of the intexinal body 61-72% of the total spore diameter.

Occurrence. K; *rare*.

Remarks. Occasionally, the exoexine seemingly extends equatorially simulating a "single-layered zona": demonstrably cavate forms were documented. This equatorial "flange" may be folded in towards the poles.

Comparisons. *Grandispora* sp. F bears a very superficial resemblance to *Archaeozonotriletes aculeatus* Naumova (1953; Pl. XIII, fig. 1): primarily this latter species differs in displaying a larger intexine to exoexine ratio, as well as a ≈sparser, irregular ornament. *Grandispora inculta* Allen (1965) bears a denser, conate sculpture. *Grandispora gracilis* (Kedo) Streel (in Becker *et al.*, 1974; p. 26, Pl. 19, figs. 1-3) exhibits a larger intexine : exoexine ratio, appears camerate in construction, and also displays a somewhat "denser" sculpture. *Samarisporites* sp. of Boumendjel *et al.* (1988) bears a resemblance to *Grandispora* sp. F (herein), although is ≈larger (≈90μm, taken from the illustration). Note that the exact nature of the distal ornament of *Samarisporites* sp. *sensu* Boumendjel *et al.* (1988) is uncertain, due to the opacity of the central body: it is difficult to ascertain from the illustration alone whether the distal sculpture is discrete or fused, "cristate".

Grandispora cf. *velata* (of the present study) is slightly larger, usually appears demonstrably camerate, and displays a coarser, more bulbous conate/spinose ornament: the intexine to exoexine ratio of *Grandispora* cf. *velata* is also smaller. Refer also to the comparisons noted for *Grandispora* cf. *velata* (earlier).

Grandispora sp. G

Plate 3.23, figs. 7, 9-12.

Description. Trilete, camerate-?zonate miospores with a subcircular, rounded triangular to distinctly triangular amb in polar compression. The outline of the intexinal body is either concentric with the equatorial margin, or appears more rounded. The suturae extend 4/5 to the full radius of the intexinal body, are straight, simple or labrate (labra ≤6μm in height, ≤2.5μm wide). The labra are thin, flexuous, or "ragged" in appearance, and tend to propagate the laesurae almost to the equatorial margin of the spore: the laesurae are occasionally terminated by faint curvaturae imperfectae. The contact areas lack pronounced sculpture. The intexinal body is laevigate, robust and rigid (rarely folded) and appears optically dense: the intexine is ≤2μm thick equatorially. The exoexine is laevigate to finely scabrate and ≤1.75μm thick at the spore circumference. The exoexine ±generously extends beyond the intexinal body, and resembles a rigid, "zona-like" flange. The proximo-equatorial and distal regions are sculptured with subdued, discrete, largely biform coni and spinae, interspersed with rare grana and diminutive mammae. These elements vary in profile from rounded to attenuate-pointed, or may be surmounted by a fine grana or slender capitate spine. The ornament ranges in height from 0.5μm to 1.25μm (rarely exceeds 1.5μm), and ≤0.25-1.5μm in basal diameter: elements are regularly distributed, ≤0.25-2.5μm apart (rarely 3-5μm). Both exinal layers lack compressional folds.

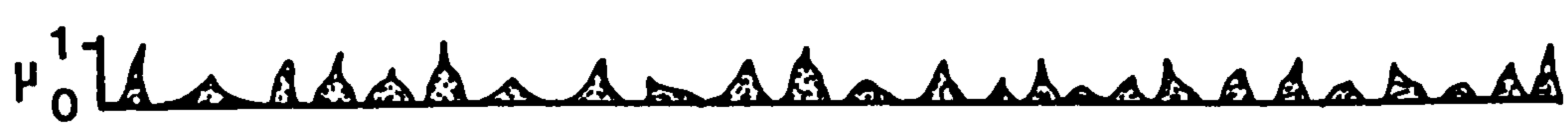


Figure 3.3.85: Sculptural elements of *Grandispora* sp G, lateral view.

Dimensions. Maximum spore diameter 44-59μm, mean 55μm; maximum intexinal body diameter 32-43μm, mean 40μm (15 specimens measured). Diameter of the intexinal body 70-76% of the total spore diameter.

Occurrence. K; *rare.*

Remarks. The exoexine occasionally resembles a rigid, ?single layered zona, rather than a distinct camera.

Comparisons. *Grandispora echinata* Hacquebard (1957) and *G. tenuispinosa* (Hacquebard) Playford (1971) are similar in relation to overall morphology, but are slightly larger in spore diameter and bear a coarser, more elongate sculpture. *Perotrilites conatus* Richardson (1965; p. 580, Pl. 91, figs. 10-11) ranges up to 132μm in diameter, displays a denser, coarser ornament ($\leq$4μm in length) and an intensely wrinkled "perisporal membrane". *Grandispora inculta* Allen (1965) displays a thinner, more diaphanous, voluminous and irregularly distorted pseudosaccus, which is ornamented by a dense conate sculpture. *Grandispora gracilis* (Kedo) Streel (in Becker *et al.*, 1974; p. 26, Pl. 19, figs. 1-3) appears similar in overall construction, but bears a sparser, more uniformly spinose ornament. *Calyptosporites spinosus* Tiwari & Schaarschmidt (1975; p. 43, Pl. 24, fig. 4 - holotype only) is larger in diameter (94-160μm) and is densely ornamented by elongate, spinose sculptural elements (4-8μm in length). *Grandispora daemonii* Loboziak, Streel & Burjack (1988; p. 357, Pl. VI, figs. 2-6) appears $\approx$homologous, but displays a slightly coarser, denser sculpture (Note: *Grandispora daemonii* closely resembles *G. inculta*, and may in fact prove to be conspecific with this taxon). *Grandispora riegelii* Loboziak & Streel (1989; p.190, Pl. V, figs. 1-5; Pl. IX, figs. 10-13) is larger (80-120μm) and displays a denser, slightly coarser sculptural cover (1-3μm in size).

Grandispora cf. *velata* (of the present study) is larger, and displays a coarser, more varied and bulbous conate/spinose ornament. Furthermore, the intexine to exoexine ratio of *Grandispora* cf. *velata* is smaller.

Genus *Hystricosporites* McGregor, 1960.

Type species. *Hystricosporites delectabilis* McGregor, 1960.

Discussion.

McGregor (1960, p. 31) proposed *Hystricosporites,* placing this genus within the Subturma Azonotriletes Luber, Infraturma Apiculati (Bennie & Kidston) Potonié. He distinguished this genus from *Archaeotriletes* (Naumova) Potonié (1958) due the absence of a flange, or any apparent concentration of appendages in the equatorial region. Owens (1971) and later Playford (1976, p. 32-33) demonstrated that hystricospores were partly, although not strongly, cavate: cameration usually subtle, as the two layers are commonly closely appressed. Streel (in Becker *et al.*, 1974) regarded the construction of *Hystricosporites* as problematic, and reflected this in the assignation of this plexus to an *incertae sedis* category.

Within the circumscription of *Hystricosporites porcatus,* Allen (1965, p.699) remarked upon previously unrecorded proximal radial muri, although Richardson (1962) had in fact illustrated radial "striations" in his sketch of *H. corystus*, but had payed no mention to this attribute in the text. Indeed, Vigran (1964, p. 15) earlier commented on Richardson's (1960) incomplete description of this taxon in this respect. Subsequently Owens (1971) emended the generic circumscription of *Hystricosporites* to accommodate a greater diversity of haptotypic characteristics, including proximal "ribbing". Furthermore, Owens (1971, p. 27) perceived *Dicrospora* (Winslow, 1962 p. 49-52) to be synonymous with *Hystricosporites*.

Ancyrospora (Richardson 1962, emend. Richardson 1965) displays similar bifurcate-tipped appendages, but is distinguished from *Hystricosporites* by the presence of an equatorially extended "pseudoflange". *Nikitinsporites* Chaloner (1959) displays a somewhat larger, elevated "apical prominence", coupled with poorly defined contact areas (*sensu* McGregor, 1960; Owens, 1971, p. 27). The sculpture morphology of *Nikitinsporites* is somewhat unique, comprising robust processes with subtle bifurcate terminations, constricted below their base. *Trichodosporites* Chi and Hills (1976, p.725) is similar to *Hystricosporites* in terms of gross morphology, but the processes lack bifurcate tips.

Unfortunately, despite the recovery of abundant hystricospores from north Devon, the vast majority have been left in open nomenclature. This was in part due to specimen opacity and the poor preservation of the element termini. For such material, differences in process morphology, element disposition and overall spore diameter provide the basis for speciation (herein). Haptotypic features were usually unresolved and specimens commonly opaque or translucent, even after lengthy oxidation.

The nomenclature devised by Owens (1971) to convey variation in process-tip morphology is applied below.

Hystricosporites ?corystus Richardson.

Plate 3.24, fig. 1.

? 1962 *Hystricosporites corystus* Richardson, p. 173-174, Pl. 25, figs. 1, 2; text-fig. 2.

non 1962 *Hystricosporites ?corystus* Richardson, in Richardson p. 174, Pl. 25, figs. 3.

Description. Trilete, camerate (laminate) miospores with a circular, subcircular to rounded-triangular amb: a thin intexinal body may be distinguishable, although commonly closely appressed to, and inseparable from, the exoexine. When discernible, the suturae are straight and obscured by flexuous, pronounced labra: the labra typically range in height from ≤11μm to 18μm at the proximal pole (very occasionally up to 36μm), are ≤7μm wide, and "ragged" or rounded in lateral profile. The laesurae extend 2/3 to 7/8 the spore radius, tapering in width and height towards the equatorial margin. The thickness of both exinal layers is uncertain, although when discernible the inner body appears markedly thin, folded and membraneous, ≤?2μm thick. In comparison, the exoexine is "thickened", robust (≤?8μm thick equatorially), and rarely laevigate, commonly finely granulose (individual grana/coni ≤0.25-0.75μm in dimensions), or shagreenate in texture. The contact areas are either ill-defined or distinct, and may be delimited equatorially by variably developed curvaturate ridges: the exine of the contact areas commonly appears thinned, unsculptured, or with faint "striations" radial about the proximal pole (3 to 6 per inter-radial, ≤3-4.5μm in width). The proximo-equatorial and distal regions display a distinct sculpture comprising long and robust processes (straight, rarely flexed), which are terminated by a pronounced bifurcation. Elements are usually 21-48μm in length (rarely ≤12-15μm), and are ≤5-14μm in basal diameter (average 6-8μm): the shafts of the appendages are either parallel-sided, or taper gradually from a bulbous, laterally expanded base. The processes may be constricted at one or more points along their length: the bifurcations are ≤4-16μm in width. These terminations are extended triangular, triangular-laterally extended, to laterally extended and partially reflexed in form. The shafts and the bifurcate termini are laevigate: the bulbous bases may appear distinctly granulose, or shagreenate. Elements are usually ≤12-38μm apart, with five to nineteen processes projecting at the equatorial margin (commonly 11-16).

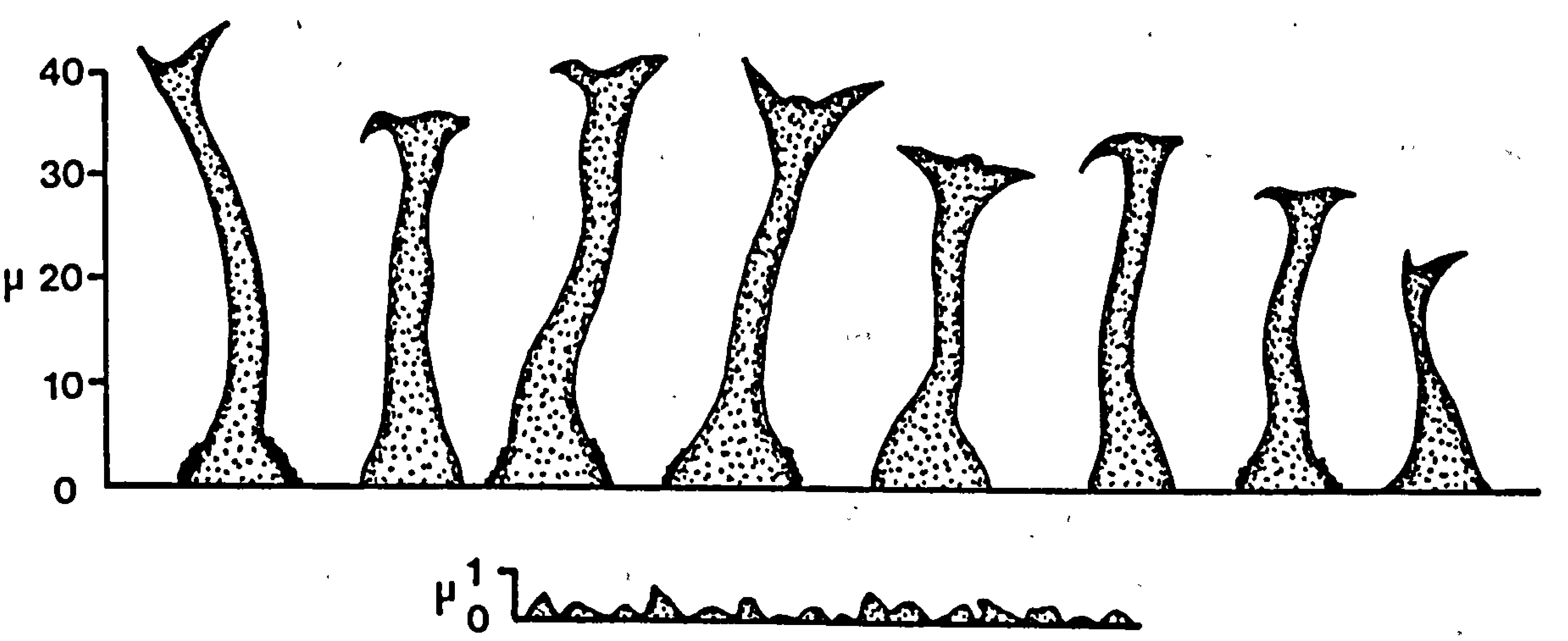


Figure 3.3.86: Sculptural elements of *Hystricosporites ?corystus*, lateral elevation.

Dimensions. Maximum spore diameter (polar compression, excluding sculpture), 102-124μm, mean 114μm (10 specimens measured).

Occurrence. LN; *common*. R, S, LH; *rare*.

Remarks. The population recovered from north Devon differ to *Hystricosporites corystus, sensu stricto* Richardson in being slightly smaller in overall spore diameter (102-124μm *vs.* 129-213μm quoted by

Richardson, 1962, p. 173), and in displaying a greater number of processes projecting beyond the equatorial margin (Richardson quotes 5-10 processes, ≤66μm in length).

In the present study, specimens were commonly recovered in polar compression, and due to their opacity haptotypic characteristics proved difficult to evaluate. Labra were rarely preserved intact, and bifurcate terminations were quite often missing. Low numbers of processes projecting at the equatorial margin may simply be due to breakage.

Comparisons. *Hystricosporites delectabilis* McGregor (1960; p. 32, Pl. 11, figs. 13, 14; text-fig. 1) is larger (145-340μm), and displays a denser, more bulbous and elongate sculpture: McGregor (1960) notes appendage length as being 1/3 to 2/3 the spore body radius. *Hystricosporites ?corystus* Richardson in Richardson (1962) is larger (140-260μm), and the sculpture seemingly lacks well defined, reflexed bifurcate terminations. *Hystricosporites gravis* Owens (1971; p. 31-32, Pl. VIII, figs. 1-3; text-fig.9) bears a denser, more bulbous-based and robust sculpture, that ranges up to 89.1μm in length and 19.9μm in basal diameter. *Hystricosporites* sp. B of Owens (1971; p. 33-34, Pl. IX, fig. 2) displays far coarser, more elongate processes, that range in length from 69.3μm to 132μm. *Hystricosporites* cf. *corystus* in Riegel (1973; p. 87, Pl. 12, fig. 3) bears more pronounced labra (25-70μm), and ranges in size up to 147μm: the bifurcate termini to the appendages appear more reflexed. *Hystricosporites elegans* Tiwari & Schaarschmidt (1975; p. 30-31, Pl. 13, figs. 10-13; text-fig. 22) is smaller in overall diameter (60-105μm) and display a somewhat denser sculpture, that may range up to 90μm in overall length (Note: the processes of *H. elegans* Tiwari & Schaarschmidt figured on Pl. 13 fig. 12 resembles those recorded above). *Hystricosporites triangulatus* Tiwari & Schaarschmidt (1975; p. 30, Pl. 13, figs. 6-9; text-fig. 21) is slightly smaller in diameter (78-110μm), and displays a predominance of laterally extended/reflexed bifurcate terminations. The processes of *H. elongatus* Chi & Hills (1976) are similar in morphology, but larger.

Hystricosporites sp. B (of the present study) is ≈smaller in overall diameter (63-95μm) and bears more slender, shorter appendages, which are terminated predominantly by reflexed bifurcations.

Hystricosporites sp. A.
Plate 3.24, fig. 2.

Description. Trilete, ?acamerate miospores; subcircular, ovate to subtriangular amb. When discernible the suturae are straight to openly arcuate, simple, ruptured or paralleled by subdued, flexuous labra, ≤6μm high and wide at the proximal pole. The laesurae extend 1/2 to 4/5 the spore radius, ±tapering equatorially and occasionally terminated by faint curvatural ridges. The contact areas are ill-defined, with the exine over the proximal pole seemingly thinned and bearing faint, radial "ribs", ≤2μm high and wide. A comparatively thin (≤?2μm thick), laevigate, distorted intexinal body may be distinguishable, closely appressed to the exoexine. The exoexine is robust, ≤5μm thick equatorially, and scabrate to finely granulose. The equatorial and distal regions display regularly spaced, prominent and discrete processes. These appendages appear robust, rarely flexed, and are comparatively uniform in gross morphology. Elements are typically ≤12-27μm in length (rarely exceed 30μm): the shafts are parallel-sided or planoconcave in lateral profile, ≤5μm wide midlength and rising from a relatively flared base (≤4-9μm in basal diameter). The bifurcate terminations are

≤3-8.5μm in width, and range in morphology from triangular to laterally extended, rarely reflexed. Sculptural elements are densely spaced, ≤2-7μm apart: 29 to 47 elements project at the equatorial margin (rarely greater than 39 elements).

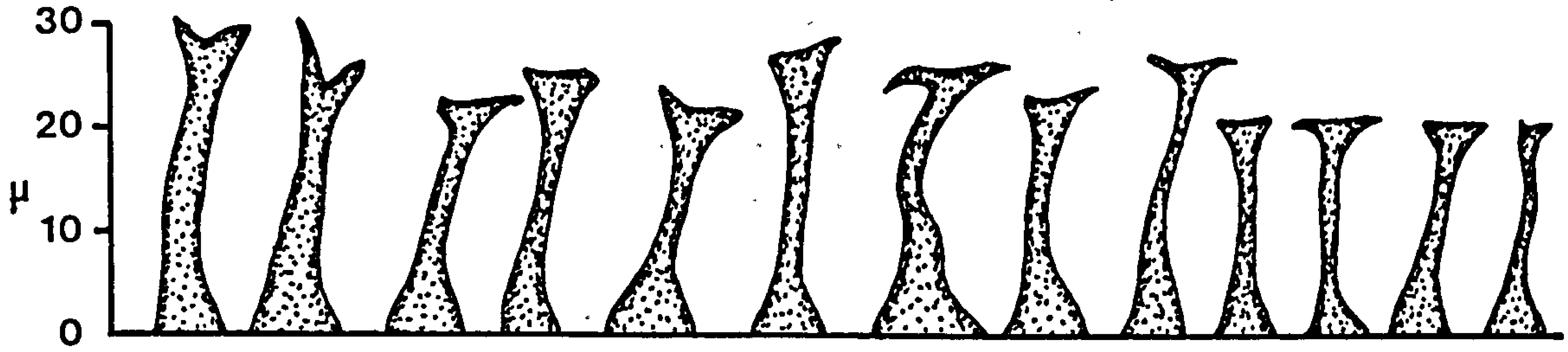


Figure 3.3.87: Sculptural elements of *Hystricosporites* sp. A, lateral view.

Dimensions. Maximum spore diameter (polar compression, excluding sculpture), 65-79μm, mean 68μm (15 specimens measured).

Occurrence. LN; *common.* H; *rare.*

Comparisons. The amb and size of the spore, coupled with the morphology and density of the sculpture merits this form distinct from all previously described hystricospores. *Hystricosporites porcatus* (Winslow) Allen (1965; p. 699, Pl. 95, figs. 4-6), *H. porrectus* (Balme & Hassell) Allen (1965; p. 698-699, pl. 95, figs. 1-3) and *H. mitratus* Allen (1965; p. 699-700, Pl. 95, figs. 7, 8) are generally larger (collectively within the range 84-184μm), are seemingly more robust and rounded in polar compression and display a somewhat sparser sculpture. *Hystricosporites microancyreus* Riegel (1973, p. 88-89, Pl. 12, fig. 6-8; Pl. 13, figs. 1-3) ranges in size down to 61μm, but bears sculptural elements that are morphologically different, sparser and somewhat smaller in overall size (10-15μm in length).

Hystricosporites sp. B

Plate 3.24, figs. 3, 4.

Description. Trilete, ?acamerate miospores; amb subcircular to convex subtriangular. When discernible the suturae are straight to openly arcuate, simple or obscured by thickened, robust but subdued labra (≤4μm in total width, ≤11μm in height at the proximal pole): the laesurae extend 2/3 to 3/4 the spore radius, ±tapering towards the equatorial margin. The contact areas are ill-defined, lacking pronounced sculpture. The exine is thickened (≤?5μm at the equator) and appears laevigate to coarsely shagreenate. A thin, membraneous intexinal body is (rarely) differentiated. The equatorial and distal surfaces display discrete, elongate, and slender processes. These elements comprise parallel-sided or tapering shafts, rising from a ≈bulbous base, ≤4-9μm in diameter: these appendages are usually kinked or flexed midlength (≤1.5-4μm wide). Process terminations are distinctly bifurcate: the tips are generally ≤7-11μm wide, laterally-extended, reflexed and occasionally expanded, rarely extended. Elements are ≤5-18μm apart (rarely 20μm+) - 13 to 24 processes project equatorially.

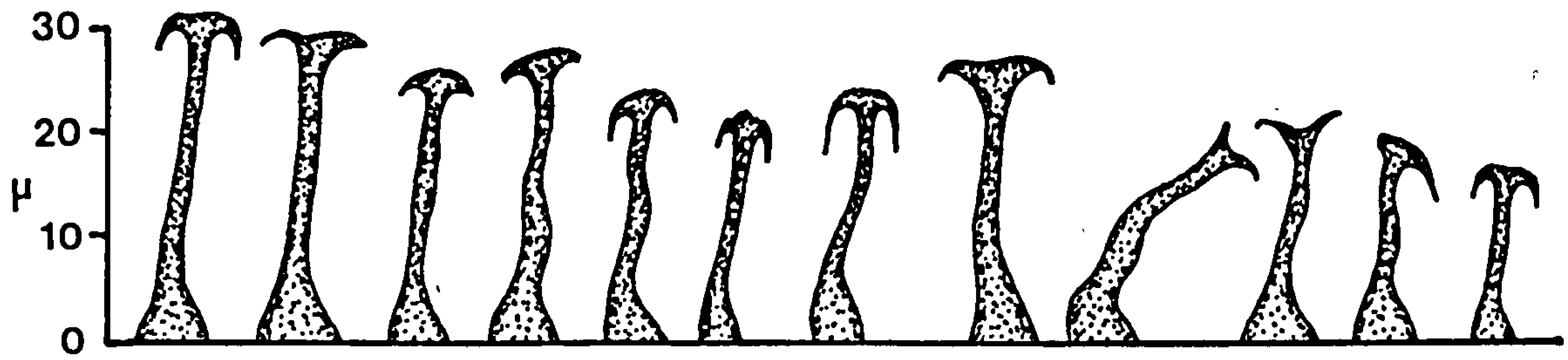


Figure 3.3.88: Sculptural variation of *Hystricosporites* sp. B, lateral elevation.

Dimensions. Maximum spore diameter (polar compression, excluding sculpture) 63-95μm, mean 69μm (10 specimens measured).

Occurrence. LN, H; *rare.*

Remarks. Spore opacity often limits resolution of haptotypic characteristics.

Comparisons. The small size of *Hystricosporites* sp. B, coupled with its slender, elongate and sparse sculpture (that display pronounced, reflexed terminations) distinguishes this form from all other species of hystricospore. *Hystricosporites* cf. *corystus* in Riegel (1973; p. 87, Pl. 12, fig. 3, 4) bears a morphologically similar, but denser sculpture, and is slightly larger in overall size (108-147μm), displaying more pronounced labra (ranging from 25μm to 70μm in height).

Hystricosporites sp. C.
Plate 3.24, fig. 5.

Description. Trilete, camerate miospores; amb subcircular, subtriangular to convex triangular. Exinal stratification barely perceptible to distinct. The intexinal body is retracted away from, or closely appressed to, the exoexine: the intexine may be intensely folded, appearing $\leq$1μm thick (membraneous), and texturally laevigate to finely scabrate. Conversely, the exoexine is robust and rigid in appearance ($\leq$4μm thick equatorially), laevigate, scabrate or finely shagreenate in texture, and lacks compressional folds. When discernible, the suturae are straight to openly arcuate, and commonly paralleled by subdued labra, typically $\leq$6μm high and wide (rarely range up to 18μm in dimensions). The laesurae extend 2/3 to 7/8 the spore radius, $\approx$tapering gradually towards the equatorial margin and may be terminated by curvaturae imperfectae. The contact areas are either readily discernible or ill-defined: the exine is slightly thinned, lacks prominent sculpture, and may display faint radial "striae", $\leq$1μm in width (up to 11 per contact area). The equatorial and distal surfaces display distinct, discrete spinae, $\leq$5-12μm in length (rarely exceed 15μm), and $\leq$3-7μm wide at their base: these processes are terminated by a distinct to barely perceptible triangular, or triangular-reflexed bifurcation, $\leq$3-5μm in lateral width. The bifurcate termini tend to be laevigate, whereas the process shafts appear longitudinally striated and/or coarsely shagreenate. The appendages may be constricted below the bifurcate termination, and the shafts flexed, bent. Elements are $\leq$1-6μm apart (rarely greater than 12μm), with 21 to 38 processes projecting from the spore equator.

Figure 3.3.89: Sculptural elements of *Hystricosporites* sp. C, lateral elevation.

Dimensions. Maximum spore diameter (polar compression, excluding sculpture) 55-69μm, mean 57μm (15 specimens measured).

Occurrence. CM, K; *rare.*

Comparisons. This forms differs to *Ancyrospora ancyrea* var. *brevispinosa* Richardson (1962) primarily in basic construction, and in displaying less robust, seemingly more membraneous sculptural elements. *Hystricosporites costatus* Vigran (1964; p. 14-15, Pl. V, fig. 3-5) is larger (75-165μm), thicker walled (2-layered exine 4-12μm thick) and displays a coarser sculpture. *Hystricosporites furcatus* Owens (1971; p. 28-29, Pl. VI, figs. 7-9, text-fig. 6) and *Hystricosporites reflexus* Owens (1971; p. 29-30, Pl. VII, figs. 1-4, text-fig. 7), first described from the Arctic Archipelago, are both substantially larger (exceed 82.5μm in diameter), and display somewhat coarser, more elongate sculptural elements (15-46.2μm and 9-35 in length, respectively). These forms commonly display distinct inter-radial ribbing over the proximal surface.

This species differs to all other hystricospores described from north Devon in being stratigraphically "isolated", and in displaying a substantially smaller, less robust sculpture.

Genus *Insculptospora* Marshall, 1985.

Type species. *Insculptospora confossa* (Richardson) Marshall, 1985.

Synonymy.

? 1988 *Ambagisporites* Balme, p.134.

Discussion.

Marshall formally defined the genus *Insculptospora* in 1985 (p. 453-470), although homologous forms are reported in the literature as early as 1925 (Spore-type B of Lang): such morphotypes have variously been attributed to *Punctatisporites* (Richardson, 1965, p. 561-562; Riegel, 1968, p.80) and *Archaeozonotriletes* (Mortimer & Chaloner 1972, p. 39).

Recently Balme (1988, p. 134) proposed the genus *Ambagisporites,* based upon material isolated from the Upper Devonian (early Frasnian) strata of the Carnarvon Basin. Balme interpreted the construction of these spores to be three layered; the outer and inner layers are homogeneous, with an intervening "mesexinous" layer sculptured by a fine (≤1μm) "...system of sinuous, discrete anastomosing tubes". In the present study, the validity of this genus is questioned. A number of representatives of *Insculptospora confossa* recovered from north Devon display closely appressed intexinal and exoexinal layers, and in terms of overall morphology bear a striking resemblance to those specimens figured by Balme (1988, p. 134, Pl.7, figs. 3-7) as *Ambagisporites daedaleus*. However, the specimens illustrated by Balme do appear "thick-walled", and may conceivably be three-layered.

In comparison, *Geminospora* (Balme) Owens 1971 displays a differentially thickened, sculptured exoexine, relative to the intexinal body. *Videospora* (Higgs & Russell, 1981) differs in being acamerate and possessing an external ornament confined to the proximal surface: Marshall (1985) mentioned that specimens of *Insculptospora* may resemble *Videospora* if the intexine is exposed through ruptured suturae. Playford (1983a, p. 274-276) proposed the Carboniferous camerate spore genus *Ascetospora*, which is broadly similar in construction to that of *Insculptospora*, but differs in the disposition of the exinal sculpture: the intexine and exoexine are externally laevigate, but the exoexine of *Ascetospora* bears a sculptured inner surface.

Insculptospora confossa (Richardson) Marshall
Plate 3.24, figs. 6-16.

1925 Spore-type B in Lang (pars), p. 256, Pl. I, fig. 4.
1965 *Punctatisporites confossus* Richardson, p. 561-562, Pl. 88, fig. 2.
1968 *Punctatisporites intromatus* Riegel, p. 80, Pl. 16, fig. 1-5.
1972 *Archaeozonotriletes incrustatus* Arkhangelskaya, in Mortimer & Chaloner (pars) p.39, Pl. VII, fig. 7.
1975 Spore Type A, Higgs, p.402, Pl. 7, fig. 2.
1985 *Insculptospora confossa* (Richardson) Marshall, p. 453-470, Pl. 1, figs. 1-7, Pl. 2, figs.1-9, 11-13, text-fig. 2, 3.
? 1988 *Ambagisporites daedaleus* Balme, p.134, Pl. 7, figs. 3-7.

Description. Trilete, camerate miospores; amb oval, circular, subcircular to irregular convex-triangular. The shape of the intexinal body may either parallel the outline of the exoexine, or may appear more irregular, plicated (dependant upon the degree of appression of the two exinal layers). The suturae are straight to openly arcuate, simple, or occasionally paralleled by exinal "thickenings" (individually ≤2μm wide). The laesurae extend 1/3 to 7/8 the spore radius (usually 3/4), are non-curvaturate, and taper equatorially. The intexine and exoexine are attached principally adjacent to the trilete mark; elsewhere the intexine may be indiscriminately folded. A concave-triangular to rounded-triangular polumbra may cover the proximal polar region (herein is interpreted as reflecting the area of attachment between the two exinal layers. The exoexine is laevigate to finely scabrate, of ≈uniform thickness (≤1μm-2.75μm), and rarely folded proximo-equatorially: conversely the distal surface of the exoexine may be severely distorted, displaying between three and eight(+) ±major plications. The intexine is somewhat thinner, ≤?0.5-0.75μm thick and more membraneous in appearance, commonly bearing concentric folds which are usually independent of the exoexine. The intexine bears an obvious, dense and usually even sculpture, comprising grana, diminutive broad-based coni and mammae, with very rare spinae and biform elements: ornament ≤1μm in height and ≤2μm in basal diameter. Elements are discrete, ≤0.5-1.5μm apart (usually 0.5μm), or may be fused into irregular, "beaded" rugulae or vermiculae (which range up to 4.5μm long). Very occasionally this ornament appears "patchy", forming an uneven sculptured "veneer", with the intervening intexine laevigate.

Figure 3.3.90: Sculptural elements on the intexinal body of *Insculptospora confossa*, lateral & plan views.

Dimensions. Maximum exoexinal diameter, 38-94μm (mean 53μm); intexinal body diameter 56-95% of the total spore diameter (60 specimens measured).

Occurrence. S; *abundant.* LH, WP, L, CM, K; *common.* R, M; *rare.*

Remarks. Within the population of *Insculptospora confossa* recovered from north Devon, the vermiculate sculpture on the intexine rarely resembled an ordered microreticulum: the degree of cameration also proved highly variable.

Specimens were occasionally recovered with a veneer of fine, globular tapetal residue on the exoexine (refer to Pl. 3.9, figs. 8, 9, herein).

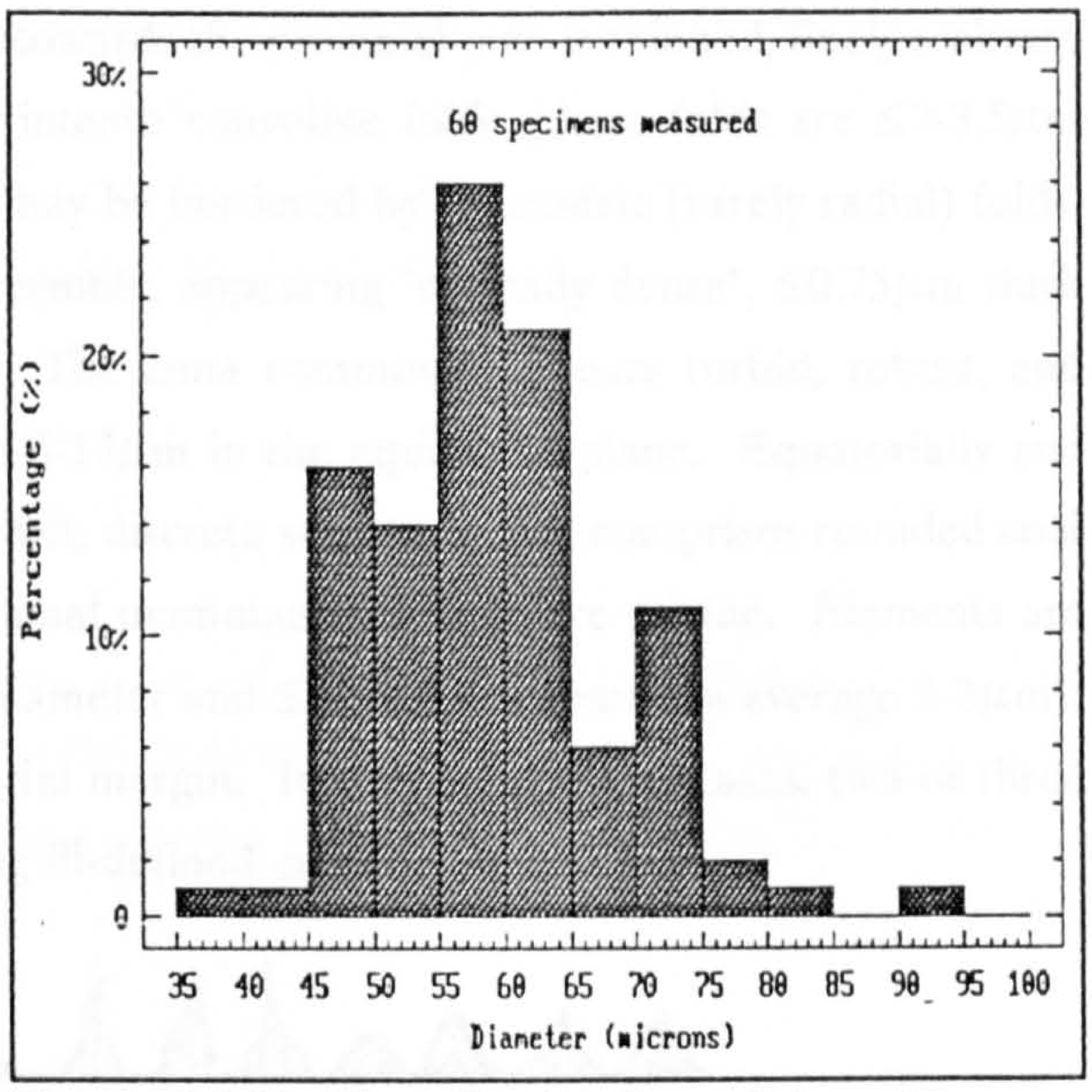


Figure 3.3.91: Size distribution of *Insculptospora confossa* (Richardson) Marshall (1985).

Comparisons. *Videospora glabrimarginata* (Owens) Higgs & Russell (1981) is acamerate and displays a granulate exinal ornament confined to the proximal surface. *Insculptospora incrustata* (Arkhangelskaya) Marshall (1985) is a megaspore, considerably larger in overall spore size (210-360μm in diameter).

Genus *Kraeuselisporites* Leschik emend. Owens, Mishell and Marshall, 1976.

Type species. *Kraeuselisporites dentatus* Leschik, 1956.

Discussion.

Leschik (1956) proposed the genus *Kraeuselisporites* for Mesozoic, alete and zonate miospores. Owens *et al.* (1976) subsequently emended the circumscription of this plexus, so as to encompass Carboniferous, trilete spores, of zonate-camerate construction. More recently McGregor & Camfield (1982, p. 29, 52) applied this generic concept to Devonian material (in the sense of Scheuring, 1974), acknowledging the potential ambiguity in morphology with *Cristatisporites: Kraeuselisporites* is reserved for spores with exclusively (*vs.* dominantly) discrete sculptural elements.

Kraeuselisporites sp.
Plate 3.25, figs. 1, 2.

Description. Trilete, zonate-?camerate miospores; amb convex triangular to subcircular. The suturae are indistinct, straight to tightly sinuous, and are commonly obscured by thin, sinuous and flexuous labra, ≤6μm in height and ≤2-4μm wide at the proximal pole. The laesurae are non-curvaturate, extend 4/5 to the full radius of the spore, and taper slightly towards the equatorial margin. The contact areas lack pronounced sculpture: the wall towards the proximal pole is thinned, finely scabrate to sparsely granulose, or displays comparatively intense convolute folds (these folds are ≤2-3.5μm in width and height). The thinned apical region may be bordered by concentric (rarely radial) folds. An occasional, diffuse, "inner" body may be discernible, appearing "optically dense", ≤0.75μm thick and ≈conformable with the equatorial margin. The zona commonly appears turbid, robust, and relatively uniform in equatorial extent: extends ≤6-17μm in the equatorial plane. Equatorially and distally the exine is ≤2μm thick, and bears a distinct, discrete sculpture, that comprises rounded coni and grana, attenuate, broad-based spinae, occasional mammae and very rare cristae. Elements are usually ≤1-2.25μm in height, ≤1.25μm in basal diameter and ≤0.5-4.5μm apart (on average 2-3μm): ornament size may decrease towards the equatorial margin. In very exceptional cases, two or three adjacent elements coalesce at their base, forming ill-defined cristae.

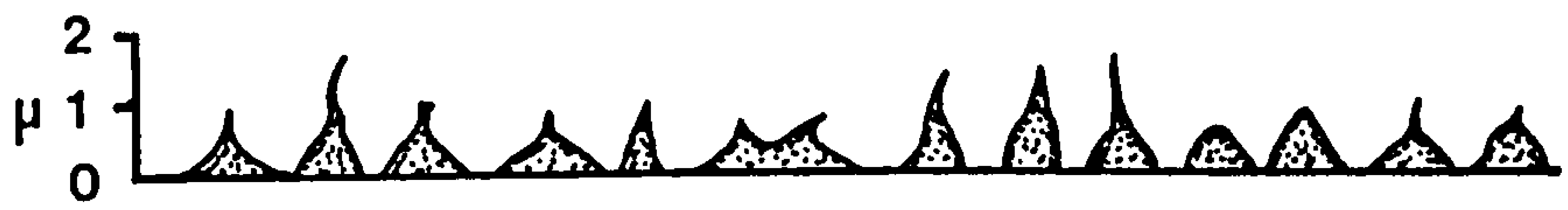


Figure 3.3.92: Sculptural elements of *Kraeuselisporites* sp., lateral view.

Dimensions. Maximum spore diameter, 63-72μm, mean 69μm (5 specimens measured).

Occurrence. CM; *very rare.*

Remarks. A faint inner feature (intexinal body) in some specimens was considered still within the emended concept of *Kraeuselisporites, sensu* Owens *et al.* (1976).

Comparisons. *Kraeuselisporites rugosus* (Owens) McGregor & Camfield (1982; p. 53, Pl. 14, figs. 11, 12, text-fig. 84) is larger (83-139μm), and displays a seemingly more diaphanous zona. Both *Kraeuselisporites acerosus* (Arkhangelskaya) McGregor & Camfield (1982, p. 52) and *Kraeuselisporites ?spinutissimus* (Naumova ex. Kedo) McGregor & Camfield (1982, p. 53) appear optically denser and more intensely sculptured.

Kraeuselisporites sp. differs to *Cristatisporites triangulatus* (Allen) McGregor & Camfield (1982) in the morphology of the zona (the intexine of the former is less well defined), in the overall equatorial outline of the spore, and also in the nature/disposition of the sculpture: *C. triangulatus* exhibits a predominance of laterally fused, cristate elements.

Grandispora sp. E (of the present study) is larger, camerate and bears a considerably coarser sculpture. *Grandispora* sp. G (of the present study) differs primarily in construction, being camerate, and displays a more even, regular sculptural cover.

Genus *Leiotriletes* (Naumova) Potonié & Kremp 1954.

Type species *Leiotriletes sphaerotriangulatus* (Loose) Potonié & Kremp, 1954.

Discussion

McGregor (1973, p. 16), McGregor & Camfield (1982, p. 33) and more recently Ravn (1986, p. 21) have favoured the use of the post-Palaeozoic genus *Deltoidospora* Miner (1935), being identical in morphology to the Palaeozoic genus *Leiotriletes,* but differing merely in its stratigraphic occurrence. Indeed, these authors believe that a separation in geological time is not a valid criterion for differentiating these two form genera. However, this kind of problem is unfortunately not unique to *Leiotriletes* and its homonyms, as pointed out by Playford (1962, p. 573) and also Smith & Butterworth (1967, p. 121): note the discussion in Smith & Butterworth (1967, p. 121)

Leiotriletes sp.

Plate 3.25, fig. 3.

Description. Trilete, acamerate miospores; amb triangular to convex rounded-subtriangular. The suturae are straight, simple or obscured by thin, slightly flexuous and irregular labra, ≤1.75μm in total width and height. The laesurae ±taper in width towards the proximal pole, and may be terminated equatorially by faint curvaturae imperfectae. The exine is laevigate to finely scabrate, and ≤1μm thick equatorially.

Dimensions. Maximum overall diameter 53-67μm, mean 62μm (12 specimens measured).

Occurrence. S; *rare.* LN, H, R, LH; *very rare.*

Comparisons *Leiotriletes inermis* (Waltz) Ishchenko (1952) is comparable in size (50-68μm), but displays simple suturae and is occasionally polumbrate. From the line drawings, *Leiotriletes trivialis* Naumova (1953; p. 45, Pl. V, fig. 14; p. 104, Pl. XVI, fig. 6; p. 121, Pl. XVIII, figs. 7, 8) resembles *Leiotriletes* sp., in displaying thickened "suturae", but is somewhat smaller: ranges from 25μm to 40μm in diameter. *Leiotriletes sphaerotriangulus* (Loose) Potonié & Kremp (1954) is similar, but the suturae are simple and interradially the spore margin appears somewhat "straighter". *Leiotriletes tumidus* Butterworth & Williams (1958) is slightly smaller in size (34-52μm) and the suturae paralleled by pronounced, thickened labra. *Deltoidospora priddyi* (Berry) McGregor (1973, p. 16, Pl. 1, figs. 6, 7) is smaller, and the labra less well developed (≤1μm wide). *Deltoidospora* sp. in McGregor & Camfield (1982; p. 33, Pl. 6, fig. 15) is likewise smaller (21-36μm) and displays relatively enlarged, robust labra, ≤2μm wide and high.

Genus *Perotrilites* Couper emend. Evans 1970.

Type species. *Perotrilites granulatus* Couper 1953.

Discussion.

Evans (1970) reassessed the holotype of *Perotrilites granulatus* and concluded that the genus circumscribes double-layered spores, with a single-layered equatorial zona. Subsequently there has been some debate as to the distinction between *Perotrilites* and *Kraeuselisporites*: Scheuring (1974) perceives the latter to be distally single-layered, whereas (earlier) Jansonius (1962) and Segroves (1970) regard *Kraeuselisporites* to accommodate both camerate and acamerate forms. Until this ambiguity is resolved, the distinctions proposed by Evans (1970) and Scheuring (1974) are sustained.

Perotrilites ?bifurcatus Richardson.
Plate 3.25, figs. 4, 5.

? 1962 *Perotrilites bifurcatus* Richardson, p. 174-175, Pl. 25, figs. 4, 5 text-fig. 3.
1982 *Perotrilites bifurcatus* Richardson, in McGregor & Camfield, p. 55, Pl. 15, figs. 13-15. Text-fig. 87.

Description. Trilete, zonate-camerate miospores with a rounded subtriangular to irregular subcircular amb. The suturae are distinct, straight to openly arcuate, and commonly obscured by thin, flexuous labra, ≤2μm wide and ≤7μm high at the proximal pole. The laesurae taper towards the margin of the intexinal body: the labra ±propagate the trilete rays to the spore circumference. The contact areas are laevigate to finely scabrate, lacking pronounced sculpture and may be delimited equatorially by very faint curvaturae imperfectae. A faint, diffuse ≈triangular polumbra may be discernible. The central body is laevigate to finely scabrate, optically dense and ≤3μm thick equatorially. The intexinal body is closely appressed to the exoexine over the distal surface: the exoexine extends in the equatorial plane as a ≈thin, diaphanous, single-layered "flange", ≤1μm thick and ≤2-14μm in lateral extent. Equatorially and distally the exoexine displays a discrete sculpture, comprising broad based, attenuate, but diminutive coni and spinae: elements typically ≤4μm in height (rarely exceed 7μm) and ≤2.75-7μm in basal diameter. Sculptural elements are commonly ≤2μm to 11μm apart, rarely greater than 14μm. The distal tips to these elements may be simple-pointed tips, although more commonly are blunted or display subtle, minute bifurcations, ≤0.5μm in lateral width. The exine may be concentrically folded over the distal surface.

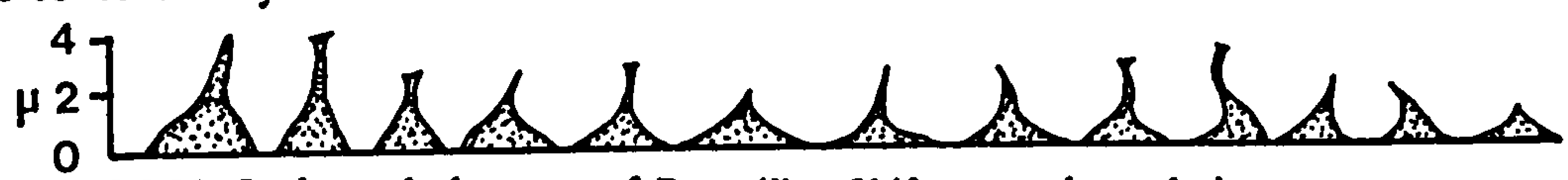


Figure 3.3.93: Sculptural elements of *Perotrilites ?bifurcatus*, lateral view.

Dimensions. 53-67μm, mean 58μm; diameter of the central body 41-49μm, mean 44μm (10 specimens measured).

Occurrence. K; *rare.*

Remarks. The holotype of *Perotrilites bifurcatus* illustrated by Richardson (1962, Pl. 25, fig. 4) differs in size (88μm) and in displaying larger, more robust spines (5-8μm long), which are clearly bifurcate-tipped. In more general terms, the size range of *Perotrilites bifurcatus* from the Middle Old Red of Scotland is quoted by Richardson (1962) as spanning 80-103μm: larger than recorded in the present study. However, McGregor & Camfield (1982) recently noted this species to range in overall diameter from 62μm to 122μm.

Comparisons. From the illustrations of the holotype, the distinction between *Ancyrospora ancyrea* var. *brevispinosa* Richardson (1962; 179-180, Pl. 25, fig. 8; text-fig. 9A) and *Perotrilites bifurcatus* Richardson (1962) appears difficult to sustain: both are of comparable size and gross morphological appearance. However, *Perotrilites bifurcatus* displays a somewhat shorter sculpture, and the exine over the polar regions appears looser, more intensely plicated ("wrinkled"). *Perotrilites ergatus* Allen (1965; p. 731-732, Pl. 102, figs. 16-20) is larger (71-124μm) and bears a simple conate sculpture, 1-3μm in height, with no mention made in the diagnosis to the presence of bifurcate terminations. Furthermore, according to Allen these elements may coalesce, defining an imperfect reticulum. *Perotrilites pannosus* Allen (1965; p. 732-733, Pl. 102, figs. 14, 15) is similar in size (40-74μm), but displays a conate sculpture (elements 1-2.5μm in height), $\pm$surmounted by diminutive, capitate spines. The proximo-equatorial and distal regions of this species display a distinct pattern of muroid folds, that may appear arcuate or anastomosing and define an imperfect reticulum.

Genus *Punctatisporites* (Ibrahim) Potonié and Kremp, 1954

Type species. *Punctatisporites punctatus.* (Ibrahim) Ibrahim, 1933.

Discussion.

Smith & Butterworth (1967) view the exine of *Punctatisporites* to be thicker than that of *Calamospora* Schopf, Wilson & Bentall (1944), lacking clearly defined contact areas and bearing fewer compressional folds. *Triletes* Erdtman ex Potonié (1956) is a megaspore equivalent, with or without an apical "polumbra". *Videospora* Higgs & Russell (1981) displays subtle sculpture on the proximal surface.

Punctatisporites planus Hacquebard.

Plate 3.25, fig. 7.

1957 *Punctatisporites planus* Hacquebard, p.308, Pl. 1, fig. 12.

1967 *Stenozonotriletes clarus* Ishchenko, in Mortimer, Pl. I, P.

Description. Trilete, acamerate miospores; amb well rounded to subcircular. The exine is uniformly laevigate to finely scabrate. The suturae are distinct, straight and extend 2/3 to 3/4 (rarely 4/5) the total spore radius. The exine is $\leq$1-2.75μm thick equatorially, and unfolded.

Dimensions. Maximum diameter 44-69μm, mean 56μm (8 specimens measured).

Occurrence. M; *rare.*

Remarks. Representatives recovered from north Devon were occasionally slightly smaller than the size specifications quoted by Hacquebard (1957; 50-64μm). However, the exinal thickness and development of the trilete rays were comparable.

Off-polar compressions were common. The suturae were very occasionally ruptured, and the proximal polar region noted to display a mottled, ill-defined polumbra.

Comparison. *Leiotriletes rotundus* Naumova (1953; p. 43, Pl. V, figs. 3, 4; p. 120, Pl. XVIII, fig. 4, 5) and *Leiotriletes simplex* Naumova (1953; p. 21, Pl. I, fig. 2; p.44, Pl. V, fig. 9) are comparable in size, but from the line drawings do not appear to be thickened equatorially. *Stenozonotriletes simplicissimus* Naumova (1953; p. 69, Pl. X, fig. 1, 2) is slightly smaller in size (30-40μm) and ?thicker equatorially. *Stenozonotriletes pumilus* Naumova (1953; p. 36, Pl.111, fig. 16; p. 69, Pl. X, fig. 4-6) is substantially smaller. *S. lasius* Naumova (1953; p. 37-38, Pl III, fig. 21; p. 111, Pl. XVII, fig 4) is smaller, thicker walled and the exine seemingly "textured". *Stenozonotriletes laevigatus* Naumova (1953; p. 70, Pl. X, figs. 9, 10; p. 111, Pl. XVII, fig. 5) is similar in size (50-70μm), but appears thicker walled and also displays a "textured" exine. *Punctatisporites solidus* Hacquebard (1957, p. 308, Pl. 1, fig. 13) is similar in size (50-64μm) but the exine is notably thicker equatorially (3-4μm thick).

Punctatisporites sp. A. (the present study) is larger, and displays a relatively thinner exine.

Punctatisporites sp. A.

Plate 3.25, fig. 6.

Description. Trilete, acamerate miospores; amb circular to subcircular. The exine is comparatively thin, ≤0.5-2.25μm thick equatorially, appearing uniformly laevigate to finely scabrate, and lacks any differential haptotypic or proximo-distal features. The suturae are distinct, straight and simple, very rarely obscured by exinal "thickening" (?labrate), which are ≤1μm in total width. The laesurae extend 1/4 to 2/3 the spore radius. The exine is unfolded.

Dimensions. Maximum spore diameter 68-89μm, mean 72μm (4 specimens measured).

Occurrence. S; *rare.* R, LH; *very rare.*

Comparisons. The line drawings of *Leiotriletes rotundus* Naumova 1953 (p. 43, Pl. V, figs. 3, 4; p. 120, Pl. XVIII, fig. 4, 5) appear similar, but the size range specified for this species much smaller (30-45μm): furthermore, some of the illustrations of *Leiotriletes rotundus* Naumova (1953) show the suturae as ruptured. *Leiotriletes simplex* Naumova (p. 21, Pl. I, fig. 2; p.44, Pl. V, fig. 9) is smaller (20-35μm) and more triangulate in outline. *Punctatisporites planus, sensu stricto* Hacquebard (1957, p. 308, Pl. 1, fig. 12) is smaller (50-64μm), and displays longer trilete rays (extend 2/3 to 3/4 the spore radius). *Punctatisporites solidus* Hacquebard (1957; p. 308, Pl. 1, fig. 13) is likewise slightly smaller in size (50-64μm) and exhibits a rigid, thickened wall (3-4μm thick). *Calamospora pannucea* Richardson (1965, p. 563) is similar in size (62-146μm), but differs in appearing markedly thinner-walled (which may be intensely folded), and in displaying thinned contact areas. *Triletes langii* Richardson (1965) is substantially larger (236-440μm), and bears laesurae which are only distinct over the contact areas: this taxon displays a triangular polumbra. *Punctatisporites* sp. A *sensu* McGregor (1973; p. 17, Pl. 1, fig. 10) is larger (86-117μm), and thicker walled (2.5-4.5μm) and the equatorial outline more irregular. *Punctatisporites* sp. B, *sensu* McGregor (1973; p. 17, Pl. 1, fig. 11) is ≈similar in size (72-92μm), but with a more intensely folded exine.

Genus *Raistrickia* Schopf, Wilson & Bentall,
emend. Potonié & Kremp, 1954.

Type species: *Raistrickia grovensis* Schopf in Schopf, Wilson & Bentall, 1944.

Discussion.

Schopf, Wilson & Bentall (1944, p. 55) defined the genus *Raistrickia* for acamerate spores with an even, verrucose to spinose sculpture. The sculptural elements were simple-blunted, or were subtly bifurcate to multifurcate tipped. Subsequently, Potonié & Kremp (1954, p. 85) emended the circumscription of *Raistrickia*, by discussing in far greater detail the variation in sculpture. In this emendation, Potonié & Kremp (1954) noted a predominance of bacula in association with conate elements, that were simple-rounded, blunted, and generally lacking pointed extremities. The termini to these elements were simple or noted to split into two or more "papillae".

(Also note to the remarks in Ravn, 1986, p. 45).

The identification of *Raistrickia* within the present study was on occasion considered arbitrary, as the predominant sculptural type was not elongate bacula, but comprised more spatulate to verrucate elements. Furthermore, in certain cases there was some uncertainty whether the distinct serration or multifurcation to the tips of the sculpture was a either primary or secondary attribute.

Raistrickia sp. A.
Plate 3.25, figs. 8-10.

Description. Trilete, acamerate miospores; amb circular, subcircular to convex subtriangular. The exine is laevigate to scabrate, $\leq 3\mu$m thick equatorially (usually 1-2μm) and optically dense. The suturae are simple, straight to openly arcuate and extend 1/3 to 4/5 the total spore radius. The exine immediately adjacent to the trilete rays may be slightly darkened, $\leq 5\mu$m in total width. The contact areas are ill-defined, displaying diminutive or sparse grana, verrucae or squat bacula: elements rarely exceed 4μm in width, and $\leq 2\mu$m in height. Proximo-equatorially and distally the exine is sculptured predominantly with baculate and clavate elements, as well as subordinate verrucae, spatula and rare coni. This ornament is $\leq$3-7.5μm in height, $\leq$2-4.5μm in width (rarely exceeds 6μm): element height usually exceeds width. In profile the sculptural elements may be constricted at one or more places along their length, are parallel-sided or rarely laterally expanded: in plan these elements are subcircular, ovate to subpolygonal in basal outline. Element terminations are either subtly serrated, or distinctly multifurcate, rarely simple, smooth, blunted or surmounted by a solitary capitate spine/grana. Between three to six secondary spinae, grana or coni surmount each primary element. The primary ornamentation tends to be discrete, evenly distributed and relatively symmetrical around the equatorial margin: sculptural elements are $\leq$2-11μm apart (rarely exceeds 16μm), with two to three very occasionally contiguous at their base. Between twelve and sixteen elements commonly project from the spore circumference (rarely exceeds 25).

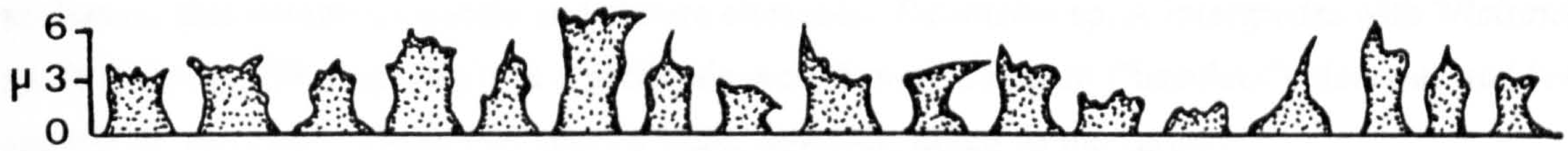


Figure 3.3.94: Variation in sculpture on *Raistrickia* sp. A, lateral view.

Dimensions. Maximum spore diameter (excluding sculpture) 34-70μm, mean 52μm (35 specimens measured).

Occurrence. L, CM; *common.* S, LH, WP, K; *rare.*

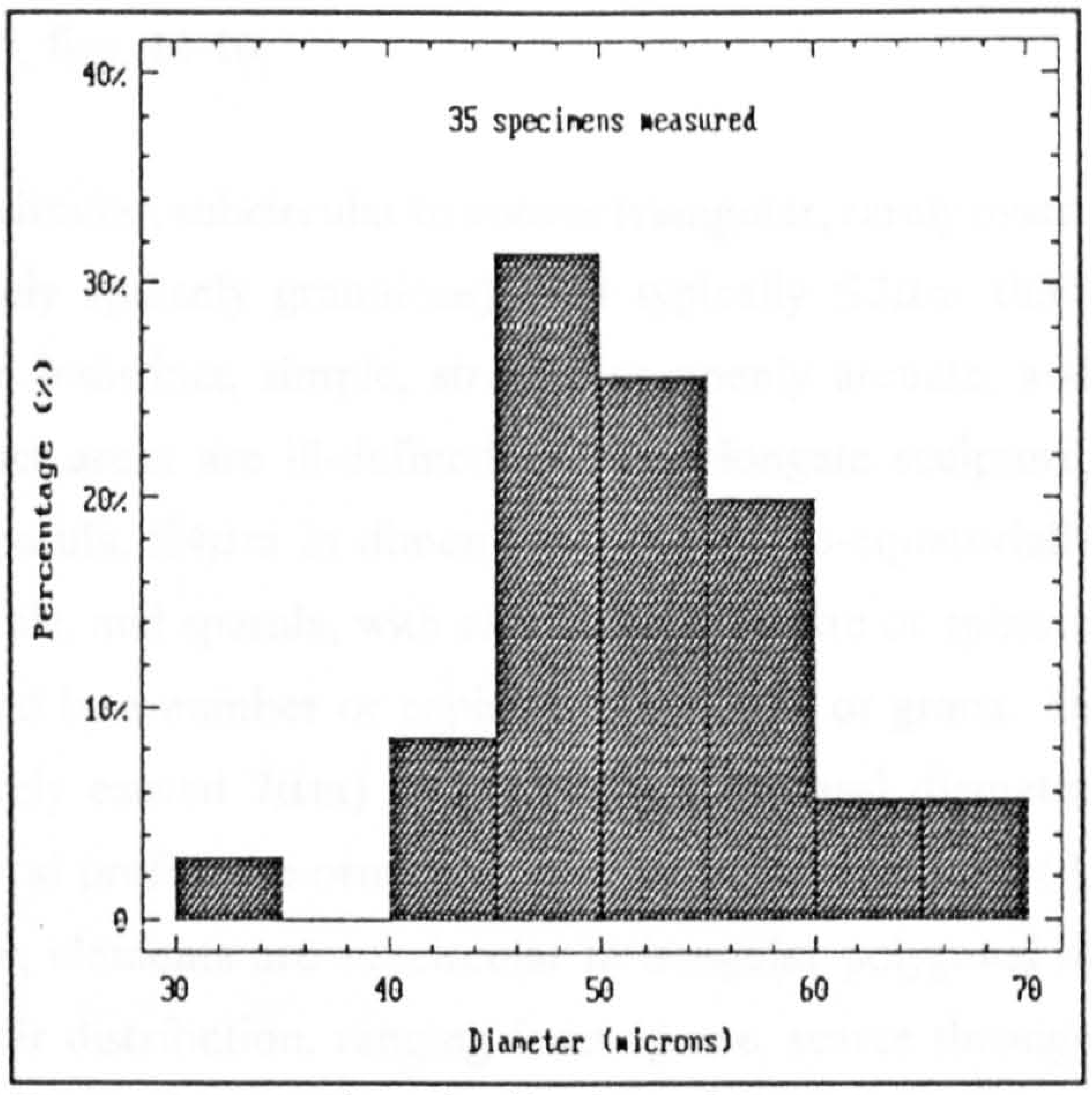


Figure 3.3.95: Size distribution of *Raistrickia* sp. A.

Remarks. The morphology of the sculpture that adorns these specimens is reminiscent of Late Devonian-Carboniferous species of *Raistrickia*. *Dibolisporites* (al. *Acanthotriletes*) *uncatus* (Naumova) McGregor & Camfield (1982 p. 38) displays grana, spinae, coni and verrucae, these elements "..mostly longer than wide". Although the primary elements on *D. uncatus* are surmounted by secondary elements, McGregor & Camfield's (1982) illustration of sculptural variation (Text-figure 55) does not show such pronounced "furcation", as was visible on both *Raistrickia* sp. A or ?*Raistrickia* sp. B (of the present study). In view of McGregor & Camfield's (1982) assignation of *uncatus* to *Dibolisporites*, both *Raistrickia* sp. A and ?*Raistrickia* sp. B (herein) may conceivably be more appropriately affiliated with *Dibolisporites*.

Comparisons. The sculpture of *Raistrickia clavata* (Hacquebard, 1957) is comparable in density, but the elements are longer (7-8.5μm in length) and the terminations more bulbous, hemispherical and smooth. The holotype of *Raistrickia setosa* (Loose) Schopf, Wilson & Bentall (1944) is 78μm in diameter. The population of *R. saetosa* (Loose) Schopf, Wilson & Bentall described and illustrated by Smith & Butterworth (1967, p. 181-182, Pl.8, fig. 21) from the Thorne Colliery, Yorkshire (Carboniferous) is similar in size range (41-62μm) and overall gross morphology. However, this species population differs in displaying a coarser baculate sculpture, that ranges up to 14μm in length (also refer to Ravn, 1986; p. 47-48, Pl. 8, fig. 9). *Raistrickia variabilis* Dolby & Neves (1970, p. 636, Pl. 1, fig. 6) is similar in size but displays a coarser sculpture. *Raistrickia spathulata* (Winslow) Higgs (1975; p. 396, Pl. 2, fig. 11) is substantially larger in overall diameter (66-125μm in diameter) and the ornament longer (5-24μm). The sculpture of *Raistrickia corynoges* Sullivan (1968; p. 119, Pl. 25, fig. 6) and *R. condylosa* Higgs (1975; p.396, Pl. 2, figs. 15, 16) appears more slender, elongate and somewhat denser. *Raistrickia lacerota* Peppers (1970) in Ravn (1986; p. Pl. 8, figs. 7, 8) exhibits a more bulbous, denser sculpture. *Verrucosisporites scurrus* (McGregor & Camfield, 1982) is densely sculptured with relatively smooth-tipped verrucae and baculae.

Baculatisporites sp. (of the present study) displays a smaller, more rounded and smooth sculpture, that comprises bacula and clavate elements. *Raistrickia* sp. A intergrades with *?Raistrickia* sp. B (herein), differing simply in a predominance of more elongate ("baculate") elements and fewer spatula or verrucae. These two species were, however, noted to intergrade.

?Raistrickia sp. B
Plate 3.25, figs. 11-16.

Description. Trilete, acamerate miospores; amb circular, subcircular to convex triangular, rarely ovate. The exine is laevigate to finely scabrate (rarely sparsely granulose), and typically $\leq 2\mu m$ thick equatorially (rarely up to $4.5\mu m$). Suturae are indistinct, simple, straight to openly arcuate, and extend 1/3 to 7/8 the spore radius. The contact areas are ill-defined, lacking elongate sculpture, merely displaying diminutive grana, bacula or spatula, $\leq 4\mu m$ in dimensions. Proximo-equatorially and distally the exine bears discrete verruca, bacula, and spatula, with rare clavate, conate or spinose elements: these primary elements are surmounted by a number or capitate spinae, pila or grana. In general elements are ≤ 2-$4.5\mu m$ in height (rarely exceed $7\mu m$) and ≤ 5-$8.5\mu m$ in basal diameter (rarely less than $3\mu m$ or exceed $10\mu m$). In lateral profile the ornament may be basally constricted, parallel-sided or laterally expanded: in plan view, elements are subcircular to irregular polygonal in outline. Sculptural elements are variable in their distribution, ranging from sparse, scarce through to notably dense: elements commonly ≤ 1-$9\mu m$ apart (rarely exceed $12\mu m$) and occasionally coalesce, defining short, irregular muri, $\leq 15\mu m$ in overall length. Commonly 18 to 31 elements project at the spore circumference (rarely fewer than 14 or greater than 35).

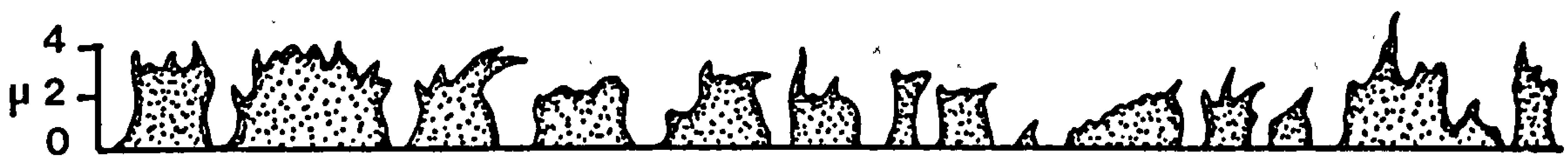


Figure 3.3.96: Sculptural variation on *?Raistrickia* sp. B., lateral view.

Dimensions. Maximum spore diameter 52-$73\mu m$, mean $58\mu m$ (20 specimens measured).

Remarks. The predominance of subdued verrucae and spatulate elements over bacula justifies the tentative allocation to *Raistrickia*. However, the similarity in the morphology of the ornament on this form, with that of *Raistrickia* sp. A (*i.e.* elongate, serrated-tipped elements), confirms that this complex of spores are more appropriately affiliated with *Raistrickia* than with *Dibolisporites* Richardson emend. Playford (1976).

Conceivably, a few specimens attributed to *?Raistrickia* sp. B may in fact be poorly preserved, corroded representatives of *Verrucosisporites scurrus* (Naumova) McGregor & Camfield (1982).

Comparisons. In terms of gross morphology, *?Raistrickia* sp. B resembles *Verrucosisporites scurrus* (Naumova) McGregor & Camfield (1982, p. 62), but the sculpture of *V. scurrus* is more rounded, lacking serrated termini and ranges up to $12\mu m$ in height. *D. uncatus* does not display such distinctly serrated terminations, being more rounded in morphology (Note: this distinction is acknowledged to be somewhat ambiguous, and indeed forms attributed herein to *?Raistrickia* sp. B may well prove to be within the species concept of *Dibolisporites uncatus, sensu* McGregor & Camfield, 1982).

The sculpture of *Raistrickia* sp. A (of the present study) is more elongate, sparser and isolated, and is predominantly baculate. Sculpturally the two species intergrade.

?*Raistrickia* sp. C.
Plate 3.25, figs. 17, 18.

Description. Trilete, acamerate miospores; amb circular, subcircular to ovate. The exine is scabrate, rarely laevigate, and ≤4μm thick equatorially. The suturae are commonly indistinct, but if discernible appear simple, straight to openly arcuate and are non-curvaturate, extending 1/3 to 2/3 the total spore radius. The contact areas are ill-defined, lacking pronounced sculpture or displaying squat coni, bacula or spatula. The proximo-equatorial and distal regions display distinct, discrete, robust but scarce sculptural elements, typically 8-17μm in height (rarely less than 6μm or exceed 20μm), and ≤3-14μm in basal diameter. These elements are elongate, and exhibit simple-rounded/pointed, bifurcate, although more usually multifurcate terminations. These primary elements are commonly surmounted by numerous grana, coni or diminutive spinae. In lateral profile the sculpture is considerably varied, appearing constricted towards their base, parallel-sided, or towards ±gradually their distal extremities. Elements are generally discrete, well spaced, usually ≤6-22μm apart (rarely less than 5μm or greater than 25μm). Two to three adjacent elements may coalesce at their base, forming irregular, elongate spatula. 8-24 distinct elements project at the spore circumference (rarely greater than 20).

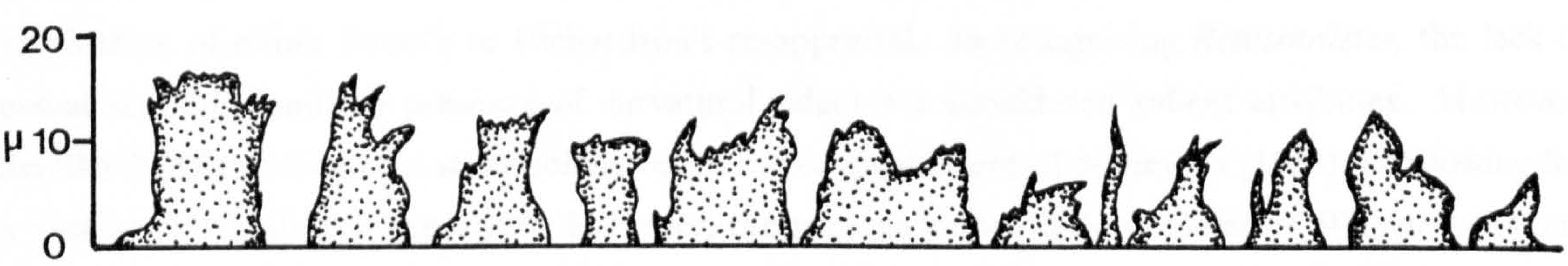


Figure 3.3.97: Sculptural elements of ?*Raistrickia* sp. C, lateral view.

Dimensions. Maximum spore diameter 39-77μm, mean 50μm (35 specimens measured).

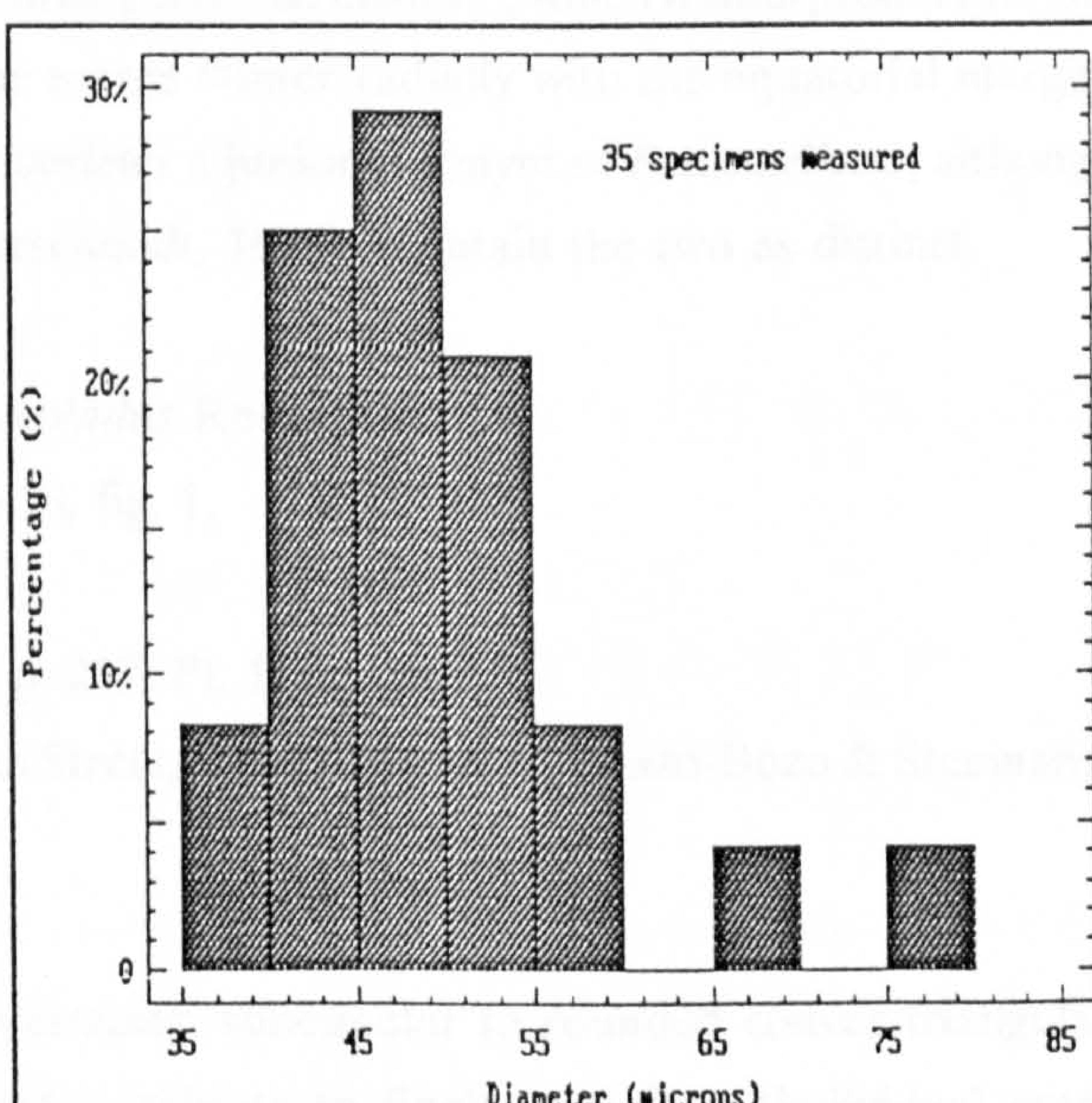


Figure 3.3.98: Size distribution of ?*Raistrickia* sp. C.

Remarks. Forms are only tentatively affiliated with *Raistrickia,* due to the lack of baculate sculpture. ?*Raistrickia* sp. C is believed to form one end member of a morphologically intergrading complex of spores, that encompasses ?*Raistrickia* sp. B and at the opposite extreme *Raistrickia* sp. A: variation in the dimensions and disposition of the serrated-tipped sculpture allows differentiation.

In describing *Verrucosisporites premnus* Richardson (1965, p. 572) remarked that the the sculpture may display "....flat, slightly curved, and lobed and serrated apices". However, neither specimen of *V. premnus* figured by Richardson (1965, Pl. 90, figs. 1, 2) displays such pronounced apical serration, as was noted on specimens of *?Raistrickia* sp. C documented herein.

Specimens invariably proved difficult to oxidise: haptotypic and distal characteristics were thus difficult to resolve.

Comparisons. *Verrucosisporites premnus* Richardson (1965) bears comparable, enlarged sculptural elements (4-16μm in height), but these are notably more rounded and smooth in profile view.

The scarcity and size of the sculpture clearly distinguish this form from *Raistrickia* sp. A and *?Raistrickia* sp. B: intergradational forms were noted with *?Raistrickia* sp. B.

Genus *Retusotriletes* (Naumova) emend. Streel 1964.

Type species. *Retusotriletes simplex* Naumova 1953.

Discussion.

The original diagnosis of *Retusotriletes* by Naumova (1953, p. 29) circumscribed miospores that displayed three distinct contact areas. Subsequently two emendations were independently published, one by Streel (1964 p. 6-7) and the other by Richardson (1965, p. 563-564), which attempted to constrain the concept of this genus to azonate, unornamented, and curvaturate miospores. With the notable exceptions of Schultz (1968) and Lanninger (1968) there is general consensus favouring the application of either Streel's or Richardson's re-appraisal. In recognising *Retusotriletes,* the lack of exinal sculpture and the presence of curvatural ridges are considered salient attributes. However, Schultz (1968) advocated a strict adherence to the original intent of Naumova (1953), in allowing for a variety of exinal ornamentation. However, the present author follows Owens (1971, p. 9-11) and McGregor (1973, p. 18) in favouring the emendation of *Retusotriletes* by Streel (1964), largely because this emended circumscription appears far more flexible than that of Richardson (1965). Richardson (1965, p. 563-564) refers to the presence of "curvaturae perfectae distinct", which if interpreted literally may exclude retusoid spores where the curvaturae merge $\approx$inter-radially with the equatorial margin.

Streel (1967, p. B23) considered *Phyllothecotriletes* a junior synonym of *Retusotriletes*, although many subsequent workers (*e.g.* Tiwari and Schaarschmidt, 1975) maintain the two as distinct.

Retusotriletes aureoladus Rodriguez

Plate 3.26, fig. 1.

1978 *Retusotriletes aureoladus* Rodriguez, p. 219, Pl. 1, fig. 10.

1981 *Retusotriletes aureoladus* Rodriguez, in Streel, Fairon-Demaret, Otazo-Bozo & Steemans, p. 183, Pl. 1, fig. 1.

Description. Trilete acamerate miospores; amb circular, subcircular to rounded convex-triangular. The exine is $\leq$1.25μm thick equatorially, laevigate, scabrate to finely granulose (individual grana $\leq$0.5μm in diameter). The suturae are distinct, straight or tightly sinuous towards the proximal pole, and are simple, or partially obscured by labra, which generally increase in thickness towards the equatorial margin: ≤3.25μm in width and height, rarely ranging up 5μm. Conversely, the laesurae may appear indistinct equatorially, or ruptured towards the proximal pole. The exine paralleling the laesurae is commonly thinned. The trilete rays extend 3/4 to the full radius of the spore, and are joined equatorially by ±distinct curvatural ridges: the curvaturae may either appear indistinct, coinciding in part with the spore margin, or conversely are pronounced and discrete from the spore circumference, ranging up to 1.75μm in thickness. The exine is comparatively uniform in thickness and homogenous in appearance, apart from three subcircular to ovate, diffuse or distinct apical papillae. These apical "spots" commonly extend over ≤15-35% of each contact area, and range in ≈diameter from 8μm to 14μm. Concentric, equatorial folds are rare.

Dimensions. Maximum spore diameter 49-59μm, mean 52μm (6 specimens measured).

Occurrence. LN; *rare.* L, CM, K; *R.*

Remarks. Rodriguez (1978) specifies the size range of *R. aureoladus* as 20-30μm, and thus slightly smaller than that noted herein. Furthermore, the apical papillae on the holotype appear more irregular in morphology than those observed on specimens recovered from north Devon. These disparities are considered inconsequential.

The occasional, turbid, and seemingly degraded appearance to some of the apical papillae suggested that these may in fact represent remnant, ill-preserved polumbra.

Comparisons. *Retusotriletes goensis, R. rotundus* and *R. triangulatus* display "complete" polumbras. *Retusotriletes ocellatus* McGregor (1973; p. 22, Pl. 2, fig. 5) is substantially larger in size (70-104μm), and the interradial papillae displaced more towards the centre of each contact area. *Retusotriletes maculatus* McGregor & Camfield (1976, p. 26, Pl. 1, fig. 6) is similar in overall size (35-58μm), but the single papillae apparent upon each contact face are better defined, and appear located more centrally (*i.e.* near the mid-point of each interradial area).

Retusotriletes ?pychovii Naumova
Plate 3.26, figs. 3, 4.

? 1953 *Retusotriletes Pychovii* Naumova, p. 88, Pl. XIV, fig. 5; p. 110, Pl. XVI, fig. 41; p. 123, Pl. XVIII, fig. 19.
? 1973 *Retusotriletes pychovii* Naumova, in McGregor, p. 19-20, Pl. 2, fig. 3.
? 1982 *Retusotriletes pychovii* Naumova, in McGregor & Camfield, p. 58, Pl. 16, fig. 12.
1986 *Retusotriletes pychovii* Naumova, in Turnau, p. 347-348, Pl. II, fig. 13.

Description. Trilete, acamerate miospores; amb circular, subcircular to convex triangular. The exine is laevigate to finely scabrate, and ≤3μm thick proximo-equatorially and distally. The suturae are straight to openly arcuate, extend 3/4 to 7/8 the spore radius, and may be simple or partially obscured by thin, ±flexuous labra. The labra may appear tightly sinuous and narrow at the proximal pole, thickening up to 2.75μm in total width towards the spore circumference. The trilete rays are joined equatorially by pronounced curvaturae perfectae, which are ≤1.25-3.5μm thick inter-radially, and usually slightly thicker (up to 5.5μm) radially. The curvaturae are invariably discrete from the equatorial margin of the spore, being situated well upon the proximal face. The contact areas either appear homogeneous, lacking sculpture and depressed, or may display a faint, irregular apical darkening ("diffuse polumbra"). The contact areas are further accentuated by a pronounced thinning of the exine (≤1-1.75μm in thickness), as well as being sharply delimited by curvaturate ridges.

Dimensions. Maximum spore diameter 41-68μm, mean 62μm (25 specimens measured).

Occurrence. LN; *rare.* H, S, LH, WP; *very rare.*

Remarks. Although the population of *Retusotriletes ?pychovii* recovered from north Devon are compatible with the size specifications of Naumova (1953, p.88; 45-50μm; p. 123, 65-70μm), specimens noted herein are subtly different in morphology to the line drawings of Naumova (1953; Pl. XIV, fig. 5; Pl. XVI, fig. 41). Forms recovered from Devon occasionally display distinct labra, and as lack a substantially thickened exine. On the rare occasions that the curvaturae coincide inter-radially with the equatorial margin, the exine appears ≤4.75μm in thickness.

Schultz (1968) regarded *Retusotriletes pychovii* to be cingulate.

Comparisons. *Retusotriletes communis* Naumova (1953, p. 97, Pl. XV, figs. 15-17; p. 110, Pl. XVI, fig.42) is ≈similar in size (20-60μm) and appears labrate, but equatorially the exine is thickened, the curvaturae less well developed, and the contact areas not so apparently thinned. *R. famenensis* Naumova (1953, p. 98, Pl. XV, fig. 18) displays thickened, labrate laesurae, and asymmetric contact areas (refer to the figured specimen in Mortimer & Chaloner, 1972; Pl. V, fig. 3). *R. parvimammatus* Naumova (1953; p. 89, Pl. XIV, fig. 8) is slightly larger in size (80-90μm), and conversely *R. simplex* (Naumova, 1953; p. 29, p. 97; 30-40μm) somewhat smaller, and seemingly thinner walled.

Retusotriletes laevigatus Guennel (1963, p. 255) is slightly smaller (38-43μm), and Guennel quotes the "cingulum" of this species to be ≈8μm broad. *R. paraguayensis* Menendez & Pöthe de Baldis (1967) is thick walled, but larger in overall diameter (75.7-85.2μm). *R. communis major* (Schultz, 1968, p. 15-16) is similarly larger in diameter (≈125μm). *Retusotriletes dittonensis* Richardson & Lister (1969; p. 215, Pl. 37, figs. 1, 2) is similar in size (35-57μm), but the curvatural ridges are somewhat thinner (≤0.5μm wide) and the contact areas finely striate, infragranulate or shagreenate in texture.

Retusotriletes actinomorphus Chibrikova (1962) in McGregor (1973; p. 18, Pl. 1, fig. 12-14) may display a polumbra as well as faint radial striae upon each contact face. *Retusotriletes digressus* Playford (1976; p. 9-10, Pl. 1, figs. 1-10) ranges up to 109μm in diameter, and the exine outside of the contact areas far greater in thickness (2.5-8.5μm).

Retusotriletes rugulatus Riegel
Plate 3.26, figs. 9-11, 13, 14.

p 1965 *Retusotriletes dubius* (Eisenack) Richardson p. 564, Pl. 88, fig. 6 (only).

1972 *Retusotriletes biarealis* McGregeor, in Mortimer & Chaloner, p. 14, Pl. I, fig. 10.

1973 *Retusotriletes rugulatus* Riegel, p. 82, Pl. 10, figs. 2-5.

non 1978a *Retusotriletes* cf. *rugulatus* Riegel, in Richardson & Rasul, p. 427-428, Pl. 1, fig. 7.

1980 *Retusotriletes rugulatus* Riegel, in Loboziak & Streel, Pl. I, fig. 1.

1982 *Retusotriletes rugulatus* Riegel, in McGregor & Camfield, p.58-59, Pl. 17, figs. 1-5.

1985 *Retusotriletes rugulatus* Riegel, in Paris *et al.*, Pl. 22, fig. 5.

1986 *Retusotriletes rugulatus* Riegel, in Turnau, Pl. IX, fig. 4.

1988 *Retusotriletes rugulatus* Riegel, in Marshall, Fig. 3 (2).

1989 *Retusotriletes rugulatus* Riegel, Loboziak & Streel, Pl. I, fig. 1.

For additional synonymy refer to McGregor & Camfield (1982, p.58).

Description. Trilete, acamerate miospores; amb circular, subcircular to convex-triangular. Outside of the contact areas the exine is laevigate to finely scabrate, rarely folded and ≤1-2.5μm thick at the equatorial margin: the exoexine ranges up to 3.75μm thick distally. The suturae are straight, rarely openly arcuate, and simple about the proximal pole, with thin labra developing towards the equatorial margin. Individually the labra are ≤0.5-1.75μm wide: the laesurae extend 2/3 to the full radius of the spore. The contact areas are delineated equatorially by distinct to perceptible curvaturate ridges, ≤2.25μm thick, ±invaginated. The curvaturae perfectae usually coincide with the spore circumference interradially. The contact areas bear an ornate sculpture, incorporating an apical polumbra, coupled with rugulate and/or subreticulate ribs, plications or "wrinkles": in general these "folds" are radial about the proximal pole. The polumbra varies in outline from subcircular to convex/concave triangular, and appears either homogenous, granulose (grana ≤0.75μm), striated or "zoned" (comprising a thinned, ±laevigate and lightened inner zone, and an outer, darkened "annulus"). The polumbra generally extends over 1/5 to 1/2 of each contact area: the remainder of the contact faces display morphologically diverse, radial plications, on average ≤0.75-2.25μm in individual width and height (rarely exceed 3.5μm). These rugulae appear sinuous (rarely straight) and are of variable extent, extending across ≤1/5 to 4/5 of each contact area: may be simple, bifurcating or anastomose. Dependant upon the development of the polumbra, such rugulation may cover up to 80% of each contact area. The morphology of all three contact areas is constant on one individual specimen.

Dimensions. Maximum spore diameter 46-98μm, mean 63μm (70 specimens measured).

Occurrence. S, L, CM, K; *common.* LN, H, LH, WP; *rare.* M; *very rare.*

Remarks. According to taxonomic details provided by Mortimer (1969, p. 34-35), the size range of the "*R. biarealis*" complex (recovered from subsurface Devonian strata in southern England) spans 40-105μm. This is in part more compatible with the size specifications of *Retusotriletes rugulatus* Riegel (1973; 53-79μm) than with those of *R. biarealis* McGregor (1964; 93-127μm). Mortimer (1969, p. 35) also remarks that many of the specimens recovered from southern Britain occasionally displayed proximal, radial "scabration" (homologous to that noted by McGregor (1964) upon the contact areas of *R. biarealis*). In view of the broadened size range note for *R. rugulatus* in the present study, the "*biarealis*" population of Mortimer (1969) and subsequently of Mortimer & Chaloner (1972) is herein regarded as synonymous with *Retusotriletes rugulatus* Riegel (1973).

Within the population of *R. rugulatus* documented from north Devon, the exine appeared up to ≈6μm in thickness when the curvaturae coincide with the equatorial margin.

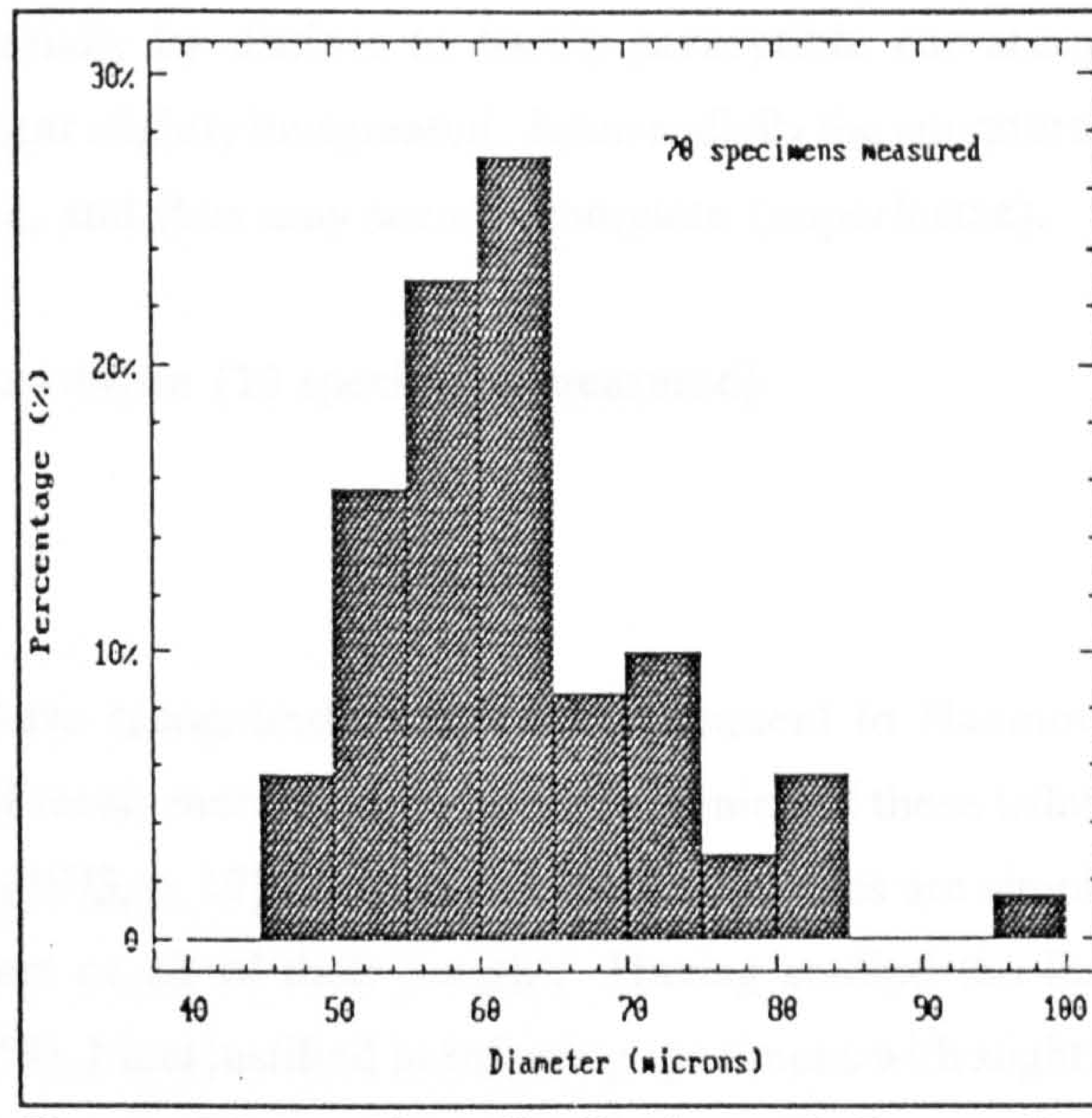


Figure 3.3.99: Size distribution of *Retusotriletes rugulatus* Riegel (1973).

Comparisons. *R. rugulatus* Riegel (1973) differs to all other species of *Retusotriletes* due to its distinctive, coarsely rugulate contact areas. *Retusotriletes actinomorphus* Chibrikova *sensu* McGregor (1973) may display faint, radial striations upon the contact areas, but these appear somewhat more subtle than those of *R. rugulatus*. *R. incomptus* McGregor (1973; p. 22, Pl. 2, fig. 6) is similar in size (38-61μm) but is thinner walled (1-1.5μm thick), and the interradial muri seemingly more diffuse. The contact areas of *Retusotriletes piperatus* Playford (1976, p. 10-11) are ill-defined, but exhibit a polumbra which may appear faintly striated. The contact areas of *Retusotriletes phillipsii* Clendening *et al.* (1980) are more clearly structured, lacking such intense and chaotic rugulate sculpture.

A few species of *Emphanisporites* bear a superficial resemblance to *R. rugulatus*, in displaying thin, sinuous muri, which are radial about the proximal pole. However, such features are rarely as intense, morphologically diverse or as chaotic as noted upon *R. rugulatus*. *Emphanisporites neglectus* Vigran (1964; p. 10-11, Pl. I, figs. 14-16) is markedly smaller in size (9.5-17μm). *E. epicautus* Richardson & Lister (1969; p. 223-224, Pl. 38, figs. 13-15) is likewise smaller (25-40μm), and displays comparatively uniform, finer, radial muri (≤0.5-1.5μm high and wide) upon each contact area.

The morphology of the proximal surface of ?*Retusotriletes* sp. B (of the present study) is similar to that of *R. rugulatus*, but the interradial muri are far more subtle, are of comparatively uniform width, and appear far more orderly in their arrangement.

Retusotriletes simplex Naumova.

Plate 3.26, figs. 12, 15, 16.

1953 *Retusotriletes simplex* Naumova, p. 29, Pl. II, fig. 9; p. 97, Pl. XV, fig. 14.

? 1967 *Retusotriletes simplex* Naumova, in Mortimer Pl. 1, fig. J.

? 1973 *Retusotriletes simplex* Naumova, in McGregor p. 19, Pl. 2, fig. 2.

Description. Trilete, acamerate miospores; amb circular, subcircular to rounded subtriangular. The exine is laevigate to finely scabrate, homogeneous, uniformly ≤1μm thick and rarely folded. The suturae are straight to openly arcuate, simple or finely labrate: the laesurae are ≤1.25μm in width and height. The trilete rays may be joined equatorially by distinct to barely perceptible curvaturae perfectae, which are ≤ 0.5-1μm thick and may appear slightly invaginated. Inter-radially the curvaturae commonly coincide with the spore circumference, and thus may seem incomplete (imperfectae).

Dimensions. Maximum diameter 34-52μm, mean 44μm (10 specimens measured).

Occurrence. LN, *rare.*

Remarks. Many Devonian palynologists who have recognised *R. simplex* subsequent to Naumova (1953) usually describe the suturae as simple, and rarely mention any subtle thickening of these trilete rays (*e.g.* Lele & Streel, 1969, p. 93). McGregor (1973, p. 19) does remark that the sutures are simple and may "...have weak or strong folds along part or all of their length". Having studied the line drawings of *R. simplex* provided by Naumova (1953), I feel justified in referring specimens with slightly "thickened" laesurae to *R. simplex* Naumova. Naumova (1953, p. 29, p. 97) defines the size range of *Retusotriletes simplex* as 30-40μm. The population recovered from north Devon range up to 52μm.

The contact areas of the specimen figured by McGregor (1973, Pl. 2, fig. 2) as *Retusotriletes simplex* Naumova appear in part to be markedly thinner than the remainder of the exine. This apical thinning is somewhat reminiscent of the Late Devonian/Early Carboniferous taxon *Retusotriletes leptocentrum* Higgs (1975).

Comparisons. *Retusotriletes semizonalis* of Streel (1967; *partim,* Pl. I, fig. 12) is similar, but the curvatural ridges are slightly thicker. Both *Retusotriletes warringtonii* Richardson & Lister (1969; p. 216, Pl. 37, figs. 7, 8) and *Retusotriletes* cf. *minor* Kedo in Richardson & Lister (1969; p. 217, Pl. 37, fig. 12) range down to less than 20μm in diameter, and display pronounced labra, 0.5-2μm in height. *Retusotriletes* sp. B *sensu* Richardson & Lister (1969; p. 273, Pl. 1, figs. 20, 21) and *Retusotriletes* sp. D *sensu* Richardson & Lister (1969; p. 273, Pl. 2, fig. 1, 2) are similar in all respects to *Retusotriletes simplex* (as recognised herein), apart from subtle, differential thickening of the contact areas.

Retusotriletes goensis Lele & Streel (1969), *R. rotundus* (Streel) Lele & Streel (1969) and *R. triangulatus* (Streel) Streel (1967) bear an apical polumbra of variable morphology. *Retusotriletes witneyanus* (Chaloner) Streel (1967, B 26-27) likewise displays a polumbra and is substantially larger in overall spore diameter. *Retusotriletes* sp. A in Richardson & Rasul (1978a, p. 432, Pl. 1, fig. 4) is similar, but the exine exhibits numerous compressional folds.

The *rotundus* Morphon.

McGregor (1973, p. 20-21) discusses the difficulty of consistently distinguishing between *Retusotriletes rotundus* (Streel) Lele & Streel (1969), *R. goensis* Lele & Streel (1969) and *R. triangulatus* (Streel) Streel (1967), as overall their morphological features are identical: these three taxa have been differentiated solely upon the variable design of the polumbra. McGregor (1973) remarked on the gradation in polumbra morphology and subsequently rationalised this plexus, favouring the consolidation of these three taxa to within one species concept, with *Retusotriletes rotundus* assuming taxonomic priority. The basic simplicity in construction of *Retusotriletes* spp. does, however, limit the number of variable parameters that can be used in speciation.

Within the population of *Retusotriletes* documented from north, the three species mentioned earlier were usually quite easy to recognise, although intergradational forms were (rarely) recovered. Therefore if present, I consider the variability in polumbra design to be of primary significance in the speciation of *Retusotriletes*. Thus, in the present study *R. goensis, R. rotundus* and *R. triangulatus* are recognised as discrete.

Retusotriletes goensis Lele & Streel.

Plate 3.26, fig. 2.

1967 *Phyllothecotriletes rotundus* Streel in Mortimer, Pl. 1, fig. G.

1969 *Retusotriletes goensis* Lele & Streel, p. 93-94, Pl. 1, figs. 12-16.

non 1976 *Retusotriletes goensis* Lele & Streel, in Massa & Moreau-Benoit, Pl. 4, fig. 8.

Description. Trilete, acamerate miospores; amb circular, subcircular to rounded convex-triangular in polar compression. The exine is laevigate to finely scabrate, $\leq$1.25 μm thick, with very occasional concentric folds distorting the exine (located preferentially towards the equatorial margin). The suturae are usually simple, straight to openly arcuate, and extend 1/4 to 7/8 the spore radius: the laesurae may appear thickened (labrate) towards the equatorial margin, ranging in total width from $\leq$1.5μm to 2.25μm. The trilete rays are joined equatorially by either well developed or indistinct curvaturae perfectae, $\leq$1.75μm thick: the curvaturae may be invaginated, and are commonly distinct from the equatorial margin. The exine is unsculptured, homogeneous, apart from a ?thickened, circular to subcircular, rarely rounded convex-triangular polumbra, which develops over the proximal pole and usually extends 1/5 to 1/3 (rarely 1/2) the spore radius. The margin of this apical darkening may be diffuse of distinct.

Diameter. Maximum spore diameter 47-65μm, mean 56μm (25 specimens measured).

Occurrence. LN, S; *common.* H, R, LH, WP, L, CM, K; *rare.*

Remarks. Few specimens exceed 60μm in diameter. Lele & Streel (1969, p. 93) record *R. goensis* to range up to 80μm in diameter.

Patchy, globular tapetal residue was occasionally observed adhering to the spore exine.

Comparisons. The polumbra of *Retusotriletes rotundus* (Streel) Lele & Streel (1969) is "zoned", and comprises a darkened "halo" which encircles ?thinned, lightened exine centred on the proximal pole. *R. triangulatus* (Streel) Streel (1967) is comparable to *R. rotundus* but exhibits a distinctly triangular polumbra. For *R. goensis,* this apical darkening is undifferentiated, appearing uniform over the polar region. *Retusotriletes biarealis* McGregor (1964, p. 7, Pl. 1, figs. 13-15) is substantially larger (93-127μm), exhibit a triangular polumbra and also displays textured (scabrate) contact areas.

Retusotriletes rotundus (Streel) Lele & Streel.

Plate 3.26, figs. 5-8, 20.

1964 *Phyllothecotriletes rotundus* Streel, p. 4, Pl. I, figs.1 and 2.

1967 *Retusotriletes rotundus* (Streel) Streel, p.25, Pl. I fig. 11, Pl. II, figs. 16 & 17.

1969 *Retusotriletes rotundus* (Streel) Streel emend. Lele & Streel, p. 94, Pl. 1, figs. 18-20.

1976 *Retusotriletes rotundus* (Streel) Streel, in McGregor & Camfield, p. 26, Pl. 5, fig. 9.

non 1982 *Retusotriletes rotundus* (Streel) Lele & Streel, in Marshall & Allen, p.284, Pl. 30, fig.6.

Description. Trilete, acamerate miospores; amb circular, subcircular to ovate, rarely convex triangular. The exine is laevigate, scabrate, rarely finely granulose: $\leq 1.75\mu m$ thick equatorially with rare folds. The suturae are distinct, straight to openly arcuate, and extend 3/4 to 7/8 the spore radius. Towards the proximal pole the suturae are commonly simple and "ragged", becoming indistinct equatorially or obscured by pronounced, thickened labra (≤ 1-$4.75\mu m$ in total width). The laesurae are connected equatorially by well defined curvaturae perfectae, which may be slightly invaginated and are also usually discrete (inter-radially) from the spore circumference: the curvaturae are $\leq 3.25\mu m$ in width. A darkened, circular to subcircular and ?thickened, "zoned" polumbra (the darkened "annulus" $\leq 4.5\mu m$-$11.5\mu m$ in width), is centred upon the proximal pole: this polumbra encircles a lightened, ?thinned, apical area. The margins of the polumbra may be distinct or diffuse, and commonly extend between 1/5 to 1/2 the length of the laesurae, from the proximal pole. Rare, equatorial, concentric folds may be present.

Diameter. Maximum spore diameter 42-$89\mu m$, mean $58\mu m$ (60 specimens measured).

Occurrence. LN, S, WP, L, K; *common*. H, R, LH, CM; *rare*.

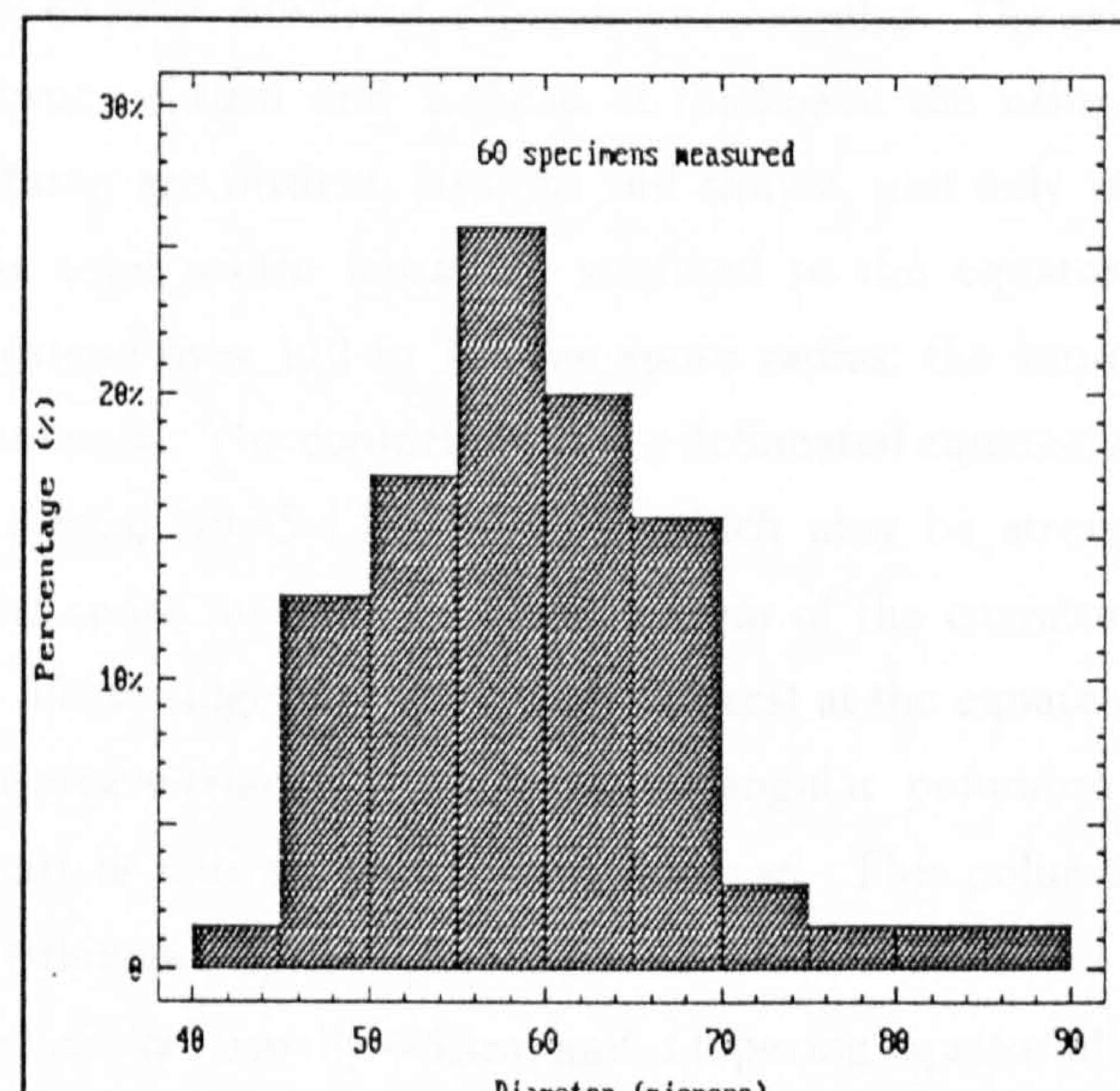


Figure 3.3.100: Size distribution of *Retusotriletes rotundus* (Streel) Lele & Streel (1969).

Remarks. As already discussed, McGregor (1973) recognised the practical problems of confidently differentiating between *R. rotundus*, *R. triangulatus*, and *R. goensis*. Consequently, he rationalised this plexus to within the concept of *Retusotriletes rotundus*. Whether variability in polumbra morphology can assume taxonomic priority is debatable. However, in view of the extreme differences in polumbra character observed for the population of *Retusotriletes* spp. documented from north Devon, and also due to the lack of other suitable characteristics that may allow speciation within this plexus, the present author believes *R. rotundus, R. goensis* and *R. triangulatus* to be justifiably distinct. However, rare intergradational forms were noted between these "end-member" species, as noted by McGregor (1973).

Comparisons. *Retusotriletes triangulatus* displays a demonstrably triangular, "zoned" polumbra, which commonly parallels the trilete rays. *R. goensis* exhibits a homogeneous polumbra, centred on the proximal pole. (Note the comparisons listed overleaf for *Retusotriletes triangulatus*).

Retusotriletes triangulatus (Streel) Streel.
Plate 3.26, figs. 17-19.

1964 *Phyllothecotriletes triangulatus* Streel, p. 5, Pl. I, figs. 3,4 and 5.
p ? 1965 *Retusotriletes dubius* p. 564, Pl. 88, fig. 5 only (fig. 6, *R. rugulatus* Riegel, 1973).
1967 *Retusotriletes distinctus* Richardson, in Mortimer, Pl. 1, fig. H.
1967 *Retusotriletes triangulatus* (Streel) Streel, p. 24, PL. II, figs. 18, 19, and 20.
1967 *Retusotriletes* (Naumova) Richardson, Pl. III, fig. A.
p 1969 *Retusotriletes* cf. *triangulatus* (Streel) Streel, in Richardson & Lister, p. 217-218, Pl. 37, figs. 3, 4, (only); text-fig. 3.
? 1973 *Retusotriletes dubiosus* McGregor, p. 21-22 (p. 37), Pl. 2, fig. 1.
1977 *Retusotriletes triangulatus* (Streel) Streel, in Owens, Downie & Reynolds, Pl. 2, figs, 1, 2.
1978a *Retusotriletes* cf. *triangulatus* (Streel) Streel, in Richardson & Rasul, p. 428,430, Pl.1, fig.10.
1982 *Retusotriletes rotundus* (Streel) Lele & Streel, in Marshall & Allen, p. 284, Pl. 30, fig. 6.
1982 *Retusotriletes rotundus* (Streel) Streel, in McGregor & Camfield, p. 58, Pl. 16, fig. 13.

Description. Trilete, acamerate miospores; amb circular, subcircular to convex-triangular. The exine appears laevigate or scabrate, and ranges between $\leq 1\mu m$ and $2.75\mu m$ in thickness: the exine is $\leq 3.5\mu m$ thick over the distal surface. The suturae are distinct, straight and simple, and only very occasionally are paralleled by labra, $\leq 2\mu m$ in total width: labra are confined to the equatorial extremities of the trilete rays. The laesurae extend over 1/2 to 7/8 the spore radius: the suturae become increasingly distinct towards the proximal pole. The contact areas are delineated equatorially by distinct to barely perceptible curvaturate ridges, ≤ 0.75-$4.25\mu m$ thick, which may be strongly invaginated and in general are distinct from the spore margin: the inner margin of the curvaturae tends to be distinct, and the outer edge diffuse. These ridges are commonly thickest at the equatorial terminations of the laesurae. A triangular, concave-triangular or convex-triangular polumbra is centred upon the proximal pole, and may in part or entirely parallel the laesurae. This polumbra usually appears "zoned", comprising an inner, $\approx$thinned, apical lightened zone which is bordered by a distinct, darkened band (≤ 2.5-$9\mu m$ wide interradially , usually $\approx 6\mu m$, and $\pm$tapering equatorially). This apical darkening may either appear diffuse, or conversely more homogeneous and uniform: in either case the polumbra still appears strikingly triangular in outline. The polumbra tends to parallel the suturae over 1/3 to 7/8 their full length.

Dimensions. Maximum spore diameter 41-$87\mu m$, mean $54\mu m$ (60 specimens measured).

Occurrence. LN, R, S, WP, CM, K; *common.* H, LH, L, M; *rare.*

Remarks. Streel (1964, B.5, Fig. 1) plots the size distributions of *Retusotriletes* (al. *Phyllothecotriletes*) *rotundus* and *Retusotriletes* (al. *Phyllothecotriletes*) *triangulatus*. According to this plot, the two species are comparatively distinct, with *R. triangulatus* the larger (36-64μm *vs.* 58-84μm, *sensu* Streel, 1964). Similar plots were produced herein, based upon measurements of specimens recovered from north Devon: the two species were found to have very similar size ranges and means (both comparable to the *Retusotriletes* cf. *triangulatus* plot of Richardson & Lister, 1969, p. 218, text-fig. 3). The data base in the present study is far more extensive than that of Streel (1964; which was based upon a total of 12 specimens of *R. rotundus* and 23 of *R. triangulatus*), and therefore considered more representative. Clearly the two species cannot be differentiated based simply upon disparities in size.

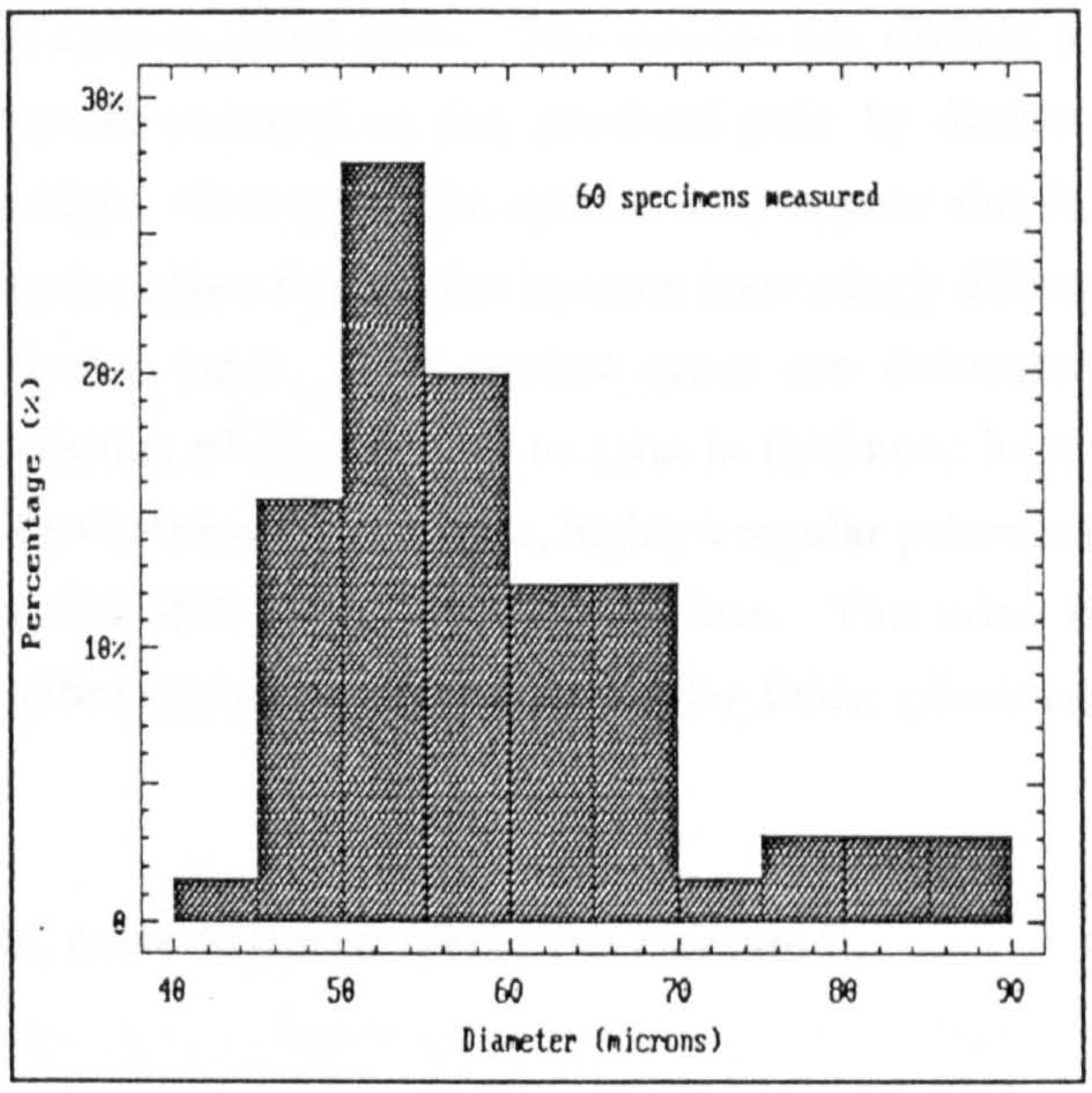


Figure 3.3.101: Size distribution of *Retusotriletes triangulatus* (Streel) Streel (1967).

Richardson (1965, p. 564) and subsequently McGregor (1973, p. 21) remark that *Retusotriletes dubiosus* (al. *dubius, partim*) is a simple retusoid spore that commonly displays a triangular apical darkening. McGregor (1973) specified the size range for *R. dubiosus* as 67-119μm, with Richardson & Rasul (1978a, p. 427) subsequently quoting its size as 65μm-80μm. The figured specimen of *R. dubiosus* in McGregor (1973, Pl. 2, fig. 1) appears comparatively thick walled and displays a diffuse, seemingly homogeneous, subtriangular polumbra. Clearly the dimensions and gross morphology of *R. dubiosus* conform (in essence) with those of *R. triangulatus,* and thus the two may well prove to be synonymous: *Retusotriletes triangulatus* would assume taxonomic priority.

Gradational forms were noted with *R. goensis* and *R. rotundus.*

Comparisons. *Retusotriletes biarealis* McGregor (1961) similarly displays a triangular polumbra, but is substantially larger (93-127μm), with scabrate, ≈radially striated contact areas. *R. rotundus* (Streel) Lele & Streel (1969) exhibits a distinctly circular, "annulate" polumbra, whereas that of *R. goensis* Lele & Streel (1969) is homogeneous-"complete", and generally circular in outline. *Retusotriletes planus* Dolby & Neves (1970) is comparatively simple in design: the laesurae are paralleled by a diffuse darkened zone, which is not as well defined as the polumbra of *R. triangulatus. Retusotriletes witneyanus* (Chaloner) Streel (1967, B 26-27) is substantially larger in overall spore diameter (110-196μm; in Chaloner, 1963; p. 101-102).

Retusotriletes sp. A

Plate 3.27, figs. 4, 5.

Description. Trilete, acamerate miospores; amb subcircular to irregular subtriangular. The exine is scabrate to finely granulose, rarely homogeneously laevigate, and ≤0.75-1.25μm thick equatorially:

the exine is distorted by pronounced, concentric and/or radial folds. The suturae are distinct to perceptible, straight to openly arcuate, and may be obscured at the proximal pole by distinct, diaphanous labra, ≤0.5-1μm wide and ≤7.25μm high. Conversely the suturae may appear simple, nonlabrate. The laesurae extend 4/5 to 7/8 the spore radius: the suturae become increasingly diffuse towards the equatorial margin, and/or the laesurae taper. The contact areas are delineated equatorially by faint to discernible curvaturae perfectae, which range up to 1μm in thickness: inter-radially the exine is ±clearly laevigate, and occasionally thinned. A diffuse, highly irregular polumbra may extend over the proximal pole, and covers ≤20-55% of the proximal surface. The exine is variably distorted by between three to eleven, either broad or narrow, lenticular folds: plications ≤1.5-14μm in width.

Dimensions. Maximum spore diameter 52-71μm, mean 67μm (8 specimens measured).

Remarks. Globular tapetal residue, resembling isodiametric grana (≤1.75μm in diameter), may form a sparse "sculptural" cover over the exine.

Comparisons. *Retusotriletes* sp. A differs to previously described species of *Retusotriletes,* due to the combination of a thin, scabrate exine, the irregular, diffuse polumbra, and the intensity of exinal folds. Indeed, *Retusotriletes* sp. A displays all the key attributes of calamaspores (namely thin, distorted exine, ±polumbra), but differs in possessing ≈pronounced curvatural ridges.

Retusotriletes simplex Naumova (1953) is smaller, morphologically simple and lacks such pronounced exinal folds. *Retusotriletes goensis* Lele & Streel (1969), *R. rotundus* (Streel) Lele & Streel (1969), and *R. triangulatus* (Streel) Streel (1967) display more distinct, structured polumbras. *Retusotriletes witneyanus* (Chaloner) Streel (1967) is substantially larger, lacks such chaotic compressional folds, and bears a more conservative, discrete, apical darkening.

?*Retusotriletes* sp. B.
Plate 3.27, figs. 1-3, 6.

Description. Trilete, acamerate miospores; amb circular, subcircular to convex triangular. The suturae are distinct to discernible, straight to openly arcuate and extend between 1/2 to 7/8 the spore radius: the suturae may appear simple or variably obscured by either pronounced or barely perceptible labra, ≤1-4.25μm wide and ≤3μm high. The labra may appear splayed at their equatorial extremities, ranging up to 7.5μm in width. Proximo-equatorially and distally the exine is laevigate, scabrate to finely granulose, and is ≤2-2.75μm thick equatorially. The exine of the contact areas appears slightly thinned, scabrate to granulose and delineated equatorially by distinct, thickened curvaturae perfectae, which are robust, ≤2-7.25μm in width (usually thinning interradially), with an irregular but distinct inner (polar) margin, and either a diffuse or sharp outer edge. The curvaturae may be strongly invaginated, and inter-radially may coincide with the equatorial margin: when the two coincide, the spore circumference may seem ≤6μm in thickness. The contact areas display a varied sculpture, incorporating a laevigate to microgranulose, irregular-subcircular to subtriangular, thinned apical zone, which extends over ≤20-35% of the contact surface. The remainder of the contact areas bear distinct to diffuse striations, radial about the proximal pole. These "muri" are simple (rarely bifurcate or anastomose), and straight, openly arcuate to tightly sinuous, extending over ≤1/3 to 3/4 of the contact area radius: muri are ≤0.5-2.75μm in width equatorially, usually tapering or becoming increasingly diffuse towards the proximal pole. These striae often degenerate towards the proximal pole, into less well defined, more irregular, "beaded" rugulae, or simple rows of discrete grana (individual grana ≤0.5μm in diameter). Overall these radial elements are ≤1-2.5μm apart (rarely exceed 3μm), with approximately 15-23 per interradial area.

Dimensions. Maximum spore diameter 53-81μm, mean 64μm (15 specimens measured).

Occurrence. S; *common.* R, LH; *rare.*

Remarks. There is some question as to the most appropriate generic repository for spores of this type. The distinct, depressed and thinned contact areas, as well as the laevigate exine (apart from the subtle interradial sculpture) and pronounced curvatural ridges are common attributes of the genus *Retusotriletes.* Certain species of *Emphanisporites* display a comparable morphology (*e.g. E. epicautus* Richardson & Lister, 1969), but *Retusotriletes* is considered the more appropriate generic repository.

Comparisons. *Emphanisporites annulatus* McGregor (1961), *E. rotatus* McGregor (1961) and *E. mcgregorii* (Cramer 1967) are comparable in size, but display variably coarser, more pronounced and distinct radial ribs, and furthermore lack curvatural ridges. *Emphanisporites neglectus* (Vigran; 1964, p. 10-11, Pl. I, figs. 14-16) and *E. minutus* (Allen; 1965, p. 709, Pl. 97, fig. 20) are markedly smaller (≤30μm), and lack such robust, well differentiated curvaturate ridges. *Emphanisporites epicautus* Richardson & Lister (1969; p. 223-224, Pl. 38, figs. 13-15) is broadly similar in morphology to that of *?Retusotriletes* sp. B, but is smaller (25-40μm in diameter) and the proximal ribbing more pronounced. *Emphanisporites* sp. of Riegel (1973; p. 87, Pl. 18, fig. 11) ranges down to 44μm in spore diameter, and displays better defined interradial ribs.

Of the *Retusotriletes* plexus, *Retusotriletes rugulatus* Riegel (1973) bears the closest resemblance to *?Retusotriletes* sp. B. However, *R. rugulatus* displays a more chaotic, wrinkled to subreticulate interradial sculpture, and usually bears a ±darkened, "?thickened" polumbra. The haptotypic striations on *Retusotriletes actinomorphus* Chibrikova (1962; p. 404, Pl. V, fig. 1) are more indistinct. *Retusotriletes incomptus* McGregor (1973; p. 22, Pl. 2, fig. 6) is comparable in size (38-61μm) and also displays a faint interradial sculpture, but is thinner walled (≈1-1.5μm thick), and exhibits finer, less robust curvaturate ridges: according to McGregor (1973) these are ≤1μm in width and height.

Genus *Rhabdosporites* Richardson, emend. Marshall & Allen 1982.

Type species. *Rhabdosporites langii* (Eisenack) Richardson, 1960.

Discussion.

Richardson (1960, p. 53) proposed the genus *Rhabdosporites* to circumscribe non-limbate, camerate spores, that bear a homogeneous, dense cover of truncated, "rod-like" sculptural elements. He contrasted *Rhabdosporites* with *Remysporites,* which differed in possessing a smooth to microreticulate bladder, and similarly with *Glomospora*, which displayed an ornament comprising "slightly raised, spiral or parallel ridges". Subsequently, a number of authors have referred species to this plexus, that not only display a diversity of other sculptural elements, but more significantly lack any baculate sculpture (*e.g. R. firmus*, Guennel 1963; *R. scamnus*, Allen 1965; *R. cuvillieri*, Taugourdeau-Lantz, 1967). In addition, a far greater diversity in sculpture has been recognised for the genotype, *Rhabdosporites langii*, subsequent to the original diagnosis of Richardson, 1960 (*e.g.* Streel 1972, p. 210; Tiwari & Schaarschmidt 1975, p. 39).

Lele & Streel (1969; p. 102-103) remarked upon the predominance of a conate sculpture on species of *Rhabdosporites* recovered from Givetian strata at Goé, Belgium. Baculate sculptural elements were seldom present upon these specimens, which lead Lele & Streel to question whether such sculpture was in fact primary: they suggested that this ornamentation may be corroded. Furthermore, this "atypical" ornament suggested to Lele & Streel (1969) a potential affinity with the *Geminospora* plexus. Owens (1971, p. 59-60) subsequently emended the circumscription of *Geminospora*, allowing for a far greater diversity of ornament, but payed little attention to the potential homology with *Rhabdosporites:* Owens (1971) was more directly concerned with rationalising, in part, the heterogeneous *Archaeozonotriletes* complex of Naumova (1953) - refer to the earlier discussion under *Geminospora.*

Higgs & Russell (1981, p. 30) remarked that the population of "*Rhabdosporites parvulus*" documented from the Upper Devonian strata of the Moll's Gap Quarry, County Kerry (Ireland), displayed a preponderance of coni over baculate sculpture. In this respect Higgs & Russell concord with the observations of Lele & Streel (1969), and thus only tentatively identified *Rhabdosporites*, remarking also upon the similarity in ornamentation and construction of such forms with *Geminospora*.

McGregor & Camfield (January, 1982, p. 59) addressed the restrictive circumscription of *Rhabdosporites, sensu* Richardson (1960), by examining specimens of *R. langii* from Edderton Burn and Coal Heugh (localities of Richardson, 1965). They corroborated Richardson's earlier findings that the predominant sculptural-type was minute bacula, but also noted grana, coni and truncated coni in association. Consequently McGregor & Camfield (1982) proposed a more flexible and realistic expanded diagnosis of the genus *Rhabdosporites*, allowing for grana, coni, and minute spinae, as well as bacula. These authors do note, however, that in well preserved specimens, bacula are always the most predominant sculptural type.

Later that year, Marshall & Allen (April; 1982, p. 294) formally emended the circumscription of *Rhabdosporites*, similarly allowing for a far greater variation in sculpture (low bacula, coni and grana), as well as synonymising a number of what they regarded were superfluous taxa. This emendation is not too dissimilar to the expanded diagnosis proposed by McGregor & Camfield earlier that year. However, Marshall & Allen (1982) do allow for the optional presence of a limbus (as remarked upon by Owens 1971, being present in Eisenacks' original illustration): this feature was not discussed by McGregor & Camfield (1982). The emendation of Marshall & Allen is therefore adopted herein.

In comparison, Neves & Owens (1966, p. 342-344) proposed the genus *Spelaeotriletes*, being reminiscent in construction to that of *Rhabdosporites*, but differs in bearing a more varied exoexinal sculpture (encompassing discrete or fused coni, grana and verrucae). In rationalising *Rhabdosporites*, Marshall & Allen (1982) acknowledged the morphological similarity with *Geminospora* (Balme) Owens (1971), but considered geminospores distinguishable by virtue of their construction: *Geminospora* is typified by a thin-walled intexine, which is closely appressed to, or variably separated away from, a sculptured, distally thickened exoexine. However, Marshall & Allen (1982) note that without recourse to microtome sectioning, differentiation becomes increasingly difficult when limbate *Rhabdosporites* have a high intexine to exoexine ratio: also note the comments in Playford (1983, p. 315). Marshall & Allen (1982) also remark that camerate spores with a "coarse" sculpture can be accommodated within genera other than *Rhabdosporites* (*e.g. Grandispora*). Unfortunately, the diagnoses of many genera such as *Rhabdosporites* and *Grandispora* are at present ambiguous, and not mutually exclusive. Indeed, the status and validity of many Devonian camerate spore complexes urgently require verification.

Rhabdosporites langii (Eisenack) Marshall and Allen
Plate 3.27, figs. 7-9.

1944 *Triletes langi* Eisenack, p. 112, Pl. 1, figs. 3-6.
1960 *Rhabdosporites langi* (Eisenack) Richardson, p. 54, Pl. 14, figs. 8, 9.
1965 *Rhabdosporites parvulus* Richardson, p.588, Pl. 93, figs. 3-7.
1972 *Rhabdosporites parvulus* Richardson, in Mortimer & Chaloner, p. 14, Pl. I, fig. 8.
1972 *Rhabdosporites langi* (Eisenack) Richardson, in Mortimer & Chaloner, p.28, Pl.IV, fig.4.
1976 *Rhabdosporites langii* (Eisenack) Richardson, in McGregor & Camfield, p. 27, Pl. 7, fig. 7.
1980 *Rhabdosporites langii* (Eisenack) Richardson, in Loboziak & Streel, Pl. III, fig. 2.
1980 *Rhabdosporites parvulus* Richardson, in Loboziak & Streel, Pl. III, fig. 3.
1981 *Rhabdosporites parvulus* Richardson, in Loboziak & Streel, Pl. III, fig. 1.
1982 *Rhabdosporites langii* (Eisenack) Richardson, in McGregor & Camfield, p.59-60, Pl. 17, figs. 6-11, 13, text-fig. 91.
1982 *Rhabdosporites langii* (Eisenack) Marshall & Allen, p. 295-296, Pl. 32, figs. 8-10.
1986 *Rhabdosporites langii* (Eisenack) Richardson, in Turnau, Pl. IX, fig. 8.
1988 *Rhabdosporites langii* (Eisenack) Marshall & Allen, in Marshall, Fig. 3 (1).
? 1989 *Rhabdosporites langii* (Eisenack) Richardson, in Loboziak & Streel, Pl. III, fig. 4.

For additional synonymies refer Moreau-Benoit (1980, p.29-30) and Marshall & Allen (1982, p. 295).

Description. Trilete, camerate miospores; amb subcircular or irregular subovate, rarely convex-triangular. The outline of the intexinal body may either parallel the equatorial margin, or conversely may appear more irregular, distinctly circular or subtriangular in form. The exinal layers are discrete, well separated, with attachment seemingly confined to the proximal polar region. The suturae are indistinct, straight to openly arcuate, and typically extend 3/4 to the full radius of the intexinal body. The suturae are commonly obscured by robust, and/or thin-flexuous, elevated labra, $\leq$6-11μm in height and $\leq$5μm in total width at the proximal pole: the laesurae usually taper towards the equatorial margin, are simple, non-curvaturate. Pronounced exinal folds may parallel the trilete rays, and $\pm$propagate the laesurae to the spore circumference. The intexine is laevigate, distinct, and optically dense: appears relatively robust, rigid and rarely folded, typically ≤1-2.5μm thick equatorially (rarely exceeds 3μm). In contrast the exoexine appears ≈membraneous, ≤1-2.25μm thick equatorially (rarely exceeds 2μm). The exoexine may be irregularly limbate, ≤5.5μm in thickness: such compressional thickening may appear highly variable in width around the spore circumference. Other than the extent of the laesurae, haptotypic characteristics are often difficult to discriminate: the contact areas are ill-defined, coarsely scabrate to finely granulose in texture and may merely be distinguishable by a juxtaposition in sculpture. The proximo-equatorial and distal regions display a dense, even sculpture, comprising bacula, coarse grana, coni and rare spinae: sculptural elements are variably smooth, rounded or truncated in lateral profile, and subcircular to polygonal in plan view. Elements are typically 1μm in width and height, and only very occasionally range up to 1.5μm: the ornament is densely distributed, individual elements commonly ≤0.25-0.5μm apart (rarely 0.75μm). The exoexine may display intense radial or concentric folds, commonly independant of the intexinal body.

Figure 3.3.102: Sculptural elements of *Rhabdosporites langii*, lateral view.

Dimensions. Maximum exoexinal diameter 57-137μm, mean 88μm. Intexinal body diameter 39-102μm, mean 61μm (125 specimens measured). Mean diameter of the intexinal body, 76% of the total spore diameter.

Occurrence. S, WP, L; *common*. R, LH, CM, K; *rare*. M; *R*.

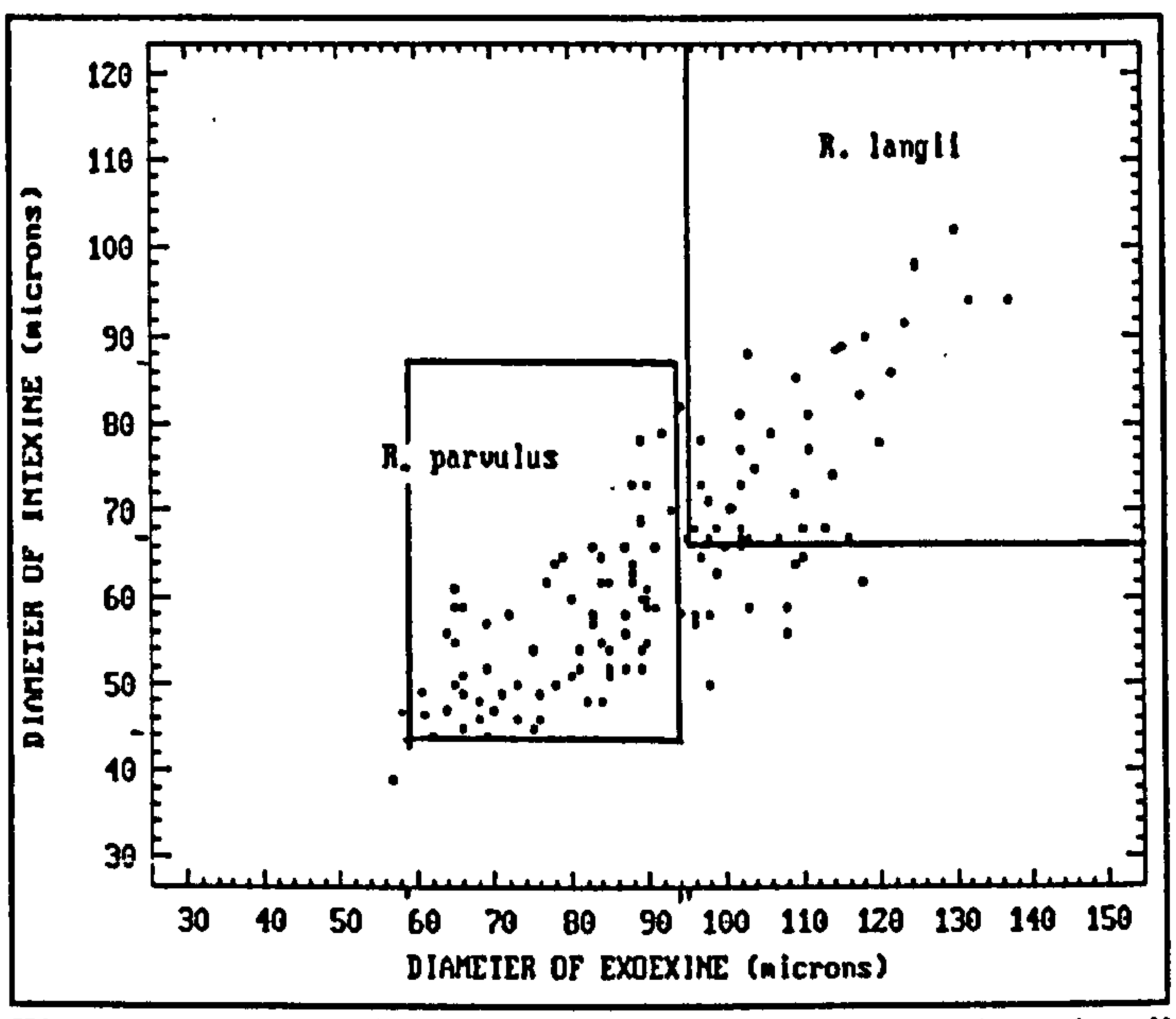


Figure 3.3.103: Size variation in *Rhabdosporites langii* (Eisenack) Marshall & Allen (1982).

Remarks. Despite striking similarities in morphology, Richardson differentiated two species of *Rhabdosporites*, namely *R. langi* Richardson (1960) and *R. parvulus* Richardson (1965), based upon disparites in overall spore size (95-190μm *vs.* 44-87μm respectively) and variable intexine to exoexine ratios.

Using a statistical approach, Marshall & Allen (1982) questioned the validity of the species *Rhabdosporites parvulus* Richardson (1965), noting no obvious distinction in size for populations of "*langii*" (*sensu stricto*) and "*parvulus*" (*sensu* Richardson) recorded from Fair Isle (Scotland): note "size" was compared by plotting intexinal body diameter against that of the exoexine. Further to Bonamo & Banks (1967), Marshall & Allen (1982) considered the two original species of Richardson to merely represent subtle ontogenetic variants within one species population, and consequently regarded *R. parvulus* as a junior synonym of *R. langii*.

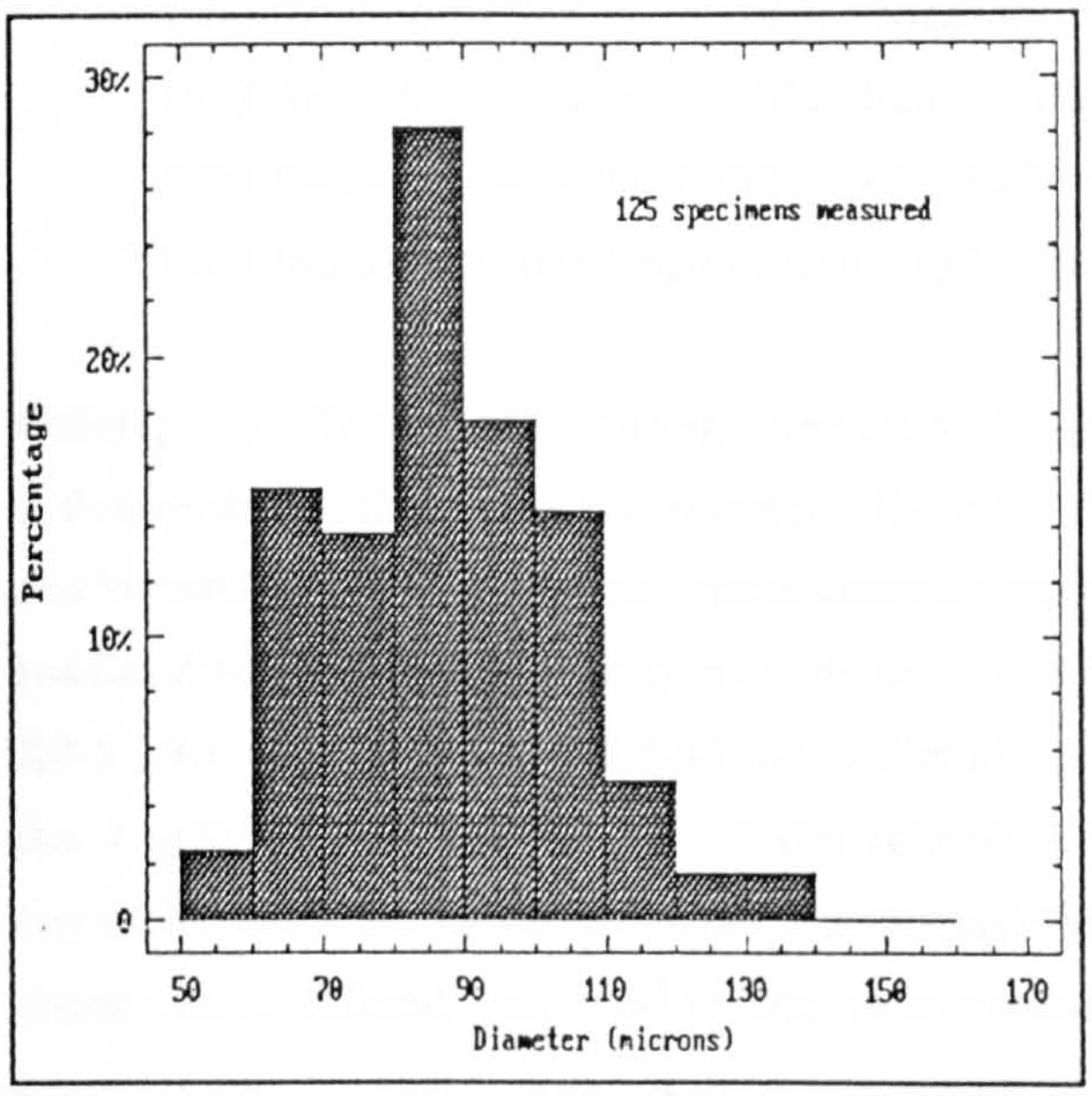


Figure 3.3.104: Frequency histogram plot of exoexinal diameters of *Rhabdosporites langii.*

A methodology similar to that of Marshall & Allen (1982) was adopted in the present study, and concurred with their observations: *Rhabdosporites langii* and *R. parvulus* are inseparable based solely upon a disparity in size (as cited by Richardson, 1960, 1965). Figure 3.3.103 illustrates the variation in size (intexine to exoexine plot) for the population of *Rhabdosporites langii* documented from north Devon (the limits of *R. langi, sensu* Richardson 1960, and *R. parvulus* Richardson 1965, are indicated). Figure 3.3.104 is a frequency histogram plot of exoexinal diameter for the population of *Rhabdosporites langii* recorded in the present study. Interestingly, the mean exoexinal diameter of this species population is greater than the upper size limit specified by Richardson (1965) for *R. parvulus* (87μm), but less than the minimum spore diameter quoted for *R. langi* by Richardson (1960).

Contrary to the original restriction imposed on sculptural morphology by Richardson (1960), and in agreement with a number of subsequent workers (*e.g.* McGregor & Camfield, 1982; p. 59), forms of *Rhabdosporites langii* documented from north Devon were noted as displaying a more varied sculpture.

Comparisons. The re-appraisal of *Rhabdosporites langii* by Marshall & Allen (1982, p. 295) and the associated synonymy list is acknowledged in the present study. In comparsion, *Rhabdosporites* sp. A, *sensu* Richardson (1965) displays three distinct exinal layers. *R. scamnus* Allen (1965) displays a number of ≈radial, symmetrically disposed muroid folds. *Grandispora inculta* Allen (1965) is broadly comparable, but bears a preponderance of slightly longer (1-2μm), conate sculpture: furthermore *G. inculta* displays a more "membraneous" pseudosaccus. *Rhabdosporites minutus* Tiwari & Schaarschmidt (1975, p. 39-40, Pl. 21, figs. 4-6) is small (45-57μm), displays a "leathery", thick-walled exoexine (2-3μm thick) and is sculptured with diminutive bacula, 0.5μm in size. *Rhabdosporites* sp. of McGregor & Camfield (1982) displays a thinner, more diffuse intexinal body, and a coarser exoexinal sculpture.

The problem of differentiating between small forms of *Rhabdosporites langii* and *Geminospora lemurata,* alluded to by Marshall & Allen (1982), was not encountered in the present study.

Rhabdosporites sp. A, *sensu* Richardson 1965.

Plate 3.27, figs. 10, 12, 13.

1965 *Rhabdosporites* sp. A., Richardson, p. 589, Pl. 93, fig. 7.

1972 ?*Calyptosporites* sp. A. Mortimer & Chaloner, p. 18, P. II, fig. 4.

1974 *Rhabdosporites* sp. A. of Richardson, in Moreau-Benoit, p. 202, Pl. 15, fig. 5.

1980 *Rhabdosporites* sp. A. of Richardson, in Moreau-Benoit, p. 31. Pl. 10, fig. 4.

1982 *Rhabdosporites* sp. A., Marshall & Allen, p.297, Pl. 32, figs. 6, 7.

1988 *Rhabdosporites langii* (Eisenack) Richardson, in Loboziak, Streel & Burjack, Pl. VII, fig.1.

? 1989 *Rhabdosporites langii* (Eisenack) Richardson in Loboziak & Streel, Pl. III, fig. 4.

Description. Trilete, camerate miospores; amb subcircular, ovate to irregular subtriangular. Exine is demonstrably three layered: in general the central ("intexinal") body and the middle exinal layer are conformable in outline with the spore circumference. The suturae are straight to openly sinuous and confined to the central body: commonly obscured by elevated, either flexuous or robust/rigid labra, ≤2-5.5μm in total width and ≤9.75μm in height at the proximal pole. The labra tend to propagate the trilete rays to the margin of the middle layer or occasionally beyond, reaching the spore circumference: the laesurae ≈taper equatorially and appear simple, noncurvaturate. The contact areas are ill-defined, and tend to lack pronounced sculpture. The central body and middle exinal layer appear laevigate, scabrate to finely granulose: the innermost intexinal body is optically dense, robust, and ≤?2-3μm thick. In contrast, the middle and outermost exinal layers are comparatively membraneous, usually folded (in sympathy), and rarely exceed ≤1-1.75μm in thickness. The outermost layer may be irregularly thickened equatorially: this limbus ranges in width from ≤3μm to 5μm. The outermost exinal layer exhibits a distinct, dense, apiculose sculpture, comprising diminutive bacula, coni and grana, with rare spinose elements interspersed: ≤0.5-1.25μm in width and height. The ornament may form either a comparatively homogeneous sculptural cover over the entire exoexine, or conversely may appear slightly reduced/?absent towards the proximal pole. The exinal layers are often ruptured, fragmented, and/or display radial or concentric folds ±independant of one another: the central body is usually the least distorted.

Figure 3.3.105: Sculptural elements of *Rhabdosporites* sp. A, *sensu* Richardson (1965).

Dimensions. Maximum exinal parameters (45 specimens measured); Outer wall 59-129μm, mean 92μm. Middle wall 53-113μm, mean 81μm. Intexinal body 40-98μm, mean 61μm.

Diameter of the intexinal body 52-87% (mean 67%) of the total spore diameter. Diameter of the middle exinal layer 74-93% (mean 87%) of the total spore diameter.

Occurrence. WP, CM; common. L, K; *rare.*

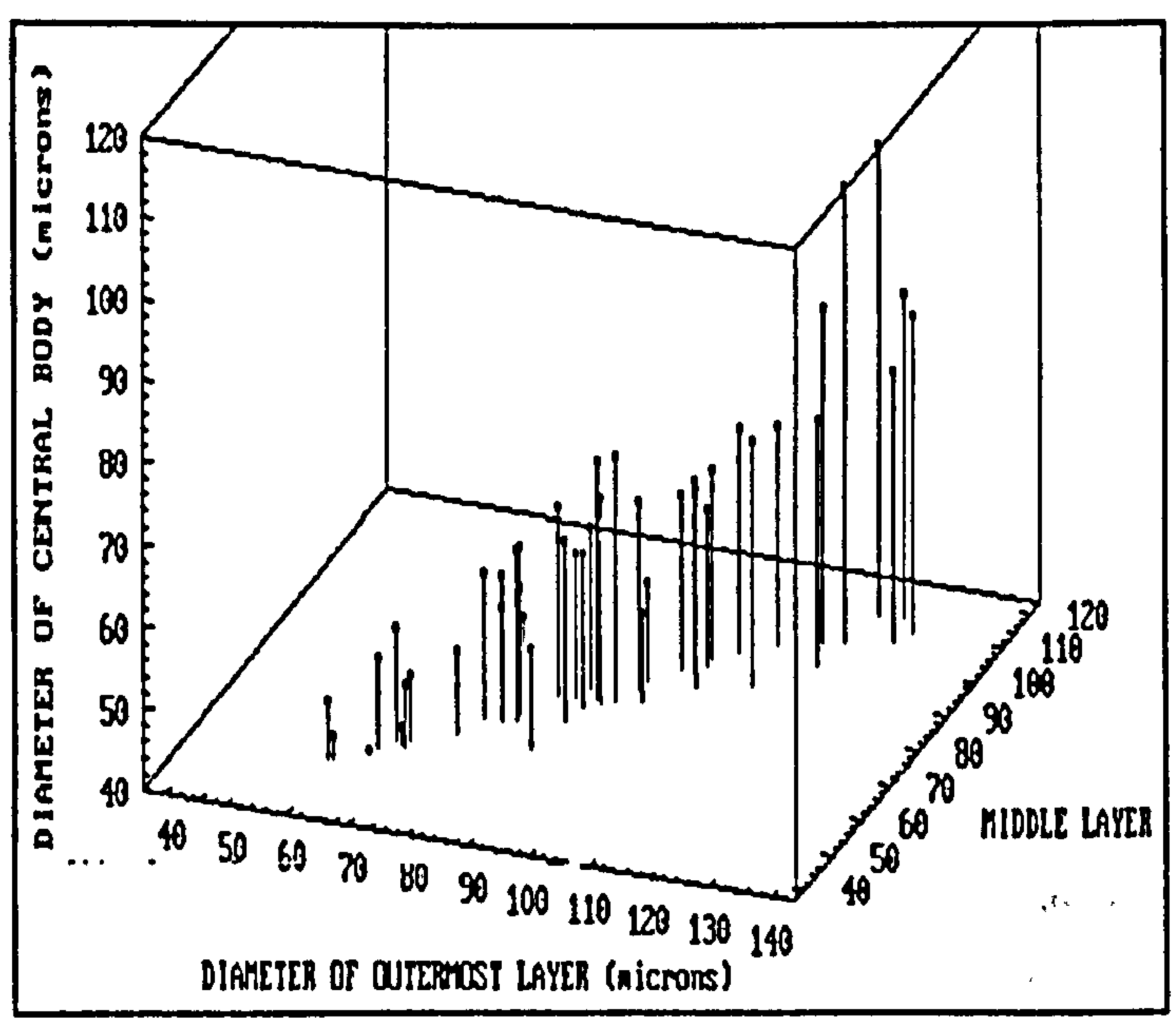


Figure 3.3.106: Size variation in *Rhabdosporites* sp. A, *sensu* Richardson (1965).

Remarks. *Rhabdosporites* sp. A *sensu* Richardson (1965) was first described from the Eday Beds (Middle Devonian sediments) of the Orcadian Basin, Scotland. Since then, either this species or forms identical in construction have been reported from a limited number of localities around the globe. Hemer & Nygreen (1967) illustrate a three layered spore as *Rhabdsporites* sp., but did not provide systematic details. ?*Calyptosporites* sp. A in Mortimer & Chaloner (1972) was recovered from the Harmansole and Wyboston Boreholes of southern England (Middle and Upper Devonian strata respectively). According to the systematic palaeontology provided by Mortimer (1969, p. 195-197) and Mortimer & Chaloner (1972, p. 18), this morphotype was similar in size to *Rhabdosporites* sp. A *sensu* Richardson (maximum diameter 115-210μm), but was differentiated due to a "patchy", predominantly rounded conate sculpture. According to these authors, Ozolinya (1960; Pl. 1, fig. 29) figures a spore (250μm in diameter) as *Archaeozonotriletes micromanifestus* var. *minor* Naumova, that appears three layered in construction. Moreau-Benoit (1974, 1980) recognised *Rhabdosporites* sp. A, *sensu* Richardson within Devonian spore assemblages from Libya, noting the size range in the latter publication to be 128-140μm. Subsequently, Marshall & Allen (1982, p. 297) defined a form of *Rhabdosporites* sp. A, distingushing this complex from that of Richardson (1965, p. 589) largely due to a discrepency in overall spore diameter (90-101μm, Marshall & Allen, *vs.* 146-224μm of Richardson 1965), as well as minor differences in sculpture. More recently, a specimen identified as *Rhabdosporites langii* from subsurface Devonian strata of the Parana Basin (Brasil) by Loboziak *et al.* (1988) clearly exhibits a subtle three-layered wall construction, and thus is more appropriately assigned to *Rhabdosporites* sp. A, *sensu* Richardson (1965).

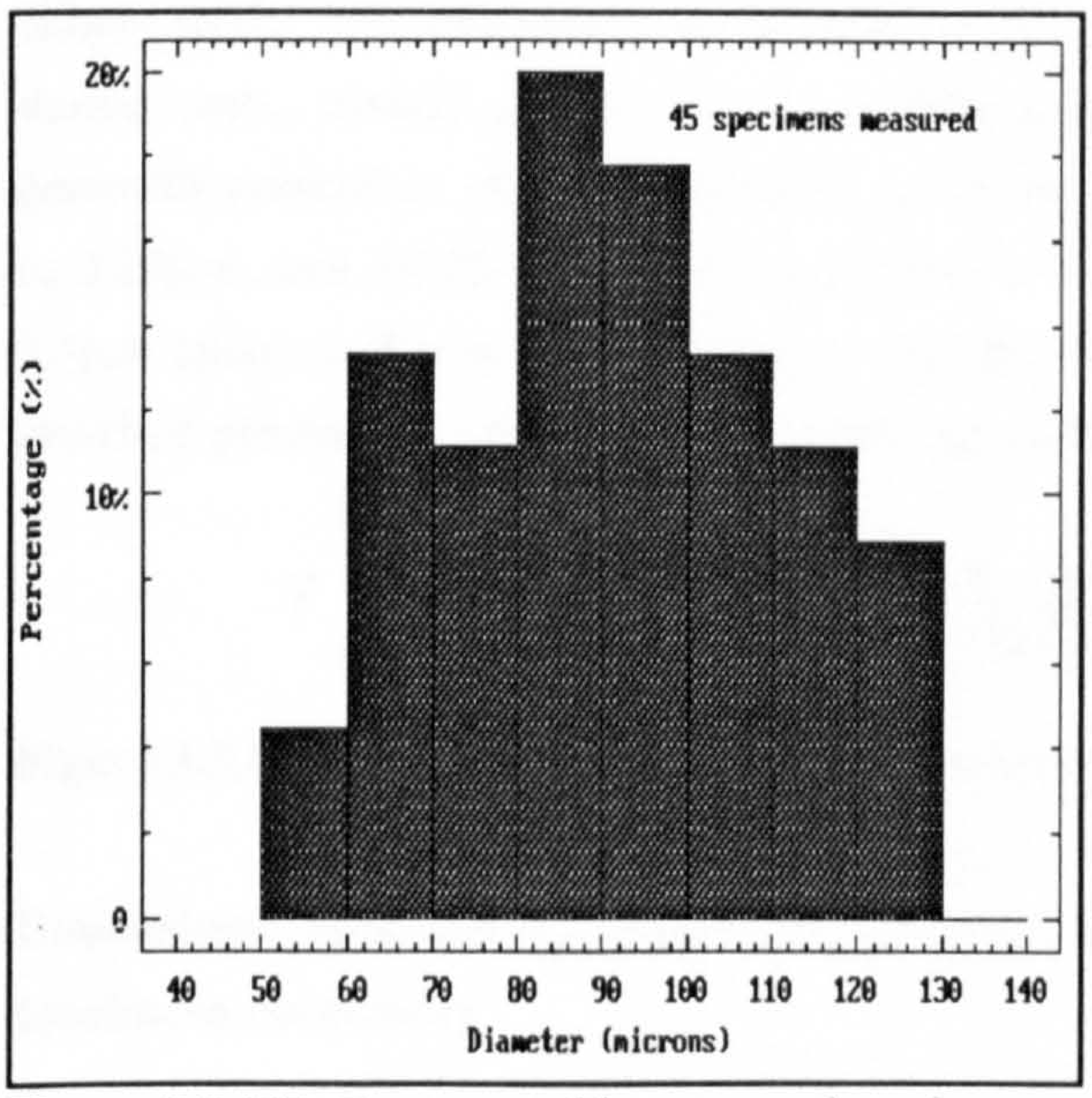


Figure 3.3.107: Frequency histogram plot of outer-most exinal diameters for *Rhabdosporites* sp. A.

The dimensions of specimens recovered from north Devon compare favourably with those of Marshall & Allen (1982). However, in reviewing all previous measurements of this species, there is a clear progression through from small specimens (*sensu* Marshall & Allen, and the present study) to enlarged representatives (as originally noted by Richardson, 1965: based upon six specimens). The construction of this spore type is unique within the *Rhabdosporites* plexus, and therefore should assume taxonomic priority over any other subtle disparities such as spore size or sculptural morphology.

Small numbers of this spore type were noted *in situ* within sporangia of *Tetraxylopteris schmidtii* by Bonamo & Banks (1967), occurring in association with *Rhabdosporites langii* and *R. parvulus*. Bonamo & Banks (1967) believed the third, "intermediate" layer was probably due to the splitting of one of the other exinal walls. Subsequently, Marshall & Allen (1982) were unable to clarify whether this feature was a primary or secondary attribute. Within the population noted from north Devon the three layers were consistantly discrete, well separated and commonly parallel to one another, and thus are considered primary in origin.

The opacity of the central body often obscures resolution of haptotypic characteristics.

Comparisons. The three layered construction of *Rhabdosporites* sp. A *sensu* Richardson (1965) is unique to this species. *Rhabdosporites langii* (Eisenack) Marshall & Allen (1982) is similar in size range and sculpture, but the exine is merely two-layered.

Species of the Late Devonian/Early Carboniferous morphon *Diducites* Van Veen (1981a) are similarly three layered in construction, but the outermost layer appears to be diaphanous, more membraneous and less rigid, lacking such pronounced sculpture. Moreover, the two outermost exinal layers of *Diducites* are very closely appressed, and commonly difficult to differentiate.

Rhabdosporites sp. B.

Plate 3.27, fig. 11.

Description. Trilete, camerate miospores; amb circular, subcircular to convex triangular. The intexinal body is generally conformable in outline with the spore circumference. The suturae are indistinct, straight to openly arcuate and usually obscured by slightly thickened, subdued labra, ≤2μm in width and height. The laesurae extend 3/4 to the full radius of the spore, are ≈uniform in thickness along their length, and may be terminated equatorially by faint curvaturae imperfectae. The contact areas are ill-defined, scabrate or displaying a diminutive ?sculpture: "elements" ≤1μm in dimensions. The intexinal body is laevigate to finely granulose, rarely folded and optically dense, ≤2μm thick. The exoexine is membraneous (≤1μm thick), and not notably voluminous, bearing a dense, even, conate, spinose or occasionally baculate ornament: sculptural elements are either generally pointed or rounded in profile, rarely truncated (blunted), and range in length from ≤0.75 to 2.25μm, and ≤0.25-0.75μm in basal diameter (rarely greater than 1μm). Elements are ≤0.25-0.5μm apart, and seemingly reduced or absent over the proximal surface. The two exinal layers are attached proximally, and detached but closely spaced elsewhere.

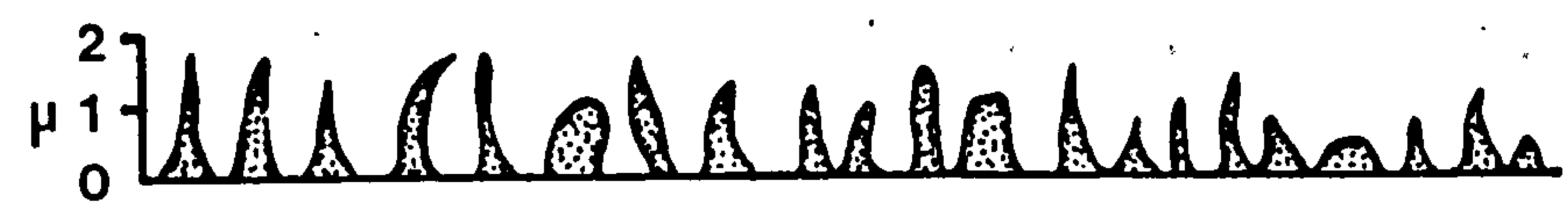


Figure 3.3.108: Sculptural elements of *Rhabdosporites* sp. B, lateral elevation.

Dimensions. Maximum spore diameter 49-63μm, mean 58μm; intexinal body diameter 42-57μm (10 specimens measured).

Occurrence. LN; *rare*. H; *very rare*.

Remarks. In view of the revised circumscription proposed by Marshall & Allen (1982), *Rhabdosporites* was considered the most appropriate generic repository for this spore type. The exoexine showed no preferential thickening over the equatorial and distal polar regions, thus discounting allocation to *Geminospora:* the exoexine of *Rhabdosporites* sp. B was in fact notably thinner and substantially more membraneous than the intexinal body. Affiliation with *Grandispora* was considered inappropriate, in view of the density and morphology of the sculpture.

Riegel (1973; p. 96, Pl. 15, fig. 8) describes and illustrates a species of *Rhabdosporites* of ≈similar size (57-73μm), with a restricted, densely sculptured but thin "saccus" (≤1μm) and a thick intexinal body (2-3μm). However, Riegel details the sculpture as merely baculate, 0.5-1.5μm in length. Clearly the differences in ornament between *Rhabdosporites* sp. of Riegel (1973) and *Rhabdosporites* sp. B (of the present study) are somewhat trivial, and indeed the two may well prove to be conspecific.

The specimen figured herein is typical of the preservation and oxidised appearance of this species: the opacity of the central body limited resolution of polar morphology.

Comparisons. *Rhabdosporites minutus* Tiwari & Schaarschmidt (1975) is comparable in size (45-57μm), but bears a substantially thicker exoexine (2-3μm thick), which is "leathery" in appearance and displays a diminutive sculpture (bacula, 0.5μm in dimensions). At its lower size range, *Rhabdosporites langii* (Eisenack) Marshall & Allen (1982) is similar in gross morphology, but lacks such pronounced, elongate and predominantly spinose ornamentation

cf.*Rhabdosporites* sp. *sensu* McGregor & Camfield, 1982.
Plate 3.27, fig. 14.

cf. 1982 *Rhabdosporites* sp., McGregor & Camfield, p. 60, Pl. 18, figs. 1-3, text-fig. 93.

Description. Trilete, camerate miospores; amb subcircular to irregular subtriangular. The suturae are distinct to barely perceptible, straight, openly arcuate or "ragged", and are obscured equatorially by thickened, robust exinal folds (≤6μm wide and ≤8μm in height). The laesurae extend 3/4 to 7/8 the spore radius, and are simple, noncurvaturate. The contact areas are ill-defined, commonly scabrate, or bearing sparse, diminutive grana and coni, ≤1μm in width and height. The intexinal body is subcircular to convex-triangular in outline, ?limbate (≤3.25μm "thick" equatorially), laevigate to finely granulose and rarely folded. The exoexine is thinner than the intexinal body, of uncertain thickness («?0.75μm), ?limbate (limbus up to 3μm wide), and scabrate to finely granulose in texture. Outside of the contact areas the exoexine displays a pronounced, dense sculpture, comprising rounded coni, irregular grana, with simple bacula the predominant sculptural type: elements ≤1.25-2.5μm in width and height (usually ≈2μm), and typically ≤0.75-2.5μm apart (rarely greater than 4μm). The sculpture may appear slightly sparse and scarce towards the equatorial margin.

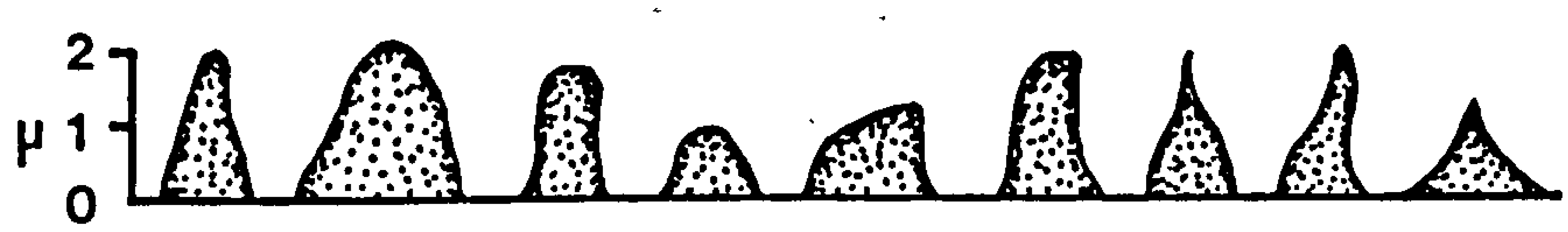


Figure 3.3.109: Sculptural elements of cf.*Rhabdosporites* sp. *sensu* McGregor & Camfield, lateral view.

Dimensions. Maximum exoexinal diameter 79-102, mean 84μm; intexinal body diameter 49-78μm, 54μm (4 specimen measured). Diameter of intexinal body 62-77% of the total spore diameter.

Occurrence. S; *very rare.*

Remarks. The few specimens documented from north Devon proved smaller than the size specifications quoted by McGregor & Camfield (1982, p. 60; 112-165μm), with a seemingly "thicker" exoexine and a more discernible intexinal body. Occasionally the sculptural elements on forms noted herein appeared more isolated.

Comparisons. *Rhabdosporites langii* (Eisenack) Marshall & Allen (1982) bears a smaller sculpture. *Geminospora micropaxilla* (Owens) McGregor & Camfield (1982; p. 41, Pl. 8, figs. 16-18; Pl. 9, figs. 1-3, text-fig. 58) displays differential intexine and exoexinal wall thicknesses, as well as a smaller sculpture.

Genus *Rugospora* Neves & Owens, 1966.

Type species. *Rugospora corporata* Neves & Owens, 1966.

Rugospora sp.

Plate 3.28, figs. 1, 2.

Description. Trilete miospores; amb subcircular to convex-triangular. The exine is laevigate, scabrate to granulose in texture, and ranges in equatorial thickness from $\leq 1\mu$m to 3.25μm, with no pronounced exinal stratification. The suturae are distinct to barely perceptible, straight to openly arcuate, and commonly obscured by robust, sinuous labra, $\leq 5\mu$m in total width and height at the proximal pole. The trilete rays commonly extend 4/5 to the full radius of the spore, tapering equatorially where they are terminated by distinct to discernible curvaturae imperfectae. The contact areas are usually scabrate to finely granulose in texture and lack pronounced sculpture: the exine over the proximal pole may appear thinned and two layered, with the outer "perinous" layer usually ruptured, torn or folded (convolute folds parallel the laesurae). The equatorial and distal surfaces display an irregular, patchy sculpture, comprising discrete verrucae, coni and coarse grana. These elements are $\leq 2.25\mu$m in height, and ≤ 1-4.25μm in basal diameter (usually 2-3μm), and may coalesce to form irregular, "beaded", sinuous or "straight" rugulae, up to 9.5μm in total length: rugulae are indiscriminately distributed, although may show a propensity for being concentrated over the distal pole. Overall, this ornament appears somewhat sparse, with individual elements usually ≤ 1-3μm apart (rarely exceed 4μm).

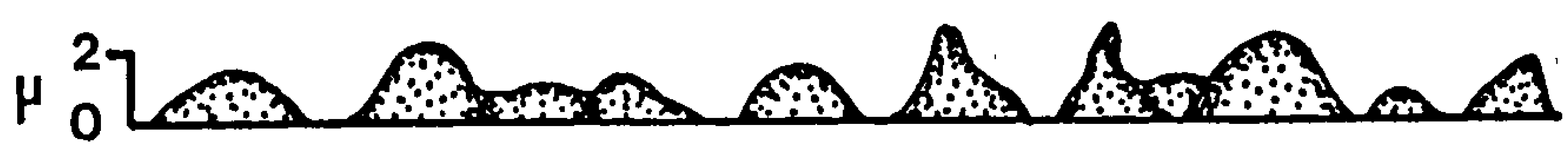


Figure 3.3.110: Sculptural variation on *Rugospora* sp., lateral elevation.

Dimensions. Maximum spore diameter 47-59, mean 56μm (10 specimens measured).

Occurrence. M; *very* rare.

Remarks. The sculpture (rugulae interspersed with verrucae/coni/grana) is typical of small-sized *Rugospora* (*e.g. Rugospora flexuosa* (Juschko) Streel 1974).

Morphologically, *Rugospora* sp. intergrades with coarsely sculptured forms of *Crassispora* *catenata* also recovered from the Morte Slates (in the present study): feasibly these two morphotypes may represent different ontogenetic growth stages variants of the same "botanical" species.

Comparisons. *Convolutispora* Hoffmeister, Staplin & Malloy (1955) bears a denser, predominantly rugulate sculpture, with discrete elements the rarity. *R. flexuosa* (Juschko) Streel (1974) is morphologically similar, but may exhibit a distinct intexinal body, and also tends to display simple suturae, with a denser, more intensely rugulate sculpture noted over the distal surface. The ornament of *Crassispora catenata* Higgs (1975) comprises a mixture of smaller grana and thinner vermiculate sculptural elements. *Verrucosisporites polygonalis* Lanninger (1968) and *Verrucosisporites bulliferus* (Taugourdeau-Lantz) Richardson & McGregor (1986) display a preponderance of somewhat coarser, more discrete and well defined verrucae. *Rugospora radiata* (Juschko) Byvscheva (1985) bears a dense distal sculpture of verrucae and rugulae, which characteristically are arranged radial about the distal pole. *R. bricei* Loboziak & Streel (1989; p. 191, Pl. III, figs. 1, 2) bears a more subdued, indistinct vermiculate and verrucate sculpture: wall separation may be distinct.

Stenozonotriletes (Naumova) Potonié (1958).

Type species. *Stenozonotriletes conformis* Naumova (1953).

Discussion.

Naumova (1953) proposed the genus *Stenozonotriletes:* from her line drawings appears to circumscribe essentially unsculptured, equatorially thickened spores. Subsequently, McGregor (1964, p. 10) regarded *Stenozonotriletes* Naumova (1953) and *Ambitisporites* Hoffmeister (1959) as synonymous, the former assuming priority. Richardson & Lister (1969, p. 228-229) later remarked upon the ambiguity between *Stenozonotriletes* (Naumova) Potonié (1958), *Ambitisporites* Hoffmeister (1959) and *Asterocalamotriletes* (Luber) Potonié (1958), as all three complexes circumscribe smooth-walled spores that display a narrow, equatorial thickening (crassitude). Richardson & Lister questioned the status of *Stenozonotriletes*, noting the type species, *S. conformis,* as lacking any equatorial "thickening" (also refer to Playford, 1976; Balme, 1988, p. 123). However, the observation of Richardson & Lister is herein considered invalid, as the line drawings of *Stenozonotriletes conformis* Naumova (1953; p. 36, Pl. III, fig, 15; p. 70, Pl. X, figs. 11, 12; p. 100, Pl. XV, fig. 31, 32; p. 130, Pl. XIX, figs. 12-14) clearly show a "thickened" equatorial margin. Recently, Ravn (1986, p. 99) references the thorough discussion of *Stenozonotriletes* by Smith & Butterworth (1967), and notes that in practice the precise structure of this equatorial thickening is invariably difficult to ascertain (*i.e.* whether cuneiform or not). Indeed, certain species of thick-walled *Punctatisporites* and *Deltoidospora* appear homologous in construction to that of *Stenozonotriletes.*

In comparison, *Camarozonotriletes* Naumova 1939 ex. Ishchenko (1952) displays a thickened interradial crassitude, and may either be smooth walled or sculptured (refer to McGregor & Camfield, 1982, p. 22-23). *Leiozonotriletes* was proposed by Hacquebard (1957, p. 314) following his rationalisation of the genus *Archaeozonotriletes* Naumova (1953): *Leiozonotriletes* circumscribes equatorially thickened spores, that exhibit a discernible to indistinct intexinal body. Crassitudinous spores that display verrucate/muronate sculpture are assigned to the genus *Synorisporites* Richardson & Lister (1969). *Aneurospora* (Streel) Richardson *et al.* (1982) bears a granulose sculpture (refer to the discussion of *Aneurospora* herein).

Stenozonotriletes cf. *simplex* Naumova
Plate 3.28, fig. 3.

cf. 1953 *Stenozonotriletes simplex* Naumova, p. 36-37, Pl. III, fig. 17; p. 69, Pl. X, fig. 3; p. 100, Pl. XV, fig. 33; p. 112, Pl. XVII, fig. 7; p. 130, Pl. XIX, figs. 16, 17.
cf. 1968 *Stenozonotriletes simplex* Naumova, in Lanninger, p. 139, Pl. 24, fig. 6.

Description. Trilete, crassitudinous miospores; amb circular to irregular convex-triangular. The suturae are usually simple, straight to openly arcuate and extend 4/5 the spore radius, or reach the inner margin of the crassitude: very occasionally the suturae are partially obscured by thin, flexuous "labra", which range up to 2.5μm in height and are $\leq$1.5μm wide. The laesurae taper equatorially, and are noncurvaturate. The exine is laevigate to very finely scabrate, and appears relatively thin proximo-distally. The spore circumference is uniformly thickened, $\leq$4μm wide in the equatorial plane.

Dimensions. 41-53μm, mean 44μm (4 specimens measured).

Occurrence. S, LH; *very rare.*

Remarks. The trilete mark on a few specimens recovered in the present study appeared "?labrate" (refer to specimen figured herein, Pl. 3.28, fig.3).

Comparisons From her line drawings, a number of species of *Stenozonotriletes* illustrated by Naumova appear subtriangular to convex-triangular in outline. *Stenozonotriletes pumilus* (Waltz) Naumova (1953; p. 36, Pl. III, fig. 16; p. 69, Pl. X, figs. 4-6) is smaller (10-30μm in diameter), and is occasionally shown as displaying "labra", or a diffuse exinal thickening parallel to the trilete rays. Conversely *S. manifestus* Naumova (1953; p. 71, Pl. X, fig. 14; p. 101, Pl. XV, fig. 34) consistently bears pronounced labra. The exinal layers of *S. ornatus* Naumova (1953; p. 74, Pl. XI, fig. 1, 2) and *S. conspersus* Naumova (1953; p. 101, Pl XV, fig. 35; p. 112-113, Pl. XVII, fig. 10) appear "textured". *S. conformis* Naumova (1953) is more circular in outline. *Archaeozonotriletes regularis* Naumova (1953; p. 82, Pl. XIII, fig. 5) is presumably camerate, with a ?thin outer wall. *Stenozonotriletes inspissatus* Owens (1971; p. 37, Pl. X, figs. 3, 6, 10) is larger (62.7-99μm), and the cingulum 4-12.5μm in lateral width (also note the comparisons in Owens, 1971).

Genus *Tholisporites* Butterworth & Williams, 1958.

Type species. *Tholisporites scoticus* Butterworth & Williams, 1958.

Discussion.

Butterworth & Williams (1958, p.382) interpreted the patina of *Tholisporites* to be thickest in the equatorial plane, and remarked upon a superficial similarity with densospores. Subsequently

Allen (1965, p. 721) emended the concept of *Archaeozonotriletes* Naumova (1953), based upon a reappraisal of the construction of the type species, *A. variabilis* Naumova. Allen interpreted this form to display a uniformly thick or distally thickened patina, and thus unlike the perceived construction of *Tholisporites,* or indeed that of the densospore complex. Furthermore, Allen (1965, p.721) believed the disparity between *Archaeozonotriletes* and *Tholisporites* lay not only in the location of the patina, but also in the manner by which the exine differentially thins over the proximal surface. Allen (1965) integrated observations from microtome sections in a taxonomic re-evaluation of *Archaeozonotriletes,* and although its patinate construction was thus considered "distinct", Chaloner & Streel (1968, p. 94) later voiced concern over the ambiguous definition and recognition of a patina in transmitted light microscopy.

Richardson & Lister (1969, p.235), following Allen (1965), distinguished *Tholisporites* from *Archaeozonotriletes* on the basis of the position of "maximum patina thickness", but commented that "in practice...(it is) very difficult to separate these two taxa". Owens (1971, p. 39) questioned the ability to assess the relative thickness of a patina equatorially and over the distal surface, when dealing with proximo-distally compressed specimens. Subsequently, McGregor (1973, p. 56-57) adopted a more realistic and practical approach in evaluating the problematic construction of such genera. McGregor assessed whether certain species were demonstrably patinate, and consequently considered that a number of taxa should more appropriately be accommodated within the concept of *Tholisporites*, and not *Archaeozonotriletes*. More recently McGregor & Camfield (1982, p. 20-21) concede that invariably it is impossible to determine the true variation in patina thickness proximo-distally, and furthermore note that such a parameter may realistically be of minimal use in differentiating genera (also note comments in McGregor & Camfield 1976, p. 28).

The distinction between *Archaeozonotriletes* and *Tholisporites* is still ambiguous. Allen (1965) noted that the validation of *Archaeozonotriletes* precedes that of *Tholisporites* by one month, and that the former genus would thus assume taxonomic priority if the two were placed in synonymy (according to the I.C.B.N. rules of priority). A detailed reappraisal of the morphology of both type species, based upon microtome sections and observations in transmitted light of topotypic material, may resolve the current ambiguity. Until such a time, the use of *Tholisporites* herein follows that of McGregor (1973): in following McGregor, I am not advocating the complete synonymy of these two generic groupings, which Owens (1971, p. 39) had viewed plausible. It is interesting to note, however, that the thickness of the patina in the holotype line drawing of *Archaeozonotriletes* Naumova (namely *A. variabilis*) is problematic: McGregor & Camfield (1982, p. 21) speculate that this may well be of "*Tholisporites*-construction".

In comparison *Stenozonotriletes* (*Ambitisporites*) is a laevigate miospore complex that is equatorially thickened, "crassitudinous". *Cyrtospora* (Winslow 1962) displays distal "tubercules". *Cliviospora* (Staplin & Jansonius 1964) and *Camptozonotriletes* (Staplin 1960) are interpreted as cingulicavate. *Densosporites* Berry emend. Butterworth *et al.* (in Staplin & Jansonius 1964) displays a differentiated, distal and zonal ornament (refer to the earlier discussion under *Densosporites*). *Chelinospora* (Allen, 1965 p. 728) exhibits a reticulate or foveoreticulate sculpture (also note emendation in McGregor & Camfield, 1976, p.14). Allen (1965, p. 725) also proposed the genus *Cymbosporites* for patinate spores that display a variable ornament of cones, spines and/or granules.

Tholisporites chulus (Cramer) McGregor (1973) var. *chulus*.

Plate 3.28, fig. 4-7.

1966 *Retusotriletes chulus* Cramer, p.74, Pl. 2, fig.14.

1969 *Archaeozonotriletes chulus* (Cramer) Richardson & Lister var. *chulus* Richardson & Lister, p. 235, Pl. 43, figs. 1-6.

1973 *Tholisporites chulus* (Cramer) McGregor var. *chulus*, p.56-57, Pl. 7, figs. 13-15.

1976 *Tholisporites chulus* (Cramer) McGregor var. *chulus*, in McGregor & Camfield, p. 28, Pl. 1, figs. 19, 20.

1988 *Tholisporites chulus* (Cramer) McGregor var. *chulus*, in Boumendjel, Loboziak, Paris Steemans, & Streel, Pl. 1, figs. 4, 5.

1988 *Tholisporites chulus* (Cramer) McGregor var. *chulus*, in Ravn & Benson, Pl. 4, figs. 4, 5, 13, 14, 17.

Description. Trilete miospores, with a broadly convex-triangular, oval to subcircular amb in polar compression (rarely circular). Sutures are straight, simple or obscured by thin, flexuous labra, which range up to 1.5μm in total width at the proximal pole, broadening up to 4.5μm equatorially. The laesurae extend 2/3 to the full radius or spore (excluding the equatorial thickening), and may appear curvaturate. A diffuse, irregular to concave-triangular apical darkening may extend over the proximal pole. The exine is either homogeneously laevigate, or finely scabrate, rigid equatorially and optically dense, lacking folds over the proximo-distal surfaces. The equatorial "thickening" typically ranges between 4μm and 9μm in lateral width, rarely $\leq$2μm or exceeds 11μm: may appear marginally narrower radially: the exine is "thinned" proximo-distally. A rim or "fold" of exine (?curvaturate ridges) may parallel, or appears closely appressed to, the inner edge of the thickened equatorial margin: this "rim" is commonly 1-1.75μm in thickness.

Dimensions. Maximum spore diameter (polar compression) 41-68μm, mean 53μm (65 specimens measured).

Occurrence. LN; *common.* H; *rare.*

Remarks. The relative thickness of the distal and proximal polar regions proved difficult to assess, largely because all specimens were compressed proximo-distally rather than equatorially. Even after extreme oxidation, many specimens remained optically dense, further limiting a detailed appraisal of preferential wall thickening: the thickened ("patinate") equatorial margin was however obvious. In view of the ≈regularity in width to

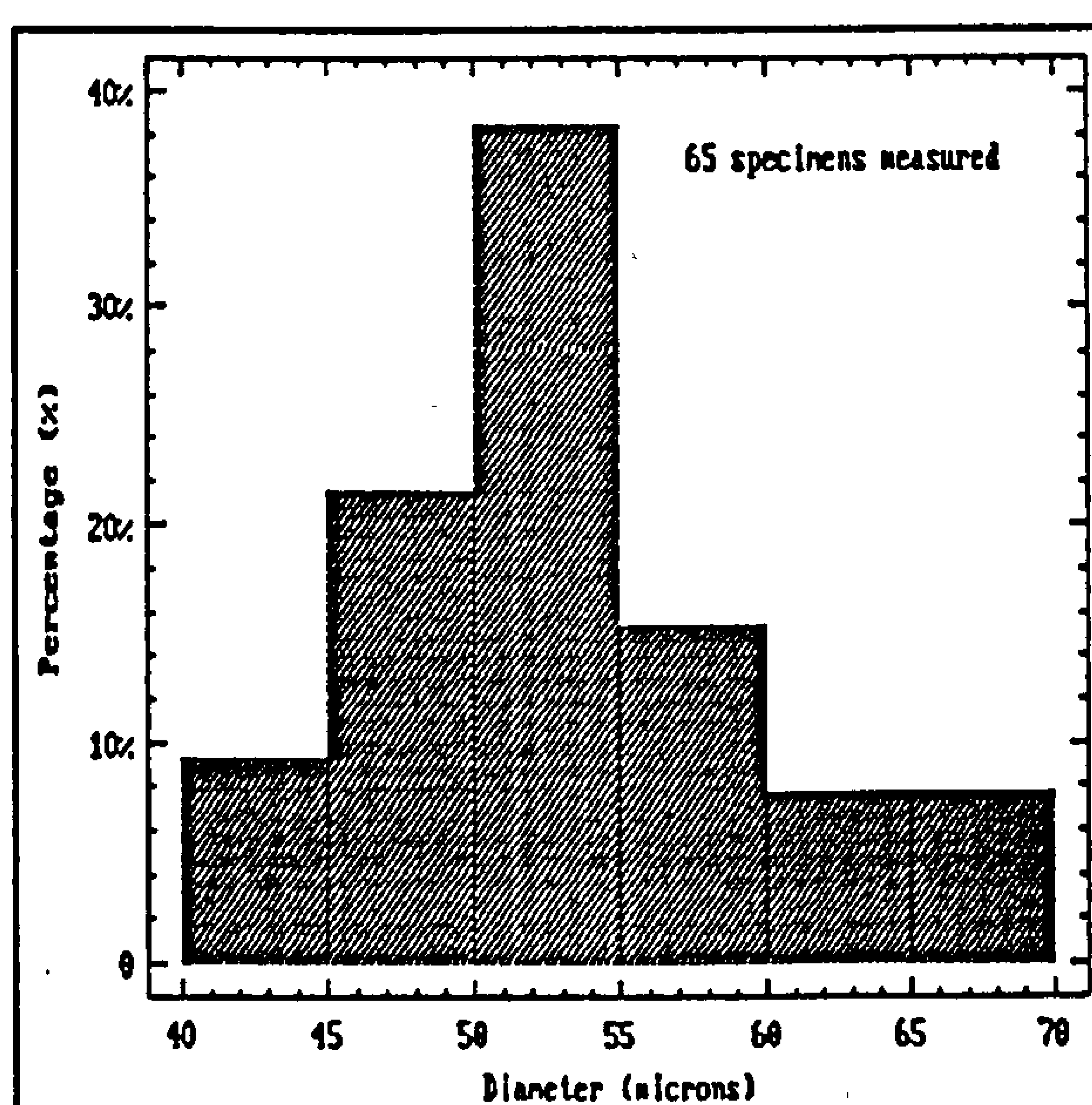


Figure 3.3.111: Size distribution of *Tholisporites chulus* var. *chulus*.

the equatorial margin, coupled with the exclusive recovery of proximo-distally compressed specimens, the exinal thickening of *chulus* var. *chulus* is considered most likely to be an equatorial and not distal feature. In comparison, the width of the equatorial margin of the genotype *Archaeozonotriletes variabilis* Naumova (1953) appears highly variable (as noted in the emended circumscription by Allen, 1965, p. 721-722, Pl. 100, figs. 3-6), and thus substantiates an interpreted patinate condition for this plexus.

The described regularity in morphology of *chulus* var. *chulus* thus favours affiliation with *Tholisporites,* rather than *Archaeozonotriletes.*

Certain specimens within the population of *Tholisporites chulus* var. *chulus* recovered from north Devon displayed a degraded, superficially "sculptured" exine. However, such a corrosive feature was readily identifiable as secondary. Tetrads were occasionally recovered from the Lynton Formation.

Comparisons. *Chelinospora* Allen (1965) and *Cymbosporites* Allen (1965) are interpreted as patinate in construction, and furthermore are sculptured. *Archaeozonotriletes columnus* Allen (1965; p. 723, Pl. 100, figs. 8-10) displays a homogeneous, infragranulate or finely/coarsely punctate patina. *Tholisporites ancylus* Allen (1965; p. 724-725, Pl. 101, figs. 1-7) is two-layered, with a consistently "corroded" outer patinate exinal layer.

Richardson & Lister (1969, p. 234-238) differentiated three varieties of *Archaeozonotriletes* (al. *Retusotriletes*) *chulus* (Cramer) comb.nov., namely *chulus* var. *chulus, chulus* var. *inframurinatus* and *chulus* var. *nanus.* "*Archaeozonotriletes*" *chulus* var. *inframurinatus* was distinguished from the other subspecies due to the presence of a murornate infrastructure. "*Archaeozonotriletes*" *chulus* var. *chulus* and "*A.*" *chulus* var. *nanus* were differentiated simply upon differences in overall spore diameter: according to Richardson & Lister (1969) 36-60μm and 23-35μm respectively (Note: D'Erceville (1979) regards these two subspecies as synonymous). *Tholisporites divellomedium* (Chibrikova) Turnau lacks any trace of a trilete mark. *Tholisporites salantaicus* (Arkhangelskaya) Turnau (1986; p. 349, Pl. IV, figs. 16-18) is very similar to "*Archaeozonotriletes*" *chulus* var. *inframurinatus* Richardson & Lister (1969) in appearance, but the "sculpture" is an external and not an infrastructural characteristic.

Tholisporites divellomedium (Chibrikova) Turnau
Plate 3.28, fig. 9.

1959 *Archaeozonotriletes divellomedium* Chibrikova, p.65-66, Pl.9, fig.4.
p 1968 *Densosporites atavus* De Jersey, in Schultz, p. 140, Pl. 24, fig. 7.
? 1976 *Archaeozonotriletes divellomedium* Chibrikova, in Massa & Moreau-Benoit, Pl. 1, fig. 1.
1981 *Archaeozonotriletes divellomedium* Chibrikova, in Steemans, Pl. 1, fig. 7.
1986 ?*Archaeozonotriletes* cf. *divellomedium* Chibrikova, in Richardson & McGregor, Pl.1, fig.10.
1986 *Tholisporites divellomedium* (Chibrikova) Turnau, p.349, Pl.II, fig. 12; Pl.VI, fig. 14.

Description. Miospores; amb convex subtriangular to subovate, rarely subcircular. Laesurae are not discernible. The exine is laevigate to finely scabrate: the equatorial margin is thickened, typically ranging in lateral width from ≤3μm to 6.5μm (rarely exceeds 8μm). The exine upon the (?presumed) proximal surface may display a narrow fold (?curvaturae) ≤1.5μm thick, that either parallels, or is closely appressed to, the inner margin of this "thickened" equatorially "feature".

Dimensions. Maximum spore diameter (polar compression) 46-62μm, mean 47μm (8 specimens measured).

Occurrence. LN, H; *very rare.*

Comparisons. *Tholisporites chulus* var. *chulus* displays a distinct trilete mark. (Also refer to the comparisons made earlier for *Tholisporites chulus* var. *chulus*).

Genus *Verruciretusispora* Owens, 1971.

Type species. *Verruciretusispora dubia* (Eisenack) Richardson & Rasul, 1978a.

Verruciretusispora dubia (Eisenack) Richardson & Rasul.

Plate 3.28, fig. 10.

p 1944 *Triletes dubius* Eisenack, p.115, Pl.2, fig. 7, text-figure 14.
1968 *Retusotriletes macrotuberculatus* Schultz, p. 16, Pl. 2, fig. 3.
1968 *Retusotriletes infrapunctatus* var *macrotuberculatus* Schultz, in Lanninger, p.114, Pl.21, fig.4.
1968 *Retusotriletes multituberculatus* Lanninger, p. 114-115, Pl. 21, fig. 5.
1971 *Verruciretusispora robusta* Owens, p. 21-22, Pl. 4, figs. 7, 8, 10, 11.
1973 *Verruciretusispora* cf. *macrotuberculata* (Schultz) Riegel, p. 85-86, Pl. 11, figs. 10, 11.
1973 *Verruciretusispora multituberculata* (Lanninger) McGregor, p. 36, Pl. 4, figs. 13, 14.
1978a *Verruciretusispora dubia* (Eisenack) Richardson & Rasul, p.443-444, Pl. 1 fig. 6.
1978b *Verruciretusispora dubia* (Eisenack) Richardson & Rasul, Pl. 1 fig. 3.
non 1979 *Verruciretusispora multituberculata* (Lanninger) McGregor, in Moreau-Benoit, p. 44, Pl. 6, fig. 4.
1982 *Verruciretusispora dubia* (Eisenack) Richardson & Rasul, in McGregor & Camfield, p. 60-61, Pl. 18, figs. 4-7, text-figure 94.
1986 *Verruciretusispora dubia* (Eisenack) Richardson & Rasul, in Turnau, Pl. VI, fig. 22.
1988 *Verruciretusispora dubia* (Eisenack) Richardson & Rasul, in Marshall, Fig. 3 (15).

Description. Trilete acamerate miospores; subcircular, oval to convex-triangular amb. The exine is laevigate, finely scabrate, or occasionally shagreenate in texture, and ≤0.75-2μm thick equatorially (rarely exceeds 3.5μm). The suturae are simple, straight to openly arcuate, and extend 2/3 to the full radius of the spore: the suturae may be partially or entirely obscured by either subdued, subtle or conversely distinct labra, ≤2.75μm wide and thickening towards the spore circumference. The contact areas are delimited equatorially by pronounced, radially thickened curvaturae perfectae, which may become increasingly diffuse interradially. These curvaturate ridges are ≤2-7.5μm in width and height, ±invaginated: inter-radially such curvaturae commonly coincide in part with the spore margin, such that the exine ±appears up to 8μm thick. The exine of the contact areas is commonly slightly thinned, depressed, and consistently lacks distinct sculptural elements. A diffuse apical darkening, subtriangular or ≈irregular in form, may extend over 15-35% of the proximal surface. Proximo-equatorially and distally the exine displays an ornament comprising elongate or subdued, bulbous verrucae, with occasional, broad, truncated coni and rare spatulate elements: the sculpture may appear highly variable upon one individual specimen. In lateral profile these elements are smooth, rounded, and generally ≈hemispherical: in plan, appear subcircular in outline, rarely polygonal. Sculptural elements range between ≤1.5 and 5.75μm in height, and ≤3.5μm to 6.5μm in basal diameter (rarely ≤2μm): this ornament is irregularly distributed but ≈discrete, typically 3-12μm apart (rarely greater than 15μm) - very occasionally three to five elements cluster, separated by ≤1μm. Up to 28 elements project (asymmetrically) at the spore circumference (usually 8-15). Subordinate, diminutive verrucae and grana may be interspersed amongst the coarser, larger elements: these subsidiary elements are ≤1-2μm in size.

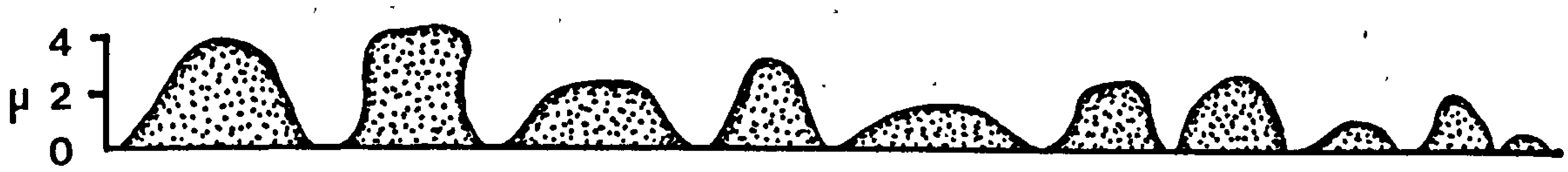


Figure 3.3.112: Sculptural elements of *Verruciretusispora dubia*, lateral view.

Dimensions. Maximum spore diameter 53-94μm, mean 78μm (10 specimens measured).

Occurrence. LN, S; *rare.* R, LH; *very rare.*

Remarks. Richardson & Rasul (1978a, p. 444) note the dimensions of *V. dubia* as 70-130μm: specimens recovered from north Devon are more compatible in size with the population documented by McGregor & Camfield (1982, p. 60-61) from the Canadian Arctic (dimensions quoted as 46-96μm).

Specimens proved very difficult to oxidise, which may be a reflection of the "?rigidity" and thickening of the exine. The laesurae rarely rupture.

Comparisons. The presence of curvaturae assumes generic priority over a predominantly verrucate sculpture. *Verrucosisporites* spp. circumscribes forms that lack such pronounced curvaturae. *Apiculiretusispora* spp. displays a markedly finer, more attenuate-spinose ornament.

Genus *Verrucosisporites* Ibrahim emend. Smith, 1971.

Type species. *Verrucosisporites verrucosus* (Ibrahim) Ibrahim 1933.

Synonymy.

Converrucosisporites Potonié & Kremp, 1954.

Discussion

The genus *Verrucosisporites* was validated by Ibrahim (1933), and over the following decades became the repository for a diversity of simple, acamerate, ±verrucate sculptured spores. Consequently Smith (1971) rationalised this plexus, considering the predominance of discrete verrucae as diagnostic of *Verrucosisporites* and thus allowing differentiation from other acamerate spores that similarly display discrete, apiculose sculpture (*e.g. Granulatisporites* (Ibrahim) Potonié & Kremp, 1954; *Cyclogranisporites* Potonié & Kremp, 1954; *Lophotriletes* (Naumova) Potonié & Kremp, 1954; *Planisporites* (Knox) Potonié, 1960).

In comparison, the ornament of *Camptotriletes* and *Convolutispora* comprises rugulae, anastomosing ridges or other forms of contiguous sculpture. *Dibolisporites* circumscribes forms that display biform ornamentation. Despite obvious similarities between certain species of *Raistrickia* and *Verrucosisporites*, the former complex displays a sculpture that comprises essentially elongate, baculate elements (length typically exceeds width).

Verrucosisporites bulliferus (Taugourdeau-Lantz) Richardson & McGregor
Plate 3.28, fig. 8, 11-13, 17.

1967 *Verrucosisporites bullatus* Taugourdeau-Lantz, p.50, Pl. 2, figs. 9, 10.
1968 *Lophozonotriletes grumosus* Naumova, in Schultz p. 39, Pl. 4, figs. 14, 14a.
1971 *Verrucosisporites bullatus* Taugourdeau-Lantz, in Taugourdeau-Lantz, p. 26-27, Pl. I, figs. 13, 14, & 17.
1976 *Verrucosisporites bullatus* Taugourdeau-Lantz, in Massa & Moreau-Benoit, Pl. 7, fig. 6.
1981 *Verrucosisporites bullatus* Taugourdeau-Lantz, in Loboziak & Streel, Pl. I, figs. 9, 10.
non 1985 *Verrucosisporites bullatus* Taugourdeau-Lantz, in Paris *et al.*, Pl. 29, fig. 8.
1986 *Verrucosisporites bulliferus* (Taugourdeau-Lantz) Richardson & McGregor, p.18, Pl. 17, fig. 2.
non 1988 *Verrucosisporites bulliferus* Richardson & McGregor, in Loboziak, Streel & Burjack, Pl. VII, fig. 6 (refer to *Geminospora boleta*).
1989 *Verrucosisporites bulliferus* (Taugourdeau-Lantz) Richardson & McGregor, in Loboziak & Streel, Pl. I, fig. 6.

Description. Trilete, acamerate miospores; circular, subcircular to broadly convex-triangular amb. The exine is single layered, non-laminate, ≤2.25μm thick equatorially, and is laevigate to finely scabrate, rarely finely granulose in texture. The exine may appear compressionally "thickened", forming an opaque, irregular, equatorial "rim", resembling a diffuse crassitude (≤5μm in width). The suturae are straight to openly arcuate, simple or obscured by distinct labra, ≤4.25μm high and wide at the proximal pole. The laesurae extend 3/4 to the full radius of the spore, tapering towards the spore circumference, where they may be terminated by faint to pronounced curvaturae imperfectae. The contact areas are distinct, lacking elongate and enlarged sculptural elements, although commonly appear coarsely scabrate in texture. Equatorially and distally the exine is regularly sculptured with discrete, predominantly well rounded, squat verrucae. In lateral profile these elements are smooth, rounded-hemispherical or parallel-sided, occasionally constricted towards their base: individual elements are ≤0.75-2.5μm in height. In plan view, the sculpture is circular, subcircular, rarely subpolygonal in outline, 2.25-6.25μm in basal diameter (usually 3-4μm). In general the sculpture forms a comparatively regular and dense cover over the exine: elements range from ≤0.5μm to 5μm apart (commonly 1-2.5μm), with two to four occasionally fused or clustered. Subordinate grana, squat coni, and diminutive verrucae, ≤0.75-1.75μm in width and height are commonly interspersed amongst these larger sculptural elements. 20-35 elements typically project at the spore circumference (rarely exceed 45).

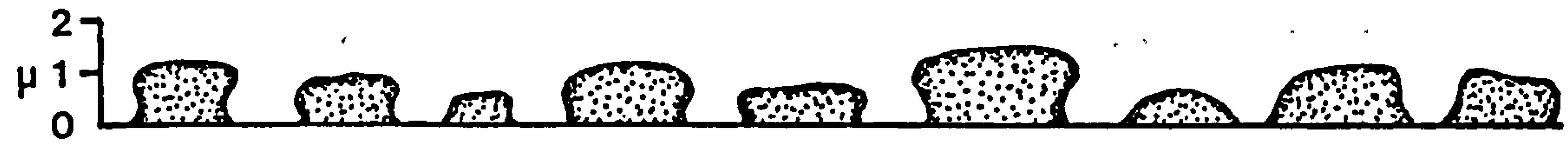


Figure 3.3.113: Sculptural elements of *Verrucosisporites bulliferus*, lateral elevation.

Dimensions. Maximum spore diameter 41-57μm, mean 49μm (30 specimens measured).

Occurrence. K, M; *common.*

Remarks. The sculpture of *Verrucosisporites bulliferus* is virtually identical to that of *Geminospora boleta* Higgs & Russell (1981). As discussed earlier, the two differ primarily in construction: *G. boleta* is demonstrably cavate, whereas *V. bulliferus* is (regarded herein) as clearly non-laminate, acamerate in form. Unfortunately, problems of differentiating between these two taxa were encountered, notably when the intexinal body of *Geminospora boleta* is diffuse, indistinct, or closely appressed to (and thus seemingly inseparable from) the exoexine. Due to this ambiguity, only forms that were demonstrably acamerate (single layered) were herein attributed to *Verrucosisporites bulliferus.*

Verrucosisporites rarituberculatus Curry (1975) may prove a junior synonym of *V. bulliferus,* if on re-examination, the construction of this species proves to be single layered and not "stratified" as the holotype appears (refer to the earlier comments made in relation to *G. boleta*).

Poorly oxidised specimens occasionally displayed a comparatively regular, opaque equatorial "feature" (≤4.25μm wide), somewhat similar in appearance to the crassitude noted for *Aneurospora greggsii* (McGregor) Streel (refer to Pl. 3.28, fig. 13 herein). This feature may reflect the poor oxidation of a compressionally thickened, robust exinal layer, and is not believed primary.

In a few examples, the contact areas were delimited equatorially by curvaturae perfectae.

Comparisons. Taugourdeau-Lantz (1971, p. 27) remarked upon the comparability of *Verrucosisporites bullatus* and *V. morulatus* (Knox) Potonié & Kremp (1955): the concept of this latter species was later emended by Smith & Butterworth (1967, p. 152). Taugourdeau-Lantz (1971) considered these two species distinct, based largely upon disparities in the width and (more importantly) the height of the verrucate sculpture: the ornament of *V. morulatus* is ≤4μm high and ≤6μm in basal diameter. *Verrucosisporites polygonalis* Lanninger (1968) displays a finer, denser, verrucate sculpture. *Verrucosisporites tumulentus* Clayton & Graham (1974) usually exhibits a more diffuse, subdued and generally irregular sculpture. *Geminospora boleta* Higgs & Russell (1981) is demonstrably camerate in construction. The original holotype illustration of *Cymbosporites* (al. *Lycospora*) *magnificus* (McGregor) McGregor & Camfield (1982, p. 32) in McGregor (1960, Pl. 13, fig. 13) clearly differs to *Verrucosisporites bulliferus* in the morphology and disposition of the sculpture.

Verrucosisporites cf. *polygonalis* Lanninger

Plate 3.28, fig. 14.

cf. 1968 *Verrucosisporites polygonalis* Lanninger, p. 128, Pl. 22, fig. 19.

cf. 1976 *Verrucosisporites polygonalis* Lanninger, in McGregor & Camfield, p. 28, Pl.3, figs.22-24.

non 1978a ?*Verrucosisporites polygonalis* Lanninger, in Richardson & Rasul, p. 444-445, Pl.2, fig.9.

cf. 1983 *Verrucosisporites polygonalis* Lanninger, in Le Herissé, p. 27, Pl. 3, figs. 13-14.

cf. 1989 *Verrucosisporites polygonalis* Lanninger, in Steemans. p. 160, Pl. 46, figs. 28-30.

Form additional synonymy refer to Steemans (1989, p. 160).

Description. Trilete, acamerate miospores; amb subcircular to convex-triangular. The suturae are distinct to barely perceptible, straight to openly arcuate and commonly extend 2/3 to 4/5 the spore radius. The suturae appear simple, non-curvaturate, or may be paralleled by a diffuse thickening in the exine, $\leq 7\mu m$ in width. The exine is laevigate to finely scabrate, $\leq 1.5\mu m$ thick equatorially, and may appear compressionally thickened, forming a diffuse equatorial "wall-feature" up to $6\mu m$ wide. The exine displays a comparatively regular, even sculpture comprising rounded diminutive verrucae and coarse grana: elements are ≤ 2-$3.25\mu m$ in basal diameter, and ≤ 0.75-$1.75\mu m$ in height. The exine is densely sculptured, elements typically ≤ 0.25-$0.75\mu m$ apart (rarely exceed $1.5\mu m$). The sculpture appears more discrete towards the equatorial margin, and increasingly fused, clustered, towards the distal polar region, $\pm$coalescing into short, sinuous and irregular rugulae. Occasionally, this basal fusion is so extreme that individual elements are indistinguishable.

Figure 3.3.114: Sculptural elements of *Verrucosisporites ?polygonalis,* lateral elevation.

Dimensions. Maximum spore diameter 56-$67\mu m$, mean $59\mu m$ (3 specimens measured).

Occurrence. LN; ?*R.*

Remarks. In the literature a number of forms have been described which appear homologous to *Verrucosisporites polygonalis; e.g. V. depressus* Winslow in Van Veen (1981; Pl. II, fig. 1). Clearly, the concept of this species may require a more circumspect definition to resolve such ambiguities.

Although the sculptural elements on *Verrucosisporites polygonalis* Lanninger (1968; Pl. 22, fig. 19) are crowded (forming a negative reticulum), they are still discrete. Forms recovered from north Devon lack the pronounced labra remarked upon by Lanninger (which may range up to $10\mu m$ in height).

Comparisons. *Cyclogranisporites* Potonié & Kremp (1954) generally circumscribes thinner walled spores that display a smaller ornament. The sculpture upon *Verrucosisporites bulliferus* is larger and more isolated.

Verrucosisporites premnus, Richardson

Plate 3.28, figs. 15, 16, 18, 19.

1965 *Verrucosisporites premnus*, Richardson, p. 572, Pl. Pl. 90, figs. 1, 2.

1965 *Raistrickia* sp. A., Richardson, p. 574, Pl. 90, figs. 1,2.

1965 *Raistrickia* cf. *clavata* Hacquebard, Richardson, p. 575, Pl. 90, fig. 5.

non 1968 *Verrucosisporites premnus* Richardson, in Lanninger, p. 128, Pl. 22, fig. 20.

? 1980 *Chelinospora concinna* Allen, in Loboziak & Streel, Pl. II, fig. 16.

1980 *Verrucosisporites premnus* Richardson, in Loboziak & Streel, Pl. I, fig. 3.

1982 *Verrucosisporites premnus* Richardson, in McGregor & Camfield, p.61, Pl. 18, figs. 8, 9, text-fig. 95.

1985 *Verrucosisporites* cf. *premnus* Richardson, in Paris *et al.*, Pl. 23, figs. 7.

1985 *Verrucosisporites premnus* Richardson, in Paris *et al.*, Pl. 29, figs. 9, 10.

non 1988 *Verrucosisporites premnus* Richardson, in Loboziak, Streel, & Burjack, Pl. VII, fig. 5.

1989 *Verrucosisporites premnus* Richardson, in Loboziak & Streel, Pl. I, fig. 7.

Description. Trilete, acamerate miospores with a subcircular to rounded triangular amb: in off-polar compression, the proximal surface may appear somewhat flattened. The suturae are distinct to barely perceptible, straight, and extend 1/2 to 7/8 the spore radius. Excluding sculpture, the exine is ≤2.5-4μm thick over the equatorial and distal surface, appearing somewhat thinner proximally (≤1-2μm). The exine is laevigate to finely scabrate, robust and unfolded. The proximo-equatorial and distal regions display a coarse, distinct sculpture, highly variable in size, comprising elongate verrucae, bacula and spatula, with rare truncated coni. In lateral profile this ornament is smooth and rounded, or with very occasional weakly serrated extremities: elements are lobed, blunted or rarely simple-attenuate, and ≤3-11μm in height (rarely exceed 14μm). The sculptural elements may be slightly constricted at their base, or are simple parallel-sided. In plan, the elements are subcircular to irregular-polygonal in basal outline, and typically ≤2.5-16μm in diameter (occasionally up to 22μm): the ornamentation varies quite considerably in size and shape upon a single specimen. The most robust, enlarged elements tend to project preferentially at the equatorial margin (for those compressed proximo-distally). Elements are generally discrete, asymmetrically spaced and ≤1.5-12μm apart: may fuse into irregular, short, robust "muri". 7-14 elements typically project at the spore circumference (rarely 23).

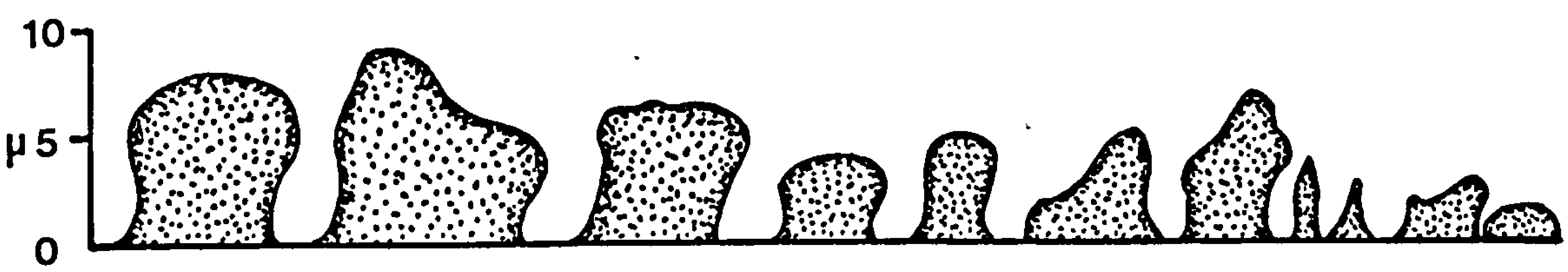


Figure 3.3.115: Sculptural variation of *Verrucosisporites premnus*, lateral elevation.

Dimensions. Maximum spore diameter (excluding sculpture), 34-75μm, mean 49μm (20 specimens measured).

Occurrence. S, L, CM, K; *rare.* LH, WP; *very rare.*

Remarks. McGregor & Camfield (1982, p. 61) remark that in view of the occasionally high number of bacula that adorn some specimens of *V. premnus* (recovered from Middle Devonian strata of the Canadian Arctic), this species may justifiably be attributed to *Raistrickia.* Indeed, both Richardson (1965, p. 572) and later Smith (1971, p. 79) questioned its assignation to *Verrucosisporites.* However, the present author concurs with McGregor & Camfield (1982) in preferring assignment to the *Verrucosisporites* plexus, largely because of the interpreted morphological gradation of *V. premnus* and *V. scurrus.*

Specimens proved very difficult to oxidise completely. Specimens illustrated as figures 16 and 19 of Plate 3.28 (herein) show the typical preservation of certain specimens of *V. premnus,* even after quite lengthy and severe oxidation. The discrete, rounded spatulate/baculate sculpture projecting from the spore circumference is diagnostic of this species, and allows identification. Specimens were rarely recorded in perfect polar compression,

Comparisons. *Chelinospora ligurata* Allen (1965, p. 729, Pl. 102, figs. 1-7) is patinate in construction and bears an irregular, dense, verrucate, conate and seemingly baculate sculpture. The ornament of cf.*Lophozonotriletes rarituberculatus* (Luber) Kedo in Mortimer & Chaloner (1972; p. 34, Pl. VI, fig.4) is sparser, more rounded and notably more subdued. Coarsely sculptured forms of *V. scurrus* (Naumova) McGregor & Camfield (1982) are similar in morphology, intergrading with that of *V. premnus*, and indeed aberrant forms may prove difficult to differentiate: in general the ornament of *V. scurrus* is far smaller, denser and less spatulate in form.

Richardson (1965, p. 572) remarked that the ornament extremities of *V. premnus* may appear serrated. Although this feature was noted on a limited few specimens recovered from north Devon, such multifurcation was not as pronounced as that of ?*Raistrickia* sp. B and ?*Raistrickia* sp. C (of the present study).

Verrucosisporites scurrus (Naumova) McGregor & Camfield
Plate 3.28, figs. 20, 21; Pl. 3.29, figs. 1-3.

1953 *Lophozonotriletes scurrus*, Naumova, p. 38, Pl. III, figs. 22, 23.
1965 *Raistrickia aratra* Allen, p. 701-702, Pl. 96, figs. 3, 4.
1976 *Lophozonotriletes gibberulus* Naumova, in Massa & Moreau-Benoit, Pl. 6, fig. 1.
1979 *Verrucosisporites nitidus* (Naumova) Playford, in Moreau-Benoit, p. 42, Pl. 6, fig. 3.
1982 *Verrucosisporites scurrus* (Naumova) McGregor & Camfield, p. 61-62, Pl. 18, figs. 10-17, text-fig. 96.
1985 *Verrucosisporites scurrus* (Naumova) McGregor & Camfield, in Paris *et al.*, Pl. 23, figs. 4, 5, 9.
? 1985 *Raistrickia* cf. *aratra* Allen, in Paris *et al.*, Pl. 23, fig. 8.
1985 *Lophozonotriletes* sp., in Paris *et al.*, Pl. 23, fig. 8.
1985 *Verrucosisporites scurrus* (Naumova) McGregor & Camfield, in Paris *et al.*, Pl. 29, fig. 11.
1988 *Verrucosisporites scurrus* (Naumova) McGregor & Camfield, in Balme p. 130, Pl. 5,

figs. 5-9.

? 1988 *Verrucosisporites scurrus* McGregor & Camfield, in Marshall Fig. 3 (6).

1988 *Verrucosisporites scurrus* McGregor & Camfield, in Loboziak, Streel, & Burjack, Pl. VII, fig. 4.

1989 *Verrucosisporites scurrus* McGregor & Camfield, in Loboziak & Streel, Pl. I, figs. 8, 9.

Description. Trilete, acamerate miospores; amb circular, subcircular, rarely convex-triangular. The laesurae are simple, straight to openly arcuate and extend 1/3 to 4/5 the spore radius: the suturae are occasionally ruptured at the proximal pole. The exine appears robust, laevigate to finely scabrate and ≤2-3.75μm thick equatorially. Proximo-equatorially and distally the exine displays a varied sculpture, comprising verrucae, bacula, and spatulate elements, with rare pila, spinae, and truncated coni: elements typically range from ≤3μm to 6μm in height, and ≤4-9.5μm in basal diameter (rarely greater than 11μm), and are usually slightly broader than high. The distal terminations are rounded and smooth, rarely serrated and only very occasionally surmounted by a small cone or grana. Elements are even to irregular in their distribution, discrete, although commonly densely spaced; typically ≤2-6.5μm apart, rarely up to 8.5μm. Two to five elements may coalesce forming short, irregular "muri". The contact areas are ill-defined, over which the exine is thin (≤?1μm thick) and displays a markedly reduced or absent sculpture.

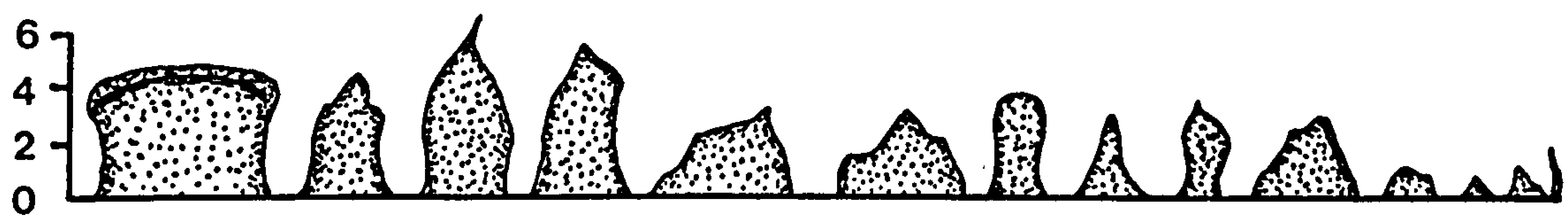


Figure 3.3.116: Sculptural elements of *Verrucosisporites scurrus*, lateral view.

Dimensions. Maximum spore diameter (excluding ornament) 39-59μm, mean 47μm (20 specimens measured).

Occurrence. L; *common.* R, S, LH, WP, CM; *rare.* M; *R.*

Remarks. In the present study, specimens attributed to *Verrucosisporites scurrus* bear a strong resemblance to one of the specimens of *Lophozonotriletes scurrus* figured by Naumova (1953; Pl. III, fig. 22). The other line drawing of *L. scurrus* provided by Naumova (1953; Pl. III, fig. 23) appears thicker walled, and displays a sparser sculpture. The form illustrated by Marshall (1988, Fig. 3 (6)) displays a dense, more rounded, and predominantly baculate sculpture, that is strikingly dissimilar to both these line drawings.

The size range of *Verrucosisporites scurrus* (Naumova) McGregor & Camfield recorded in the present study is more compatible with the size specifications of Naumova (1953, p. 38; 35-40μm), than with those quoted by McGregor & Camfield (1982, p. 61-62; 30-86μm).

In agreement with the observations of McGregor & Camfield (1982) forms of *Verrucosisporites scurrus* gradational in morphology with those of *V. premnus, sensu stricto* and *V. tumulentus, sensu stricto* were observed. Distinct end-members of these three species are easily recognisable, but forms with an intermediate morphology are more difficult to place. A small number of specimens attributed herein to *V. scurrus* were also noted to intergrade with *Convolutispora* sp. A (of the present study), as sculptural elements become increasingly confluent. Realistically, a few specimens assigned to *?Raistrickia* sp. B may in fact represent corroded, poorly preserved forms of *Verrucosisporites scurrus*.

Comparisons. *Verrucosisporites scurrus*, *V. tumulentus* Clayton & Graham (1974) and *V. premnus* Richardson (1965) are arbitrarily differentiated according to the predominant size and morphology of the sculpture: the ornamentation of *V. tumulentus* is generally smaller, more subdued, whereas that of *V. premnus* is much larger and coarser. *Dibolisporites uncatus* (McGregor & Camfield, 1982) displays more distinct biform sculpture, although aberrant forms of *Verrucosisporites scurrus* are difficult to distinguish from this species. Balme (1988, p. 129) admits it is often difficult to differentiate *Convolutispora caementosa* Balme (1988; p. 129, Pl. 5, figs. 1-3) from *Verrucosisporites scurrus,* although from the figured specimens the ornament does (arbitrarily) appear to be more subdued and contiguous.

?Raistrickia sp. B (herein) bears a predominance of serrated-tipped sculptural elements.

Verrucosisporites tumulentus, Clayton & Graham.
Plate 3.29, figs. 4-6.

1974 *Verrucosisporites tumulentus* Clayton & Graham, p. 574, Pl. I, figs. 12.
1982 *Verrucosisporites tumulentis* Clayton & Graham, in McGregor & Camfield, p.62-63, Pl. 18, figs. 18-21; text-figure 97.

Description. Trilete acamerate miospores; amb ovate, circular to convex-triangular. The exine is laevigate to finely scabrate, and ≤1-2.75μm thick equatorially: the exine thickness appears comparatively uniform over the entire spore. The suturae are straight, rarely arcuate, simple, and extend 1/3 to 4/5 the spore radius. The contact areas are ill-defined, scabrate to finely granulose, or bearing a diminutive verrucose sculpture: the remainder of the exine is covered by relatively subdued verrucae and grana, with the occasional truncated coni, broad-based spinae and very rare mammae, typically ≤1-2.25μm in height (rarely exceed 3μm). In lateral profile, the sculptural elements are smooth, generally flat-topped or rounded: in plan, elements are subcircular to polygonal in outline, and range up to 7μm in basal diameter. Very occasionally such elements are surmounted by a single, diminutive, coni or grana, «0.25 in height. Elements tend to encroach onto the contact areas: in general the ornament is comparatively dense in its distribution, but also discrete, ≤0.5-2μm apart - the sculptural elements rarely appear so crowded that the exine seems pseudoreticulate. Two to four adjacent elements may coalesce to form short, irregular, subdued "rugulae" ≤11μm in length.

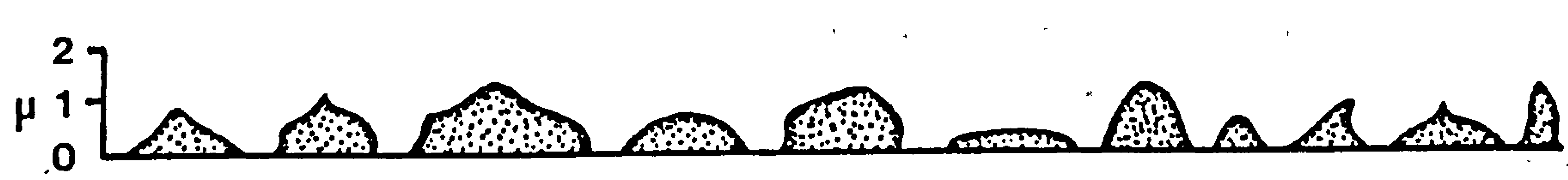


Figure 3.3.117: Sculptural elements of *Verrucosisporites tumulentus*, lateral view.

Dimensions. Maximum spore diameter (excluding ornament) 43-56μm, mean 51μm (15 specimens measured).

Occurrence. R, S, LH, WP, L, CM; *rare.* K; *very rare.*

Remarks. Forms of *Verrucosisporites tumulentus* recovered from north Devon were far more conservative in their morphological variation, than those illustrated by Clayton & Graham (1974, Pl.I, figs. 12-14): the figured specimens of Clayton & Graham (1974) display what is presumed to be "natural" intraspecific variation in morphology. The specimen illustrated by Clayton & Graham on plate I, figure 12 bears the closest resemblance to forms documented from north Devon. The sculpture upon the holotype of *Verrucosisporites tumulentus* (Pl. I, fig. 13) appears somewhat more subtle, diffuse and subdued.

The size range of *Verrucosisporites tumulentus* recorded herein is more compatible with the specifications quoted by Clayton & Graham (1974; 38-(47)-54μm) than with those of McGregor & Camfield (1982; 43-(59)-73μm). However, Clayton & Graham (1974) describe the simple presence of verrucae, and/or short ridges. In accordance with McGregor & Camfield (1982), a slightly greater variation in sculpture was recognised in the present study.

Specimens were usually observed in off-polar compression.

Comparisons. The ornament of *Verrucosisporites nitidus* (Naumova) Playford (1964) is coarser, more uniform and dense in its distribution. *Verrucosisporites polygonalis* Lanninger (1968) displays a finer, more uniform verrucate sculpture, which appear so dense that the exine seems pseudoreticulate. *Verrucosisporites confertus* Owens (1971; p. 19-20, Pl. IV, figs. 3-6) bears a superficial resemblance to *Verrucosisporites tumulentus* Clayton & Graham (1974), but differs in being substantially larger (73.4-108.9μm), and also in displaying more elongate (3-12μm), higher (3-6μm) verrucae. *V. scurrus* (Naumova) McGregor & Camfield (1982) and *V. premnus* Richardson (1965) bear markedly larger sculptural elements. *Verrucosisporites bulliferus* (Taugourdeau-Lantz) Richardson & McGregor (1986) displays more uniform, regularly disposed sculptural elements.

Spore Types.

Spore Type A
Plate 2.29, fig. 7.

Description. Trilete miospores; amb subcircular to convex-triangular. The exine is laevigate, $\leq$0.75μm thick equatorially and commonly folded. The suturae are distinct at the proximal pole, becoming increasingly diffuse equatorially, and are straight to openly arcuate, noncurvaturate. A diffuse, irregular-subcircular to subtriangular polumbra may extend over the proximal pole. The exine lacks structure, appearing unsculptured, apart from an "incomplete", reticulate "cover" (?layer). This reticulum appears only partially attached to the "exine proper", fusion of the ?2 layers confined to the equatorial region: this reticulum extends only part-way over the distal surface (the distal polar region is unsculptured). The lumina of this reticulum are variably 1.75-3μm in diameter (rarely isodiametric), subcircular to polygonal in outline, and defined by muri ≤0.5-1μm in width.

Dimensions. Maximum spore diameter 56μm, 63μm (2 specimens measured).

Occurrence. Exclusive to S20; *very rare.*

Remarks. The reticulate "layer" was poorly preserved (incomplete) on both specimens studied.

Comparisons. Mortimer & Chaloner (1972; Pl. II, fig. 9) figure a spore, *Acinosporites* sp., that is slightly smaller in size (≈40μm; from the illustration) and displays a comparable but "complete" reticulate sculpture. *Acinosporites lanceolatus* Streel in Massa & Moreau-Benoit (1976; Pl. 2, fig. 2) displays a perfect reticulum, and appears thicker walled. *Retialetes legionis* Pernelle in Streel *et al.* (1981; p. 185, Pl. 2, fig. 13) is also similar, but likewise displays a "complete" reticulum that appears composed of larger lumina.

Spore Type B
Plate 3.29, figs. 13-17.

non 1953 *Archaeozonotriletes perlotus* Naumova, Pl. XIV, fig. 2.
1972 *Dictyotriletes perlotus* (Naumova) Mortimer & Chaloner, Pl. VI, fig. 3.
p 1974 *Dictyotriletes perlotus* (Naumova) Mortimer & Chaloner, in Clayton & Graham, p. 576, Pl. III, fig. 7 (only).
1981 *Dictyotriletes perlotus* (Naumova) Mortimer & Chaloner, in Higgs & Russell, p. 28, Pl. 2, fig. 7.
? p 1988 *Bascaudaspora collicula* (Playford) Higgs *et al.*, p. 65, Pl. 7, figs. 16, 17.

Description. Trilete, camerate miospores; amb subcircular, oval to convex-triangular. Suturae are distinct, straight to openly arcuate, and may be paralleled by pronounced labra, which individually are 0.5-2.25μm wide. The laesurae extend 1/3 to 7/8 the spore radius, and may be terminated equatorially by curvaturae imperfectae. The contact areas lack distinct sculpture. The intexine is distinct to diffuse, laevigate, and usually somewhat eccentric in its disposition relative to the spore circumference. The degree of cameration is variable: the intexine may either be closely appressed to, or conversely markedly retracted away from the exoexine. The exoexine may appear irregularly thickened equatorially (?limbate, ≤2-4.75μm): the inner margin of this equatorial feature is diffuse and highly irregular. The exoexine is laevigate to coarsely scabrate, and proximo-equatorially and distally is sculptured with sinuous, simple or irregular ("beaded") muri: ?cristate elements and coni are rare, interspersed amongst these muri. The muronate sculpture is ≤1.75μm-3μm in width, and ≤2.25μm in height, and collectively define an irregular, loose and imperfect reticulum: lumina are polygonal to irregular-subcircular in outline, rarely complete (range in diameter from ≤5μm to 16μm). The intexine and exoexine are commonly folded, independent of one another.

Dimensions. Maximum exoexinal diameter 44-63μm, mean 49μm. Intexine 26-47μm, mean 38μm

(18 specimens measured).

Occurrence. M; *rare.*

Remarks. Owens (1983) proposed the genus *Bascaudaspora* to circumscribe acamerate, distally murornate miospores that display an equatorial crassitude: the equatorial thickening was deemed of prime taxonomic importance. Subsequently, Higgs *et al.* (1988) formally proposed new combinations of two taxa, namely *Bascaudaspora collicula* and *B. perlota,* which previously had been attributed variously to *Asperispora, Cristatisporites,* and *Dictyotriletes.* Specimens defined as Spore Type B (of the present study) display a murornate sculpture that resembles, in part, certain species of *Bascaudaspora* and *Dictyotriletes.* However, the presence of a well defined and discrete intexinal layer in these forms, and the absence of a pronounced, uniformly thickened equatorial crassitude makes identification somewhat problematic. Of interest, Van der Zwan (1980, p. 223) does note the presence of an intexine within the population of *D. submarginatus* recorded from Ireland, although most workers still perceive *Dictyotriletes* as an acamerate spore (attributed to the Suprasubturma *Acameratitriletes* Neves & Owens 1966). *Asperispora* (*sensu* Van der Zwan, 1980, p. 226-228) does exhibit a pseudoreticulate ornament, although individual sculptural elements are typically discrete or only partially contiguous.

Specimens of *Dictyotriletes perlotus* (Naumova) Mortimer & Chaloner figured by Mortimer & Chaloner (1972; Pl. VI, fig. 3) and subsequently by Higgs & Russell (1981; Pl. 2, fig. 3) display a faint "wall-feature" (?intexinal body) within the lower part of each illustration. These forms are thus considered synonymous with Spore Type B (herein). However, certain specimens of Spore Type B recovered from north Devon display a notably dense murornate sculpture (forming a more complete reticulum): the murornate sculpture apparent on *D. perlotus* figured by Mortimer & Chaloner and Higgs & Russell appears more open (lumina are less well defined).

Above, forms of Clayton & Graham (1974) and Higgs *et al.* (1988) are only partly synonymised with Spore Type B, as the exine on certain specimens figured by these workers does appear more uniformly thickened at the equatorial margin ("crassitudinous"). In contrast, the irregularly thickened equatorial margin occasionally observed for Spore Type B was believed a compressional attribute.

Comparison. Both *Dictyotriletes devonicus* Naumova (1953; p. 59, Pl. VII, fig. 25) and *Dictyotriletes perlotus* Naumova (1953; p. 87, Pl. XIV, fig. 2; p. 100, Pl. XV, fig. 29) appear thicker walled, and display a more complete, irregular pseudoreticulate sculpture. *Dictyotriletes varius* Naumova (1953; p. 110, Pl. XVI, fig. 40) is slightly smaller in size (40-45μm) and also thinner walled, but does appear to display a somewhat similar, widely spaced, "open" reticulum: in the line drawing of this species, Naumova does not illustrate any distinct "internal feature" (intexinal body). *Reticulatisporites emsiensis* Allen, in Lanninger (1968; p. 131, Pl. 23, fig. 4) displays a more complete, better defined reticulum, and appears to lack an intexinal body. *Dictyotriletes fimbriatus* (Winslow) Kaiser in Massa & Moreau-Benoit (1976; Pl. 8, fig. 7) exhibits a more robust, irregular murornate sculpture, that define a near perfect reticulum. *Pustulatisporites* (al. *Polymorphisporites*) *rugulatus* (Taugourdeau-Lantz) Loboziak & Streel (1981, p. 51, Pl. I, figs. 3, 4) was originally described as cingulate, acamerate, and bearing an irregular, sparse, rugulate sculpture: elements rarely coalesce, defining perfect lumina.

Bascaudaspora canipa Owens (1983, pp. 46, 48; Pl. 1, figs. 1, 5, 9) is visibly cingulate (5-10μm wide), not demonstrably camerate, and displays a "tighter", more regular reticulum.

Spore Type C

Plate 3.29, figs. 18, 19.

Description. Trilete, camerate, three-layered miospores; amb subcircular to ovate. The suturae are distinct to diffuse, straight to openly arcuate, and extend 2/3 to 4/5 the spore radius. The suturae may be bordered by robust, sinuous labra, $\leq 3\mu$m thick, or merely appear simple, ruptured. The exine is $\approx$three layered, with the outer two layers usually closely appressed and occasionally inseparable: the innermost layer is diffuse, indistinct, and laevigate, $\leq ?1\mu$m in thickness. The outermost, diaphanous, "perisporal" layer is usually intensely wrinkled and folded, notably over the distal surface, appearing comparatively undistorted proximally. This outer-most, "perinous" layer appears "sculptured", bearing diminutive spinae, coni, grana and rare bacula: "elements" are in general $\leq 2.25\mu$m in height and ≤ 0.75-3μm in basal diameter. The sculpture is dense, elements rarely exceed 0.75μm in isolation. Overall the spore appears comparatively robust and rigid in appearance.

Figure 3.3.118: Sculptural elements of Spore Type C, lateral elevation.

Dimensions. Maximum overall spore diameter 64-83μm, mean 69μm (6 specimens measured).

Occurrence. M; *very rare.*

Comparisons. Representatives of the *Diducites* morphon Van Veen (1981a) display a similar construction, but the outermost perinous layer tends to lack such pronounced "sculpture". Balme (1988, p. 140) recently described the megaspore ?*Grandispora fibrilabrata* from lower Frasnian strata of the Carnarvon Basin, Australia. Of the specimens illustrated by Balme (1988), figure 6 of plate 9 bears a close resemblance to Spore Type C described herein. However, Balme pays no mention to a third "perinous" layer in the diagnosis of this spore: ?*G. fibrilabrata* is also substantially larger, 144-255μm in overall diameter.

Plates 3.9-3.29.

Miospores are subsequently illustrated.

All illustrations are at x750 magnification, except were stated. For most specimens focal plane or orientation is not specified, unless the proximal or distal surfaces have been especially illustrated. In the plate descriptions, information is presented according to the following format; figure number; taxonomic name, and specimen remarks; sample number; slide code (a or b) and specimen coordinates. The specimen coordinates are presented as eastings then northings; the suffix (a) or (b) refers to a particular slide - two slides were standardly logged. All phytoclasts were logged on an Olympus BHS 313 microscope (Serial No. 582701) housed in the Department of Geology, Southampton University. Refer to Figure 2.1 (Chapter 2) for an explanation of lithostratigraphic abbreviations. For precise details of sample horizon and location refer to Appendix II and/or Figs. 2.2 & 2.3.

Details of slide number and specimen coordinates are provided for completeness, despite the probable opacity of the material if re-examined subsequent to the submission of this thesis. These have been included to allow possible infra-red microscopy (see Chapter 2, Section 2.7)

PLATE 3.9

Plate 3.9

Palynomorph preservation and miospore tetrads.

Opacity.

Fig. 1 Unoxidised miospore; K52 (a) 160.9/8.2.

Fig. 2 Unoxidised assemblage view, x140; M = Mineral, Sp = Miospore, V = Vitrinite; LN57 (a) 142.6/11.7.

Pyrite damage.

Fig. 3 Intensely pyrite-pitted miospore tetrad; CM70 - x450 magnification.

Fig. 4 Retusoid miospore, displaying remnant polygonal pyrite pits which have developed preferentially at the equator; CM40 (a) 139/15.5.

Fig. 5 Pyrite damaged *Geminospora lemurata* (Balme) Playford (1983); M42 (a) 147.5/19.2.

Fig. 6 Pyrite damaged fused retusoid pairing; S10 (a) 152.6/6.6.

Fig. 7 *Rhabdosporites langii* (Richardson) Marshall & Allen (1982); displaying distinct polygonal pyrite pits; R22 (a) 146.5/11.5.

Foreign sporopollenin adhesions.

Fig. 8 *Insculptospora confossa* (Richardson) Marshall (1985); exoexine bearing fine, apiculose tapetal residue; K14 (a) 128.5/22.5.

Fig. 9 *Insculptospora confossa* (Richardson) Marshall (1985); intexine discernible, exoexine "granulate"; excluding the intexine, this form resembles *Videospora* sp., *sensu* Higgs and Russell (1981); p. 27, pl. 1, figs. 8, 9, 12-15); K23 (a) 137.2/15.

Microbial degradation and tetrads.

Fig. 10 Degraded *Geminospora boleta* Higgs & Russell (1981); M47 (a) 150/7.9.

Fig. 11 ?Leiotriletes with coarse, globular tapetal residue; R22 (b) 150.3/11.2.

Fig. 12 Irregular to subcircular microbial scars upon a ?miospore fragment; M42 (a) 147.1/10.2.

Fig. 13 Fused, retusoid miospore-pairing (*?Retusotriletes triangulatus*); S02 (a) 132.3/14.2.

Fig. 14 Retusoid pairing with ?globular tapetal residue; S02 (a) 150.5/12.8.

Fig. 15 ?calamospore tetrad; H13 (a) 137.5/14.

Fig. 16 "diad" (see Fig. 12); S10 (b) 157/11.

Fig. 17 *Dibolisporites ?eifeliensis* (Lanninger) McGregor (1973) tetrad; LN89 (a) 132.2/9.5.

Fig. 18 ?Cyclogranisporites tetrad; LN101 (a) 157.9/21.9.

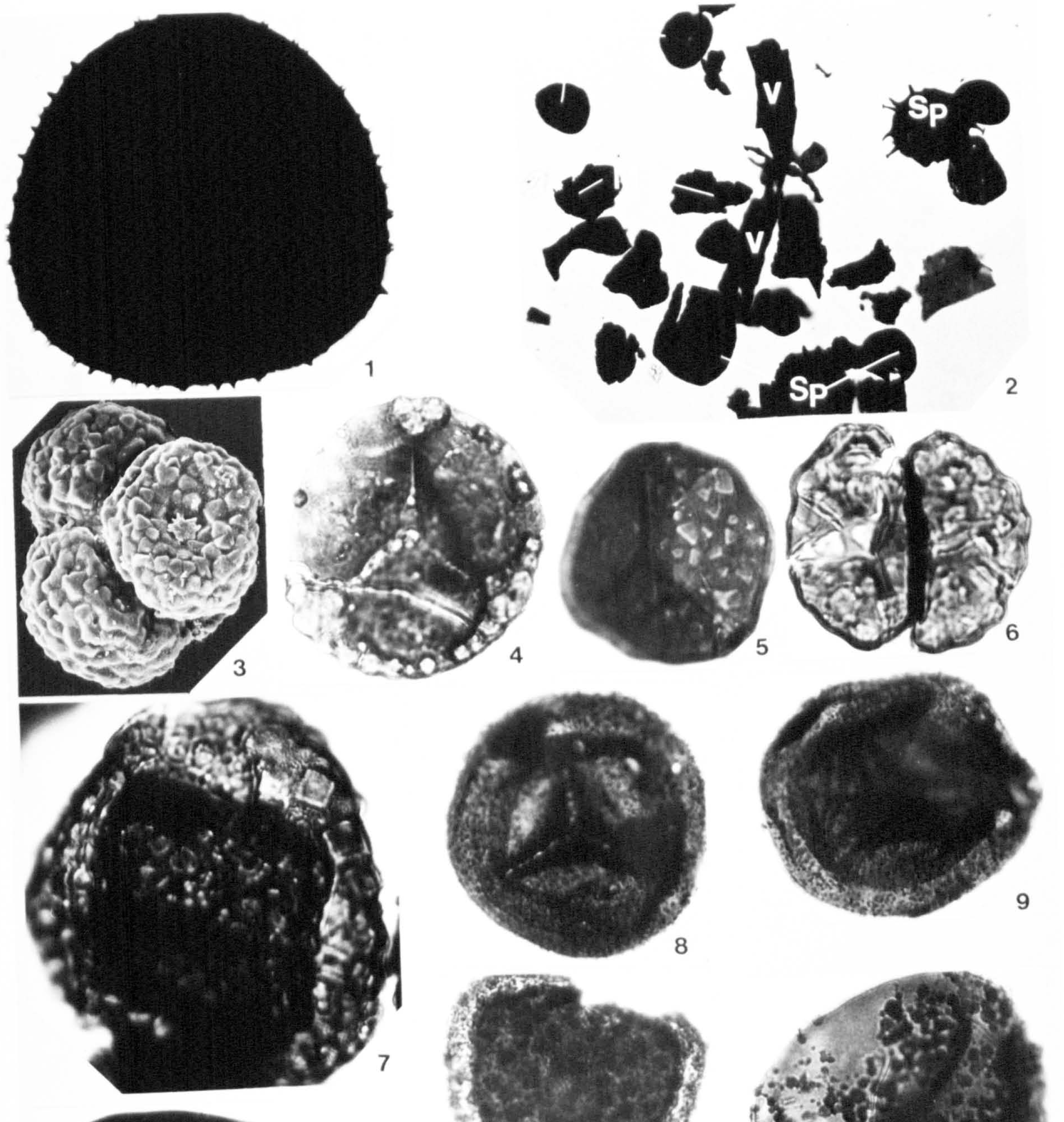


PLATE 3·9

PLATE 3.10

Plate 3.10

Fig. 1 *Acinosporites* cf. *acanthomammillatus* Richardson, 1965; S14 (a) 145.6/6.

Fig. 2 *Acinosporites* cf. *acanthomammillatus* Richardson, 1965; LH02 (a) 136.4/8.1.

Fig. 3 *Acinosporites* cf. *acanthomammillatus* Richardson, 1965; L30 (a) 154.6/10.2

Fig. 4 *Acinosporites* cf. *crassus* Riegel, 1973; detail of ornament x540; K29 (a) 144.4/14.1

Fig. 5 *Acinosporites* cf. *apiculatus, sensu* Streel, 1967; S19 (a) 151.2/13.9.

Fig. 6 *Acinosporites* cf. *apiculatus, sensu* Streel, 1967; S20 (b) 157/21.2.

Fig. 7 *Acinosporites* cf. *apiculatus, sensu* Streel, 1967; detail of ornament, x2300; H14 (a) 126.5/9.

Fig. 8 *Acinosporites* cf. *crassus* Riegel, 1973; x2300 magnification; CM02 (a) 147.19.

Fig. 9 *Acinosporites lindlarensis* Riegel var. *lindlarensis* McGregor and Camfield, 1976; H13 (a) 152/3.5:

Fig. 10 *Acinosporites lindlarensis* Riegel var. *lindlarensis* McGregor and Camfield, 1976; WP26 (a) 131.1/4.1.

Fig. 11 *Acinosporites lindlarensis* Riegel var. *lindlarensis* McGregor and Camfield, 1976; scanning electron photomicrograph; x450; WP26.

Fig. 12 *Acinosporites lindlarensis* Riegel var. *lindlarensis* McGregor and Camfield, 1976; S08 (a) 133/14.

Fig. 13 *Acinosporites* sp. A; S06 (a) 164.3/11.

Fig. 14 *Acinosporites ?macrospinosus* Richardson, 1965; proximal view; R22 (b) 146/13.

Fig. 15 *Acinosporites* sp. A; LN101 (a) 147/14.1.

Fig. 16 *Acinosporites* sp. A; LN92 (a) 130.5/11.5.

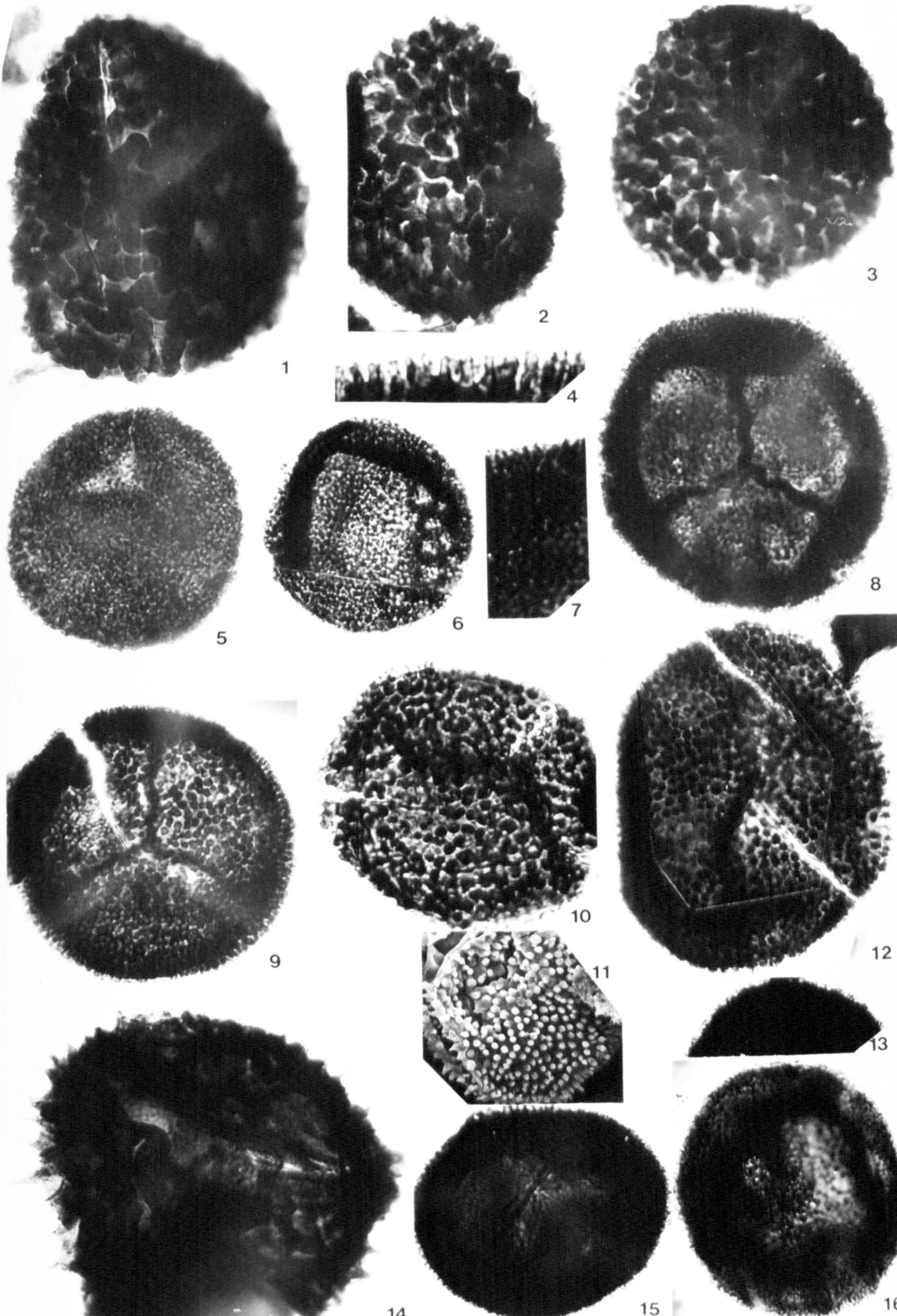


PLATE 3·10

PLATE 3.11

Plate 3.11

Fig. 1 *Anapiculatisporites* sp. A; S08 (a) 143/5.

Fig. 2 *Anapiculatisporites* sp. A; WP04 (b) 134/6.

Fig. 3 *Anapiculatisporites* sp. C; LN101 (a) 139/9.5.

Fig. 4 ?*Anapiculatisporites* sp. B; LN98 (a) 142.2/5.2.

Fig. 5 ?*Anapiculatisporites* sp. B; LN52 (a) 125/14.5.

Fig. 6 *Ancyrospora ancyrea* (Eisenack) Richardson cf. var. *brevispinosa* Richardson, 1962; CM02 (a) 150.8/4.5.

Fig. 7 *Ancyrospora ancyrea* (Eisenack) Richardson cf. var. *brevispinosa* Richardson, 1962; K12 (a) 141.2/16.7.

Fig. 8 *Ancyrospora ancyrea* (Eisenack) Richardson cf. var. *brevispinosa* Richardson, 1962; CM36 (a) 156.1/12.8.

Fig. 9 *Ancyrospora* cf. *eurypterota* Riegel, 1973; indicated top right diminutive bifurcate-tipped spine; LN38 (a) 144.5/10.5

Fig. 10 *Ancyrospora langii* (Taugourdeau-Lantz) Allen, 1965; M42 (a) 143/15.5.

Fig. 11 ?*Ancyrospora* sp. A; x470; LN101 (b) 146/11.

Fig. 12 *Ancyrospora simplex* (Guennel), Urban 1969; x1650, detail of process with laevigate bifurcate-tip preserved; K32 (a) 141.2/16.5.

Fig. 13 *Ancyrospora simplex* (Guennel), Urban 1969; x1650, detail of squat process, with laevigate bifurcate-tip preserved; M42 (a) 156.1/7.

Fig. 14 *Ancyrospora simplex* (Guennel) Urban, 1969; K40 (a) 143/17.5.

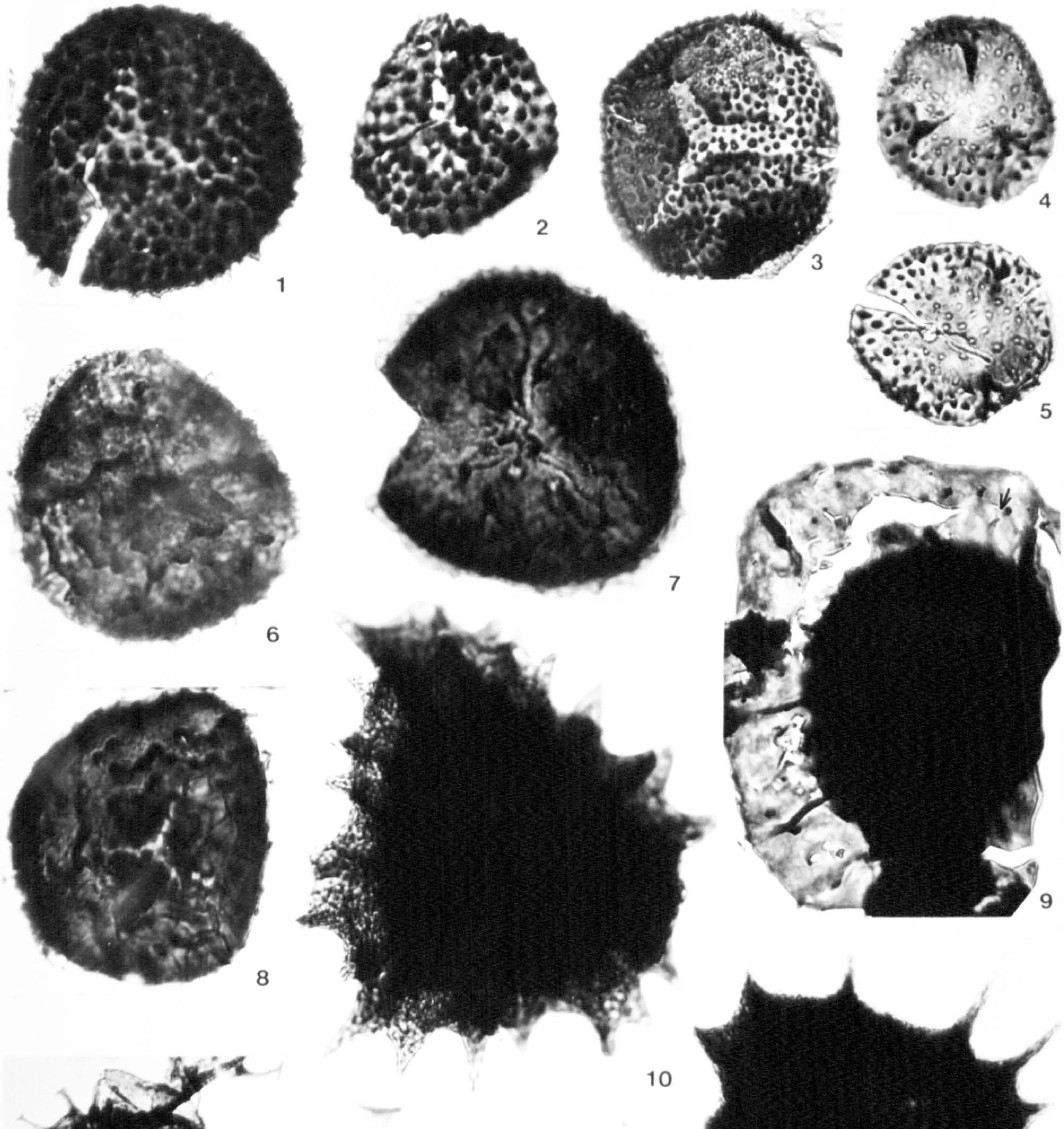


PLATE 3·11

PLATE 3.12

Plate 3.12

Fig. 1 ?*Ancyrospora* sp. A; LN98 (b) 126.3/9.8.

Fig. 2 *Ancyrospora* sp. B; CM28 (a) 147/15.

Fig. 3 *Ancyrospora* cf. *loganii* McGregor, 1973; LN31 (a) 147.2/11.

Fig. 4 *Aneurospora greggsii* (McGregor) Streel, 1974; K23 (a) 143.5/8.2.

Fig. 5 *Aneurospora greggsii* (McGregor) Streel, 1974; K41 (a) 151.8/2.5.

Fig. 6 *Apiculatisporis* sp. ; L10 (a) 150/11.9.

Fig. 7 *Apiculiretusispora brandtii* Streel, 1964; scanning electron photomicrograph, x450; H13.

Fig. 8 *Apiculiretusispora brandtii* Streel, 1964; LN101 (a) 136.2/10.9.

Fig. 9 *Apiculiretusispora brandtii* Streel, 1964; LN92 (a) 147.2/14.9.

Fig. 10 *Apiculiretusispora brandtii* Streel, 1964; LN21 (a) 156.2/5.5.

Fig. 11 *Apiculiretusispora leberidos* McGregor & Camfield, 1982; LN38 (a) 139/12.2.

Fig. 12 *Apiculiretusispora leberidos* McGregor & Camfield, 1982; LN98 (a) 148.5/16.5.

Fig. 13 *Apiculiretusispora* cf. *densiconata* Tiwari & Schaarschmidt, 1975; LN101 (a) 157.2/12.3.

Fig. 14 *Apiculiretusispora* cf. *densiconata* Tiwari & Schaarschmidt, 1975; LN60 (a) 159/21.2.

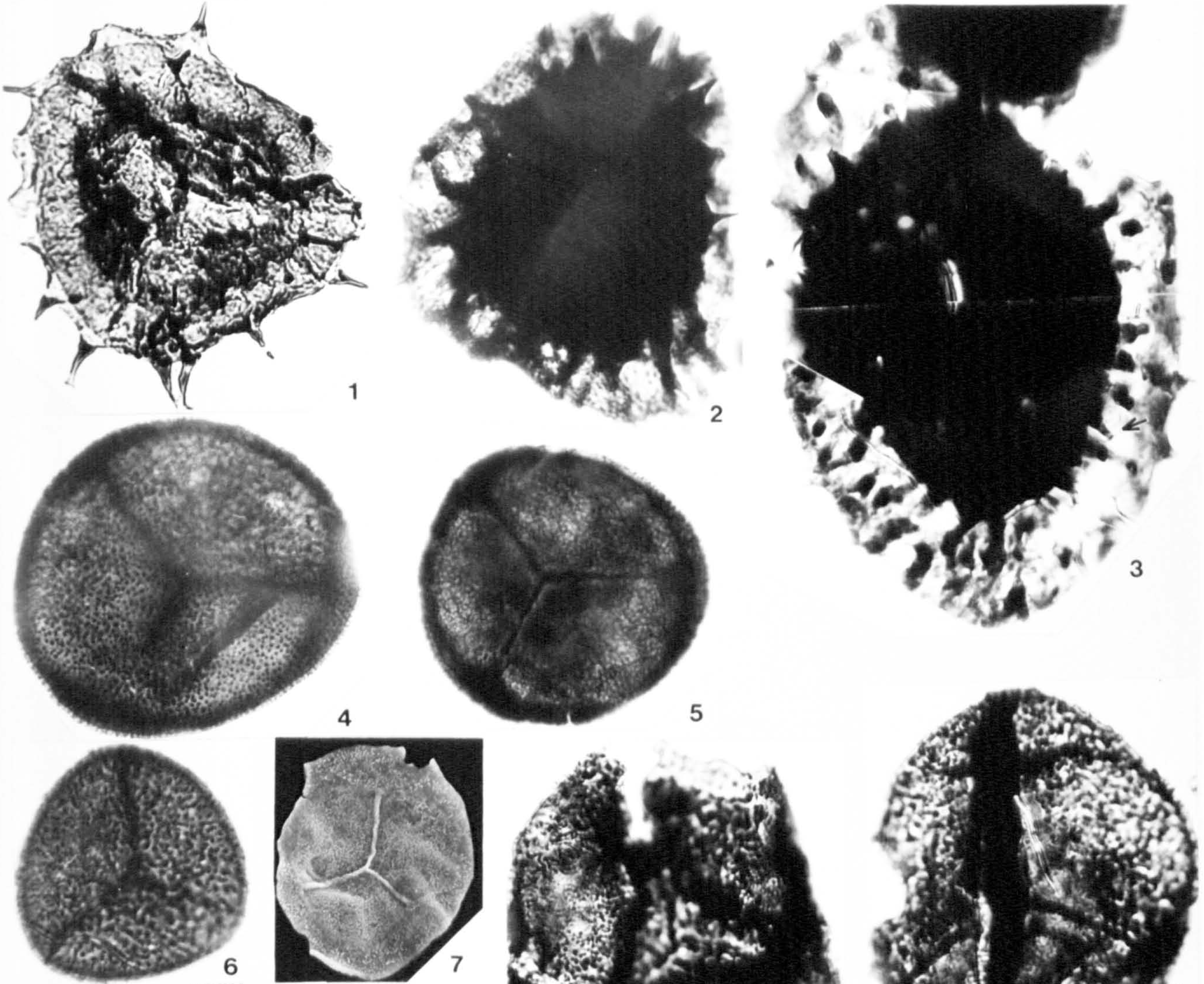


PLATE 3·12

PLATE 3.13

Plate 3.13

Fig. 1 *Apiculiretusispora magnifica* Tiwari and Schaarschmidt, 1975; S01 (a) 147/16.2.

Fig. 2 *Apiculiretusispora magnifica* Tiwari and Schaarschmidt, 1975; LN101 (a) 151.5/4.2.

Fig. 3 *Apiculiretusispora nitida* Owens, 1971; S20 (a) 130.1/16.1.

Fig. 4 *Apiculiretusispora nitida* Owens, 1971; S02 (a) 144.2/23.

Fig. 5 *Apiculiretusispora nitida* Owens, 1971; LN101 (a) 139/4.5.

Fig. 6 *Apiculiretusispora nitida* Owens, 1971; over-oxidised specimen - superficial resemblance to *Apiculiretusispora* sp. A of Richardson & Ioannides, 1973; H14 (a) 151.5/10.5.

Fig. 7 *Apiculiretusispora brandtii* Streel, 1964, ?transitional to *Apiculatasporites microconus* (Richardson) McGregor & Camfield, 1982; LN52 (a) 148.8/18.5.

Fig. 8 *Auroraspora micromanifesta* (Hacquebard) Richardson, 1960; S18 (a) 137.1/18.5.

Fig. 9 *Auroraspora* cf. *torquata* Higgs, 1975; M42 (a) 122.9/8.1.

Fig. 10 *?Baculatisporites* sp.; coarse ornamented variant, transitional form to the *Raistrickia spp.* plexus; WP31 (a) 141/16.2.

Fig. 11 *Brochotriletes ?foveolatus* Naumova, 1953; LN98 (a) 152/13.

Fig. 12 *Auroraspora micromanifesta* (Hacquebard) Richardson, 1960; x390; H14 (a) 125.2/15.4.

Fig. 13 *?Baculatisporites* sp.; L33 (a) 134/21.9.

Fig. 14 *?Baculatisporites* sp.; L23 (a) 151.1/7.

Fig. 15 *Calamospora* cf. *nigrata* (Naumova) Allen, 1965; LN101 (a) 153.1/14.2.

Fig. 16 *Calamospora* cf. *nigrata* (Naumova) Allen, 1965; S08 (a) 156/13.2.

Fig. 17 *Calamospora* cf. *nigrata* (Naumova) Allen, 1965; LN38 (a) 139.8/16.9.

Fig. 18 *Calamospora* cf. *nigrata* (Naumova) Allen, 1965; R21 (a) 140.1/6.

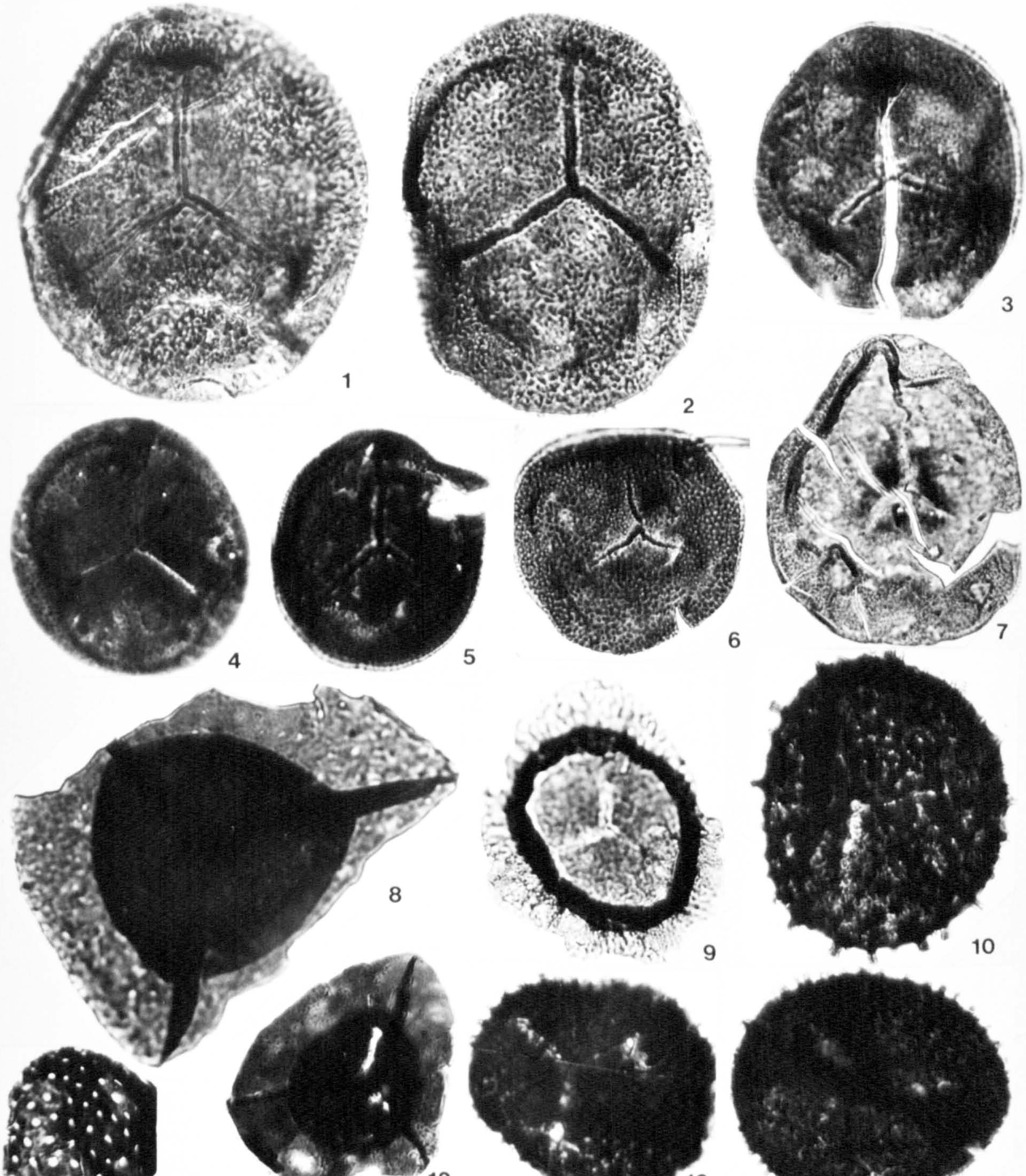


PLATE 3·13

PLATE 3.14

Plate 3.14

Fig. 1 *Calamospora pannucea* Richardson, 1965; H14 (a) 143.2/4.1.

Fig. 2 *Calamospora pannucea* Richardson, 1965; S01 (a) 134/13.5.

Fig. 3 *Camptozonotriletes mcgregorii* Ravn & Benson, 1988; LN38 (a) 142.1/14.

Fig. 4 ?*Calamospora* sp. A; LN57 (a) 141.5/10.5.

Fig. 5 ?*Calamospora* sp. A; S08 (a) 137.5/16.9.

Fig. 6 ?*Chelinospora concinna* Allen, 1965; K12 (b) 150.2/12.1.

Fig. 7 *Convolutispora* cf. *caperata* Wicander & Playford, 1985; K32 (b) 158.5/6.9.

Fig. 8 *Convolutispora* cf. *caperata* Wicander & Playford, 1985; CM68 (a) 148.5/3.1.

Fig. 9 *Convolutispora* sp. A; distal hemisphere focus; M28 (a) 145.5/10.2.

Fig. 10 *Convolutispora* sp. A; distal hemisphere focus; M26 (a) 138.4/9.2.

Fig. 11 *Convolutispora* cf. *subtilis* Owens, 1971; lateral compression - a laesura is indicated; M07 (a) 146.1/10.2.

Fig. 12 ?*Corystisporites* sp. A; detail of ornament transitional to "collared" type of ?*C. collaris*, (x750 magnification); K14 (a) 130.5/14.5.

Fig. 13 ?*Corystisporites collaris* Tiwari & Schaarschmidt, 1975; x2300, detail of ornament; K14 (a) 156.1/4.1

Fig. 14 ?*Corystisporites collaris* Tiwari & Schaarschmidt, 1975; K12 (a) 157.5/12.

Fig. 15 ?*Corystisporites collaris* Tiwari & Schaarschmidt, 1975; WP31 (a) 142.5/5.6.

Fig. 16 ?*Corystisporites* sp. A; K10 (a) 148.9/11.1.

Fig. 17 ?*Corystisporites collaris* Tiwari & Schaarschmidt, 1975; K38 (a) 150/10.5.

Fig. 18 ?*Corystisporites* sp. A; K10 (a) 152.9/5.9.

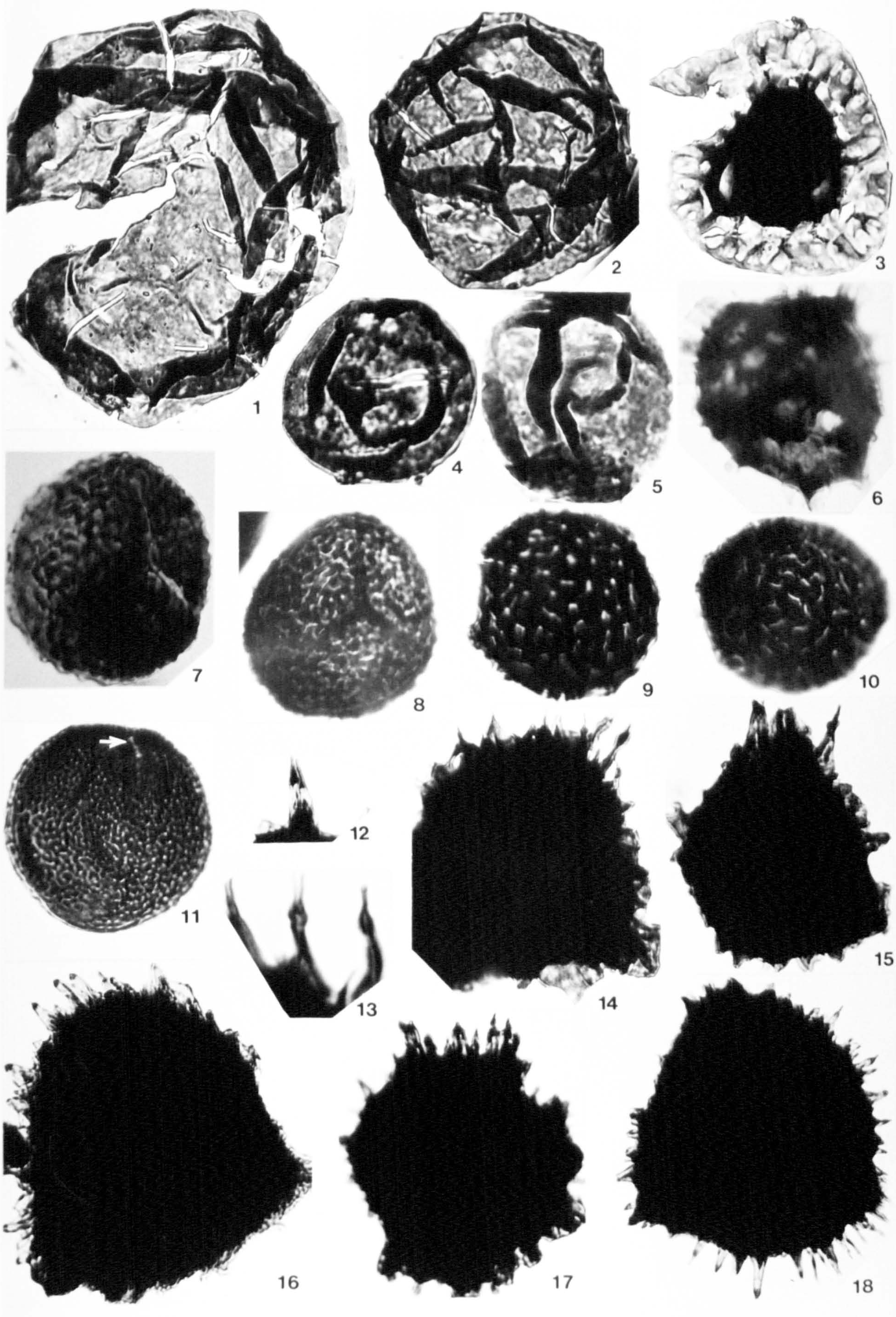


PLATE 3·14

PLATE 3.15

Plate 3.15

Fig. 1 *Crassispora catenata* Higgs, 1975; M40 (a) 159/11.5.

Fig. 2 *Crassispora* cf. *catenata* Higgs, 1975; M22 (a) 136.5/11.9.

Fig. 3 *Crassispora catenata* Higgs, 1975; transitional morphotype to *C.* cf. *catenata*; M44 (a) 129.9/23.5.

Fig. 4 *Cyclogranisporites* sp. A; H03 (b) 137/18.5.

Fig. 5 *Cyclogranisporites* sp. A; H14 (a) 140.5/11.

Fig. 6 ?*Cyclogranisporites* sp. B; distal focus; M12 (a) 146.2/13.5.

Fig. 7 *Cristatisporites triangulatus* (Allen) McGregor & Camfield, 1982; detail of convolute cristae, x2300; M15 (a) 147.5/16.5.

Fig. 8 *Cristatisporites triangulatus* (Allen) McGregor & Camfield, 1982; K08 (a) 138.5/14.1.

Fig. 9 *Cristatisporites triangulatus* (Allen) McGregor & Camfield, 1982; M42 (a) 141.6/17.2.

Fig. 10 *Cristatisporites mediconus* (Richardson) McGregor & Camfield, 1982; distal focus; S19 (a) 153.2/16.9.

Fig. 11 *Cristatisporites triangulatus* (Allen) McGregor & Camfield, 1982; ornament detail, of Fig. 9, x2300; M42 (a) 141.6/17.2.

Fig. 12 *Cristatisporites triangulatus* (Allen) McGregor & Camfield, 1982; K10 (a) 150.5/19.2.

Fig. 13 *Cristatisporites triangulatus* (Allen) McGregor & Camfield, 1982; K32 (a) 155.2/22.8.

Fig. 14 ?*Cristatisporites* sp. A, (*sensu* Loboziak & Streel, 1981) comb. nov.; equatorial ornament detail (x750 magnification); K29 (a) 140.5/16.8.

Fig. 15 *Cristatisporites triangulatus* (Allen) McGregor & Camfield, 1982; K41 (a) 141.6/16.2

Fig. 16 ?*Cristatisporites* sp. A, (*sensu* Loboziak & Streel, 1981) comb. nov.; K12 (a) 135.5/18.5.

Fig. 17 ?*Cristatisporites* sp. A, (*sensu* Loboziak & Streel, 1981) comb. nov.; K10 (a) 132.1/3.2.

Fig. 18 ?*Cristatisporites* sp. A, (*sensu* Loboziak & Streel, 1981) comb. nov.; K14 (a) 137.4/11.2.

Fig. 19 ?*Cristatisporites* sp. A, (*sensu* Loboziak & Streel, 1981) comb. nov.; ornament detail on distal surface (of fig.20), x2300 magnification; K23 (a) 142.2/12.9.

Fig. 20 ?*Cristatisporites* sp. A, (*sensu* Loboziak & Streel, 1981) comb. nov.; K23 (a) 142.2/12.9.

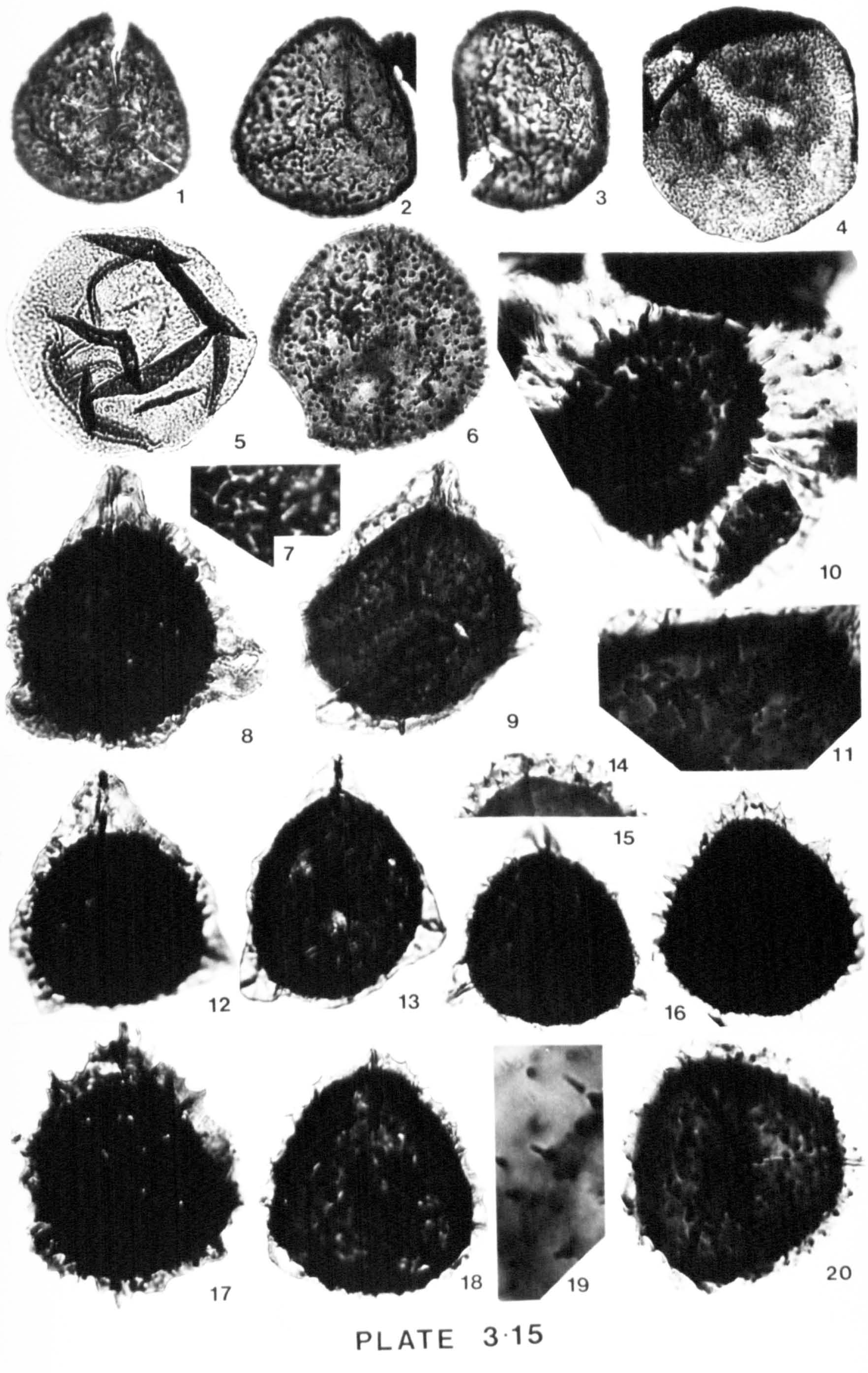


PLATE 3·15

PLATE 3.16

Plate 3.16

Fig. 1 *?Cymbosporites* sp.; LN101 (a) 137.2/7.2.

Fig. 2 *?Densosporites devonicus* Richardson, 1960; WP26 (a) 144.2/9.8.

Fig. 3 *?Densosporites devonicus* Richardson, 1960; ?transitional morphotype to *D.concinnus*; R21 (a) 151.2/16.2.

Fig. 4 *?Densosporites concinnus* (Owens) McGregor & Camfield, 1982; S14 (b) 151.2/20.5.

Fig. 5 *?Densosporites concinnus* (Owens) McGregor & Camfield, 1982; S08 (a) 136.1/13.9.

Fig. 6 *?Densosporites devonicus* Richardson, 1960; intexinal body discernible; S14 (a) 147.4/11.2.

Fig. 7 *?Densosporites concinnus* (Owens) McGregor & Camfield, 1982; K23 (a) 151/20.1.

Fig. 8 *?Densosporites devonicus* Richardson, 1960; ornament detail, x1100; S06 (a) 137.5/14.5.

Fig. 9 *Dibolisporites echinaceus* "complex" (Eisenack) Richardson, 1965; ornament detail, x2300; K12(a) 144.3/14.9.

Fig. 10 *Dibolisporites echinaceus* "complex" (Eisenack) Richardson, 1965; ornament detail, x2300; LN92 (b) 141.3/11.5.

Fig. 11 *Dibolisporites bullatus* Allen, 1965; detail of sparse sculpture, x2300; LN92 (b) 143.9/22.1.

Fig. 12 *Dibolisporites echinaceus* "complex" (Eisenack) Richardson, 1965; (= *D. radiatus* of Tiwari & Schaarschmidt, 1975); LN38 (a) 136/5.4.

Fig. 13 *Dibolisporites echinaceus* "complex" (Eisenack) Richardson, 1965; CM66 (a) 137.5/11.5.

Fig. 14 *Dibolisporites bullatus* Allen, 1965; K05 (a) 135.1/17.9.

Fig. 15 *Dibolisporites bullatus* Allen, 1965; LN101 (a) 136.2/7.5.

Fig. 16 *Dibolisporites echinaceus* "complex" (Eisenack) Richardson, 1965; (= *D.radiatus* of Tiwari & Schaarschmidt, 1975); S14 (a) 146.2/9.7.

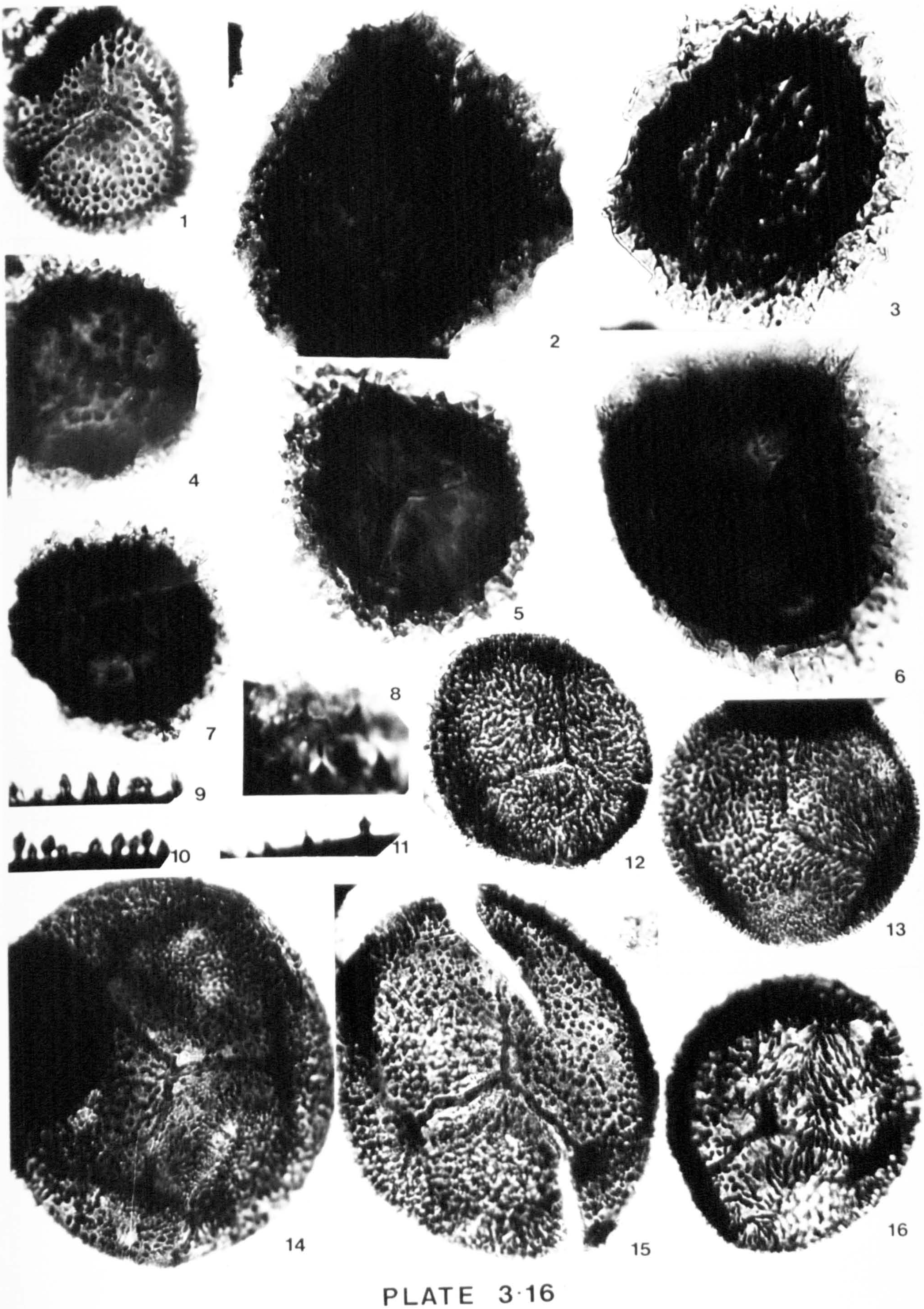


PLATE 3·16

PLATE 3.17

Plate 3.17

Fig. 1 *Dibolisporites echinaceus* "complex" Richardson, 1965; LN101 (a) 139.1/12.2.

Fig. 2 *Dibolisporites eifeliensis* (Lanninger) McGregor, 1973; LN38 (a) 146/10.8.

Fig. 3 *Dibolisporites eifeliensis* (Lanninger) McGregor, 1973; S12 (a) 147.9/15.2.

Fig. 4 *Dibolisporites ?eifeliensis* (Lanninger) McGregor, 1973; LN101 (a) 135.9/5.5.

Fig. 5 *Dibolisporites ?eifeliensis* (Lanninger) McGregor, 1973; H13 (a) 146.1/25.

Fig. 6 *Dibolisporites ?eifeliensis* (Lanninger) McGregor, 1973; LN06 (a) 150.6/20.

Fig. 7 *Dibolisporites* cf. *quebecensis* McGregor, 1973; LN98 (a) 149/18.2.

Fig. 8 *Dibolisporites echinaceus* "complex" Richardson, 1965; R21 (a) 134.9/5.5.

Fig. 9 *Dibolisporites variverrucatus* Massa & Moreau-Benoit, 1976; LN101 (a) 153.2/12.1.

Fig. 10 *Dibolisporites* sp. A var.A; S10 (a) 151.2/6.9.

Fig. 11 *Dibolisporites* sp. A var.A; S14 (a) 155.5/18.5.

Fig. 12 *Dibolisporites variverrucatus* Massa & Moreau-Benoit, 1976; LN21 (a) 135/5.3.

Fig. 13 *Dibolisporites* sp. A var.A; S08 (a) 143.2/4.1.

Fig. 14 *Dibolisporites* sp. A var.B; S02 (a) 132.9/17.

Fig. 15 *Dibolisporites* sp. A var.A; ornament detail of Fig. 13, x2300; S08 (a) 137.1/14.9.

Fig. 16 *Dibolisporites* sp. A var.B; S02 (a) 150.2/11.2.

Fig. 17 *?Dictyotriletes* sp. A; S14 (a) 138.9/6.8

Fig. 18 *?Dictyotriletes* sp. A; LH02 (a) 143/16.2.

Fig. 19. *Dictyotriletes* sp. B; K12 (a) 152.3/9.6.

Fig. 20 *Emphanisporites annulatus* McGregor, 1961; WP31 (a) 145.2/14.6.

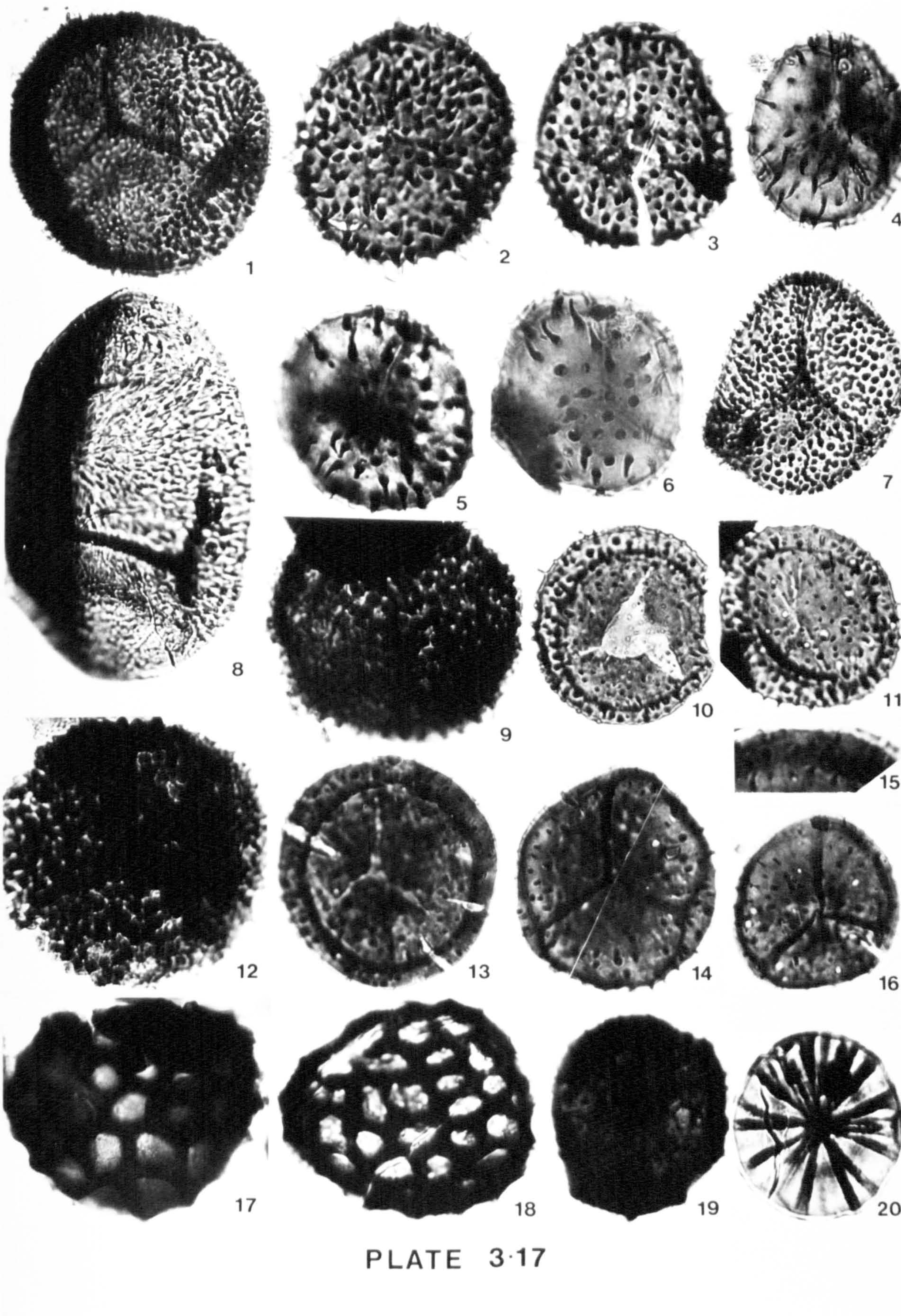


PLATE 3·17

PLATE 3.18

Plate 3.18

Fig. 1 *Emphanisporites annulatus* McGregor, 1961; LN101 (a) 157.9/22.9.

Fig. 2 *Emphanisporites annulatus* McGregor, 1961; LN98 (a) 131/10.1.

Fig. 3 *Emphanisporites annulatus* McGregor, 1961; S14 (a) 141.6/16.2.

Fig. 4 *Emphanisporites annulatus* McGregor, 1961; proximal view; LN98 (a) 126/17.1.

Fig. 5 *Emphanisporites annulatus* McGregor, 1961; WP02 (a) 149.5/9.6.

Fig. 6 *Emphanisporites annulatus* McGregor, 1961; H13 (a) 136.5/8.5.

Fig. 7 *Emphanisporites annulatus* McGregor, 1961; scanning electron photomicrograph showing the distal annulus, and radial creases of the exine on the equatorial side of this feature; x450; LN98.

Fig. 8 *Emphanisporites annulatus* McGregor, 1961; distal view of Fig. 4 - note discernible radial creases (as defined for Fig. 7); LN98 (a) 126/17.1.

Fig. 9 *Emphanisporites pseudoerraticus* Schultz, 1968; LN38 139.1/10.2.

Fig. 10 *Emphanisporites foveolatus* Schultz, 1968; LN24 (a) 156.2/4.5.

Fig. 11 *Emphanisporites foveolatus* Schultz, 1968; H06 (a) 138.2/11.1.

Fig. 12 *Emphanisporites foveolatus* Schultz, 1968; LN101 (a) 156/19.5.

Fig. 13 *Emphanisporites pseudoerraticus* Schultz, 1968; LN31 (a) 148.5/12.4.

Fig. 14 *Emphanisporites mcgregorii* Cramer, 1967b; LN101 (a) 142.1/12.

Fig. 15 *Emphanisporites mcgregorii* Cramer, 1967b; LN38 (a) 139.1/10.2.

Fig. 16 *Emphanisporites mcgregorii* Cramer, 1967b; LN38 (a) 21.2/147.8.

Fig. 17 *Emphanisporites rotatus* McGregor, 1961; scanning electron photomicrograph, proximal surface; x600; oblique proximal view; LN01.

Fig. 18 *Emphanisporites rotatus* McGregor, 1961; LN101 (a) 137/12.4.

Fig. 19 *Emphanisporites rotatus* McGregor, 1961; H12 (a) 124.3/4.7.

Fig. 20 *Emphanisporites rotatus* McGregor, 1961; S02 (a) 146.8/4.7

Fig. 21 *Emphanisporites rotatus* McGregor, 1961; scanning electron photomicrograph, proximal surface; x600; LN98.

Fig. 22 *Emphanisporites schultzii* McGregor, 1973; poorly oxidised specimen - note traces of apical proximal ribbing; LN38 (a) 132.2/10.1.

Fig. 23 *Emphanisporites* sp. A; S20 (a) 134.8/6.5.

Fig. 24 *Emphanisporites* sp. A; S19 (a) 136.2/12.2

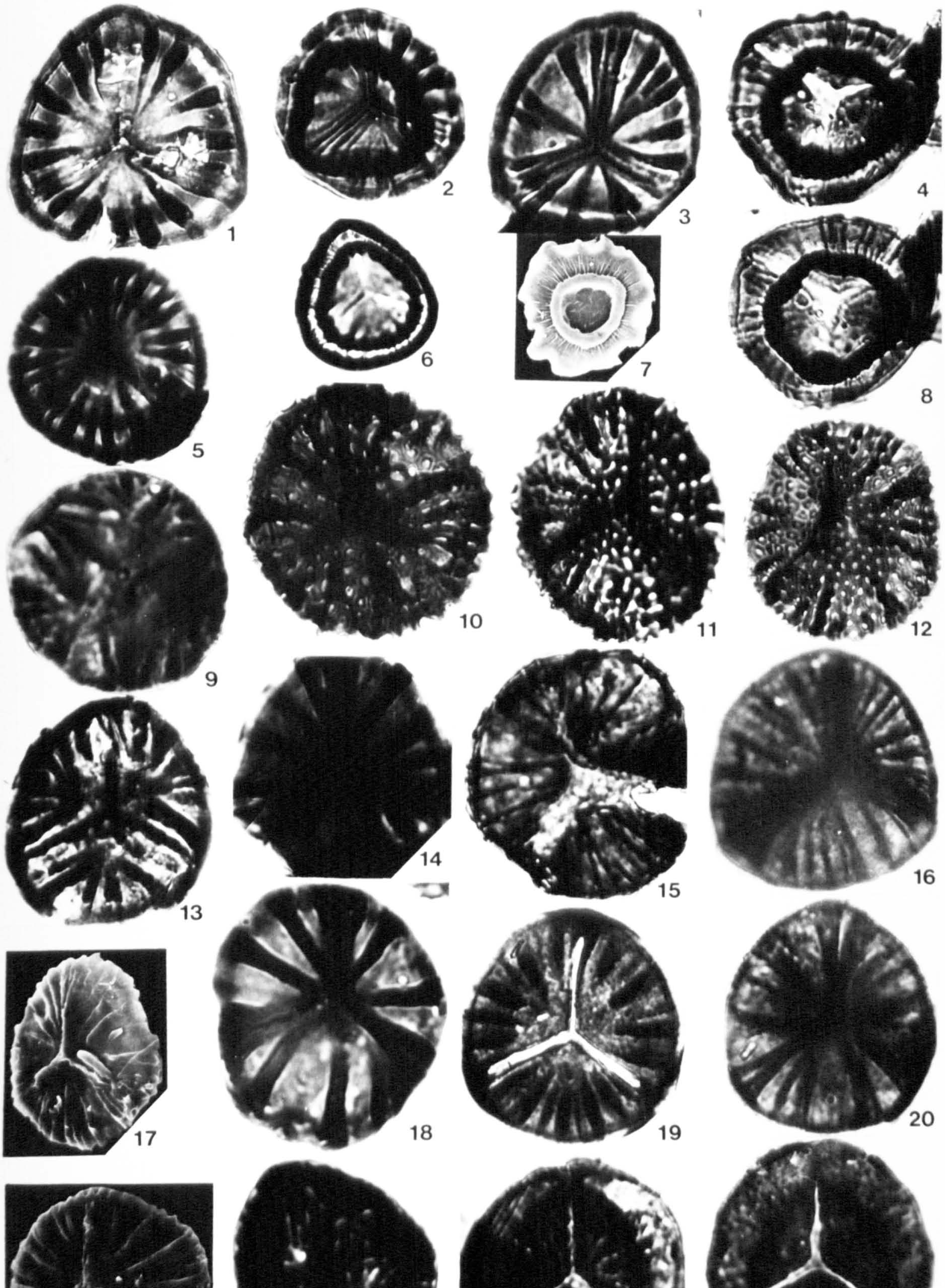


PLATE 3·18

PLATE 3.19

Plate 3.19

Fig. 1 *Geminospora boleta* Higgs & Russell, 1981; intexine enlarged and closely appressed to exoexine; M35 (a) 147.2/17.6.

Fig. 2 *Geminospora boleta* Higgs & Russell, 1981; M42 (a) 152.3/4.2.

Fig. 3 *Geminospora boleta* Higgs & Russell, 1981; ornament detail, x2300; K32 (a) 155.1/18.9.

Fig. 4 *Geminospora boleta* Higgs & Russell, 1981; K02 (a) 148.1/15.1.

Fig. 5 *Geminospora boleta* Higgs & Russell, 1981; M07 (a) 148.9/23.9.

Fig. 6 *Geminospora boleta* Higgs & Russell, 1981; x2300 magnification; K40 (a) 157.2/22.5.

Fig. 7 *Geminospora lemurata* Balme 1962, emend. Playford, 1983; M26 (a) 140.3/7.1.

Fig. 8 *Geminospora lemurata* Balme 1962, emend. Playford, 1983; K37 (a) 135.3/10.9.

Fig. 9 *Geminospora lemurata* Balme 1962, emend. Playford, 1983; L02 (a) 134/8.2.

Fig. 10 *Geminospora boleta* Higgs & Russell, 1981; M47 (a) 140.1/19.

Fig. 11 *Geminospora lemurata* Balme 1962, emend. Playford, 1983; sculptural detail, x2300; CM28 (a) 146.9/14.2.

Fig. 12 *Geminospora lemurata* Balme 1962, emend. Playford, 1983; CM68 (a) 158.2/12.5.

Fig. 13 *Geminospora lemurata* Balme 1962, emend. Playford, 1983; M31 (a) 142.1/7.4.

Fig. 14 Monolete *Geminospora lemurata* Balme 1962, emend. Playford, 1983; ornament gradational with *G. tuberculata* (Kedo) Allen var. *micromata* McGregor & Camfield, 1982 (Fig. 19, below); K50 (a) 143.6/16.2.

Fig. 15 *Geminospora lemurata* Balme 1962, emend. Playford, 1983; CM40 (a) 129/9.1.

Fig. 16 *Geminospora pilaformis* Loboziak *et al.*, 1988; K32 (a) 155.1/3.5.

Fig. 17 *Geminospora ?spinosa* Allen, 1965; M22 (a) 135.5/19.1.

Fig. 18 *Geminospora ?spinosa* Allen, 1965; M28 (a) 138.9/16.9.

Fig. 19 *Geminospora tuberculata* (Kedo) Allen var. *micromata* McGregor & Camfield, 1982; M42 (a) 152.1/6.2.

Fig. 20 *Geminospora tuberculata* (Kedo) Allen var. *tuberculata* ; CM66 (a) 152.8/15.1.

Fig. 21 *Geminospora tuberculata* (Kedo) Allen var. *tuberculata* ; K50 (a) 159/14.

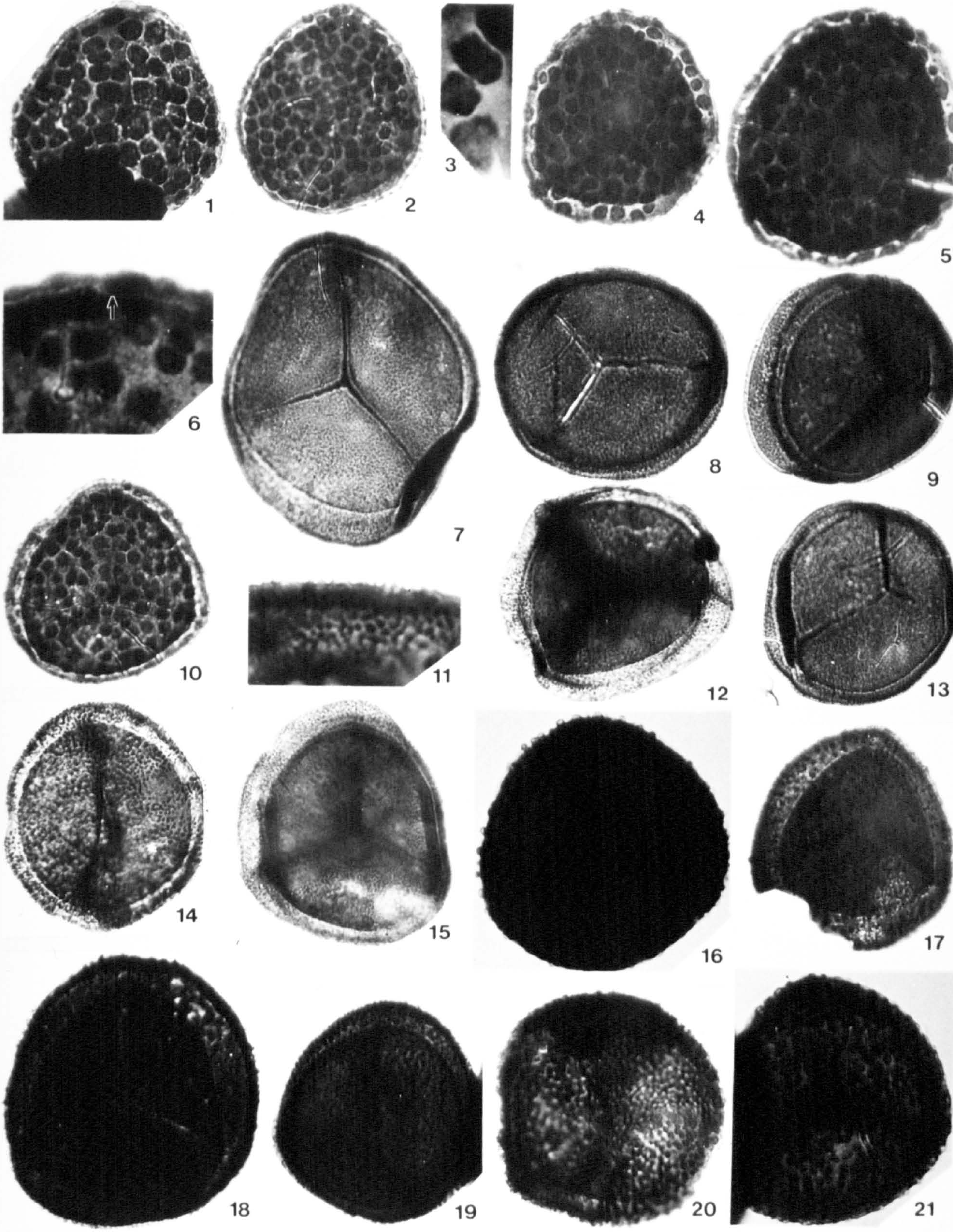


PLATE 3·19

PLATE 3.20

Plate 3.20

Fig. 1 *Grandispora* cf. *arduinnae* (Riegel) comb.nov.; LN17 (a) 144.5/8.2

Fig. 2 *Grandispora* cf. *arduinnae* (Riegel) comb.nov.; LN84 (a) 150/16.2.

Fig. 3 *Grandispora diamphida* Allen, 1965; exoexine comparatively flimsy, ?gradational towards *G. naumovii* (Kedo) McGregor, 1973 - reworked; S20 (a) 130/2.9

Fig. 4 *Grandispora diamphida* Allen, 1965; LN21 (a) 157.5/13.1.

Fig. 5 *Grandispora ?diamphida* Allen, 1965; morphological similarity with *Grandispora cassideus* (Owens) Chi & Hills, 1976. Resemblance to the figured specimen of *Grandispora diamphida* in Allen (1965, Pl. 103, fig.4); LN84 (a) 141/10.4.

Fig. 6 *Grandispora libyensis* Moreau-Benoit, 1980; detail of equatorial sculpture (x750 magnification); S14 (a) 151/12.4.

Fig. 7 *Grandispora* aff. *echinata* Hacquebard, 1957; M26 (a) 145.5/17.2.

Fig. 8 *Grandispora douglastownense* McGregor, 1973; virtually all ornament around the spore circumference unpreserved; LN96 (a) 155.2/11.3.

Fig. 9 *Grandispora eximia* (Allen) McGregor & Camfield, 1982; x470 magnification; LN101 (a) 143.6/17.2.

Fig. 10 *Grandispora eximia* (Allen) McGregor & Camfield, 1982; ornament detail (x750 magnification); LN13 (a) 141.2/19.

Fig. 11 *Grandispora libyensis* Moreau-Benoit, 1980; x750 magnification; WP31 (a) 146/23.2.

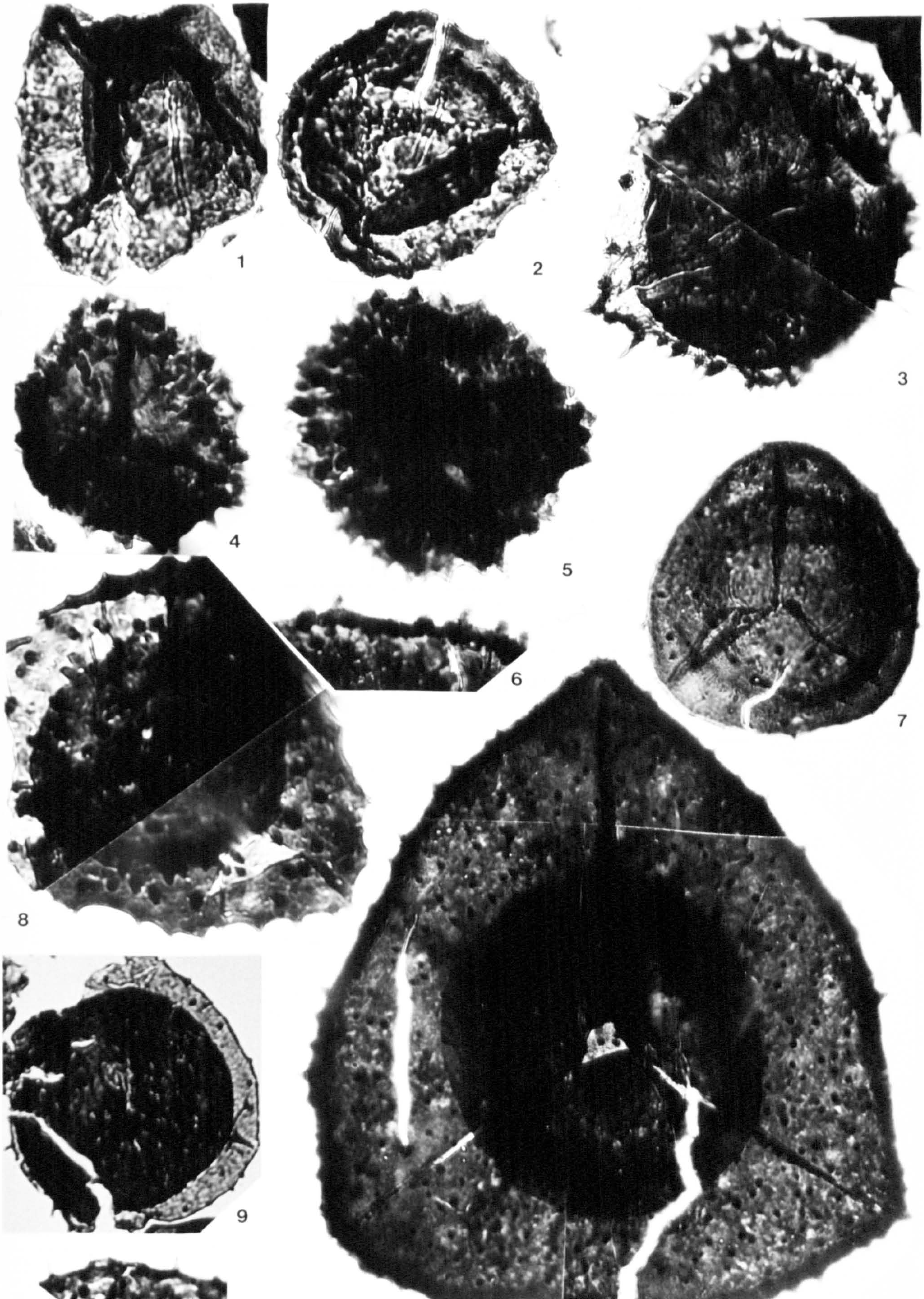


PLATE 3·20

PLATE 3.21

Plate 3.21

Fig. 1 *Grandispora naumovii* (Kedo) McGregor, 1973; L23 (a) 131.5/19.5.

Fig. 2 *Grandispora naumovii* (Kedo) McGregor, 1973; S08 (a) 157.1/11.8.

Fig. 3 *Grandispora naumovii* (Kedo) McGregor, 1973; as for Fig. 1, but with the intexine indicated. The asterixed process allows orientation between the two photomicrographs; L23 (a) 131.5/19.5.

Fig. 4 *Grandispora* cf. *protea* (Naumova) Moreau-Benoit, 1980; H14 (a) 152.2/4.1.

Fig. 5 *Grandispora protea* (Naumova) Moreau-Benoit, 1980; LN101 (a) 150.1/13.4.

Fig. 6 *Grandispora saetosa* Clayton & Graham, 1974; M42 (a) 143.1/3.9.

Fig. 7 *Grandispora tomentosa* Taugourdeau-Lantz, 1967; M35 (a) 151.3/8.2.

Fig. 8 *Grandispora* cf. *variospinosa* McGregor & Camfield, 1982; H14 (a) 141/21.9.

Fig. 9 *Grandispora* cf. *variospinosa* McGregor & Camfield, 1982; S08 (a) 155/5.5.

Fig. 10 *Grandispora* cf. *velata* (Eisenack) Playford, 1971; specimen with small, predominantly spinose ornament - transitional with *Grandispora* cf. *protea* (Naumova) Moreau-Benoit (1980), described and illustrated herein; LN101 (a) 146.1/12.5.

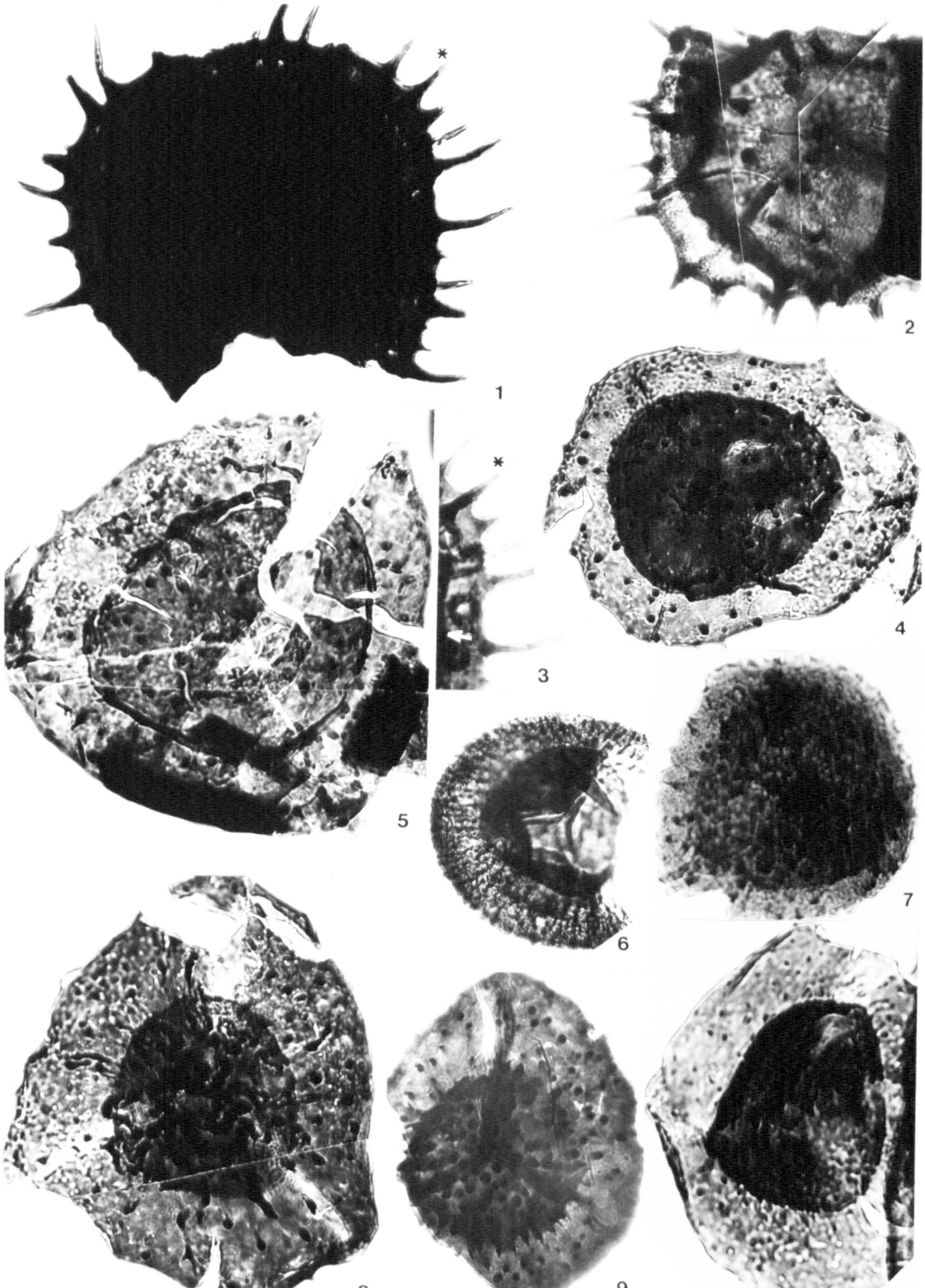


PLATE 3·21

PLATE 3.22

Plate 3.22

Fig. 1 *Grandispora velata* (Eisenack) Playford, 1971; ornament detail, x750 magnification; S20 (a) 143.2/17.8

Fig. 2 *Grandispora* sp. B; LN101 (a) 154.5/4.1.

Fig. 3 *Grandispora velata* (Eisenack) Playford, 1971; note polygonal pyrite "pitting"; K14 133.2/5.1.

Fig. 4 *Grandispora* sp. B; H14 (a) 149.8/9.2.

Fig. 5 *Grandispora* sp. A; LN84 (a) 139.9/9.6.

Fig. 6 *Grandispora* sp. A; WP29 (a) 151.9/10.2.

Fig. 7 *Grandispora* sp. C; R22 (a) 155.6/9.2.

Fig. 8 *Grandispora* sp. D; S08 (a) 152/6.3.

Fig. 9 *Grandispora* sp. D; WP31 (a) 140.5/5.6.

Fig. 10 *Grandispora* sp. D; WP31 (a) 148/14.2.

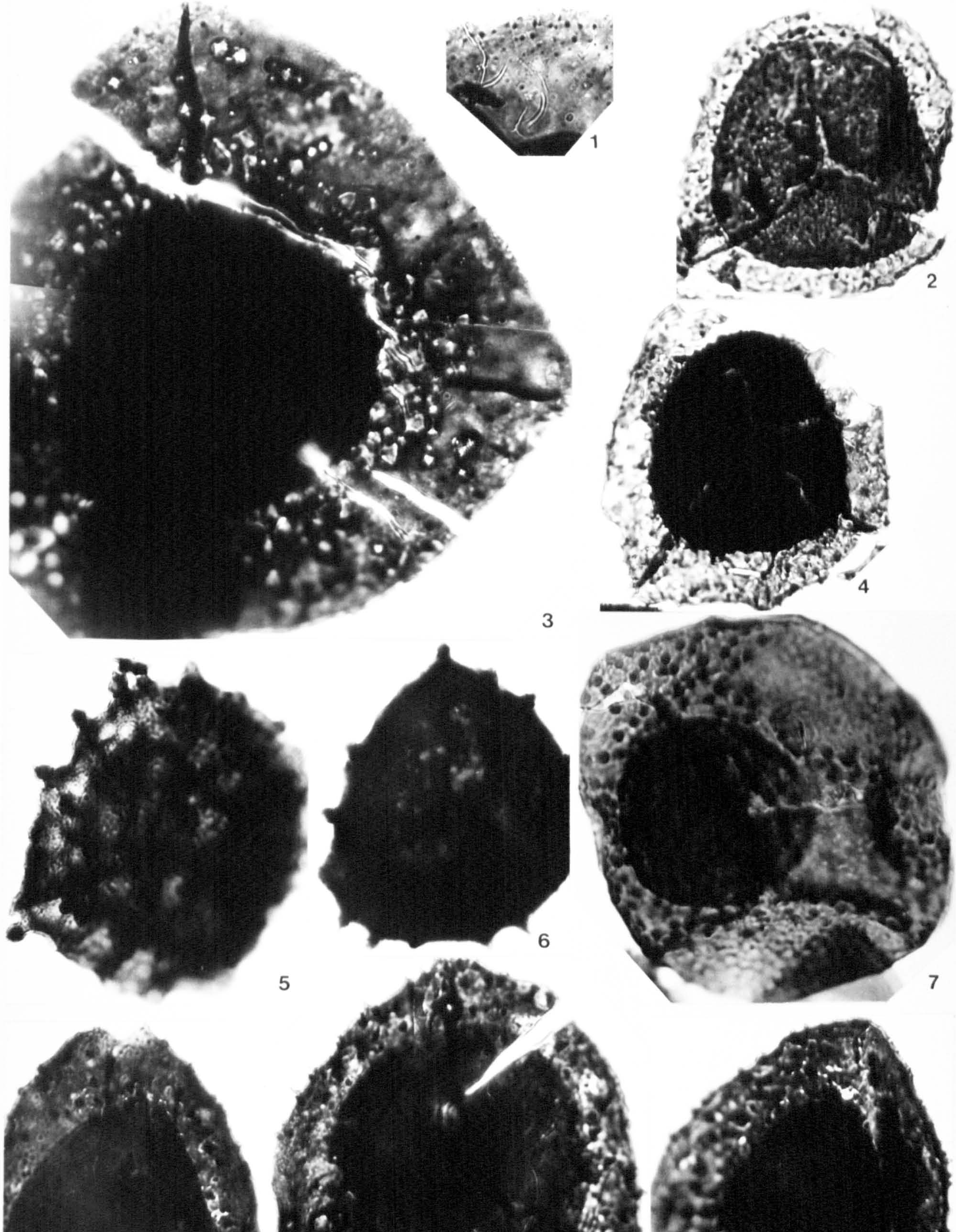


PLATE 3·22

PLATE 3.23

Plate 3.23

Fig. 1 *Grandispora* sp. E; CM34 (a) 150.5/14.2.

Fig. 2 *Grandispora* sp. E; K12 (b) 136.2/14.5.

Fig. 3 *Grandispora* sp. E; detail of ornament, x1100 magnification; CM40 (a) 133.9/6.4.

Fig. 4 *Grandispora* sp. F; K08 (a) 139.9/21.5.

Fig. 5 *Grandispora* sp. F; K12 (a) 148.2/6.1.

Fig. 6 *Grandispora* sp. E; K52 (a) 160.9/8.2.

Fig. 7 *Grandispora* sp. G; K08 (a) 146.5/22.1.

Fig. 8 *Grandispora* sp. F; K14 (a) 149.1/5.2.

Fig. 9 *Grandispora* sp. G; K08 (a) 140.5/23.5.

Fig. 10 *Grandispora* sp. G; K25 (a) 142.1/3.8.

Fig. 11 *Grandispora* sp. G; sculptural detail of Fig. 12, x2300; K23 (a) 132.2/22.2.

Fig. 12 *Grandispora* sp. G; K23 (a) 132.2/22.2.

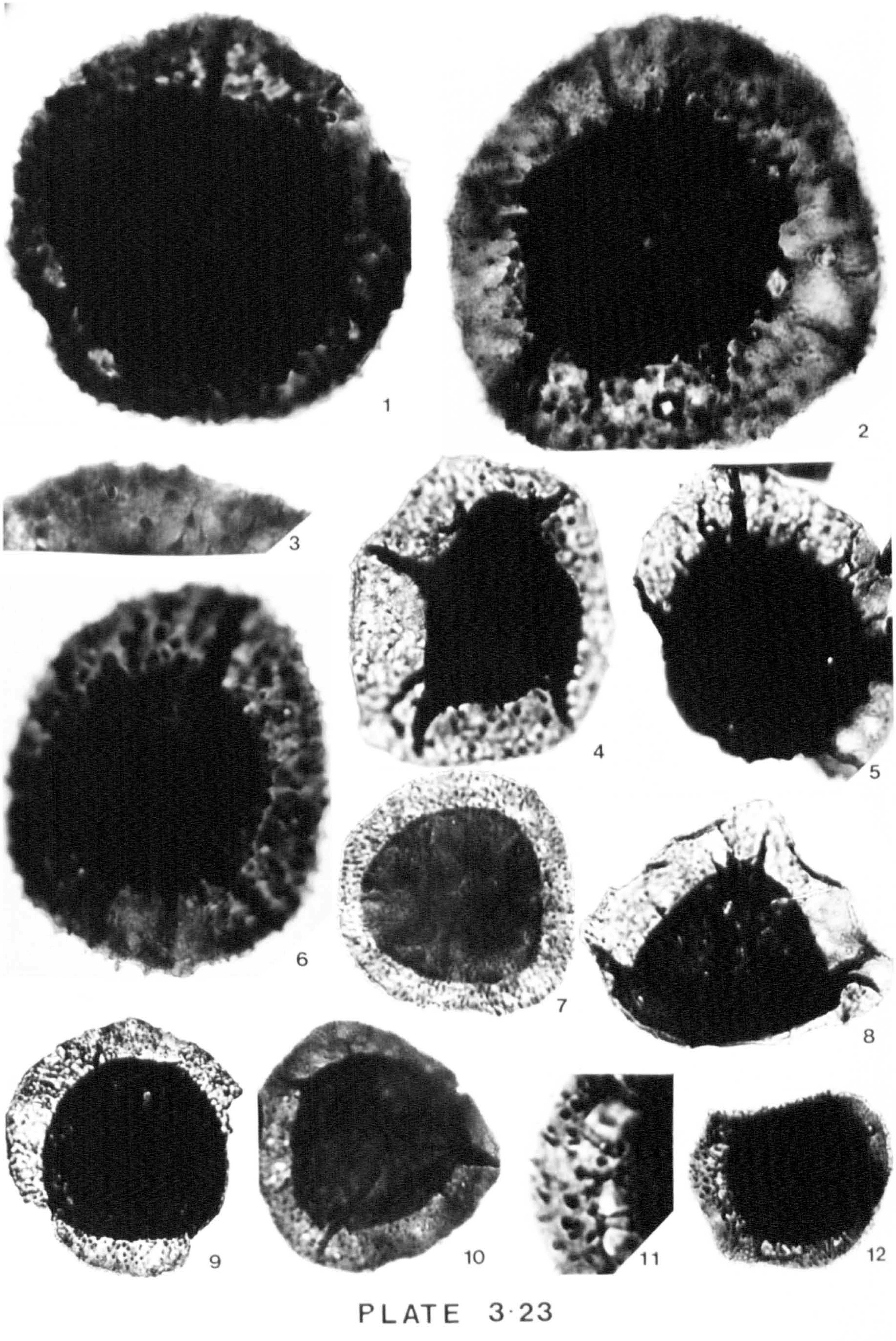


PLATE 3·23

PLATE 3.24

Plate 3.24

Fig. 1 *Hystricosporites ?corystus* Richardson, 1962; x310 magnification; R22 (a) 138.5/7.1.

Fig. 2 *Hystricosporites* sp. A; LN92 (a) 142.1/5.6.

Fig. 3 *Hystricosporites* sp. B; x400 magnification; LN92 (a) 150.6/19.1.

Fig. 4 *Hystricosporites* sp. B; H14 (a) 153.1/8.2.

Fig. 5 *Hystricosporites* sp. C; K38 (a) 133.5/16.9.

Fig. 6 *Insculptospora confossa* (Richardson) Marshall, 1985; intexine closely appressed to exoexine; M42 (a) 147.9/9.2.

Fig. 7 *Insculptospora confossa* (Richardson) Marshall, 1985; exoexine ruptured revealing textured intexine; S08 (a) 155.3/10.5.

Fig. 8 *Insculptospora confossa* (Richardson) Marshall, 1985; detail of granulate intexine, x2300 magnification; K12 (a) 148.9/11.1.

Fig. 9 *Insculptospora confossa* (Richardson) Marshall, 1985; intexine partially contracted within exoexine; CM34 (a) 143.2/9.8.

Fig. 10 *Insculptospora confossa* (Richardson) Marshall, 1985; detail of textured intexine of Fig. 11, x2300 magnification; S08 (a) 157.9/10.2.

Fig. 11 *Insculptospora confossa* (Richardson) Marshall, 1985; S08 (a) 157.9/10.2.

Fig. 12 *Insculptospora confossa* (Richardson) Marshall, 1985; intexine and exoexine closely appressed; CM34 (a) 132/11.2.

Fig. 13 *Insculptospora confossa* (Richardson) Marshall, 1985; intexine and exoexine discrete; L12 (a) 151.3/9.2.

Fig. 14 *Insculptospora confossa* (Richardson) Marshall, 1985; oblique equatorial compression, illustrating the distal folding of the exoexine independent of the intexine; K23 (a) 155.5/8.2.

Fig. 15 *Insculptospora confossa* (Richardson) Marshall, 1985; intexine confined to one half of the exoexine - attachment adjacent to the trilete rays; K29 (a) 128/16.2.

Fig. 16 *Insculptospora confossa* (Richardson) Marshall, 1985; exinal layers closely appressed; S06 (a) 140.5/8.2.

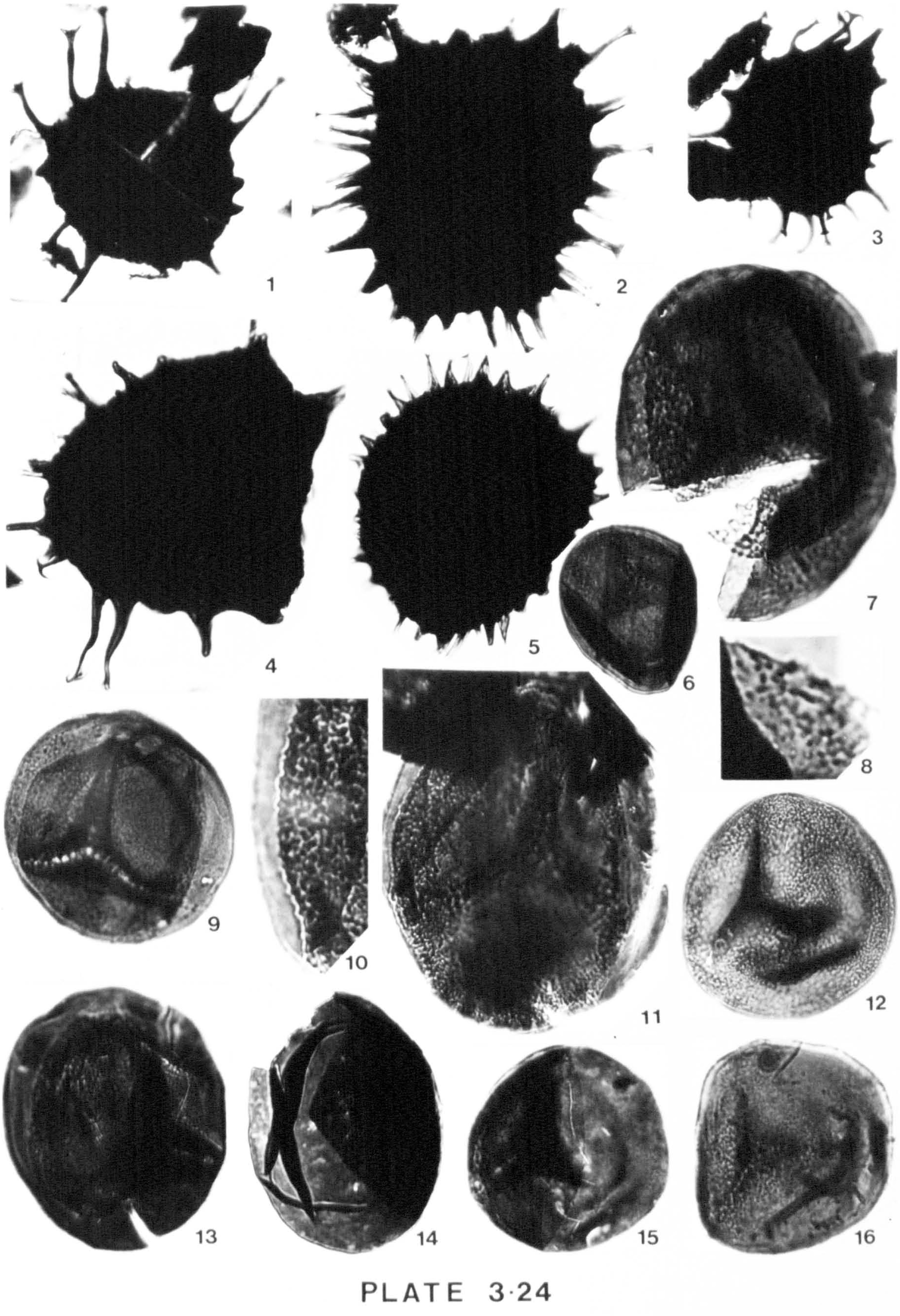


PLATE 3·24

PLATE 3.25

Plate 3.25

Fig. 1 *Kraeuselisporites* sp.; proximal focus; CM34 (a) 146.2/14.9.

Fig. 2 *Kraeuselisporites* sp.; median focus; CM34 (a) 157.2/5.4.

Fig. 3 *Leiotriletes* sp.; S20 (a) 139.8/8.5.

Fig. 4 *Perotrilites ?bifurcatus* Richardson, 1962; K14 (a) 140/8.5.

Fig. 5 *Perotrilites ?bifurcatus* Richardson, 1962; K08 (a) 155.8/17.

Fig. 6 *Punctatisporites* sp. A; R21 (a) 144.8/3.4.

Fig. 7 *Punctatisporites planus* Hacquebard, 1957; M24 (a) 145.7/6.9.

Fig. 8 *Raistrickia* sp. A; L33 (a) 150.5/5.1.

Fig. 9 *Raistrickia* sp. A; CM40 (a) 157.2/14.2.

Fig. 10 *Raistrickia* sp. A; S06 (a) 142.1/6.3.

Fig. 11 *?Raistrickia* sp. B; detail of ornament of Fig. 14, x2300; K25 (a) 132.5/8.2.

Fig. 12 *?Raistrickia* sp. B; sculptural detail - different aspect of the ornament for the specimen illustrated in Fig. 14, x2300; K25 (a) 132.5/8.2.

Fig. 13 *?Raistrickia* sp. B; ornament detail, illustrating serrated "biform" extremities, x2300; WP10 (a) 148.8/11.2.

Fig. 14 *?Raistrickia* sp. B; K25 (a) 132.5/8.2.

Fig. 15 *?Raistrickia* sp. B; CM01 (a) 143.9/14.9.

Fig. 16 *?Raistrickia* sp. B; L23 (a) 21.8/147.2.

Fig. 17 *?Raistrickia* sp. C; WP16 (a) 124.5/5.

Fig. 18 *?Raistrickia* sp. C; CM42 (a) 137.5/11.8.

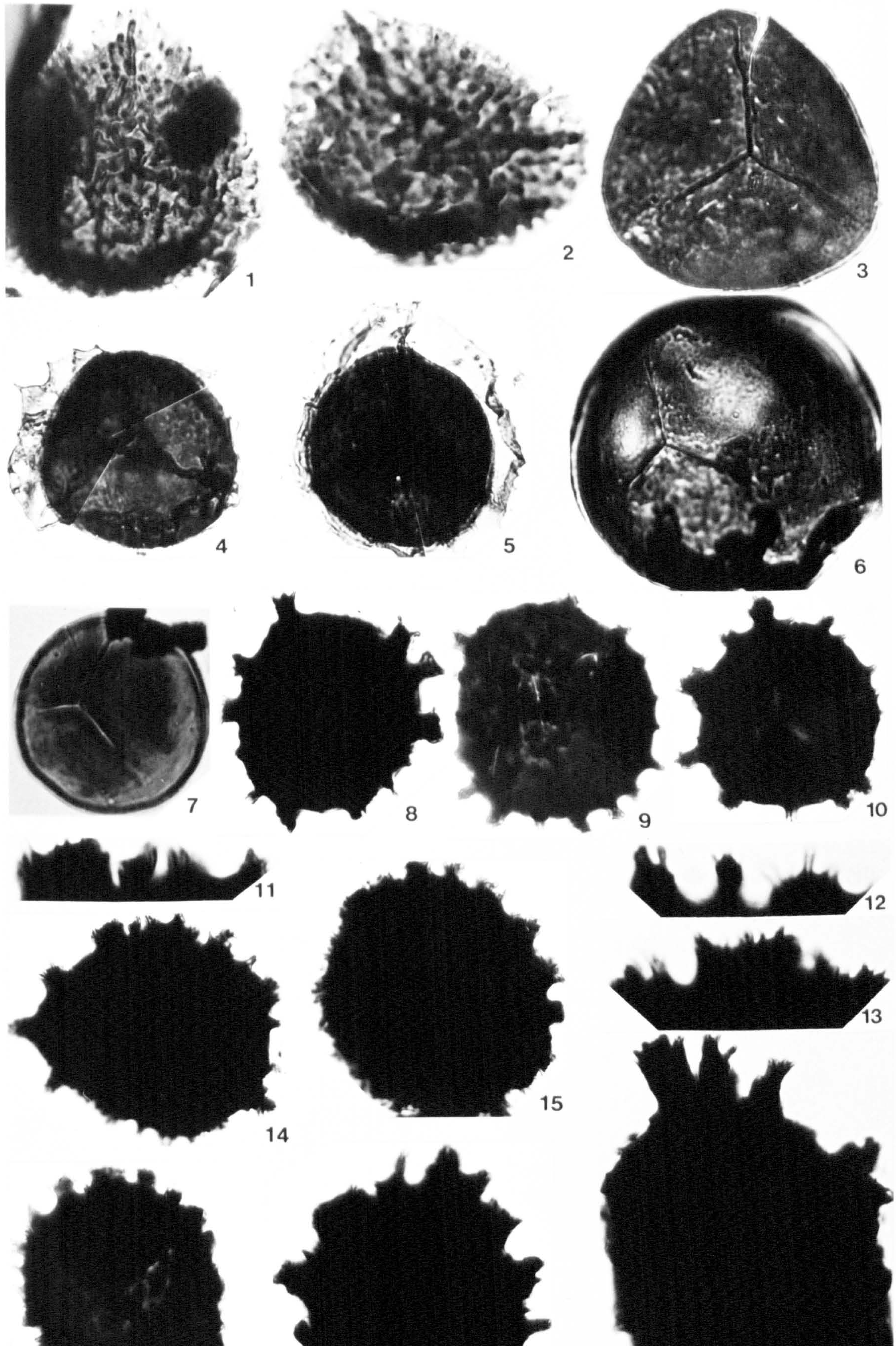


PLATE 3·25

PLATE 3.26

Plate 3.26

Fig. 1 *Retusotriletes aureoladus* Rodriguez, 1978; LN38 (a) 135.9/7.1

Fig. 2 *Retusotriletes goensis,* Lele & Streel, 1969; L14 (a) 151.2/16.3.

Fig. 3 *Retusotriletes ?pychovii* Naumova, 1953; LN101 (a) 146/10.5.

Fig. 4 *Retusotriletes ?pychovii* Naumova, 1953; S08 (a) 153.5/15.8.

Fig. 5 *Retusotriletes rotundus* (Streel) Lele & Streel, 1969; WP31 (a) 148.2/10.2.

Fig. 6 *Retusotriletes rotundus* (Streel) Lele & Streel, 1969; CM01 (a) 159.2/19.5.

Fig. 7 *Retusotriletes rotundus* (Streel) Lele & Streel, 1969; LN24 (a) 134/13.2.

Fig. 8 *Retusotriletes rotundus* (Streel) Lele & Streel, 1969; R21 (a) 140.2/4.2.

Fig. 9 *Retusotriletes rugulatus* Riegel, 1973; CM02 (a) 154.2/11.5.

Fig. 10 *Retusotriletes rugulatus* Riegel, 1973; H3 (a) 133.5/11.2.

Fig. 11 *Retusotriletes rugulatus* Riegel, 1973; R22 (a) 156/5.9.

Fig. 12 *Retusotriletes simplex* Naumova, 1953; LN98 (a) 139/12.5.

Fig. 13 *Retusotriletes rugulatus* Riegel, 1973; K08 (a) 140.5/11.

Fig. 14 *Retusotriletes rugulatus* Riegel, 1973; detail of inter-radial rugulation, x750 magnification; WP31 (a) 132.2/4.

Fig. 15 *Retusotriletes simplex* Naumova, 1953; scanning electron photomicrograph, proximal view; x450; R22.

Fig. 16 *Retusotriletes simplex* Naumova, 1953; LN101 (a) 146/9.8.

Fig. 17 *Retusotriletes triangulatus* (Streel) Streel, 1967; S02 (a) 142.5/15.9.

Fig. 18 *Retusotriletes triangulatus* (Streel) Streel, 1967; M10 (a) 152/2.9.

Fig. 19 *Retusotriletes triangulatus* (Streel) Streel, 1967; LN38 (a) 133.5/9.3.

Fig. 20 *Retusotriletes rotundus* (Streel) Lele & Streel, 1969; scanning electron photomicrograph, proximal view; x450; LN98.

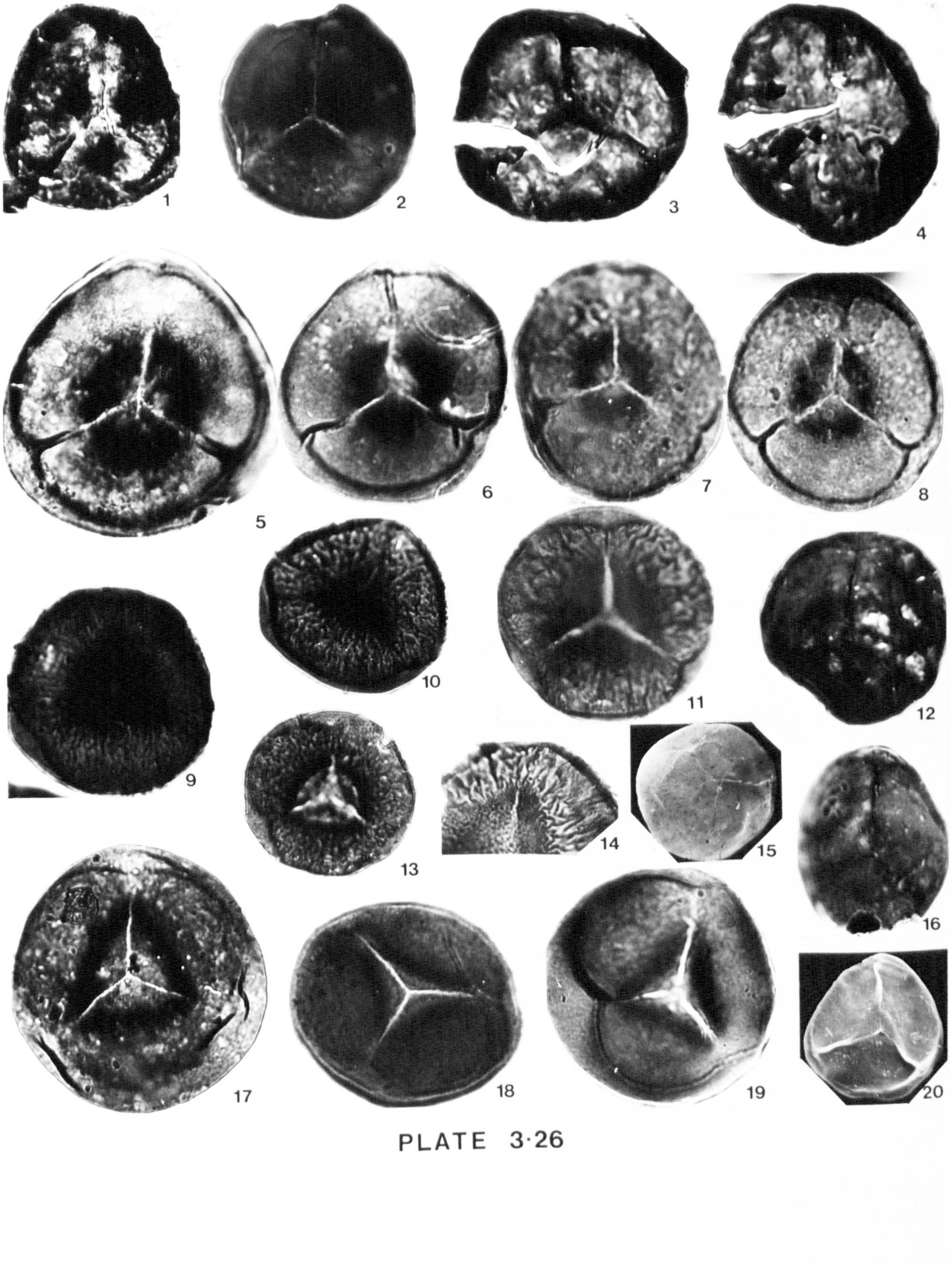


PLATE 3·26

PLATE 3.27

Plate 3.27

Fig. 1 ?*Retusotriletes* sp. B; R22 (a) 150.2/18.2.

Fig. 2 ?*Retusotriletes* sp. B; S19 (a) 141.2/3.1.

Fig. 3 ?*Retusotriletes* sp. B; S10 (a) 149.7/12.2.

Fig. 4 *Retusotriletes* sp. A; LN60 (a) 157.3/21.6.

Fig. 5 *Retusotriletes* sp. A; H14 (a) 144.2/3.1.

Fig. 6 ?*Retusotriletes* sp. B; S14 (a) 156.1/16.2.

Fig. 7 *Rhabdosporites langii* (Richardson) Marshall & Allen, 1982; WP31 (a) 151.9/12.2.

Fig. 8 *Rhabdosporites langii* (Richardson) Marshall & Allen, 1982; S14 (a) 155.4/5.9.

Fig. 9 *Rhabdosporites langii* (Richardson) Marshall & Allen, 1982; K02 (a) 138.1/15.5.

Fig. 10 *Rhabdosporites* sp. A *sensu* Richardson, 1965; tripartite exinal stratification, x2300; WP26 (a) 156.2/19.1.

Fig. 11 *Rhabdosporites* sp. B; LN17 (b) 141.2/24.5.

Fig. 12 *Rhabdosporites* sp. A *sensu* Richardson, 1965; CM02 (a) 151.5/21.1.

Fig. 13 *Rhabdosporites* sp. A *sensu* Richardson, 1965; K32 (a) 143.7/5.5

Fig. 14 cf. *Rhabdosporites* sp. *sensu* McGregor & Camfield, 1982; S20 (a) 151.5/10.4.

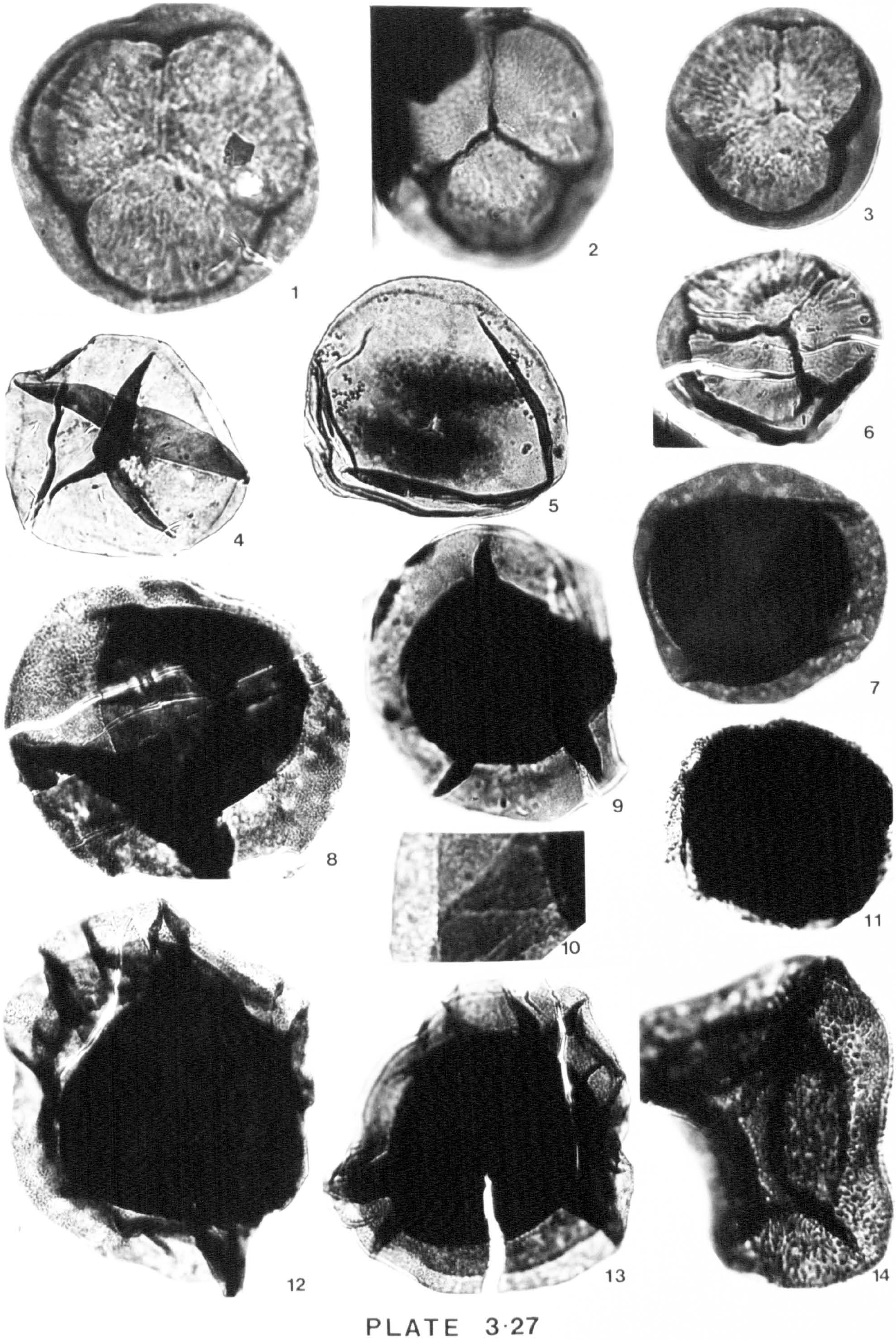


PLATE 3·27

PLATE 3.28

Plate 3.28

Fig. 1 *Rugospora* sp.; distal view; M42 (a) 124.1/4.3.

Fig. 2 *Rugospora* sp.; distal view; M12 (a) 132.5/20.3.

Fig. 3 *Stenozonotriletes* cf. *simplex* Naumova, 1953: S10 (a) 149.1/10.5.

Fig. 4 *Tholisporites chulus* (Cramer) McGregor, 1976, var. *chulus*; H13 (a) 131.2/4.2.

Fig. 5 *Tholisporites chulus* (Cramer) McGregor, 1976, var. *chulus*; scanning electron photomicrograph; x600; LN21.

Fig. 6 *Tholisporites chulus* (Cramer) McGregor, 1976, var. *chulus*; LN38 (a) 155/7.1.

Fig. 7 *Tholisporites chulus* (Cramer) McGregor, 1976, var. *chulus*; LN101 (a) 150.1/13.6.

Fig. 8 *Verrucosisporites bulliferus* (Taugourdeau-Lantz) Richardson & McGregor, 1986; detail of sculpture projecting at the circumference of Fig. 11, x2300; M42 (a) 152.3/17.1.

Fig. 9 *Tholisporites divellomedium* (Chibrikova) Turnau, 1986; LN101 (a) 138.2/12.1.

Fig. 10 *Verruciretusispora dubia* (Eisenack) Richardson & Rasul, 1978a; LN31 (a) 149.2/6.9.

Fig. 11 *Verrucosisporites bulliferus* (Taugourdeau-Lantz) Richardson & McGregor, 1986; M42 (a) 152.3/17.1.

Fig. 12 *Verrucosisporites bulliferus* (Taugourdeau-Lantz) Richardson & McGregor, 1986; sculptural detail, x2300; K34 (a) 144.2/11.

Fig. 13 *Verrucosisporites* cf. *bulliferus* (Taugourdeau-Lantz) Richardson & McGregor, 1986; opaque equatorial feature; K10 (a) 157.2/8.2.

Fig. 14 *Verrucosisporites* cf. *polygonalis* Lanninger, 1968; LN31 (a) 137.2/6.1.

Fig. 15 *Verrucosisporites premnus* Richardson, 1965; CM44 (a) 145/14.3.

Fig. 16 *Verrucosisporites premnus* Richardson, 1965; CM01 (a) 139.4/21.5.

Fig. 17 *Verrucosisporites bulliferus* (Taugourdeau-Lantz) Richardson & McGregor, 1986; distal and equatorial ornament, x2300 magnification; M42 (a) 141.7/11.2.

Fig. 18 *Verrucosisporites premnus* Richardson, 1965; partially degraded specimen; S20 (a) 145/14.9.

Fig. 19 *Verrucosisporites premnus* Richardson, 1965; K14 (a) 140.5/14.5.

Fig. 20 *Verrucosisporites scurrus* (Naumova) McGregor & Camfield, 1982; scanning electron photomicrograph; x450; CM70.

Fig. 21 *Verrucosisporites scurrus* (Naumova) McGregor & Camfield, 1982; CM66 (a) 143.5/9.1.

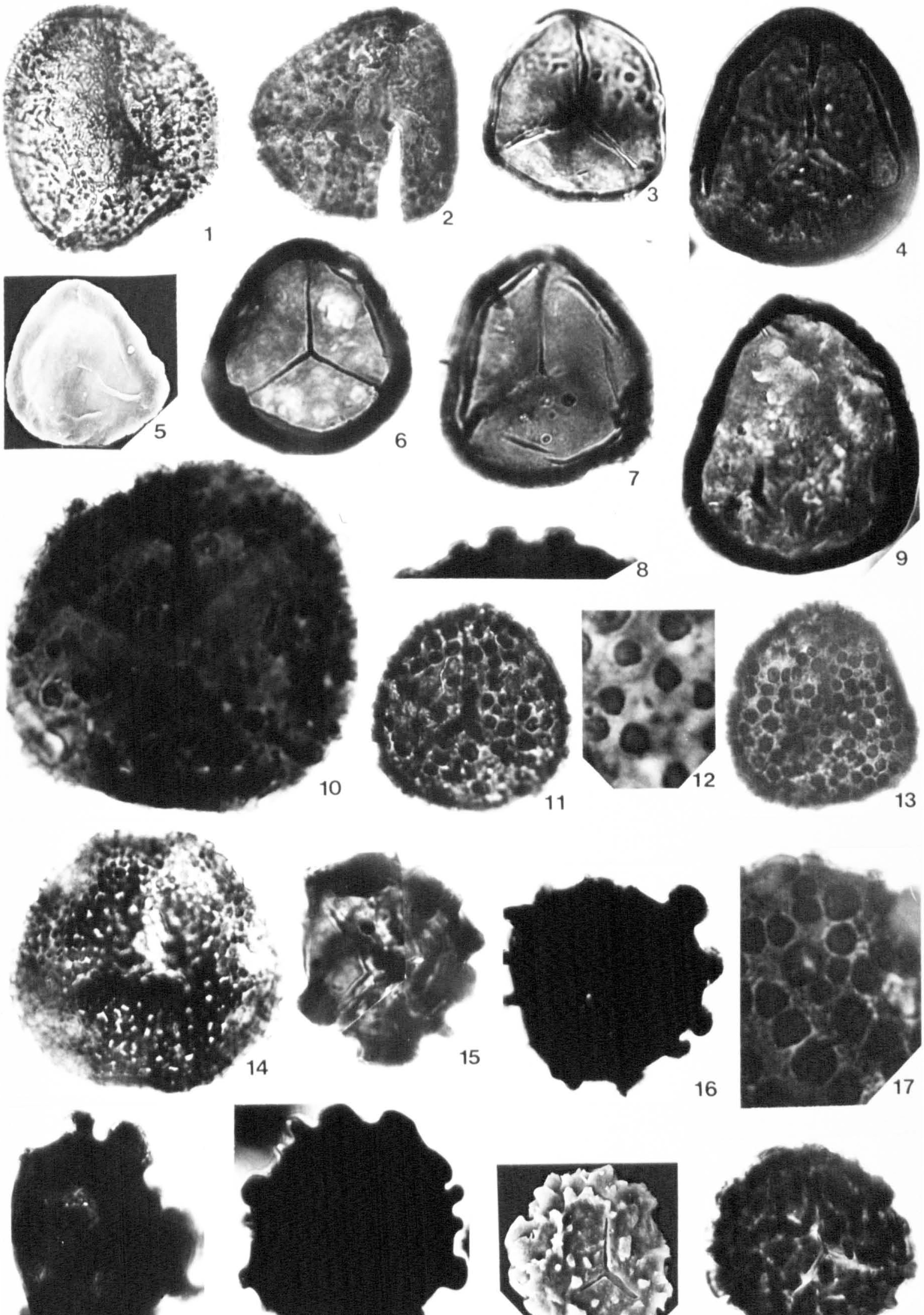


PLATE 3·28

PLATE 3.29

Plate 3.29

Fig. 1 *Verrucosisporites scurrus* (Naumova) McGregor & Camfield, 1982; S14 (a) 148.5/9.1.

Fig. 2 *Verrucosisporites scurrus* (Naumova) McGregor & Camfield, 1982; WP02 (a) 141.6/19.3.

Fig. 3 *Verrucosisporites scurrus* (Naumova) McGregor & Camfield, 1982; CM28 (a) 156.2/9.5.

Fig. 4 *Verrucosisporites tumulentus* Clayton & Graham, 1974; ornament transitional to *V. scurrus* (Naumova) McGregor & Camfield, 1982; S08 (a) 153/20.2.

Fig. 5 *Verrucosisporites tumulentus* Clayton & Graham, 1974; CM42 (a) 144.5/11.2.

Fig. 6 *Verrucosisporites tumulentus* Clayton & Graham, 1974; CM02 (a) 160.2/3.1.

Fig. 7 Spore Type A; S20 (a) 142.5/5.5.

Fig. 8 *Diaphanospora reticulata* Guennel, 1963; M44 (a) 138.9/8.1.

Fig. 9 *Diaphanospora reticulata* Guennel, 1963; M42 (a) 156.2/16.7.

Fig. 10 *Diaphanospora reticulata* Guennel, 1963; three layered wall structure discernible (outer layer indicated), x2300; M40 (a) 146.8/9.1.

Fig. 11 *Diaphanospora reticulata* Guennel, 1963; indicated thin, diaphanous third layer; M38 (a) 136.8/10.2.

Fig. 12 *Diaphanospora reticulata* Guennel, 1963; M44 (a) 130.5/7.9.

Fig. 13 Spore Type B; M42 (a) 149.8/7.2.

Fig. 14 Spore Type B; M35 (a) 140.3/19.4.

Fig. 15 Spore Type B; proximal view; M42 (a) 146.5/15.2.

Fig. 16 Spore Type B; distal view of Fig. 15; M42 (a) 146.5/15.2.

Fig. 17 Spore Type B; M02 (a) 147.2/6.1.

Fig. 18 Spore Type C; M18 (a) 139.9/11.2.

Fig. 19 Spore Type C; M42 (a) 146.5/15.4.

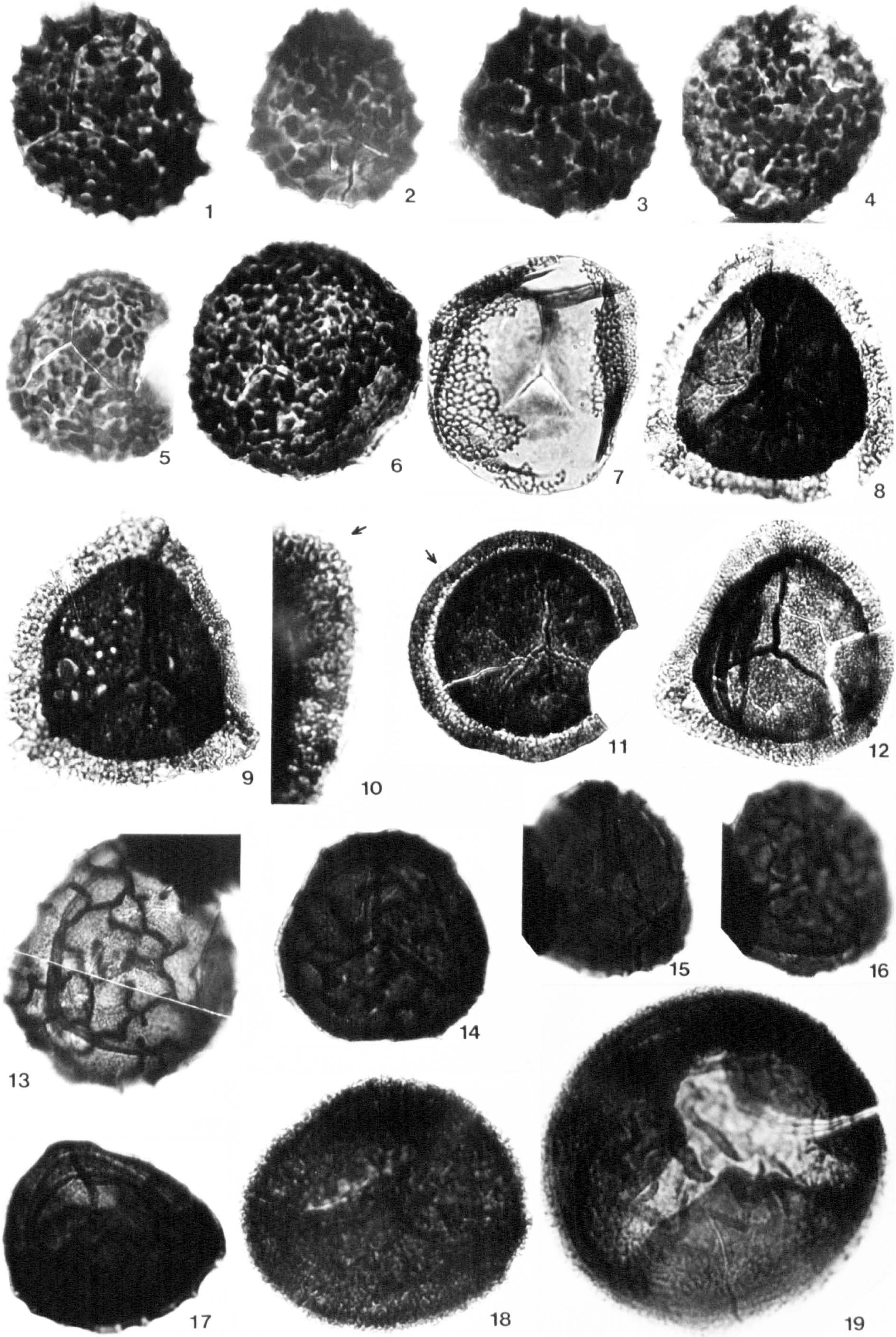


PLATE 3·29

All forms of acritarch and chitinozoa isolated from north Devon are described below, and representative specimens illustrated, coupled with a selection of the scolecodont and "wood" types also recovered. For the microplankton and chitinozoa described below, details of occurrence are provided in Table 4.3 of Chapter 4. Appendix II details the occurrence of scolecodonts (undifferentiated), as well as cataloguing the various "wood" types present in each sample.

ACRITARCHS.

The following systematic section details those identifiable components of the acritarch flora routinely recovered in palynological analyses. In addition to the forms documented below, fragments ?referable to the *Veryhachium*, *Diexallophasis*, *Micrhystridium* and *Multiplicisphaeridium* complexes were recorded in many of the samples studied. The poor preservation of these specimens coupled with their limited stratigraphic utility did not warrant their inclusion in the following section. Only relatively well preserved specimens, and/or those noted in comparative numbers are described systematically below. This may account for any discrepancy between recorded presence within a particular sample (as listed in Appendix II) and species occurrence as tabulated in Table 4.3.

Many authors still favour the presentation of acritarch systematics according to "subgroupings". However, Loeblich (1970) adopted a more utilitarian approach in the alphabetical ordering of Palaeozoic acritarch taxa. In view of the limited numbers of microplankton recovered in the present study, and also to conform with the format of the miospore systematics, the following acritarch systematics are presented alphabetically by genera (Note: the following systematics do not differentiate between the informal *incertae sedis* group "Acritarcha", and forms affiliated with the Division Prasinophyta (formerly part of the Chlorophyta), *e.g.* *Cymatiosphaera*, *Dictyotidium*, *Polyedryxium*, and *Maranhites*). Specimens are described using terminology currently in widespread use (for example, refer to Playford 1977, p. 9-10). The principal descriptive terms applied in the present study are shown by Figure 3.3.1. Comprehensive synonymy lists are not provided (refer to Section 3.1 herein).

Genus *Cymatiosphaera* O.Wetzel ex Deflandre, 1954.

Type species. *Cymatiosphaera radiata* O.Wetzel (1933), by subsequent designation of Deflandre, 1954.

Cymatiosphaera reticulosa (Kirjanov) Colbath

Plate 3.30, figs. 2-4; Plate 6.3, fig. 11.

1978 *Cymatiosphaeropsis reticulosa* Kirjanov, p. 32-33, Pl. 7, fig.6.

1983 *Cymatiosphaera reticulosa* (Kirjanov) Colbath, p. 253-254, figs. 16-20, 24-28.

1986 Unidentified, in Turnau, Pl. II, fig. 10.

1986 *Cymatiosphaera reticulosa* (Kirjanov) Colbath, in Wicander p. 335, Pl. II, figs. 1-4.

? 1988 *Dictyotidium* sp. A, in Ravn & Benson, Pl. 7, fig. 2.
1988 *Dictyotidium* sp. B, in Ravn & Benson, Pl. 7, fig. 3.

Description. Circular to subcircular vesicle; wall appears robust, laevigate, scabrate, occasionally infrapunctate or infragranulose, and excluding sculpture ranges in equatorial thickness from ≤1.5μm to 3.75μm. The surface is regularly divided into numerous polygonal to subcircular imperforate lacunae, 4-15μm in diameter (usually 6-9μm): ≈uniformly covering each hemisphere. Each lumina is delineated by thin, straight to openly sinuous muri, which appear laevigate, robust and/or in part membraneous: ≤0.5-1.75μm in basal width and ≤2.25μm in height. Approximately 35 to 50 complete lumina adorn each hemisphere. Muri become increasingly diffuse or thin midlength, unlike the points of intersection which are usually marked by a subtriangular to well rounded verrucae or blunted coni; typically rounded, rarely pointed in profile, ranging between 2.5-6μm in diameter (generally 3.5-4.25μm). Only very occasionally are the junctions of the muri simple. The floors of the lacunae appear gently concave, and may be ornamented with grana ≤0.75μm in diameter. Very occasionally a faint, secondary, diminutive reticulum may just be distinguished covering the floors of the larger lacunae: "subordinate" lumina ≤1-2μm in diameter. Excystment structure not observed. The vesicle walls are rarely folded.
Dimensions. Maximum vesicle diameter 41-89μm, mean 64 (15 specimens measured).

Occurrence. WP; *rare.* R, S, LH, CM, M; *very rare.*

Remarks. The subdued, low and robust nature of the muri is more reminiscent of *Dictyotidium* than of *Cymatiosphaera.* Future rationalisation of this species may confirm that it would be more appropriately attributed to *Dictyotidium.*

Wicander (1986, p. 335) details quite considerable variability in the character of the vesicle wall within each lacuna; encompassing second-order reticulate sculpture, grana and imperforate tubular canals. Such variability in lacunal morphology proved difficult to resolve on the specimens recovered from north Devon. Indeed the lacunal floors usually appeared simple-scabrate, to finely granulose, although the development of the muri did prove highly variable, ranging from pronounced to indistinct.

The scarcity of this morphotype in north Devon suggests that this species is reworked into the study area, particularly as previous reports of this taxon are from rocks of much older age.

Comparisons. The gross morphology of *Cymatiosphaera reticulosa* (Kirjanov) Colbath resembles a number of species of *Dictyotidium, e.g. Dictyotidium dictyotum* (Eisenack) Eisenack in Dorning (1983; Pl. 6, fig. 5). However, the nodal elements at the intersections of the muri appear somewhat more pronounced on *Cymatiosphaera reticulosa* (Kirjanov) Colbath. Such distinctions may prove difficult to sustain (being somewhat trivial), and as suggested earlier this species may more appropriately be circumscribed by *Dictyotidium.*

Refer also to the comparisons of *Cymatiosphaera* cf. *reticulosa,* below.

Known geologic range. Ludlow - Lockhovian; Kirjanov (1978) & Colbath (1983). Lower Devonian of the Haragan Formation, Oklahoma, U.S.A.; Wicander (1986).

Cymatiosphaera cf. *reticulosa* (Kirjanov) Colbath
Plate 3.30, fig. 5.

Dimensions. Maximum vesicle diameter 64μm, 63μm (2 specimens measured).

Occurrence. LN, H; *very rare.*

Remarks. Specimens closely resemble *C. reticulosa* described above, but differ in displaying a markedly thinner, more intensely distorted and ruptured vesicle wall (≤0.75μm in thickness), and a finer reticulate sculpture (muri more diffuse, transparent and seemingly membraneous, ≤2.25μm in width). The nodes where the muri converge are also less well defined. The vesicle wall appears slightly more granulose or infrapunctate, and may display a number of cryptosutures.

Comparisons. Both *Cymatiosphaera brevicrista* Wicander (1974) and *C. parvicarina* Wicander (1974) from the Upper Devonian-Mississipian of Ohio display fewer lumina per hemisphere, which are delineated by somewhat more robust muri. Wicander & Loeblich (1977) formally describe *Cymatiosphaera cavea* from the Upper Devonian Antrim Shale of Indiana, U.S.A: this species ranges in size from 48-74μm, appears similarly thin-walled and with a vesicle divided into numerous fields per hemisphere. However, the excystment structure is different, and the muri appear far more diffuse (≤1μm). Furthermore the surface of the lacunae in *Cymatiosphaera cavea* are reticulocristate, where subordinate, diminutive muri interconnect forming a network of tiny polygonal fields.

Cymatiosphaera sp.
Plate 3.20, fig. 1.

Description. Hollow vesicle; subcircular, ovate, to polygonal in outline. The wall is ≤1.5μm thick and rarely folded. The vesicle surface appears laevigate to scabrate, and is differentiated into broad lumina by straight to arcuate, robust to flexuous, optically dense muri. Individual muri range in width from 1.75μm to 4μm, and from 3μm to 9μm in height (usually 5μm), defining polygonal, rarely subrounded lacunae: usually ≤15-20μm in diameter. The floors to the lacunae are gently concave or convex. One to three (rarely four) distinct, complete laevigate lacunae extend over each hemisphere. The muri project from the vesicle circumference, and in cross-section resemble stout, tapering coni, commonly ≤5μm in height. These muri may thin, resembling diaphanous membranes developed perpendicular to the vesicle wall.

Dimensions. Maximum vesicle diameter (excluding murornate sculpture) 42-66μm, mean 57μm (6 specimens measured).

Occurrence. K; *very rare.*

Comparisons. *Cymatiosphaera antera* Wicander & Loeblich (1977) differs in the arrangement of the muri over each hemisphere of the vesicle (arranged in the shape of the letter "H"). The miospore *Dictyotriletes flavus* Keegan (1977) bears a superficial resemblance to this acritarch, but *Cymatiosphaera* sp. (above) lacks a distinct trilete mark.

Genus *Dateriocradus* Tappan & Loeblich, 1971.

Type species. *Dateriocradus polydactylus* Tappan & Loeblich, 1971; by original designation.

Dateriocradus sp.

Plate 3.30, fig. 6.

Description. Vesicle subcircular to convex-triangular in outline; thick walled ($\leq 2\mu m$) and laevigate to faintly granulose. Robust, straight to openly flexed processes develop from the apices of the vesicle: $\leq 5.5\mu m$ in basal diameter and tapering gradually to a simple or bifurcate tip. Processes are $\leq 33\mu m$ in length, freely communicating with the vesicle interior and may display a faint, striated ornament at the junction with the vesicle. Excystment is uncertain: an equatorial cryptosuture was noted on one of the specimens.

Dimensions. Maximum vesicle diameter, $25\mu m$ and $29\mu m$ (2 specimens).

Occurrence. R; *very rare.*

Remarks. The scarcity of such specimens suggests that their occurrence is probably reworked.

Comparisons. The concept of *Ozotobrachion furcillatus* (Deunff) Playford 1977 encompasses far greater variability in vesicle and process morphology. More significantly, the processes are plugged proximally, and the vesicle wall ornamented (note the superficial homology with *Ozotobrachion furcillatus* (al. *dicros*) as figured by Loeblich & Wicander, 1976; Pl. 7, fig. 8).

Genus *Dictyotidium* Eisenack emend. Staplin, 1961.

Type species. *D. dictyotum* (Eisenack) Eisenack, 1955; by original designation.

Dictyotidium cf. *cohora* Wicander & Wood.

Plate 3.30, figs. 11, 12; Plate 6.3, figs. 9, 10.

cf. p 1973 *Dictyotidium dictyotum* (Eisenack) Eisenack in Legault, p. 52, Pl. XI, fig. 8 (only).
cf. 1981 *Dictyotidium cohora* Wicander & Wood, p. 21, Pl. 1, figs. 8-10.
1988 *Dictyotidium* sp. cf. *D.cohora* Wicander & Wood, in Ravn & Benson, p.197, Pl.7, figs.5,6.
Refer to Wicander & Wood (1981, p. 21) for additional synonymy.

Description. Vesicle circular, subcircular to ovate in outline; appears relatively thick walled, laevigate, rarely finely scabrate and robust in appearance. The vesicle wall appears $\leq 1.5\text{-}2\mu m$ thick equatorially and generally lacks secondary folds. The vesicle surface is divided into a regular, relatively uniform reticulum; the variation in lacunae outline and size may be quite marked between specimens but uniform upon one individual. Lumina are subcircular to rounded polygonal in outline, are five to six sided and defined by low, narrow, straight to arcuate muri: 1.25-3.75μm broad at their base, ≤1-2.5μm high with rounded crests. At the vesicle margin, the muri resemble squat bacula or coni in lateral profile, and are ≤2μm in dimensions. In general the muri appear comparatively thick and robust, and may be ?compressionally broadened. The floors of the lacunae are gently concave, laevigate to finely scabrate. The maximum diameter of the lumina varies between 8μm and 17μm (rarely less than 6μm, and on average 9.5-14μm). Twelve to fifteen discrete lumina cover each hemisphere (rarely exceeds eighteen). Excystment is uncertain; occasional cryptosutures noted.

Dimensions. Vesicle diameter 39-58μm, mean 51μm (35 measurements).

Occurrence. S, LH, WP; *rare.* LN, H, R, L, K, M; *very rare.*

Remarks. The population of *Dictyotidium cohora* recovered from north Devon is similar to the specimens documented by Ravn & Benson (1988) from southwestern Georgia, in being somewhat smaller than the original complex of *D. cohora* described by Wicander & Wood (1981; 66-79μm) from the Silica Formation, Ohio, U.S.A. Specimens from north Devon are identical to that illustrated by Ravn & Benson (1988).

Comparisons. *Cymatiosphaera magnata* Pilcher (1971) displays a rounded "knot" located subcentrally on the floor of each lumina. *Dictyotidium cohora* differs to *Cymatiosphaera labyrinthica* Wicander (1974) in displaying a laevigate to slightly textured (scabrate) vesicle surface. *Muraticavea munificus* Wicander & Wood (1981, p. 24-25) is larger (72-103μm) and displays fewer, larger fields per vesicle hemisphere.

Dictyotidium cf. *cohora* differs from *Dictyotidium* sp. A (of the present study) in being somewhat larger, but more significantly in displaying fewer fields per vesicle hemisphere. ?*Dictyotidium* sp. B (herein) bears thinner, more membraneous and sinuous muri.

Known geologic range. *Dictyotidium cohora* has been reported from the Givetian of southwestern Ontario (Hamilton Formation; identified as *D. dictyotum* by Legault, 1973), and was defined on specimens recovered from the Givetian of Ohio (Silica Formation), by Wicander & Wood (1981). Ravn & Benson (1988) noted *Dictyotidium* cf. *cohora* from an unnamed subsurface Devonian unit of Emsian/Eifelian age in southwestern Georgia (U.S.A).

Dictyotidium cf. *polygonium* Staplin

Plate 3.30, fig. 15.

cf. 1961 *Dictyotidium polygonium* Staplin, p. 417, Pl. 49, fig. 14.

cf. 1983 *Dictyotidium polygonium* Staplin, in Le Herissé, p. 56, Pl. 10, fig. 5, a-b, 10.

Description. Vesicle subcircular to ovate in outline; wall laevigate to finely scabrate and relatively thin, ≤1-2μm equatorially. The surface is divided fairly uniformly into numerous, distinct, regular lacunae; circular, subcircular to ovate in outline, rarely polygonal. These lumina are defined by thickened (optically dense), arcuate (rarely straight), laevigate muri; ≤0.5-2μm in basal width and height (rarely range up to 3μm). The muri commonly thin midlength; in profile appear subdued, rarely attenuate or pointed, with simple-rounded crests. Lacunae are variable in number (between *ca.*45 and 70 per hemisphere), and ranging in diameter from 2μm to 5μm (rarely greater than 7μm). A single, distinct granule (≤1-1.5μm in diameter) may be distinguished, central within each lacunae. Alternatively this central region may merely display a diffuse opaque "spot", ≤1-3μm in diameter; conversely may lack any form of wall modification. In general the lacunae appear slightly concave outwards. Excystment is by the simple splitting of the vesicle wall (?cryptosuture).

Dimensions. Maximum vesicle diameter 44μm-52μm, mean 48μm (3 specimens measured).

Occurrence. S; *very* rare.

Remarks. The specimens documented from sample S14 (the present study) were similar in size to the larger specimens described by Le Herissé (1983) from the Lower Devonian of the Laval Syncline, Massif Armoricain (which ranged up to 48μm in diameter). The population of *Dictyotidium polygonium* identified by Staplin (1961) from the Upper Devonian of Alberta (Canada), were however somewhat smaller, ranging between 27μm and 31μm in diameter. The dimensions of the lacunae noted for the specimens recovered from north Devon were slightly larger than perceived typical for *Dictyotidium polygonium* by Staplin (1961).

Comparisons. *Dictyotidium variatum* Playford (1977, p. 18-19; note synonymy with *D. legionis* in Le Herissé, 1983, p. 56) is similar, but lacks any sculptural modification to the floors of the lacunae. Playford & Dring (1981, p. 45-46) described *Melikeriopalla venulosa* from the Late Devonian of the Carnarvon Basin, Western Australia. This forms bears a superficial resemblance to *Dictyotidium polygonium* in displaying a regular, structured reticulum, but is smaller (26-33μm) and the lacunae floors bear an irregular, dendritic ridged sculpture, which tend to radiate from the centre of each field. *Dictyotidium legionis* (Cramer) Le Herissé (1983, p. 56-57) displays a simplistic reticulum with subtle projections emanating from the points at which the muri converge; the lacunae are simplistic, unmodified.

Recently Steemans (1989; p. 116, Pl. 28, fig. 6-9), proposed *Chelinospora baculoreticulata* from Gedinnian to Siegenian strata of Belgium. This trilete miospore is of similar size (37-60μm) and also exhibits a comparable sculpture.

Known geologic range. Upper Devonian (Frasnian, Woodbend Formation, central Alberta, Canada; Staplin, 1961). Lower Devonian (Le Herissé, 1983; Massif Armoricain, France).

Dictyotidium sp. A
Plate 3.30, figs. 8, 9.

Description. Vesicle subtriangular, subcircular to well rounded; vesicle wall thin, ≤?1-2μm. Each hemisphere is divided into numerous, irregular, polygonal to subcircular lacunae; maximum diameter of individual lumina commonly 4-7.5μm (rarely less 3μm). Each lacunae is delineated by straight to slightly sinuous, subdued muri, 0.5-1.75μm in width and height; commonly thin midlength and may thicken at the points where the muri merge, ranging up to 4.25μm in width. Such thickened junctions are rare and occasionally bear a singular, diminutive cona or verruca, ≤2.5μm in height; may project visibly from the vesicle margin. The crests of the muri tend to be rounded, with the floors of the lacunae imperforate, concave outwards and scabrate to faintly granulose in texture. In well preserved specimens, this faint granulose "ornament" may appear ordered, resembling diminutive vermiculate "ridges". Collectively, the lacunae define a fairly regular reticulum. 30 to 45 lumina extend over each hemisphere. Excystment is uncertain; cryptosutures rare.

Dimensions. Maximum vesicle diameter 36-56μm, mean 46μm (10 measurements).

Occurrence. LN, S, WP, K, CM; *very rare.*

Remarks. Rare compressional folds were noted, concentric with the equatorial margin.

Comparisons. *Dictyotidium craticulum* (Wicander & Loeblich) Wicander & Playford (1985, p. 105) is substantially smaller in overall diameter (24-29μm), bearing a much finer reticulum comprising lacunae 2.2-3.1μm in diameter. Although *Dictyotidium torosum* Playford & Dring (1981, p. 23-24) is similar in overall vesicle dimensions (39-59μm), this species is thicker walled (1.6-4μm thick), and the reticulum appears much finer (individual lacunae range from 0.5μm to 3.5μm in maximum diameter).

Dictyotidium sp. A differs from *D.* cf. *cohora* (of the present study) in displaying a denser reticulum.

?*Dictyotidium* sp. B.
Plate 3.30, fig. 10, 14.

Description. Vesicle circular, subcircular to ovate in outline; wall is laevigate to faintly scabrate, ≤1.5μm thick equatorially and displays an irregular to uniform reticulum. This reticulum comprises nine to fourteen equidimensional, pentagonal to hexagonal lacunae per hemisphere, which range from 7μm to 12μm in diameter; are defined by thin, flexuous, diaphanous muri, ≤1.75-3.5μm in height and ≤1 in basal width. These muri are laevigate, tend to thin midlength and thicken at points of convergence (rarely exceed 2.5μm in width). The muri are distally "ragged", and sinuous in plan view. The lacunae floors are laevigate, occasionally finely scabrate and slightly convex outwards. Method of excystment not observed.

Dimensions: Vesicle diameter 40μm, 46μm (2 specimens).

Occurrence. R, S; *very rare.*

Remarks. The membraneous, flexuous appearance to the muri suggests a possible assignation to *Cymatiosphaera* O. Wetzel ex. Deflandre (1954).

Comparisons. *Cymatiosphaera chelina* Wicander & Loeblich (1977, p. 137) is similar in size and overall appearance, but differs in the structure of the lacunae floors, which appear scabrate to reticulocristate. This form is closely related to *D.* cf. *cohora* defined above, but varies in the thinner more membraneous nature to the muri, and the slightly fewer number of fields per hemisphere.

Dictyotidium sp. C.
Plate 3.30, fig. 13.

Description. Vesicle circular to subcircular; wall thin, $\leq 1\mu m$ thick equatorially and lacking folds. The surface is divided fairly regularly into well defined, polygonal lacunae: 5-6 sided, and defined by low, thin, membraneous muri, $\leq 1.75\mu m$ in basal width and $\leq 2\mu m$ in height. These muri are straight, rarely arcuate, with smooth or ragged crests, and in profile appear narrow, transparent, and attenuate. Lacunae are variable in number, ranging between nine to sixteen per vesicle; also of highly variable size (16-25μm in maximum diameter). The lacunae floors appear straight or slightly convex outwards, and generally laevigate to very faintly scabrate (lack any pronounced surficial sculpture). Excystment (rarely noted) is by the simple splitting of the vesicle wall.

Dimensions. Maximum vesicle diameter (excluding murornate sculpture) 36-43μm (6 specimens measured).

Occurrence. R, S; *very rare.*

Comparisons. In terms of gross morphology, some of the specimens figured by Playford & Dring (1981) as *Dictyotidium granulatum* resemble *Dictyotidium* sp. C described in the present study (*e.g.* Pl. 5, fig. 8). However, *Dictyotidium* sp. C differs primarily in lacking a distinct, granulose surficial sculpture to the vesicle wall.

Genus *Diexallophasis* Loeblich, 1970.

Type species. *Diexallophasis denticulata* (Stockmans & Willière) Loeblich, 1970.

Diexallophasis denticulata (Stockmans & Willière) Loeblich.
Plate 3.31, figs. 1, 4.

1963 *Baltisphaeridium denticulatum* Stockmans and Willière, p. 458, Pl. 1, fig. 4, text-fig. 13.
1970 *Diexallophasis denticulata* (Stockmans & Willière) Loeblich, p. 715-716, figs. 8A-E, 9A-C.
1973 *Multiplicisphaeridium denticulatum* (Stockmans & Willière) Eisenack & Cramer, p. 587-

603, 653.

1986 *Diexallophasis denticulata* (Stockmans & Willière) Loeblich, in Wicander, p. 340, 341, Pl. IV, fig. 3.

1988 *Diexallophasis denticulata* (Stockmans & Willière) Loeblich, in Ravn & Benson, p. 197, Pl. 7, fig. 18.

Description. Vesicle circular, subcircular to polygonal in outline. The wall appears notably thin (usually <0.25-0.75μm in thickness), scabrate to finely granulose (rarely homogeneous-laevigate), and commonly folded where the processes join with the vesicle. Five to eight, generally broad, hollow, essentially homomorphic processes adorn the vesicle; ranging in length from <15μm to 43μm, with the diameter of the bases 3-9.25μm (subcircular to ovate in outline). Area of (proximal) attachment rounded-angular: the processes freely communicate with the vesicle interior and appear comparatively even in their distribution ≤7-15μm apart. Despite being thin walled, the processes are comparatively robust, straight or only slightly flexed, having parallel-sided or tapering gradually to a (rare) simple or multifurcate distal termination (commonly with second to third order branching; digitate). The shafts bear a moderate to dense cover of distinct, relatively coarse, angular grana and diminutive echinae (ranging up to 2.25μm in width and height). This surficial ornament ranges between <1μm to 3.75μm apart (rarely exceeds 5μm). Excystment (rarely seen) is by the simple splitting of the vesicle wall (cryptosutre).

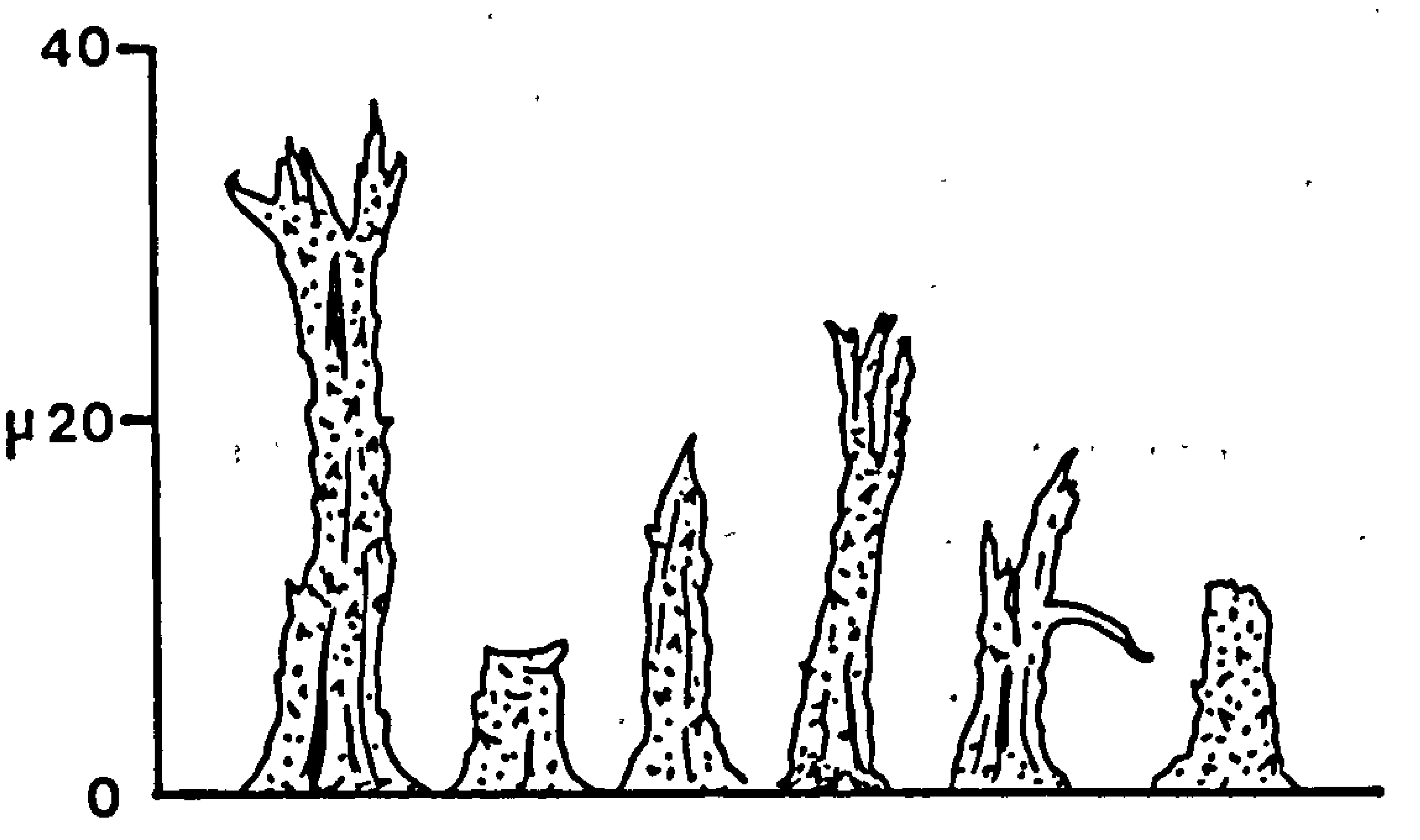


Figure 3.3.119: Process morphology of *Diexallophasis denticulata,* lateral view.

Dimensions: Maximum vesicle diameter 22-33μm, mean 29μm (5 specimens).

Occurrence. LN, S; *very rare.*

Remarks. The processes and vesicles of both *Diexallophasis denticulata* and *D.remota* are frequently ruptured and fragmented, and due to poor preservation the processes commonly appear blunted.

The criteria noted by Wicander (1986, outlined below) for differentiating *D. denticulata* from *D. remota* was evaluated and applied in the present study, and confirmed that these two species should be treated as distinct.

Comparisons. Further to the rationalisation of Playford (1977, p. 19-21), Wicander (1986, p. 340-

342) amongst others, maintains *Diexallophasis denticulata* and *D. remota* as discrete species. Although morphologically similar, these two species are differentiated on the basis of wall thickness, and the size and density of the surficial sculpture. According to Wicander, *D. denticulata* is thinner walled (<0.5μm) and the echinate ornament somewhat larger and more densely packed. In general, the processes of *Diexallophasis denticulata* appear coarse and broad, whereas those of *D. remota* are seemingly more slender.

Species of the *Evittia* Brito (1967a) complex generally display an enlarged, subquadrate, polygonal vesicle, and comparatively stout, subdued apical processes that display less complicated, digitate terminations (*e.g. Evittia cymosa* Loeblich, 1970).

Known geologic range. Ludlow to Middle Devonian; Stockmans & Willière (1963), Cramer (1964), Loeblich (1970), Jardiné *et al.* (1974), Riegel (1974), Playford (1977), Deunff (1980), Kimyai (1983), Wicander (1986).

Diexallophasis remota (Deunff) Playford.
Plate 3.30, figs. 16, 17; Pl. 3.31, 2, 3, 5 (*cf.*).

1955 *Veryhachium remotum* Deunff, p. 146, Pl. 4, fig. 8.
1970 *Evittia remota* (Deunff) Lister, p. 69-70, Pl. 4, fig. 10, 11, 13-15; Pl. 5, fig. 1.
1973 *Mulitplicisphaeridium remotum* (Deunff) Eisenack & Cramer p. 773.
p 1977 *Diexallophasis remota* (Deunff) Playford, p. 19-21, Pl. 6, figs. 12 (only).
1986 *Diexallophasis remota* (Deunff) Playford, in Wicander p. 342, Pl. IV, fig. 1, 2.
non 1988 *Diexallophasis remota* (Deunff) Playford, in Streel *et al.*, Pl. 21, figs. 4, 5.

Description. Vesicle subcircular, ovate, subtriangular to polygonal in outline; wall single-layered, ranging in thickness from 0.75μm to 1.5μm, and appears finely scabrate to granulose (rarely homogenous-laevigate). The vesicle outline is modified by distinct, discrete, hollow and slender, essentially homomorphic processes; range in length from $\leq$10μm to 59μm (rarely less than 15μm, or greater than 50μm - typically 32-42μm). These processes freely communicate with the vesicle interior: may appear straight or somewhat flexible, and are evenly distributed over the vesicle (5-17μm apart; numbering 5-8 per specimen). Processes range in basal width from $\leq$2μm to 7μm (rarely exceed 10μm), appearing subcircular to polygonal in outline; are parallel-sided or taper gradually to a fine, generally bifurcate to multifurcate termination (rarely simple). The proximal attachments of the processes are curved to angular in profile. The distal extremities display first and second order bifurcations (rarely third). These terminations are usually asymmetric and morphologically irregular. In general the shafts of the processes are scabrate, or sparse to densely granulose. This surficial ornament comprises diminutive, distinct to barely perceptible grana, rare echinae, and coni; $\leq$0.75μm in width and height. Towards the base of the shafts, this ornament may appear subaligned, forming a subsidiary, striate sculpture. Excystment (rarely seen) is by the simple rupturing of the vesicle wall; occasionally two cryptosutures may be distinguished.

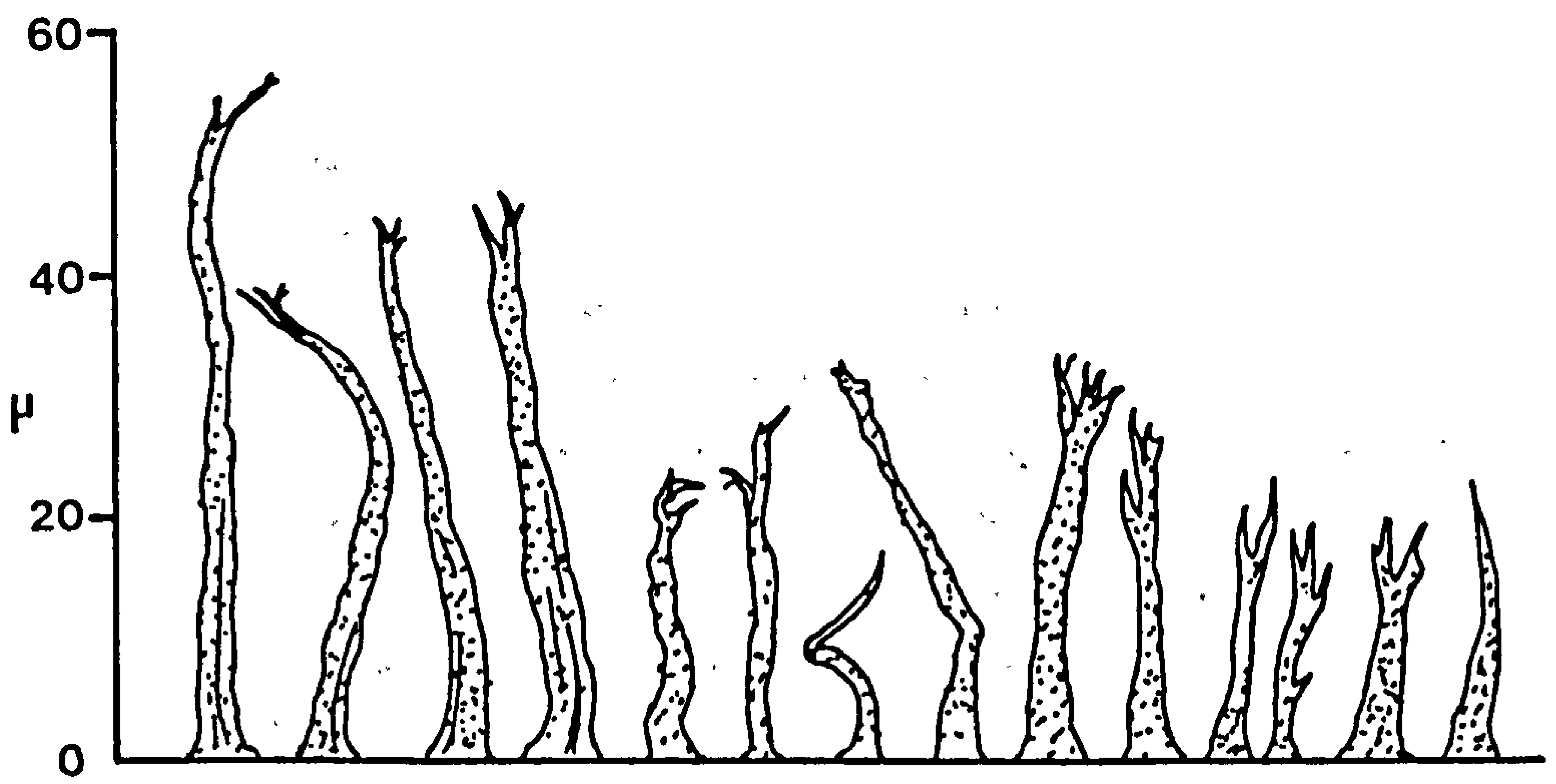


Figure 3.3.120: Variation in process morphology of *Diexallophasis remota*, lateral view.

Dimensions. Maximum vesicle diameter (excluding processes) 17-51μm, mean 33μm (25 specimens).

Occurrence. LN, S; *rare.* R, LH, WP, K; *very rare.*

Remarks. As mentioned earlier, the rationalisation of *Diexallophasis remota* by Playford (1977) has received much criticism. Wicander & Wood (1981, p.33) believe the degree of variability accommodated within Playford's (1977) revised circumscription does not truly represent a single species. Consequently, a more restricted concept of *D. remota* was applied in their study, in preference to the expanded diagnosis of Playford (1977). The approach of Wicander & Wood (1981) is followed herein.

The form identified as *Diexallophasis* cf. *remota* herein (refer to the plate caption: Pl. 3.31, fig. 5) differs from *Diexallophasis remota, sensu stricto* in displaying more elongate, attenuate processes and a substantially thickened (optically dense) vesicle wall: displays regular, equatorially displaced folds. However, the vesicle and more significantly the multifurcate-tipped processes do bear a barely perceptible to distinct granulose ornament, suggesting assignation to *D. remota.*

Comparisons. Wicander (1986, p. 340-342) differentiates *D. denticulata* and *D. remota* according to differential wall thickness, and process morphology/ornament (refer to the comparisons above, *D. denticulata*). Also note the comparisons catalogued by Playford (1977, p. 20-21).

Known geologic range. Ordovician to Late Devonian (Jardiné *et al.*, 1974; Riegel, 1974; Deunff, 1980; Playford, 1977; Vanguestaine *et al.*, 1983; Wicander, 1986; Streel *et al.* (1988 - refer to synoptic figure; Fig. 7, p.120, 121).

Diexallophasis simplex Wicander & Wood.
Plate 3.31, fig. 6.

p 1977 *Diexallophasis remota* (Deunff) Playford, p. 19-20, Pl. 7, figs. 2, 6, & 8 (only).

1981 *Diexallophasis simplex* Wicander & Wood, p. 33-34, Pl. 5, fig. 7; Pl. 6, figs. 1-3.
1985 *Diexallophasis simplex* Wicander & Wood, in Wood & Clendening, Pl. 1, figs. 3, 4.

Description. Vesicle subcircular to convex triangular in outline; wall finely scabrate, granulate to ?infrapunctate, and ≤0.5-0.75μm in thickness. The vesicle outline is modified by 6-7, hollow, cylindrical, homomorphic processes, which freely communicate with the vesicle interior; of comparatively uniform length, ranging between 26μm and 30μm in length, and averaging 4-5μm in basal diameter. The processes are rarely flexed, appearing relatively straight with simple attenuate or blunted terminations (only very occasionally subtly ?bifurcate); the shafts are ornamented with diminutive grana, squat coni and subdued spinae, typically 0.5-1μm in width and height. Excystment is by the simple equatorial splitting of the vesicle wall (cryptosuture).

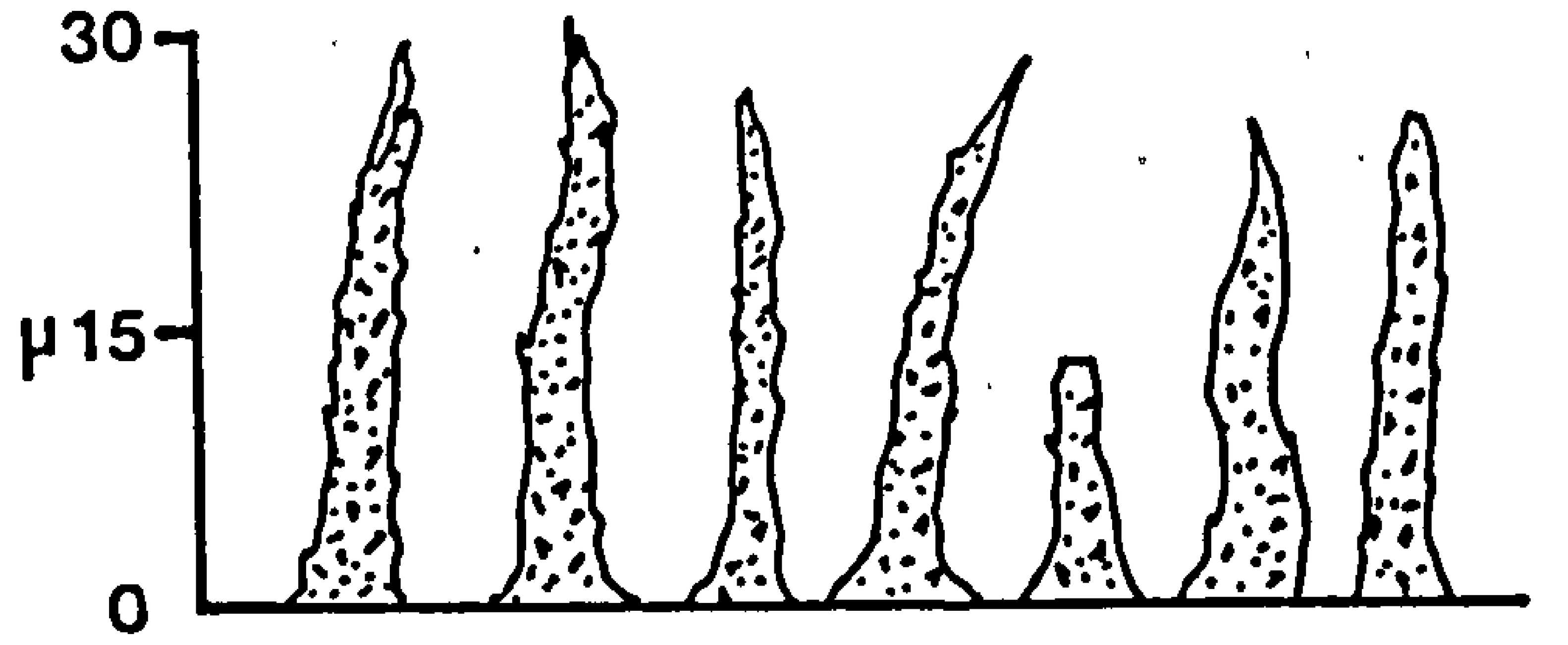


Figure 3.3.121: Processes of *Diexallophasis simplex*, lateral view.

Dimensions. Maximum vesicle diameter 26-39μm, mean 29μm (three specimens).

Occurrence. S; *very rare.*

Comparisons. Wicander & Wood (1981, p. 33) remarked that *Diexallophasis simplex* resembles certain forms assigned by Playford (1977) to *D. remota,* and that the morphological variability circumscribed by Playford's (1977) emended diagnosis was too broad (not truly representative of a single species). *D. simplex* differs to the holotype of *D. remota* (Deunff) Playford (1977) in displaying simple (rather than multifurcate) process terminations: in addition displays a textured vesicle wall. *Costatilobus undulatus* Playford (1977; p.16, Pl. 3, fig. 4-9) exhibits an irregular, granulate to rugulate vesicle sculpture, and narrow, longitudinal, ≈continuous, "blade-like" ridges (?septa - refer to the figured specimen in Ravn & Benson; Pl. 7, fig. 14). The vesicle of *Eisenackidium appendiculum* Wicander & Wood (1981; p. 35-36, Pl. 6, fig. 4; Pl 7, figs. 1, 2) is two-layered, and the processes diaphanous.

Known geologic range. ?Lower/Middle Devonian of the Moose River Basin (Playford, 1977). The Middle Devonian (Givetian) of the Silica Formation, Ohio, U.S.A. (Wicander & Wood, 1981). Wood & Clendening reported this form from the Givetian Boyle Dolomite of Kentucky, U.S.A.

Genus *Gorgonisphaeridium* Staplin, Jansonius & Pocock, 1965.

Type species *Gorgonisphaeridium spicatum* (Staplin) Staplin, Jansonius & Pocock, 1965; by original designation.

Gorgonisphaeridium sp.
Plate 3.31, fig. 9.

Description. Vesicle simple, circular to subcircular in outline; wall laevigate to finely scabrate and commonly displays concentric folds (towards the centre of each vesicle). The wall appears featureless other than displaying an even, moderately spaced sculpture comprising numerous, short, solid, and heteromorphic spinae, granae and baculae; elements ≤0.5-1μm in width and height (rarely exceeds 1.5μm), and 1-3μm apart. When discernible, these elements appear straight, and parallel-sided in profile, displaying curved proximal contacts: commonly taper to an attenuate point, rarely blunted.

Dimensions. 34-41μm, mean 37μm (6 specimens measured).

Occurrence. K; *very rare.*

Comparisons. *Gorgonisphaeridium cumulatum* Playford (1977; p. 22-23, Pl. 8, figs. 12-20) is thicker walled (2-3μm), and bears a coarser, sparser sculpture (1-3.5μm in length and up to 4μm apart). *Gorgonisphaeridium abstrusum* Playford & Dring (1981; p. 33, Pl. 8, figs. 3, 4, 15, 16) displays a similar, diminutive sculpture (≤1.5μm in length), comprising blunted spines and bacula. *Gorgonisphaeridium abstrusum* is substantially smaller in overall diameter (10-27μm), and the sculpture is somewhat denser in distribution.

Genus *Leiosphaeridia* Eisenack, 1958.

Type species. *Leiosphaeridia baltica* Eisenack, 1958; by original designation.

Leiosphaeridia sp.
Plate 3.31, fig. 8.

Description. Vesicle circular to subcircular in outline; morphologically simple. The wall is laevigate to finely scabrate, and ≤1.25μm thick; rarely folded. The wall may display a diffuse, ≈circular thinning ("annulus"), which is ≤1-3μm thick and located 1/3 to 1/2 the vesicle radius from the equatorial margin.

Dimensions. Maximum overall diameter 39-47μm, mean 44μm (10 specimens measured).

Occurrence. LN, S; *very rare.*

Remarks. Many contemporary workers merely mention but rarely describe or indeed illustrate this complex of morphologically simplistic acritarchs; *Leiosphaeridia* are known to have a long stratigraphic range (refer to Wicander & Playford 1985, p. 108; Wicander 1986, p. 346).

Genus *Maranhites* Brito emend. Burjack & Oliveira, 1989.

Type species. *Maranhites brasiliensis* Brito, 1965a, by original designation.

Maranhites gallicus Taugourdeau-Lantz.

Plate 3.31, fig. 14-16.

1968 *Maranhites gallicus* Taugourdeau-Lantz, p. 162, Pl. 13, fig. 9; Pl. 14, figs. 1-3.
1978 *Maranhites brasiliensis* Brito, in Brito, Pl. 1, fig. 9.
1981 ?*Maranhites stockmansii* Martin, p. 24-25, Pl. 4, figs. 10, 14.
1984 *Maranhites stockmansii* (Martin) emend. Martin, p. 25, Pl. 8, figs. 1, 3, 4, 7, & 10.
1988 *Maranhites gallicus* Taugourdeau-Lantz, in Le Herissé & Deunff, p. 127, Pl. 15, fig. 3-6.
1989 *Maranhites stockmansii* (Martin) Martin, in Burjack & Oliveira, p. 54-55, Pl. II, fig. 4-6.

Description. Vesicle oval, rarely approaching subcircular in outline. Two walled: the slight separation of the wall layers only discernible at the vesicle margin. The inner wall appears optically dense (displays an opaque equatorial rim), appears untextured, robust and $\leq$2-5μm thick. The equatorial margin of this inner layer is straight to undulose, or broadly scalloped; modified by rounded and/or subdued "verrucate" projections, $\leq$1.5-3μm in height and $\leq$6μm in circumferential width. The inner margin of the inner wall may be arcuate or openly undulose, rarely highly sinuous/irregular. The outer wall similarly appears robust equatorially, and varies in thickness from $\leq$1-1.5μm (rarely exceeds 2.25μm): is externally laevigate, shagreenate to faintly granulose. In general the two layers are closely appressed, and over the central "polar" regions the vesicle wall may display irregular, radial rugulae. Alternatively, a diffuse, homogeneous or annulate darkening may extend over the central regions of each vesicle "hemisphere". If discernible, at the equatorial margin the separation of the walls is $\leq$0.25-2μm: irregularities in the morphology of the inner and outer walls, coupled with the close proximity of these two layers, may induce partial or complete wall fusion; "vacuoles" develop where the two separate.

Figure 3.3.122: Peripheral structure of *Maranhites gallicus.*

Dimensions. Maximum overall vesicle diameter (including "outer wall") 59-89μm, mean 71μm (9 specimens measurements).

Occurrence. M; *very rare.*

Remarks. *Maranhites stockmansii* (Martin) Martin (1984) is herein considered synonymous with *M. gallicus* Taugourdeau-Lantz (1968); the latter species assuming taxonomic priority. Of the specimens recovered from north Devon, the thickness of the vesicle wall proved highly variable. The thin wall structure noted by Martin (1981) for *M. stockmansii* (refer to the holotype of *M. stockmansii* Martin, 1981; Pl. IV, fig. 14) was observed for some specimens recovered in the present work (*e.g.* Pl. 3.31, fig. 16); considered a morphological variant of *M. gallicus, sensu stricto.*

Specimens of *M. gallicus* recovered from north Devon are slightly smaller than the size specifications reported by Le Herissé & Deunff (1988) from the late Givetian/middle Frasnian strata of Ferques, Boulonnais - France. In terms of dimensions, the material from Devon is in fact more compatible with the specifications of *M. stockmansii,* as noted by Martin (1981; 67-90μm x 54-70μm).

All specimens lacked pronounced compressional folds.

Comparisons. *Maranhites mosesii* (Sommer) Brito (1967a), *M. pulcher* Brito (1967a) and *M. insulatus* Burjack & Oliveira (1989) display pronounced subcircular to circular thickenings towards the vesicle margin. *Maranhites brasiliensis* (Brito) Burjack & Oliveira (1989) is similar to *Maranhites stockmansii* (Martin) Martin (1984), although it differs in the construction of the inner vesicle wall (which appears distinctly scalloped on both the inner and outer margins). The holotype of *Maranhites magnus* Burjack & Oliveira (1989; Pl. III, fig. 10) bears coarser, more bulbous, and enlarged verrucae around the inner wall margin. However, the paratypes of *M. magnus* figured by Burjack & Oliveira (1989; Plate III, figs. 11, 12) display a wall structure approaching that of *Maranhites stockmansii.* The equatorial outline of *Maranhites primus* Burjack & Oliveira (1989) is far more irregular, displaying angular projections.

Known geologic range. *Maranhites gallicus* was first described by Taugourdeau-Lantz (1968) from the les Schistes de Beaulieu (reportedly of early Frasnian age). Recently *M. gallicus* has been recorded by Le Herisse & Deunff (1988) from the Formation de Beaulieu (of early to middle Frasnian age), Ferques, Boulonnais - France.

Maranhites stockmansii was reported from early Famennian sediments on the southern margin of the Dinant Basin, Belgium (Martin 1981). Burjack & Oliveira (1989) documented *M. stockmansii* from subsurface Devonian strata (Givetian-Upper Frasnian), of the Serra da Petrovina region, Brazil.

Maranhites perplexus Wicander & Playford

Plate 3.31, figs. 10-13.

? 1977 *Maranhites* sp. in Coquel, Loboziak, Stampfli, & Stampfli-Vuille, Pl. 1, fig. 16.

1985 *Maranhites perplexus* Wicander & Playford, p.110, Pl. 3, figs. 11A-B, 12.

1989 *Maranhites perplexus* Wicander & Playford, in Wilkinson & Knight, Fig. 2(7).

Description. Vesicle hollow; circular, subcircular to subovate in outline (rarely subpolygonal), comprising two distinct layers. The inner wall appears comparatively thick, robust (optically dense), with a well developed crenulate margin; is $\leq$2.5μm in thickness, laevigate to ?faintly scabrate and is rarely folded. In the equatorial plane, the inner layer is irregular, undulose, and with 15-22 hollow projections; $\leq$3-5.5μm in width and height. These elements are broad proximally, with subrounded to subangular vesicle attachments; may appear parallel-sided or taper to an irregular, simple-rounded or blunted distal termination (resemble elongate verrucae, or squat bacula). A thin, in part closely appressed, diaphanous (relatively transparent) outer layer partially or entirely encloses this thickened inner wall. This layer is ≤0.25-5μm thick and appears scabrate to faintly granulose. The close appression of these two layers on the main body of the vesicle may produce a faint, radially striated and/or shagreenate texture (this "sculpture" radial about a ±darkened vesicle centre). Conversely (and more typically) the vesicle may merely appear faintly scabrate. The outer layer is seldom preserved in its entirety, commonly projecting from the vesicle margin as an irregular, "torn, equatorial flange"; this incomplete membraneous layer may project up to 11μm from the margin of the inner wall. The two layers are clearly attached along the distal extremities of the circumferential "verrucae": delineated by opaque digitations radiating out from the tips of these elements.

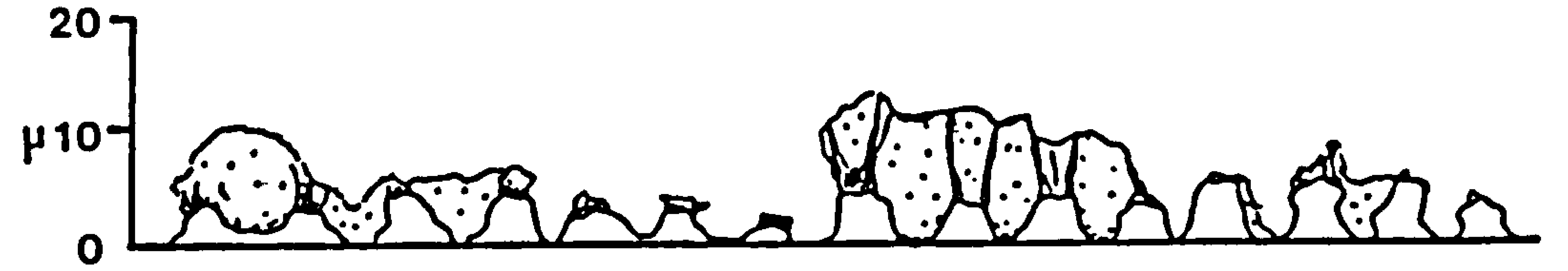


Figure 3.3.123: Peripheral structure of *Maranhites perplexus*.

Dimensions. Vesicle diameter (excluding the circumferential projections and outer membraneous layer) 42-64μm, mean 51μm (20 specimens measured).

Occurrence. M; *rare.*

Remarks. Stockmans & Willière (1969; p. 44-45, Pl. II, figs. 4, 7) proposed an early Famennian species of *Maranhites*, namely *Maranhites britoii*, which displays a virtually identical morphology to that of *Maranhites perplexus* Wicander & Playford. Indeed this homology was remarked upon by Wicander & Playford (1985), although they justified the establishment of *M. perplexus* based upon the disparity in size (*M. perplexus* being consistently smaller, 40-65μm, vs. ≈75μm of *M. britoii*). The population of this morphotype recovered in the present study compare favourably with the size range of *Maranhites perplexus* as defined by Wicander & Playford (1985): furthermore bear a strong resemblance to the (non-holotype) specimen figured by Wicander & Playford (1985; Pl. 3, fig. 12). Future reports may describe intermediates in size between the two species concepts defined by Stockmans & Willière (1969) and Wicander & Playford (1985). Subsequently these two species may prove synonymous; *M. britoii* Stockmans & Willière will assume taxonomic priority.

Wicander & Playford (1985) remarked upon the frequent fragmentation, or "sloughing off", of the outermost membraneous layer. A similar feature was reported within the population of *M. perplexus* recovered from north Devon (remnants of the outer wall were often only visible along the distal extremities to the peripheral "verrucae"). Quite often the texture of the inner wall proved difficult to resolve, largely due to the pronounced texture and/or wrinkling of the outer membraneous layer.

Comparisons. The generic diagnosis of *Tornacia* Stockmans & Willière ex Wicander (1974, p. 33) circumscribes simplistic, hollow, laevigate vesicles, that display peripheral modifications (hollow processes) but lack the second, outer membraneous layer shown by *Maranhites perplexus* Wicander

& Playford (1985). Indeed, *Maranhites perplexus* differs from all other species of the *Maranhites* plexus due to the undulose equatorial margin of the inner wall, in conjunction with the closely appressed, diaphanous outer layer.

Also refer to the comparisons noted above for *Maranhites gallicus* Taugourdeau-Lantz.

Known geologic range. *Maranhites* sp. *sensu* Coquel *et al.* (1977) was described from the upper Famennian of the Noh-Deh section, Northeast Iran. Wicander & Playford (1985) formally proposed *Maranhites perplexus* based on material from the upper Frasnian of the Lime Creek Formation, Iowa, U.S.A. More recently Wilkinson & Knight (1989) have reported this species from the upper Famennian sediments that outcrop near Porthleven, Southwest Britain.

Note: Subcircular perforations, ≤4.5μm in diameter, were occasionally noted perforating the walls of both species of *Maranhites* detailed above (refer to Plate 3.31, fig. 13). As discussed in Chapter 2, these features are interpreted as microbial in origin.

Genus *Micrhystridium* Deflandre, 1937.

Type species. *Micrhystridium inconspicuum* Deflandre, 1937; by original designation.

Remarks.

Many authors, including Wicander & Wood (1981, p.48-49) have commented upon the vast number of species which have been assigned to this structurally simple complex of acanthomorph acritarchs. Furthermore, Wicander & Wood remark upon the common inability to define or replicate established species of *Micrhystridium*, as speciation relies on simplistic but highly variable parameters. Therefore, it is often difficult to effectively constrain and circumscribe species populations.

In view of the limited number of specimens recovered in the present study, and the potential affiliation of such forms with a number of established species, specimens referred to the *Micrhystridium* plexus herein have simply been differentiated into three broad species concepts (namely species sp. A, sp. B, and sp. C). This approach follows that of Wicander & Wood (1981).

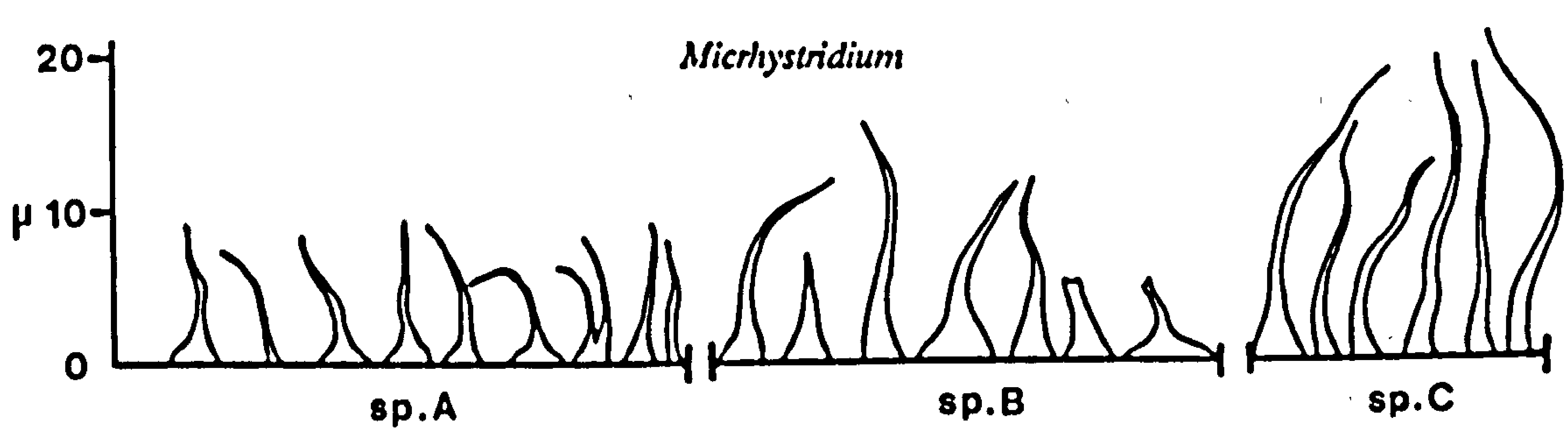


Figure 3.3.124: Variation in process morphology noted for the three species of *Micrhystridium* (sp. A; sp. B; sp. C) differentiated in the present study.

Micrhystridium sp. A
Plate 3.32, fig. 1.

Description. Vesicle circular, subcircular to broadly subpolygonal; wall relatively thin (≤0.5μm thick), laevigate, scabrate to finely granulose. The vesicle outline is strongly modified by numerous (24-30), hollow, homomorphic processes; elements comprise broad-based, straight or ≈flexible spines, ≤2-4.75μm in basal diameter and ≤7-11μm in length. The shafts to these sculptural elements are laevigate to finely scabrate: display curved proximal attachments and taper to a fine, acuminate point. These processes are principally confined to the equatorial margin of the vesicle, with few seeming to emanate from the central portion of the vesicle: range from ≤2μm to 4μm in isolation. Overall, the sculpture is comparatively even and dense at the equatorial margin of the vesicle; due to this peripheral concentration, the margin usually appears optically denser than the main body of the vesicle.

Dimensions. Maximum vesicle diameter 21-32μm, mean 26μm (4 specimens measured).

Occurrence. R, S; *very rare.*

Remarks. The vesicle wall is commonly folded at the equatorial margin (related to the compression and related distortion of the peripheral sculpture).

Micrhystridium sp. B
Plate 3.32, fig. 2.

Description. Vesicle hollow, subcircular to subpolygonal in outline. The wall appears comparatively thin (≤1μm thick), membraneous and the surface laevigate. 9-12 (on average 10) hollow, flexible (rarely straight), homomorphic processes are ≈uniformly distributed over the vesicle surface (9μm to 16μm apart). Process length ranges from 9μm to 17μm (rarely up to 22μm), and 2.5-5.75μm in basal diameter. The proximal attachments are curved, from which the sculptural elements gradually taper to a fine, attenuate point. Excystment (if observed) by the simple splitting of the vesicle wall.

Dimensions. Maximum vesicle diameter 19μm-25μm, mean 22μm (6 specimens measured).

Occurrence. LN, R; *very rare.*

Comparisons. *Micrhystridium pentagonale* Stockmans & Willière (1963) bears a close resemblance to *Micrhystridium* sp. B described above, although consistently displays a polygonal vesicle outline. The holotype of *M. pentagonale* is smaller (vesicle 14.5μm) and exhibits shorter processes. *Micrhystridium stellatum* Deflandre (1945) also displays a slightly more polygonal (*vs.* circular) vesicle outline. In comparison, the sculptural elements that adorn *Micrhystridium* sp. B are slightly larger and more attenuate than *M. stellatum. Micrhystridium adductum, sensu* Le Gall *et al.* (1985) displays a very similar morphology. *Micrhystridium ampliatum* Wicander & Playford (1985, p. 112) exhibits a more rounded vesicle, with a greater number (11-18) of somewhat coarser, longer processes projecting from the vesicle margin.

Micrhystridium sp. C.
Plate 3.32, fig. 3.

Description. Vesicle hollow, laevigate to finely scabrate; relatively thin walled (≤1μm) but appears somewhat optically dense. Vesicle outline subcircular to subpolygonal. The vesicle margin is modified by distinct, discrete, hollow and homomorphic sculptural elements; ≤15-26μm in length (usually ≈20μm) and ≤3-6μm in basal diameter. 8-14 of these spine-like elements project from the vesicle margin: appear flexible, tapering to an acuminate tip from a slightly expansive base - proximal contacts curved. Excystment by the simple splitting of the vesicle wall.

Dimensions. Maximum vesicle diameter 19-26μm, mean 21μm (4 specimens measured).

Occurrence. WP; *very rare.*

Comparisons. *Micrhystridium* sp. B of Wicander & Wood (1981) displays a marginally smaller vesicle (14-18μm in diameter) and slightly shorter, narrower processes (12-15μm in length).

Genus *Multiplicisphaeridium* Staplin
emend. Staplin, Jansonius and Pocock, 1965.

Type species. *Multiplicisphaeridium ramispinosum* Staplin 1961; by original designation.

Multiplicisphaeridium ramusculosum (Deflandre) Lister, 1970.
Plate 3.32, fig. 4.

1942 *Hystricosphaeridium ramusculosum* Deflandre, p. 476, Figs. 2-6 (nom. nud.)
1945 *Hystricosphaeridium ramusculosum* Deflandre, p. 63, Pl. 1, figs. 8-16; Figs. 38, 39.
1970 *Multiplicisphaeridium ramusculosum* (Deflandre) Lister, p. 92-93, Pl. 11, figs. 8, 11-14; Text-fig. 25a
1977 *Multiplicisphaeridium ramusculosum* (Deflandre) Lister, in Playford p. 28-29, Pl. 11, figs. 14-20; Fig.16.
1981 *Multiplicisphaeridium ramusculosum* (Deflandre) Lister, in Playford & Dring, p. 48, Pl.12, figs. 9,10.
1985 *Multiplicisphaeridium ramusculosum* (Deflandre) Lister, in Wicander & Playford, p.114, Pl. 5, figs. 3, 6.
1988 *Multiplicisphaeridium ramusculosum* (Deflandre) Lister, in Wicander & Lu Li-Chang p. 125, Pl. 2, fig. 7.

Description. Vesicle circular, subcircular to ovate in outline: wall laevigate to finely scabrate (rarely microgranulose), thin (≤0.25-0.6μm thick). 10-22 distinct, discrete, overall heteromorphic processes project from the vesicle margin. These sculptural elements are subcylindrical, hollow and freely communicate with the vesicle interior: range in length from ≤7μm to 25μm, and 3-5μm in basal diameter (rarely greater than 6μm). The proximal attachments of the processes are curved (rarely angular); the shafts are parallel-sided or taper gradually towards the distal extremity. The distal third to quarter of the sculptural elements branch to between second & fourth order (rarely initiated within the lower third of the processes). These pointed, digitate extremities appear highly irregular, ranging from simple bifurcations to intense, structurally complex multifurcate tips. Elements are comparatively regular (≈symmetrical) in their distribution over the vesicle wall, ranging from ≤6μm to 14μm apart. Excystment (rarely noted) by the simple, ragged rupturing of the vesicle wall.

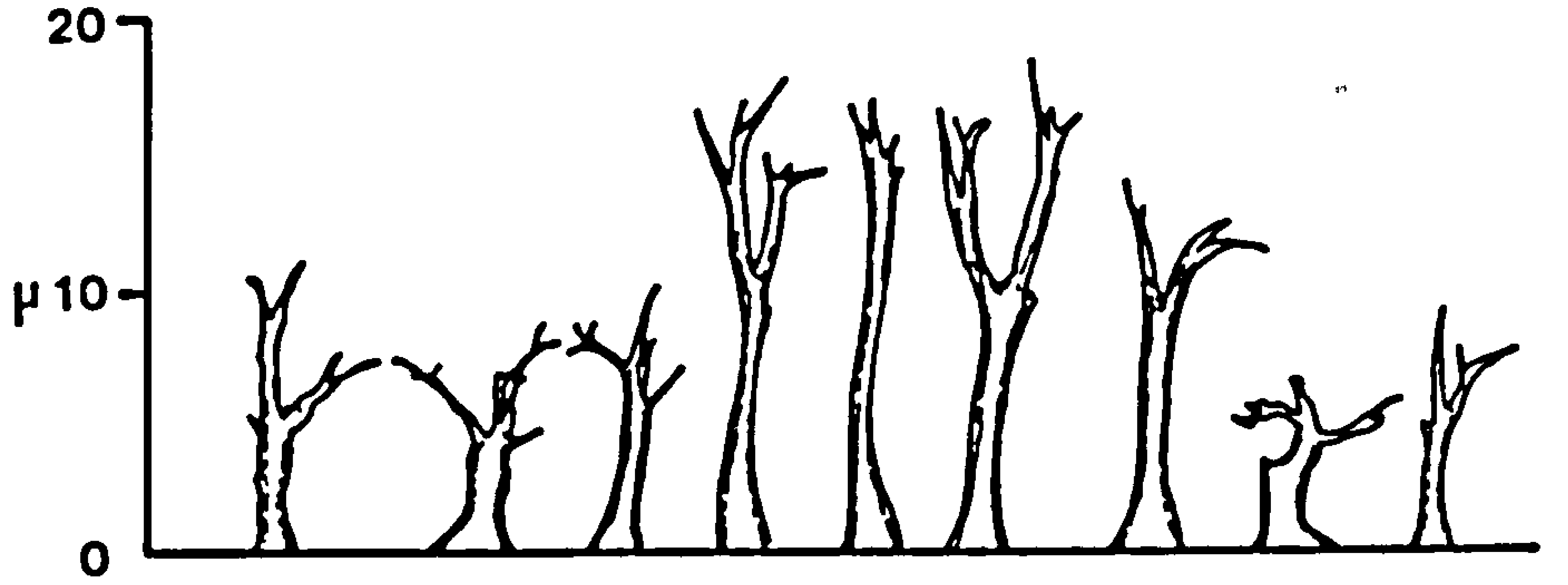


Figure 3.3.125: Sculptural elements of *Multiplicisphaeridium ramusculosum*, lateral view.

Dimensions. Maximum vesicle diameter 19-39μm, mean 29μm (10 specimens measured).

Occurrence. S; *rare.* LN, R, LH, WP; *very rare.*

Remarks. A broad circumscription of *Multiplicisphaeridium ramusculosum* was applied in the present study.

Both vesicle and processes were usually distorted and/or fragmented.

Comparisons. *Multiplicisphaeridium ampliatum* Playford (1977, p. 28) differs in displaying an irregularly shaped vesicle, and usually less numerous or slender processes.

Known geologic range. According to Wicander & Lu Li-Chang (1988, p. 125) *Multiplicisphaeridium ramusculosum* is a cosmopolitan species ranging from Upper Ordovician through to Upper Devonian.

Multiplicisphaeridium sp. A.

Plate 3.32, fig. 12.

Description. Subcircular to ovate vesicle outline; the wall appears optically dense, robust (although merely ≤0.25-0.5μm thick) and is laevigate to finely scabrate. The vesicle is ≈uniformly covered by distinct, discrete, overall homomorphic processes, ≤18μm in length and ≤7.25μm in basal diameter. These elements are relatively broad, and are hollow (freely communicating with the vesicle interior): the proximal attachments are curved to subangular, with the element shafts tapering gradually towards the distal extremity. The tips to the processes range from simple-blunted, bifurcate to trifurcate (rarely multifurcate): when preserved, digitation is confined to the distal 1/4 to 1/5 of the process length. Elements are isolated, regularly disposed over the vesicle surface: ≤6-20μm apart (average 10-15μm). 14-21 elements (or remnants of) project from the vesicle margin. Excystment not observed.

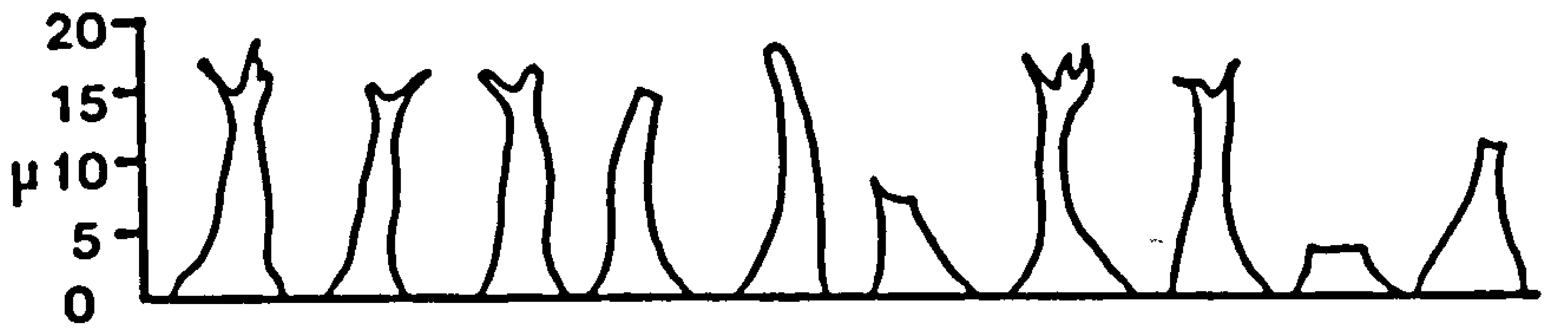


Figure 3.3.126: Sculptural elements of *Multiplicisphaeridium* sp. A., lateral elevation.

Dimensions. Maximum vesicle diameter 49-58μm, mean 53μm (8 specimens measured).

Occurrence. LN; *rare.* WP; *very rare.*

Remarks. *Multiplicisphaeridium* sp. A displays all the key attributes typical of the genus *Multiplicisphaeridium* (laevigate, thin walled vesicle and ≈regular processes that display digitate/furcate terminations). However, the morphology of the sculptural elements, and the small size of these processes relative to the overall vesicle diameter is regarded herein as somewhat atypical of this plexus.

Genus *Oppilatala* Loeblich & Wicander, 1976.

Type species *Oppilatala vulgaris* Loeblich & Wicander, 1976; by original designation.

?Oppilatala sp.

Plate 3.32, fig. 9.

Description. Vesicle subcircular to rounded ?subtriangular: wall ≤0.5μm thick, ?single layered, scabrate (≈coarse) to sparsely granulose. Three or four distinct, elongate, cylindrical and discrete processes radiate out from the vesicle: ≈regularly disposed, straight (rarely flexed), and distally branched. Processes (homomorphic) appear comparatively robust, broad based, laevigate to finely scabrate, and parallel-sided, or gradually tapering distally: 25-32μm in length, 3-6μm wide basally. Proximally the processes are plugged (≤2μm thick, preventing communication with the vesicle interior), and bear curved to subangular proximal attachments. Distally the processes branch up to the third order: branching is markedly asymmetric, irregular (rarely simple/bifurcate). Processes regularly spaced, 14-17μm apart. Excystment by the simple splitting of the vesicle wall.

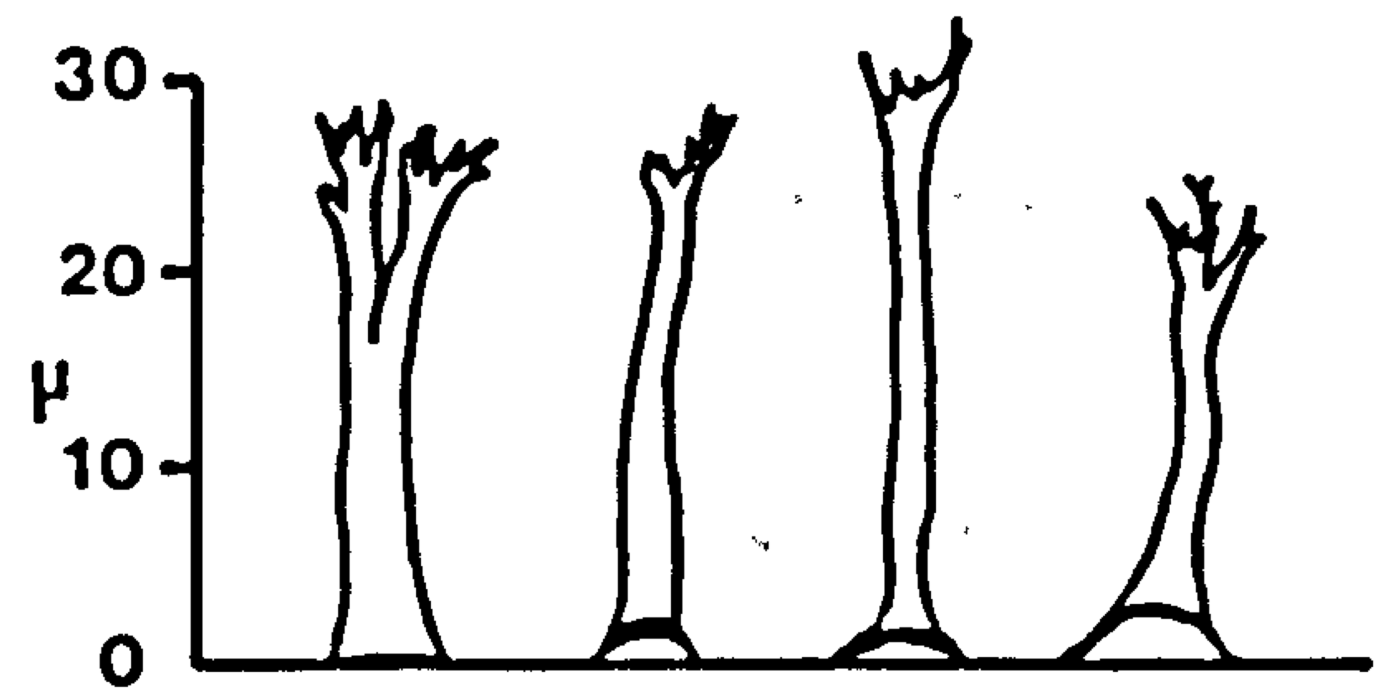


Figure 3.3.127: Process morphology of ?*Oppilatala* sp., lateral view.

Dimensions. Maximum vesicle diameter 27μm, 31μm (2 specimens measured).

Occurrence. S; *very rare.*

Remarks. Loeblich and Wicander (1976, p.19) proposed *Oppilatala* for two-layered multiplicisphaerid-type acritarchs which display proximally plugged processes. The genus *Ozotobrachion* Loeblich & Drugg (1968) is virtually identical in circumscription, but is noted to display a more triangular/polygonal vesicle. Specimens recovered from north Devon exhibit a more rounded rather than distinctly triangular vesicle outline, although this shape may be the result of the compression and associated distortion of the vesicle.

Comparisons. *Baltisphaeridium gueltaense* Jardiné *et al* (1974, p. 122, fig. 1) displays a larger vesicle (38-50μm), and a greater number (6-9) of slightly longer processes (35-50μm in length). *Ozotobrachion furcillatus* (Deunff) Playford (1977) displays a thicker walled vesicle (0.5-1.2μm), that is usually distinctly triangular in outline.

Genus *Ovnia* Cramer & Diez, 1977.

Type species. *Ovnia desertica* Cramer & Diez, 1977, by original designation.

?*Ovnia desertica* Cramer & Diez.

Plate 3.30, fig. 7.

? 1977 *Ovnia desertica* Cramer & Diez, p. 86, fig. 1-14, 16-19, 22-24.

? 1983 *Ovnia desertica* Cramer & Diez, in Le Herissé, p. 57-58, Pl. 10, fig. 11.

Description. Vesicle subcircular to ovate in outline; wall ?two-layered, thick (≤?2μm), optically dense and seemingly robust, with broad folds (concentric with the margin, and distorting the vesicle shape). The vesicle is covered by a regular microreticulum; muri are rounded or truncated in section, ≤0.25-1.25μm wide, defining diminutive lacunae (individually ≤1-2.75μm in diameter). These lacunae are circular, subcircular to polygonal in outline, and appear to be arranged in linear or openly sinuous "chains". The lacunae floors are laevigate or occasionally appear ?infragranulate.

Dimensions. Maximum vesicle diameter 47-64μm, mean 52μm (4 specimens measured).

Occurrence. M; *very rare.*

Remarks. Specimens proved very difficult to oxidise, such that the internal morphology remained unresolved.

Known geologic range. Lower Devonian; Cramer & Diez (1977), Le Herissé (1983).

Genus *Polyedryxium* Deunff ex. Deunff, 1961.

Type species. *Polyedryxium deflandrei* Deunff, 1961, by original designation.

Polyedryxium decorum Deunff

Plate 3.32, figs. 6, 7.

1955 *Polyedryxium decorum* Deunff, p. 146-147, Pl. 2, fig. 1.

1977 *Polyedryxium decorum* Deunff, in Playford, p. 33-34, Pl. 15, figs. 4-6; Pl. 16, figs. 5-7.

? 1979 *?Polyedryxium decorum* Deunff, in Lessuise, Streel & Vanguestaine, Pl. 3, fig. 17.

? 1984 *Arkonites bilixius* Legault, in Wicander, Pl. 1, fig. 4.

1985 *Polyedryxium decorum* Deunff, in Wicander & Playford, p. 114, Pl. 5, fig. 9.

Also refer to Wicander (1983, p. 67) for additional synonymy.

Description. Vesicle single layered, faintly scabrate to sparsely granulose: polyhedral in outline, consisting of 5-7 concave faces (each 11-25μm in maximum width). The vesicle surface is differentiated into a number of distinct or irregularly defined polygonal fields (commonly pentagonal to hexagonal in outline): 15-25μm in diameter, with $\approx$?4-9 per vesicle. The boundaries are marked by membraneous, transparent to optically dense ridges, which are commonly crenellated and range in height from 4μm to 7μm: the junctions of these crenulate muri commonly bear thickened, squat projections, that are "simple-baculate" or slightly bifurcate-tipped. These elements rarely project above the level of the muri. The muri are straight to openly sinuous in plan, and occasionally seem two layered (such ?laminate walls may "split" distally). The crenulation to the muri range from 3-6μm in basal width, with irregular-serrated or smooth extremities. Excystment structure is not observed.

Dimensions. Maximum vesicle diameter (including crenulate muri) 45-64μm (6 specimens measured).

Occurrence. K; *very rare.*

Remarks. Deunff (1955) described two further species of *Polyedryxium*, namely *P. evolutum* (p. 147, Pl. 4, fig. 7) and *P. simplex* (p. 147, fig. 2, fig. 4) which resemble *P. decorum* Deunff (1955). Indeed, it seems virtually impossible to differentiate between these three species: apart from *P. evolutum* and *P. simplex* showing a slightly greater number of lacunae per hemisphere, all three may well prove synonymous.

Comparisons. *Arkonites bilixius* Legault (1973; p. 52-53, Pl. XI, figs. 22, 23) displays a similar scalloped margin, but the vesicle is divided into two to four simple fields by centrally diverging ridges. *A. bilixius sensu* Wicander (1984) displays a greater number of diametrical "folds" than allowed by the circumscription of Legault (1973). *Polyedryxium bathyaster* Deunff (1961) and *P. deflandrei* Deunff (1961) display greater regularity in the arrangement of the crenulate muri, appearing prismatic and cuboid in outlines respectively. *Polyedryxium embudum* Cramer (1964) displays a cubic vesicle, and bears thin, simple and membraneous muri. *Polyedryxium carnatum* Playford (1977; p. 33, Pl. 15, figs. 7-13) ranges up to 96μm in diameter, and displays subdued, very regularly disposed muri, as well as a very fine reticulate vesicle ornament.

Known geologic range. Deunff (1955, 1966, 1971) recorded *P. decorum* from a sample of problematic age from Ontario, being possibly ?Lower/Middle Devonian in age. Cramer (1964) reported this species from the Lower Devonian of Spain, with Deunff (1967) noting its presence within a Frasnian chert at Kettle Point, Ontario. Jardiné *et al.* (1974) documented this form largely from the Mid Devonian of the Algerian Sahara. More recently Playford (1977) has reported *P. decorum* from Lower to Middle Devonian strata of the Moose River Basin, Ontario. Wicander & Playford (1985) record this taxon from the upper Frasnian Lime Creek Formation, Iowa, U.S.A. Wood & Clendening (1985) recovered *P. decorum* from the Givetian Boyle Dolomite of Kentucky (U.S.A.).

Genus *Veryhachium* Deunff ex Downie, 1959.

Type species: *Veryhachium trisulcum* (Deunff) Deunff, 1959; by subsequent designation of Downie (1959, p. 62).

?*Veryhachium europaeum* Stockmans & Willière.

Plate 3.32, fig. 8.

? 1960 *Veryhachium europaeum* Stockmans and Willière, p. 3, Pl. 2, fig. 25.

? 1962 *Veryhachium legrandi* Stockmans and Willière, p. 54, Pl. 1, figs. 3,4, text-fig. 11 a,b.

? 1985 *Veryhachium europaeum* Stockmans and Willière, in Wicander & Playford, p. 120, Pl. 7, figs. 7,8.

? 1986 *Veryhachium europaeum* Stockmans & Willière, in Wicander p. 357-358, Pl. VIII, fig. 6.

? 1988 *Veryhachium europaeum* Stockmans & Willière, in Wicander & Lu Li-Chang, p. 130, Pl. 3, fig. 7.

Description. Vesicle ≈equidimensional, triangular in outline, with straight to outwardly convex sides. The vesicle wall appears ≤0.5-1.25μm thick, laevigate to faintly scabrate, and occasionally folded. Three hollow, relatively rigid and ≈homomorphic processes develop within the same plane from the three apices of the triangular vesicle. These processes are 12-19μm in length (rarely 22μm), 3-7μm in basal diameter, and taper gradually to a simple (*i.e.* unbranched) blunted or pointed tip (≤1-2.25μm wide). All processes freely communicate with the vesicle interior, with subrounded proximal attachments. An auxiliary hollow process develops from the approximate centre of one of the vesicle faces. This additional process appears somewhat enlarged and robust; ≤15μm in basal width. Excystment (rarely seen) by the simple splitting of the vesicle wall.

Dimensions. Maximum vesicle diameter 25μm and 29μm (2 specimens measured).

Occurrence. WP; *very rare.*

Remarks. The enlarged vesicle diameter and coarseness of the fourth auxiliary process are atypical of *Veryhachium europaeum, sensu stricto* Stockmans and Willière (1960). Indeed, there is some question as to the identity proposed above for such specimens recovered from north Devon. What herein has been interpreted as the "fourth auxiliary process rising from one of the vesicle faces" may in fact be a primary process: akin to the asymmetric process morphology/arrangement reminiscent of *Tylignasoma* Playford (1977, p. 37). However, a diagnostic feature of *Tylignasoma* is that such apical processes do not freely communicate with the vesicle interior.

Comparisons. *Veryhachium colemanii* Playford & Dring (1981, p. 68, 70) is very similar in construction, but displays a distinct and highly variable surficial sculpture.

Known geologic range. Is a known cosmopolitan species, that ranges throughout the Silurian and Devonian (Wicander & Wood 1981, p. 65; Wicander 1986, p. 358).

Veryhachium trispinosum (Eisenack) Deunff "complex", *sensu* Wicander & Wood.
Plate 3.32, fig. 10.

1938 *Hystricosphaeridium trispinosum* Eisenack, pp. 14, 16, text-figs. 2,3.
1954 *Hystricosphaeridium trispinosum* (Eisenack) Deunff, p. 240, fig. 2.
1959 *Veryhachium trispinosum* (Eisenack) Deunff, in Downie p. 66, Pl. 12, fig. 7.
1981 *Veryhachium trispinosum* (Eisenack) Deunff, Wicander & Wood, p.67-71, Pl. 17, fig. 8.
1985 *Veryhachium trispinosum* (Eisenack) Deunff "complex", Wicander & Playford, p. 121, Pl. 7, fig.10-11.
1988 *Veryhachium trispinosum* (Eisenack) Deunff, in Wicander & Lu Li-Chang, p. 130, Pl. 3, fig. 8.

Refer to Wicander & Wood (1981, p. 67) for a more extensive synonymy.

Description. Vesicle equidimensional triangular: sides straight to convex outwards. The vesicle wall appears laevigate to faintly scabrate in transmitted light microscopy, and is ≤0.25-0.5μm thick (rarely 0.75μm). A single, hollow, laevigate process develops from each apex of the vesicle: commonly taper distally to a fine, regularly attenuated terminus. These homomorphic processes range from 9μm to 28μm in length (usually 12-16μm), and ≤2-4.5μm in basal diameter. Excystment structure not observed.

Dimensions. Maximum vesicle diameter 19-31μm, mean 27μm (6 specimens measured).

Occurrence. LN, S, ?K; *very rare.*

Remarks. Wicander & Wood (1981, p. 67-71) re-evaluated the complex of simplistic species of *Veryhachium*, namely *V. trispinosum*, *V. downiei*, and *V. reductum*. Following earlier authors (*inter alia* Cramer 1964, p. 306; Wicander 1974, p. 35; Playford 1977, p.38) they remarked that more often than not it is virtually impossible to consistently distinguish these three species (using conventional light microscopy). Consequently Wicander & Wood (1981) rationalised this plexus, applying the term "form group" or "complex", and furthermore commented that in future, differentiation may rely upon differences in ultrastructure (as resolved using the S.E.M.).

The vesicle size range noted for the population recovered from north Devon is somewhat larger than that recorded by Wicander & Wood (1981; 16-22μm) for the *V. trispinosum* "complex" of the (Givetian) Silica Formation, Ohio.

Known geologic range. Globally widespread, ranging from the Ordovician through to the Permian (Wicander & Wood 1981, p. 71; Wicander 1986, p. 358; Wicander & Lu Li-Chang 1988, p. 130).

?*Veryhachium* sp.
Plate 3.32, fig. 11.

Description. Commonly asymmetric, convex-triangular vesicle. Thin walled ($\leq$0.5μm thick), laevigate to finely scabrate, with very faint striations/wrinkles subparallel to the vesicle margins (appearing to originate and fan out from the base of the apical processes). A flexuous, hollow process, $\approx$38-45μm in length develops from each apex of the vesicle interior, and freely communicates with the vesicle. The shafts are subparallel, gradually tapering towards a solid, acuminate, distal tip. The proximal process attachments are rounded to subangular. The wall is commonly folded subparallel to the vesicle margins. Excystment by the simple rupturing of the vesicle wall.

Dimensions. Maximum vesicle diameter 25-33μm, mean 27μm (3 specimens measured).

Occurrence. LN; *very rare*.

Remarks. This form displays a subtle vesicle sculpture reminiscent of the genus *Arkonia* Burmann (1970, p. 298), hence the tentative generic assignment.

Comparisons. *Veryhachium pannuceum* Wicander & Loeblich (1977, p. 156) displays a distinctly triangular, smaller vesicle ($\approx$18μm in diameter), and a more pronounced ridged/wrinkled sculpture. *Veryhachium asymmetricum* Deunff (1961) is substantially larger, with *V. scabratum* Cramer (1964), although similar, displaying a subtle, rugulate/scabrate surficial vesicle structure. Le Gall *et al.* (1985, p. 242, Fig.6; 4, 8) illustrate two acritarch specimens as *Arkonia vigrata* Burmann (1970). These display a gross form comparable to *Veryhachium pannuceum* of Wicander & Loeblich (1977, p. 156), but unfortunately the synonymy of these two species cannot be confirmed as no detailed descriptions were available.

Genus *Vulcanisphaera* Deunff emend. Rasul, 1976.

Type species. *Vulcanisphaera africana* Deunff (1961).

Vulcanisphaera sp.
Plate 3.31, fig. 7.

Description. Vesicle subcircular to oval in outline: hollow. The wall is thin, single layered, and scabrate to finely granulose: $\leq 0.5\mu m$ in thickness. Numerous, ≈evenly spaced, solid, and overall heteromorphic processes project from the vesicle wall. These elements resemble irregular coni and bacula, ranging from $1.75\mu m$ to $3\mu m$ in height (average $2\mu m$, rarely up to $4\mu m$), that branch distally. The tips are digitate/multifurcate, comprising two to four attenuate spines, $\leq 2\mu m$ in overall length. Although discrete from one another, adjacent elements appear "interconnected" proximally by plications in the vesicle wall, ≤ 1-$3\mu m$ in width/height: collectively resemble an irregular pseudoreticulum. Elements are discrete, 5-$9\mu m$ apart (rarely greater than $11\mu m$). The "lacunae" appear irregular subcircular, triangular to polygonal in outline. Mode of excystment not observed.

Figure 3.3.128: Process morphology of *Vulcanisphaera* sp., side elevation.

Dimensions. Maximum vesicle diameter (excluding sculpture) 37-$61\mu m$, mean $54\mu m$ (6 specimens measured).

Occurrence. LN, S; *very rare.*

Remarks. The "pseudoreticulum" observed upon specimens assigned to *Vulcanisphaera* sp., is believed the result of wall distortion, and induced in part through the compression of the processes and the associated collapse of the vesicle wall. *Hapsidopalla* Playford 1977, p. 25) displays a primary reticulum: for *Hapsidopalla*, the bases of the sculpture are joined proximally by ≈distinct muri, that form a well defined to discernible reticulum. Specimens recovered from north Devon are atypical of this genus.

Known geologic range. Late Cambrian to Ordovician (Molyneux, *pers. comm.*); Late Ordovician to Silurian (Dorning, *pers. comm.*).

Acritarch Type A.
Plate 3.32, fig. 5.

Description. Vesicle subcircular to subpolygonal: wall laevigate to scabrate (rarely granulose), $\leq 0.75\mu m$ thick and rarely folded. The vesicle outline is modified by a number of processes, 8-$17\mu m$ in length and ≤ 2-$3\mu m$ in basal diameter (rarely $5\mu m$). The processes are comparatively rigid, straight to slightly arcuate, and taper distally from a broadened, rounded base. Proximal attachment rounded, rarely angular. The shafts of the processes appear finely granulose, and branch distally up to second order (rarely third order, commonly simple or bifurcate). Sculptural elements are discrete, 7-14μm apart. Excystment is by the simple, irregular rupturing of the vesicle wall.

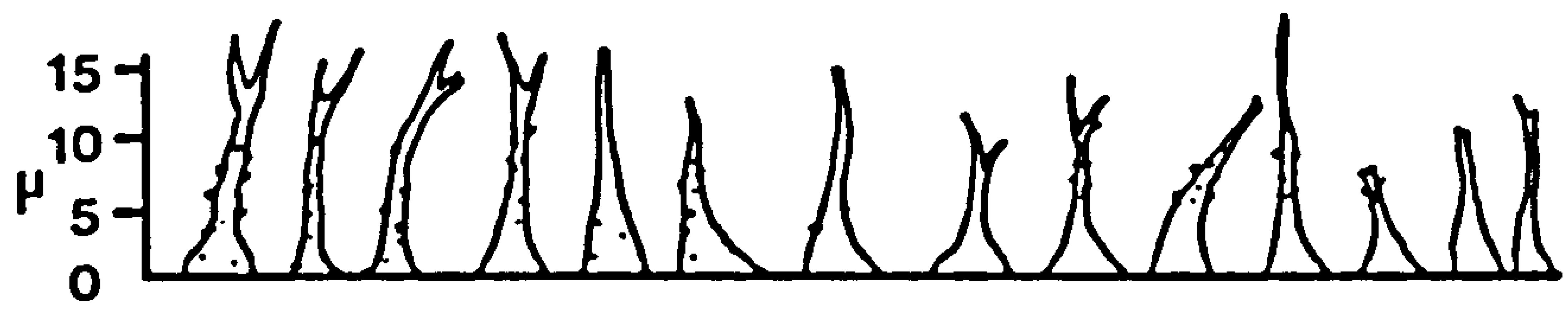


Figure 3.3.129: Sculptural elements of Acritarch sp. A, lateral view.

Dimensions. Maximum vesicle diameter 30-42μm, mean 36μm (3 specimens measured).

Occurrence. S; *very rare.*

Remarks. The subcircular to well rounded, essentially laevigate vesicle wall, coupled with the slender, bifurcate to multifurcate tipped processes are reminiscent of multiplicisphaerid acritarchs. However, the subtle and sparse granulation on the processes is more typical of the plexus *Diexallophasis* Loeblich (1970).

CHITINOZOA.

The main limitation imposed on the identification of the chitinozoa faunule recovered from north Devon proved the sporadic and/or low numbers of adequately preserved specimens. Indeed the vast majority of chitinozoa documented were fragmented, commonly lacking the basal surface or displaying a ruptured vesicle/neck. The occurrence of complete or identifiable fragments of chitinozoa is indicated in Appendix II (which does not take into account such variable specimen preservation). The majority of samples identified as containing chitinozoa simply yielded recognisable fragments of this group, which were on the whole unidentifiable even to generic level. Only those forms that were taxonomically distinctive (based upon test fragments or virtually complete specimens), are discussed below.

In a detailed study of Silurian chitinozoa from Gotland, Laufeld (1974) acknowledged the lack of stability in chitinozoan systematics, and used this observation to justify an alphabetical approach to the ordering of chitinozoan genera. This perspective was similarly adopted in the present study. Standard descriptive/orientation terminology is briefly reviewed in Figure 3.3.1. Legault (1973, p. 13-15), Wrona (1980a, p. 121-123) and Paris (1981) discuss this group and such terminology in greater detail, as well as indicating reference points for vesicle measurements.

All chitinozoa vesicles recovered from north Devon were discrete, and did not display any form of colonial habit.

Genus *Ancyrochitina* Eisenack, 1955.

Type species. *Ancyrochitina ancyrea* Eisenack, 1955.

Ancyrochitina ?taouratinensis Boumendjel

Plate 3.33, fig. 1.

? 1985 *Ancyrochitina taouratinensis* Boumendjel, p. 156, 158, Pl. 2, figs. 1, 2, 3.

? 1988 *Ancyrochitina taouratinensis* Boumendjel, in Boumendjel *et al.*, Pl. 5, fig. 2.

Description. Vesicle cylindro-conical. Chamber conical, ?two-layered; base flat or hemispherical, sides straight to slightly convex. Flexure distinct, rounded: flexure angle 62-71°. The neck is distinct, parallel-sided, cylindrical. The prosome is distinct, usually retracted within the vesicle wall, and displays ≈transverse, annulate "ribbing" which extend orally from the "flexure": the prosome occupies 30-95% of the neck. Where "unsupported" by the prosome, the neck wall appears thin ($\leq 1.5\mu m$ thick), membraneous, with the oral opening commonly ragged, irregular. When preserved, the base displays the remnants of two to five distinct, discrete processes: processes commonly fragmented, blunted, rarely terminating with pronounced, irregular digitations. These enlarged processes are aligned sub-perpendicular to the longitudinal axis of test. The "outer" vesicle wall appears homogeneous, laevigate, and is ornamented with a profusion of isolated, diminutive spines: ≤ 1-$4.25\mu m$ in length (usually 2-$3\mu m$) and $\leq 2.5\mu m$ in basal diameter. Spines are usually discrete, ≤ 4-$12\mu m$ apart (rare fusion of 2-3 individual elements), and form an even cover over most of the vesicle.

Figure 3.3.130: Vesicle sculpture on *Ancyrochitina ?taouratinensis*, lateral view.

Dimensions. (vesicle parameters) L: 82-138μm, mean 129μm. l: 27-49μm, mean 38μm. W: 69-95μm, mean 89μm. (8 specimens measured).

Occurrence. L, CM; *very rare.*

Remarks. Vesicles were rarely recovered complete, and commonly lacked the lower surface and/or aboral processes (the specimen figured on plate 3.33 shows the typical preservation). Poorly preserved specimens were near impossible to differentiate from those of *Fungochitina ?pilosa* (note the specimen illustrated on Pl. 3.33, fig. 2: may feasibly be attributable to either *A. taouratinensis* or *F. ?pilosa*).

Comparisons. *Ancyrochitina morzadeci* Paris (1980) resembles *Ancyrochitina taouratinensis* Boumendjel (1985), but the diminutive (echinate) vesicle sculpture is largely confined to the neck region and does not extend over the vast proportion of the chamber. *Fungochitina pilosa* displays a more distinct, flatted aboral surface, and lacks enlarged aboral processes.

Ancyrochitina sp. A
Plate 3.33, fig. 3-5.

Description. Cylindro-conical vesicle: chamber conical, base distinctly hemispherical (rarely flat) with straight (≈irregular) to slightly convex sides. Flexure is distinct or subtle, generally rounded: the flexure angle ranges between 58-71°. The neck is cylindrical, parallel-sided or broadening orally to a ≈distinct, flared "collar". The prosome is usually confined to the lower 1/3 to 1/2 of the neck, ≈extending orally from the flexure. The prosome appears optically dense, ?unstructured and slightly retracted away from the vesicle wall. The vesicle is laevigate, finely granulose or sparsely echinate; echinae ≤1-2μm in dimensions. 9-14 distinct, discrete but reduced appendages project from the aboral surface: ≤8μm in (?complete) length, ≤6μm in basal width tapering irregularly to ≤2-3μm. If entirely preserved, the processes are simple-attenuate or bifurcate distally.

Dimensions. (vesicle parameters) L: 83-128μm, mean 116μm. l: 16-38μm, mean 33μm. W: 61-92μm, mean 78μm. (10 specimens measured).

Occurrence. LN, CM, K; *very rare.*

Remarks. Processes are rarely preserved intact. The aboral surface is often folded back into the chamber (refer to specimen Pl. 3.33, fig. 3), or dissociated (Pl. 3.33, fig. 5). The vesicle may display a number of diminutive perforations which represent either parasitic boring, or the ?remnants of a fragmented vesicle sculpture. A similar mode of preservation has been noted by, amongst others, Paris (1988, Pl. 19, figs. 10, 13), in a study of late Givetian to Frasnian chitinozoa from the Boulonnais, France.

Ancyrochitina sp. B
Plate 3.33, fig. 6.

Description. Vesicle cylindro-conical: chamber broad, with straight to slightly undulose sides, tapering from a laterally expanded base to a comparatively constricted neck. The aboral surface appears relatively flat to slightly convex, and displays between six and eight distinct, discrete processes. The flexure is distinct, rounded: the flexure angle ranges between 55° and 61°. The neck is cylindrical, somewhat flared orally and contains an optically dense prosome; the prosome is ill-defined, diffuse, and occupies 75-90% of the total neck region. The vesicle wall is laevigate, ≤3μm thick, and commonly ruptured aborally. The appendages range in length from 27-35μm, 3-8μm in width and may bifurcate (simple).

Dimensions. (vesicle parameters) L: 92μm, 143μm. l: 26μm, 45μm. W: 81μm, 135μm. (2 specimens measured).

Occurrence. LN; *very rare.*

Remarks. The processes on the figured specimen are folded back into the chamber (indicated).

?Ancyrochitina sp. C
Plate 3.33, fig. 7.

Description. Cylindro-conical vesicle: chamber conical, 2-layered, and flat broad-based (with straight to slightly concave sides). The flexure is indistinct, rounded: flexure angle ≈45-70°. The neck is cylindrical, comparatively elongate and seemingly voluminous, relative to the contained, retracted, but distinct prosome. The prosome occupies between ≤45-65% of the neck region, appears optically dense and also unstructured. The oral part to the neck is membraneous and slightly flared, with a number of longitudinal folds. The vesicle is covered sparingly with distinct, discrete echinae, ≤3μm in height and ≤2μm in basal width; ≤5-24μm apart (commonly 8-12μm). The aboral surface appears thickened, ≤5μm, and bears the basal remnants (stubs) of processes, ≤4-6μm in diameter.

Dimensions. (vesicle parameters) L: 91-108μm, mean 96μm. l: 52-69μm, mean 63μm. W: 72-83μm, mean 77μm (3 specimens measured).

Occurrence. LN; very rare.

Remarks. The remnants of basal processes are usually indistinct, thus meriting the tentative generic identification above.

Genus *Angochitina* Eisenack, 1931.
Type species. *Angochitina echinata* Eisenack, 1931.

Angochitina sp. A.
Plate 3.32, fig. 14; Pl. 3.33, fig. 8.

Description. Broad, squat pyriform to cylindro-spherical vesicle: chamber bulbous, subcircular, thick walled (≤3-5μm) and with a slightly ≈flattened base. Flexure distinct, rounded: flexure angle 58-65°. The neck is cylindrical, comparatively short and robust. The vesicle displays a comparatively uniform sculpture, comprising discrete, diminutive, and simple echinae, coarse grana plus more rounded coni: ≤2.25μm in basal width and length. Elements are sparsely distributed, commonly ≤10-15μm apart (rarely 2-4μm). No internal morphological features were observed.

Figure 3.3.131: Sculptural elements of *Angochitina* sp. A, lateral view.

Dimensions. (vesicle parameters) L: 107-144μm, mean 119μm. l: 27-55μm, mean 39μm. W: 76-99μm, mean 83μm. (10 specimens measured).

Occurrence. LN, S, WP, L, CM, M; *very rare*.

Remarks. Specimens were rarely sufficiently oxidised allowing resolution of internal structures. Fragmentation/rupturing of the aboral surface was common.

Angochitina sp. B.
Plate 3.33, figs. 9, 10.

Description. Vesicles elongate pyriform in shape (laterally compressed), and are moderately thick walled (≤1-2.5μm). Chamber ovate, rarely subcircular, with the aboral surface rounded, rarely flattened. Flexure indistinct, rounded: flexure angle 65-73°. The neck is cylindrical, and appears robust, enclosing a barely discernible prosome. The vesicle surface is laevigate, scabrate or ?shagreenate. A regular sculpture comprising diminutive, simple echinae (≤1.25-3μm in basal width and height) is concentrated preferentially on the chamber. The neck usually lacks pronounced sculpture.

Dimensions. (vesicle parameters) L: 91-121μm, mean 112μm. l: 16-35μm, mean 29μm. W: 53-69μm, mean 63μm (5 specimens measured).

Occurrence. WP, M; *very rare.*

Remarks. Major longitudinal compressional folds are rare: the test is however commonly ruptured.

Genus *Conochitina* Eisenack, 1931 restr. 1955.
Type species. *Conochitina claviformis* Eisenack, 1931.

?*Conochitina* sp.
Plate 3.32, fig. 13 (?); Pl. 3.33, fig. 11.

Description. Simple, cylindrical vesicle. Aboral surface convex, with ?traces of a ?copula: flexure indistinct, and sides subparallel, broadly tapering towards the aperture. The vesicle wall is ≤0.5-1.5μm thick, optically dense towards the lower, aboral, surface: is laevigate to finely scabrate. Neck undifferentiated, although some form of "oral structure" appears slightly retracted from the oral wall margins. Aperture ragged, torn. The junction between the aboral surface and the vesicle margins bears an indistinct ?flange (?carina).

Dimensions. (vesicle parameters) L: 98-117μm, mean 105μm. W: 47-56μm, mean 53μm. (3 specimens measured).

Occurrence. ?CM, K; *very rare.*

Remarks. There is some question as to the generic identity of this form, as the neck appears "complex" in structure, and the aboral surface appears to exhibit a subtle "?carina". A number of species assigned to the genus *Cingulochitina* Paris (1981) display a broadly comparable morphology.

Genus *Eisenackitina* Jansonius 1964.

Type species: *Eisenackitina castor* Jansonius, 1964.

Eisenackitina castor Jansonius, *sensu* Legault (1973).
Plate 3.32, fig. 15, Pl. 3.33, fig. 12.

1964 *Eisenackitina castor* Jansonius, p. 912-913, Pl. 2, figs. 15-17.
1973 *Eisenackitina castor* Jansonius, in Legault, p. 38-39, Pl. VII, figs. 9, 10, 12; Pl. VIII, fig. 2.
? 1976 *Eisenackitina castor* Jansonius, in Massa & Moreau-Benoit, Pl. 4, fig. 14.
1985 *Eisenackitina castor* Jansonius *sensu* Legault, in Paris *et al.*, Pl. 27, figs. 1-5.
1988 *Eisenackitina castor* Jansonius *sensu* Legault, in Boumendjel *et al.*, Pl. 5, fig. 6 a,b.

Description. Vesicle subcylindrical: base flat to slightly convex with straight to slightly outward-convex, subparallel sides. Wall of variable optical density, ≤ 1-$3\mu m$ thick. The junction between the aboral surface and chamber flanks commonly appears "thickened", $\leq 5\mu m$ thick. No distinct flexure: the oral aperture is simple, or displays a slightly constricted, subtle, "lipped" collar. The vesicle surface appears evenly or sparsely sculptured with diminutive grana and/or subdued coni, occasionally scabrate: sculptural elements range from $\leq 0.5\mu m$ to $1.75\mu m$ in width and height, $<0.25\mu m$ to $7\mu m$ in isolation (usually clustered). Sculpture may appear sparse or absent towards the aperture, with an associated thinning of the vesicle wall. Specimens lack an operculum.

Dimensions. (vesicle parameters) L: 106-127μm, mean 117μm. W: 89-105μm, mean 96μm. N: 46-78, mean 63μm (based upon 6 specimens).

Occurrence. R, S, LH; *very rare.*

Remarks. The circumscription of *Eisenackitina castor* adopted herein follows the application of Legault (1973): allows for slightly smaller and somewhat more variable test morphology than was originally circumscribed by Jansonius (1964).

Known geologic range. Jansonius (1964) originally described *Eisenackitina castor* from the Hume Formation (early Givetian) of western Canada. Legault (1973, p. 38) subsequently reported this species from the Middle Devonian Hamilton Formation of Southwest Ontario. More recently Paris *et al.* (1985), Streel *et al.* (1988), and subsequently Boumendjel *et al.* (1988) have documented *E. castor* (*sensu* Legault, 1973) from Givetian strata of northeast Libya (in the former two cases) and the early Givetian of the Algerian Sahara, respectively.

Genus *Fungochitina* Taugourdeau, 1966.

Type species. *Conochitina fungiformis* Eisenack, 1931.

Fungochitina ?pilosa (Collinson & Scott) Taugourdeau.
Plate 3.33, fig. 13; Plate 6.3, fig. 14, 18.

? 1958 *Sphaerochitina pilosa* Collinson & Scott, p. 21, Pl. 3, fig. 1-5.

? 1958 *Sphaerochitina schwalbi* Collinson & Scott, p.23, Pl. 3, figs. 6-10.

? 1973 *Sphaerochitina pilosa* Collinson & Scott, in Urban & Newport, p.241, Pl. 2, figs. 1-16.

? 1976 *Fungochitina pilosa* (Collinson & Scott) Taugourdeau, Massa & Moreau-Benoit, Pl.6, fig.7.

? 1980 *Angochitina pilosa* (Collinson & Scott) Paris, p. 60, Pl. 3, figs. 7, 8, 11, 13, & 14; Pl. 4, fig. 13.

? 1985 *Fungochitina pilosa* (Collinson & Scott) Taugourdeau, in Paris *et al.*, Pl. 28, figs. 3-6.

? 1985 *Sphaerochitina pilosa* Collinson & Scott, in Wood & Clendening, p.141, Pl. 3, fig. 5-6.

? 1988 *Fungochitina pilosa* (Collinson & Scott) Taugourdeau, in Boumendjel *et al.*, Pl. 5, fig. 9.

Refer to Paris 1980b, p. 60, & Paris 1981, p. 260 for additional synonymy.

Description. Vesicle flattened-conical, to pyriform in outline; the chamber appears comparatively bulbous, with a flattened to slightly convex aboral surface. The chamber is widest towards the aboral surface (not chamber midlength), with the chamber flanks straight to convex-outwards. Flexure distinct, rounded: flexure angle 58-70°. Neck cylindrical, commonly incomplete, and terminated orally by a membraneous, translucent, "?collarette". A structured (annulate) prosome partially fills the neck (occupying between 45-95%), and is slightly retracted from, or conversely closely appressed to, the vesicle wall. The vesicle wall is $\leq$1.75-3μm thick, laevigate, scabrate to finely granulose and bears a regular, sculptured "veneer" comprising short, diminutive spines, grana and more rounded coni: typically $\leq$1.25-3μm in height (rarely 4μm+) and $\leq$1.5-2.5μm in basal diameter. These elements are dense, $\leq$2.5-8μm apart (rarely greater than 10μm). Occasionally the sculptural elements cluster, or fuse into short, irregular "cristae": $\leq$3μm in length.

Figure 3.3.132: Vesicle sculpture of *Fungochitina ?pilosa*, lateral view.

Dimensions. (vesicle parameters) L: 103-149μm, mean 124μm. l: 26-46μm, mean 32μm. W: 85-104μm, mean 91μm. (14 specimens measured).

Occurrence. S, LH, WP, L, CM, K; *very rare.*

Remarks. The population of *Fungochitina ?pilosa* documented from north Devon was somewhat smaller than the size specifications of Collinson & Scott (1958) for type material of the Cedar Valley Formation, Illinois (for which the overall length is quoted as 176-190μm). As mentioned earlier, there was an occasional problem in differentiating between poorly preserved specimens of *Ancyrochitina ?taouratinensis* (that lacked aboral surfaces) and those of *Fungochitina ?pilosa*.

The aboral surface was rarely noted to be intact, being more typically ruptured or completely missing. A number of specimens identified as *F. ?pilosa* displayed regular, ≈isodiametric perforations (≤5μm diameter), approximately located at the point of flexure. These may reflect parasite borings (refer to Laufeld 1974, or Wrona 1980).

Known geologic range. Previously recorded from both Givetian and Frasnian strata of the Western Libya (Rhadames Basin), northern France and America (Collinson & Scott, 1958; Taugourdeau, 1966; Urban & Newport, 1973; Paris 1980b). More recently *F. pilosa* has been reported from subsurface Devonian sediments (Givetian) of northeast Libya (Paris *et al.*, 1985; Streel *et al.*, 1988) and the lower Givetian sediments of the Illizi Basin, Algerian Sahara (Boumendjel *et al.*, 1988).

Genus *Hoegisphaera* Staplin, 1961

Type species: *Hoegisphaera glabra* Staplin, 1961.

?Hoegisphaera sp.

Plate 3.33, fig. 14.

Description. Vesicle ?subspherical: greater width than height. The vesicle appears comparatively thin walled, ≤1-2μm thick, and laevigate to finely scabrate. Vesicles lack any form of neck , and are commonly compressed longitudinally (orally) rather than laterally. The aperture is simple, lacking any pronounced thickening. When present, the "operculum" is partially detached, and is strongly sculptured, displaying radial striations about an opaque (?thickened) subcircular centre. The vesicle may display faint "longitudinal" lineations, but otherwise appears unstructured.

Dimensions. (Maximum vesicle parameters). W: 78μm, 71μm. Neck width: 47μm, 36μm. (2 specimens measured). **Operculum 41μm,** 1 specimen only.

Occurrence. K; *very rare.*

Remarks. Forms of *Margachitina* Eisenack (1968) are often recovered in a colonial habit, and display a structured copula/operculum comparable in morphology to the radially structured "operculum" visible on the above forms; *e.g.* refer to the figured specimens of *Margachitina catenaria* Obut *crassipes* Paris (1981; Pl. 25, figs. 13-16), or *?Margachitina leonensis* Cramer in Hill *et al.* (1985; Pl. 13, figs.9, a-b) - hence the tentative generic assignment above.

Comparisons. *?Hoegisphaera* sp. is similar in overall construction to the genotype *Hoegisphaera glabra*, but differs in being smaller in size and displaying a sculptured (radially striated) "operculum". *H. glabra* has been reported to display a simple, concentrically banded operculum.

Genus *Sphaerochitina* Eisenack, 1955

Type species: *Lagenochitina sphaerocephala*, Eisenack, 1932.

Sphaerochitina sp.

Plate 3.33, figs. 15, 16; Plate 6.3, fig. 15 (?).

Description. Vesicle pyriform, with a bulbous, well rounded chamber. Maximum chamber width tends towards test midlength (although is variable in the species population analysed). Flexure indistinct to pronounced, rounded: flexure angle 67-73°. Aboral surface distinctly convex, hemispherical and smooth. Neck distinct, cylindrical, parallel-sided or broadening orally: elongate and rigid, or ≈kinked midlength. Prosome distinct and retracted from the vesicle wall: may appear structured (annulate thickenings), and occupies 50-95% of the preserved neck region. Vesicle wall ≤1-3μm thick (rarely greater), finely scabrate, or "sculptured" with diminutive grana: ≤0.25-0.5μm (rarely 0.75μm) in width and height (do not project at the test margin). These "elements" are well spaced, discrete (≤2-5μm apart), or may cluster (≤0.25-1μm apart). The aperture ranges in appearance from ragged to smooth.

Dimensions. (vesicle parameters); L: 101-147μm, mean 126μm. l: 32-61μm, mean 37μm. W: 66-71μm, mean 69μm. (7 specimens measured).

Occurrence. LN, H, S, L, M; *very rare.*

Remarks. Specimens proved very difficult to oxidise (perhaps due to a thickened vesicle wall). Over oxidised material revealed a structured neck and the described fine vesicle sculpture (although in such extreme cases specimens usually appeared severely ruptured and fragmented). This test "ornament" was not a consistent attribute, or sufficiently pronounced to merit assignation to either *Angochitina* or *Fungochitina.*

SCOLECODONTS.

Complete and fragmented scolecodont elements (compound or "coniform") were recovered from many of the palyniferous samples collected from north Devon. In general, initial attempts of identifying the scolecodonts proved inconclusive, largely due to the lack reference texts, accessible at the time of submission. Problems of identification were further compounded by the current dualism that exist within scolecodont systematics: namely Linnaean binomials *vs.* multielement nomenclature. Adverse preservation also limited identification. A few selected "complexes" are described below, but more importantly specimens are illustrated, so that in future these may be more correctly placed.

The five heterogeneous categories defined below do not represent five distinct, taxonomic categories (multielement or other), but merely simple "form groupings" based upon very simplistic, generalised but believed consistent morphological characteristics. Realistically, these complexes circumscribe jaw elements derived from a multitude of biological genera. If possible, the dental formulae has been calculated for the few selected elements illustrated (following the methodology of

Jansonius and Craig, 1971, p. 261-264). The descriptive terminology outlined by Jansonius & Craig (1971, p. 257-261) and Bergman (1989, p. 29-30) was applied: the term "blade" loosely follows the usage as in applied conodont studies.

The most abundant and diverse types of scolecodont element recovered were primary (MI) and secondary (MII) maxillae. Although these morphotypes are perceived to have the greatest potential application to biostratigraphic studies, little systematic variation in their temporal distribution was noted through the studied sequence (?attributable to their sporadic occurrence).

Morphotype A.

Plate 3.34, figs. 1, 2.

Description. Simple, coniform elements; longitudinal axis straight to arcuate, tapering gradually to a distinctly angular or subrounded terminus. Element wall 2-6μm thick; myocoele usually distinct. In general wall laevigate and featureless, although rarely may display fine longitudinal striations, $\leq$0.25-0.75μm in width and running the $\approx$entire length of the element.

Dimensions. Variable: $\approx$75-165μm(+) in length, $\leq$25μm to 54μm in basal (aboral) diameter.

Occurrence. Sporadic and comparatively low in abundance throughout the palyniferous sections studied.

Remarks. The terminations were usually fragmented, blunted.

Morphotype B.

Plate 3.34, figs. 3, 4, 7-12, 15.

Description. Heterogeneous group that encompasses compound ?primary/secondary maxillary elements. Unifying feature: pronounced denticulation coupled with a distinct ramus/cusp. "Wall" of variable thickness (typically $\leq$3-6μm); laevigate, finely granulose or infrapunctate, with faint to pronounced ?surficial lineations/striations. In lateral profile axis arcuate, rarely straight: elements robust, wall thickened orally and may become $\approx$increasingly diaphanous towards the myocoelar opening (wall may display a polygonal, cellular structure). Elements "hollow", and open laterally or vertically in the form of a distinct, $\approx$cavenous myocoele. Wall is perforate at, or thins towards the terminations to each denticle/cusp. The denticulation is single rowed: comprises a pronounced, enlarged, hollow cusp ($\leq$10-35μm in height) or distinct ramus (ramal angle 45°-(60°)-75°, in association with numerous, subordinate, and hollow, first order denticles. This dentition may be erect, arcuate and/or preferentially orientated towards the anterior/posterior. Denticles vary from $\leq$2μm to 15μm in length (rarely exceed 18μm) and decrease $\approx$progressively in size towards the posterior terminus. If the ramus appears subdued and ill-defined, the associated ramal arch is commonly suppressed ($\rightarrow$180° in inclination). The lower surface ranges in form from being an open, expansive feature (fossa), to partially enclosed (calyx) through to strongly enclosed (antrum).

Dimensions. Typical element length; ≈80-120μm, rarely greater than 160μm. Typical number of denticles (exclusive of the cusp/ramus): 5 to 8 (rarely as great as 14).

Occurrence. This type of element was the most pervasive and abundant form recorded through the studied palyniferous sequence.

Remarks. The cusp, ramus and/or denticles may be fragmented (blunted). Considerable variation in both ultrastructural and gross morphological detail was noted within this complex of scolecodont elements, encompassing some or all of the features described above.

The ultrastructure of certain elements was noted to be similar to those features illustrated by Goodarzi & Higgins (1985).

Comparisons & possible homologies. Morphotype B accommodates a diverse suite of scolecodont morphologies. These may be further distinguished into two broad complexes, dependant upon the orientation of the myocoelar opening.

a) Laterally opening myocoele (*e.g.* Pl. 3.34, figs. 9, 10). Resemble the MI elements associated with the *Gotlandites* spp., *Kettnerites* spp., and *Lanceolatites* spp. apparatuses, *sensu* Bergman (1989).

b) Myocoele opening ≈vertically downwards (*e.g.* Pl. 3.34, figs. 4, 8, 12). The MIId element of the *Leodicites cultriformis* apparatus in Jansonius & Craig (1971, Pl. 3, fig. 5) and the MIId element of the *Albertaprion* sp. apparatus in Jansonius & Craig (1974, Pl. 4, fig.1) resembles some of the forms assigned to **Morphotype B.**

For additional homologies refer to the description of Plate 3.34.

Morphotype C.

Plate 3.34, figs. 13, 14, 16, 17.

Description. Compound elements: in lateral view, elements straight to broadly arcuate (convex upwards) - occasionally attenuate, wedge-shaped. The wall appears laevigate, scabrate, infrapunctate or cellular, and 1-5-7μm thick (rare, enlarged punctations range in diameter up to 2μm). The upper surface bears comparatively even denticulation, being ≈equidimensional or increasingly subdued towards the posterior terminus: the denticles are erect, rounded/subangular and single rowed. An enlarged, erect or inclined cusp may be discernible. Primary denticles range from ≤2μm to 16μm in height, and are erect or slightly reclined anteriorly/posteriorly. The lower margin appears broad and open (fossa), or is partially enclosed (calyx): lower margin commonly ragged (rarely well defined) in appearance, and may appear cellular in construction.

Dimensions Typical maximum element length; ≈60-120μm, rarely over 100μm. Number of denticles; 6 to 12, rarely 15+.

Occurrence. Confined stratigraphic distribution, restricted to the Upper Hangman Sandstone Group and Ilfracombe Slates.

Remarks. The described cellular structure occasionally noted along the lower margin of the fossa has previously been remarked upon by a number of authors, including Schwab (1966).

Comparisons. A number of specimens assigned to this form category resemble *Cheiridogenys'borealis* as illustrated by Jansonius & Craig (1971, Pl. 3, fig. 1), and also the various placognathid jaw elements (?MI) figured by Jansonius & Craig (1974: p. 21, Pl. 4, figs. ?6, 7, 8, 9).

Morphotype D.
Plate 3.34, figs. 5, 6.

Description. Compound elements: linear to arcuate in profile. Elements broad based (myocoelar opening simple) tapering distally to a fine, attenuated terminus. Falx ill-defined, suppressed, almost linear. The inner margin of the element bears subdued, diminutive denticles ($\leq 6\mu m$ in height, commonly $\leq 3\mu m$) and $\leq 2\text{-}3\mu m$ in basal width), which are erect or inclined towards the anterior terminus. Elements are discrete, well spaced: 2-8μm apart. The myocoele dimensions are uncertain.

Dimensions Maximum element length: $\approx$75-115μm. Number of discernible denticles: 5 to 9.

Occurrence. Exclusive to the Ilfracombe Slates.

Comparisons. Possible affiliation with **Morphotype B.** Compare favourably with a number of specimens identified and illustrated by Bergman (1989; e.g. Fig. 21, F, G, K, L) and belonging to the genus *Gotlandites*

Morphotype E.
Plate 3.34, figs. 18, 19.

Description. Compound elements, which display approximate bilateral symmetry. In profile the longitudinal axis is straight to arcuate, with a somewhat laterally expanded, cavenous myocoelar opening. The aboral margin may be broad, with the element flanks parallel-sided or tapering $\approx$progressively towards a rounded, attenuate terminus. The element sides may appear concave or straight in profile. The wall is laevigate, scabrate ($\approx$turbid), and thickened, $\leq 9\mu m$ thick (typically 3-7μm). The terminus is thickened, "plugged" and optically dense. Both lateral margins display discrete, pronounced denticulation; elements decrease in width and height towards the lower aboral margin. Denticle height $\leq$4-16μm, with the coarsest elements developed preferentially towards the terminus. Denticles $\leq 5\mu m$ apart, solid and homogeneous.

Dimensions Maximum element length; 98μm, 102μm (2 specimens recovered).

Occurrence. *Very rare.*

Comparisons. Germeraad (1980) describes and illustrates a small population of $\approx$symmetrical elements from Cainozoic sediments in Jamaica. Forms attributed to *Group 4* by Germeraad are comparable to the two specimens described herein.

MICROSCOPIC PLANT DEBRIS.

Burgess (1987) extensively studied the primordial land flora and their dissociated microscopic fragments within the Silurian and Lower Devonian sediments of the Welsh Borderlands. Based upon the taxonomic principles defined and applied by Burgess, the microscopic plant debris recovered from north Devon was categorised into four, informal, heterogeneous "complexes" (or "types"). These phytoclasts were loosely differentiated primarily because of their diversity in the studied section, but also in an attempt to evaluate any temporal variation in the distribution of such organic matter (thus assessing their biostratigraphical potential). The informal, heterogeneous categories defined have no implied palaeobotanical affiliation. Comparisons are made with the generic categories proposed by Burgess (1987), with permission.

Plant Fragment, Type A.

Plate 3.35, figs. 1-3.

Description. Heterogeneous group comprising ≈laevigate to finely scabrate (essentially homogeneous), hollow ("cylindrical") tubes: average 3μm to 8μm in diameter (rarely exceed 12μm), and range in wall thickness from thin-membraneous (≤0.25-0.5μm thick) to seemingly rigid, comparatively robust and thick walled (≤1-1.75μm thick, rarely up to 3.5μm). Tubes lack any internal structure, and may be folded longitudinally. A diversity of tube morphology is circumscribed by this category, ranging from simple straight/flexed, to branched and occasionally openly "coiled". Branching commonly comprises simple first order bifurcations. Tubes may also occur as simple, single specimens, as regularly anastomosing aggregates, or chaotic, thickly "woven" meshes. Tube length highly variable, although in general ≤200μm.

Remarks. Some tubes displayed a patchy granulose surface texture (probably secondary in origin).

Burgess (1987) proposed the genus *Laevitubus* which in part circumscribes some of the more simple forms attributed herein to the category *Plant Fragment* Type A. Burgess also defined the genus *Filomata,* accommodating branched filaments with an external ornament of grana and verrucae. Although some tubes recovered from north Devon clearly branched, any surficial texture was considered by and large secondary.

Burgess (1987) noted that in categorising these tubular forms, no direct botanical affiliation could be implied. Indeed, various plant types may have produced morphologically similar forms. Conversely, one single plant species may have been the source for a multitude of different, dissociated types of microscopic plant fragment. According to Burgess, these tubes have a speculative affiliation with certain Nematophytales.

Plant Fragment Type B.

Plate 3.35, figs. 4-9; Pl. 6.1, fig. 1(?), 5.

Description. Heterogeneous group comprising broad, laevigate to scabrate, structured (cylindrical) tubes: tubes lack branching and are ≈parallel-sided. This complex accommodates a diversity of textures and structures: tubes differentially thickened displaying internal and/or ?external transverse banding, spiralling. Such bands range from simple parallel-sided through to relatively complex, anastomosing meshes: are diametrically concentric around the tube, and average 1-3.5μm in width (rarely up to 6μm). Tubes average ≤0.5-3μm in wall thickness, 25-45μm in diameter, and rarely exceed 200μm in length (usually 80-140μm).

Remarks. Burgess (1987) proposed the genus *Porcatatubus* and *Torotubus* which are homologous to *Plant Fragment* Type B defined in the present study. Differentiation of the two genera of Burgess is dependant upon whether the banding is an internal or external feature. Using conventional transmitted light microscopy, it proved very difficult in the present study to establish whether such banding was consistently an internal or external attribute. External bands were usually expressed at the tube margin. Poorly preserved specimens simply displayed remnants of the thickened ?internal/ external bands: Note: Pl. 3.35, fig. 5, herein - the intervening "wall" is corroded &/or absent.

Comparisons. *Plant Fragment* Type B material is considerably broader in diameter than Type A (as defined above), but differing more significantly in bearing a distinct infrastructure. Some nematophytalean tube wefts show a comparable morphology. Mortimer & Chaloner (1972; Pl. III, figs. 4, 5) illustrate similar forms referred to as "(?)*Nematothallus*" wefts. McGregor (1984, Pl. 4 fig.12) also illustrates forms identical to those detailed herein, remarking that such spirally-banded tubes are "like those associated with *Nematoplexus* Lyon (1962)".

Plant Fragment Type C.

Plate 3.35, figs. 10-17; Pl. 6.1, figs. 11, 12.

Description. Heterogeneous complex: circumscribes irregularly shaped, platy fragments or structured laths, ≤3-6μm in thickness and generally ≤100μm in diameter (ranging up to ≈400μm). The surface morphology ranges from laevigate, homogeneous, scabrate to finely granulose. The unifying feature of this complex is its cellular form. Distinguishable into two distinct morphotypes namely;

(a) imperforate, pseudoreticulate "plates", upon which muri (generally ≤1.5-4.5μm wide) define irregular, polygonal to subcircular lacunae ≤5-25μm in diameter. Very occasionally porous.

(b) perforate, cellular laths and/or "plates": single layered or stacked (up to 7 separable layers). Cells elongate, subpolygonal to subcircular, ≤2-9μm in diameter, and connected longitudinally by thickened, robust (optically dense) "bands" (3-11μm in width), forming linear meshes.

Remarks. This category incorporates probable cuticle fragments; Mortimer & Chaloner (1972, Pl.III, figs. 1-3) illustrate similar cellular fragments (referred to as (cf.)*Spongiophyton* sp.), from subsurface Devonian strata in southern England. The perforate, lath-shaped fragments (group (b) differentiated above) partly resemble the vascular elements illustrated by Chitaley & McGregor (1988, Pl. 2, figs. 4-6) within the lycopsid *Bisporangiostrobus harrisii* Chitaley & McGregor.

Plant Fragment **Type D.**

Plate 3.35, figs. 18-20; Pl. 6.1, figs. 3, 6(?), 8.

Description. Irregular, longitudinally fibrous fragments: lath-shaped (often of no definable form), and bearing thickened, longitudinal "ribs", ≤3-8.5μm wide (commonly ≤5μm). Fragments typically ≤200μm x ≈50μm in size. The "ribs" are linear, arcuate or occasionally bifurcate/anastomose. Wall ≤2-6μm thick: appears overall optically dense.

Remarks. As well as *Plant Fragment* **Type C** this category forms a notable component of organic isolates, being recovered near ubiquitously throughout the palyniferous strata studied.

Plates 3.30-3.35.

Acritarchs, chitinozoa, scolecodonts
and "wood" phytoclasts are subsequently illustrated.

All illustrations are at x750 magnification, except were stated. For most specimens, focal plane or phytoclast orientation is not specified, unless a particular perspective is especially illustrated. In the plate descriptions, information is presented according to the following format; figure number; taxonomic name, and specimen remarks (*e.g.* scolecodont dental formula); sample number; slide code (a or b) and specimen coordinates. The specimen coordinates are presented as eastings then northings; the suffix (a) or (b) refers to a particular slide - two slides were standardly logged. All phytoclasts were logged on an Olympus BHS 313 microscope (Serial No. 582701) housed in the Department of Geology, Southampton University. For precise details of sample horizon and location refer to Appendix II and Figs. 2.2 & 2.3. Refer to Figure 2.1 (of Chapter 2) for an explanation of lithostratigraphic abbreviations.

Details of slide number and specimen coordinates are provided for completeness, despite the probable opacity of the material if re-examined subsequent to the submission of this thesis. These have been included to allow possible infra-red microscopy (see Chapter 2, Section 2.7)

PLATE 3.30.

Plate 3.30

Acritarchs

(all figured specimens have been oxidised)

Fig. 1 *Cymatiosphaera* sp. A; K52 (a), 142.6/14.3.

Fig. 2 *Cymatiosphaera reticulosa* (Kirjanov) Colbath, 1983; S14 (a), 134.5/5.9.

Fig. 3 *Cymatiosphaera reticulosa* (Kirjanov) Colbath, 1983; WP26 (a), 131.8/16.1.

Fig. 4 *Cymatiosphaera reticulosa* (Kirjanov) Colbath, 1983; M41 (a), 146.2/8.9.

Fig. 5 *Cymatiosphaera* cf. *reticulosa* (Kirjanov) Colbath, 1983; LN98 (b), 125.5/4.3.

Fig. 6 *Dateriocradus* sp.; R21 (a), 148.2/14.9.

Fig. 7 ?*Ovnia desertica* Cramer & Diez, 1977; M35 (a), 153/21.1.

Fig. 8 *Dictyotidium* sp. A; LN52 (a), 143.5/10.2.

Fig. 9 *Dictyotidium* sp. A; LN92 (a), 147.2/16.2.

Fig. 10 ?*Dictyotidium* sp. B; scanning electron microscope, x450 magnification; S02.

Fig. 11 *Dictyotidium* cf. *cohora* Wicander & Wood, 1981; S20 (a), 151.7/3.5.

Fig. 12 *Dictyotidium* cf. *cohora* Wicander & Wood, 1981; S14 (a), 150.4/12.2.

Fig. 13 *Dictyotidium* sp. C; R21 (a), 148/21.8.

Fig. 14 ?*Dictyotidium* sp. B; R21 (a), 137/18.5

Fig. 15 *Dictyotidium* cf. *polygonium* Staplin, 1961; S14 (a), 148.9/12.8.

Fig. 16 *Diexallophasis remota* (Deunff) Playford, 1977; S10 (a), 138.2/7.5.

Fig. 17 *Diexallophasis remota* (Deunff) Playford, 1977; S02 (a), 142.2/10.5.

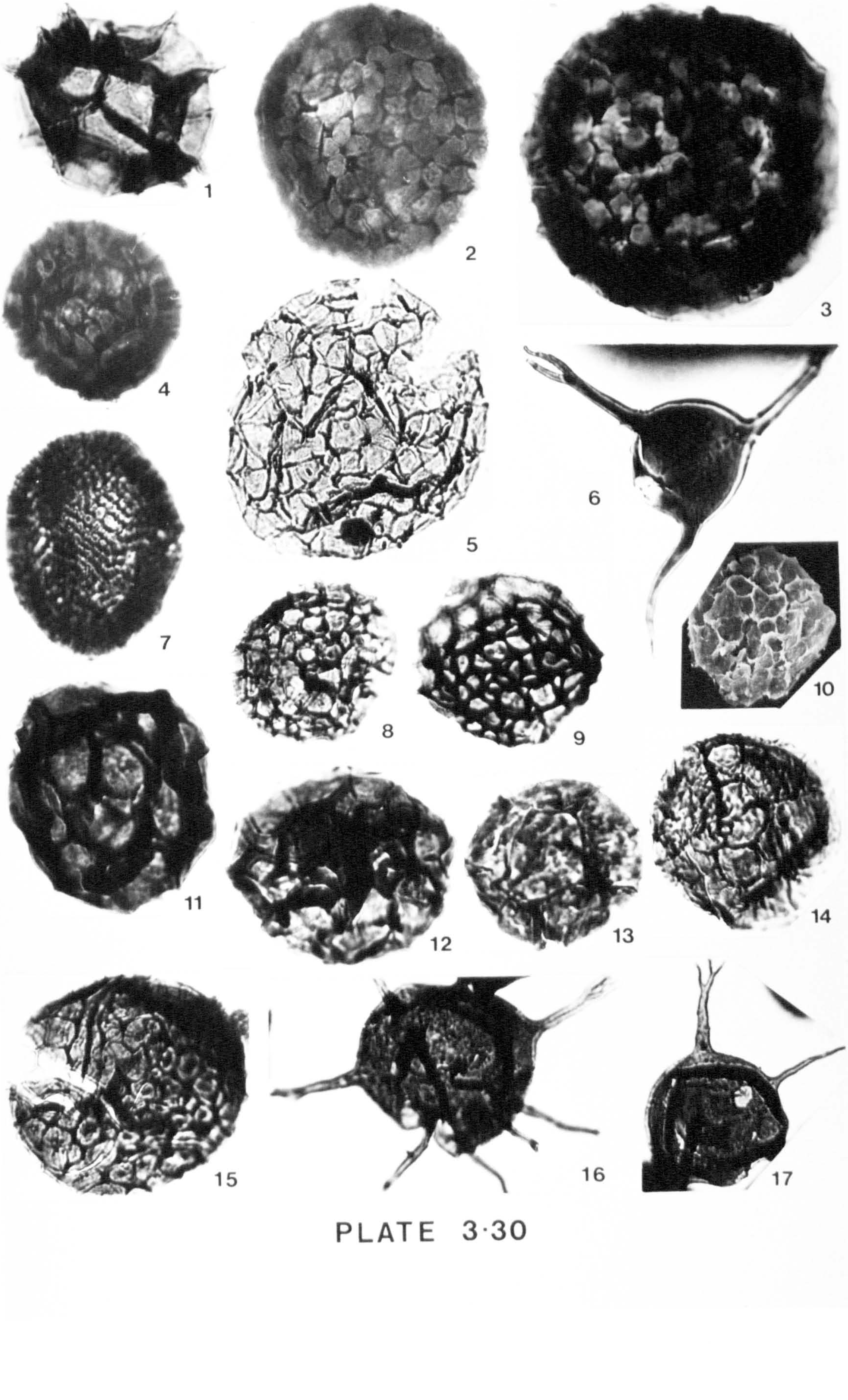


PLATE 3·30

PLATE 3.31

Plate 3.31

Acritarchs

(all figured specimens have been oxidised)

Fig. 1 *Diexallophasis denticulata* (Stockmans & Willière) Loeblich, 1970; LN92 (a), 145.2/15.2.

Fig. 2 *Diexallophasis remota* (Deunff) Playford, 1977; LN98 (a), 148.1/11.2.

Fig. 3 *Diexallophasis remota* (Deunff) Playford, 1977; LN92 (b), 138.8/13.1.

Fig. 4 *Diexallophasis denticulata* (Stockmans & Willière) Loeblich, 1970; process morphology; S20 (a), 130.2/22.2.

Fig. 5 *Diexallophasis* cf. *remota* (Deunff) Playford, 1977; LN92 (b), 132.1/20.2.

Fig. 6 *Diexallophasis simplex* Wicander & Wood, 1981; S10 (a), 138.2/7.5.

Fig. 7 *Vulcanisphaera* sp.; LN98 (b), 138.5/10.5.

Fig. 8 *Leiosphaeridia* sp.; LN96 (a), 146.2/17.2.

Fig. 9 *Gorgonisphaeridium* sp.; K32 (a), 155/20.1.

Fig. 10 *Maranhites perplexus* Wicander & Playford, 1985; M42 (a), 153.2/18.1.

Fig. 11 *Maranhites perplexus* Wicander & Playford, 1985; M12 (a), 144.4/17.1.

Fig. 12 *Maranhites perplexus* Wicander & Playford, 1985; M44 (a), 149.9/12.2.

Fig. 13 *Maranhites perplexus* Wicander & Playford, 1985; vesicle displaying subcircular ?microbial scars; M35 (a), 131.2/8.6.

Fig. 14 *Maranhites gallicus* Taugourdeau-Lantz, 1968; M42 (a), 156.9/16.3.

Fig. 15 *Maranhites gallicus* Taugourdeau-Lantz, 1968; M42 (a), 160.2/8.3.

Fig. 16 *Maranhites gallicus* Taugourdeau-Lantz, 1968; M44 (a), 139.2/17.1.

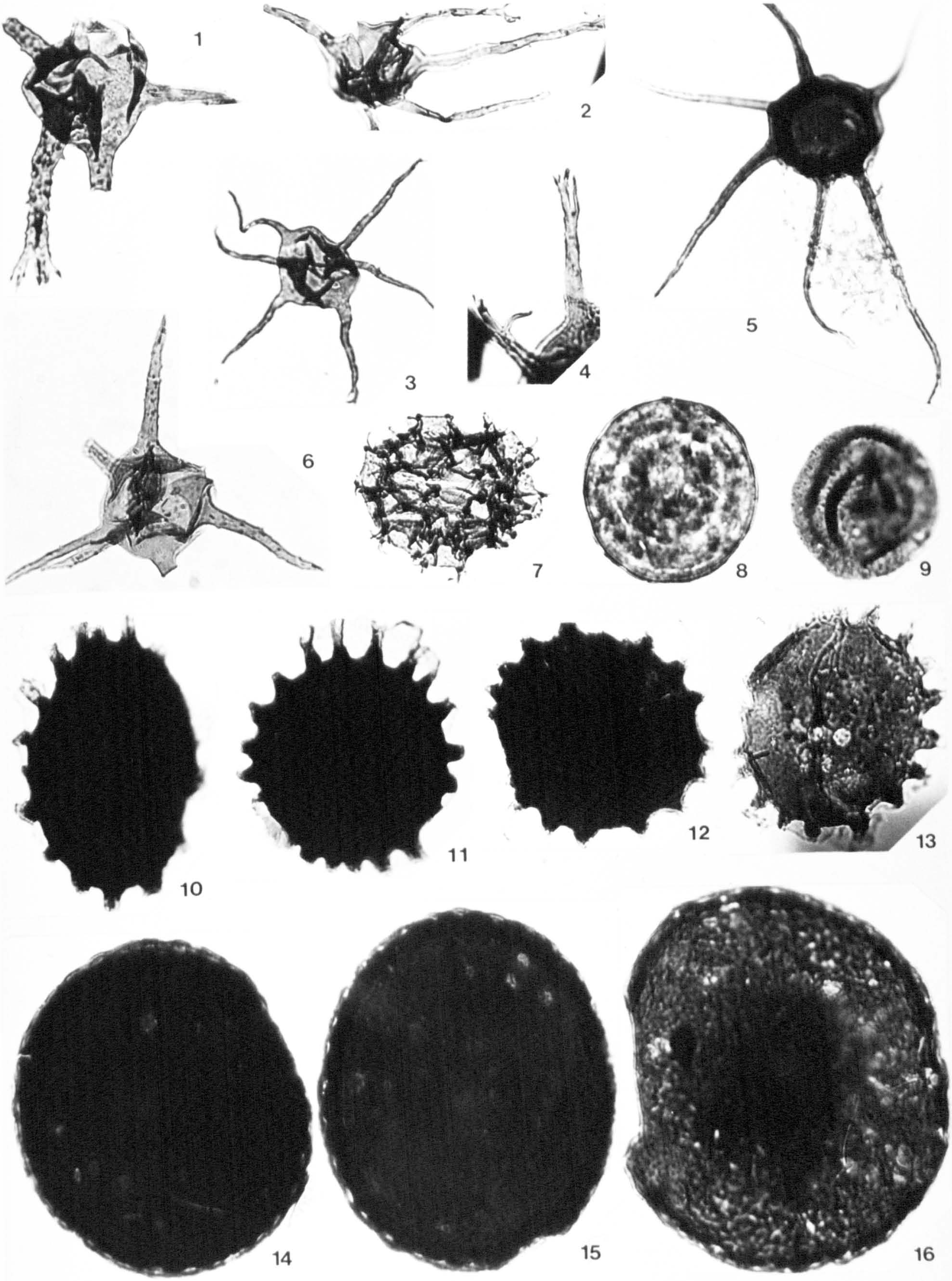


PLATE 3·31

PLATE 3.32

Plate 3.32

Acritarchs & Chitinozoa.

(all figured specimens have been oxidised)

Fig. 1 *Micrhystridium* sp. A; R21 (a), 147.1/5.3.

Fig. 2 *Micrhystridium* sp. B; LN92 (a), 139.4/7.4.

Fig. 3 *Micrhystridium* sp. C; WP12 (a), 148.2/11.4.

Fig. 4 *Multiplicisphaeridium ramusculosum* (Deflandre) Lister, 1970; WP10 (a), 153/7/11.9.

Fig. 5 Acritarch Type A; S18 (a), 141.2/4.9.

Fig. 6 *Polyedryxium decorum* Deunff, 1955; K44 (a), 143.4/6.1.

Fig. 7 *Polyedryxium decorum* Deunff, 1955; K32 (a), 152.2/8.5.

Fig. 8 ?*Veryhachium europeaum* Stockmans & Willière, 1960; WP10 (a), 156.1/7.

Fig. 9 ?*Oppilatala* sp.; S10 (a), 154.9/7.2.

Fig. 10 *Veryhachium trispinosum* (Eisenack) Deunff, 1954c "complex"; S12 (a), 145/18.2.

Fig. 11 ?*Veryhachium* sp.; LN98 (b), 138.4/5.8.

Fig. 12 *Multiplicisphaeridium* sp. A.; WP31 (a), 133/16.1.

Fig. 13 Isolated ?chitinozoan base (?*Conochitina* spp.), x750 magnification; CM66 (a), 142.2/17.2.

Fig. 14 *Angochitina* sp. A; x300 magnification; WP26 (a), 155.7/7.7.

Fig. 15 *Eisenackitina castor* Jansonius, 1964, *sensu* Legault, 1973; transversely ruptured vesicle; x300 magnification; R21 (a), 149.2/18.5.

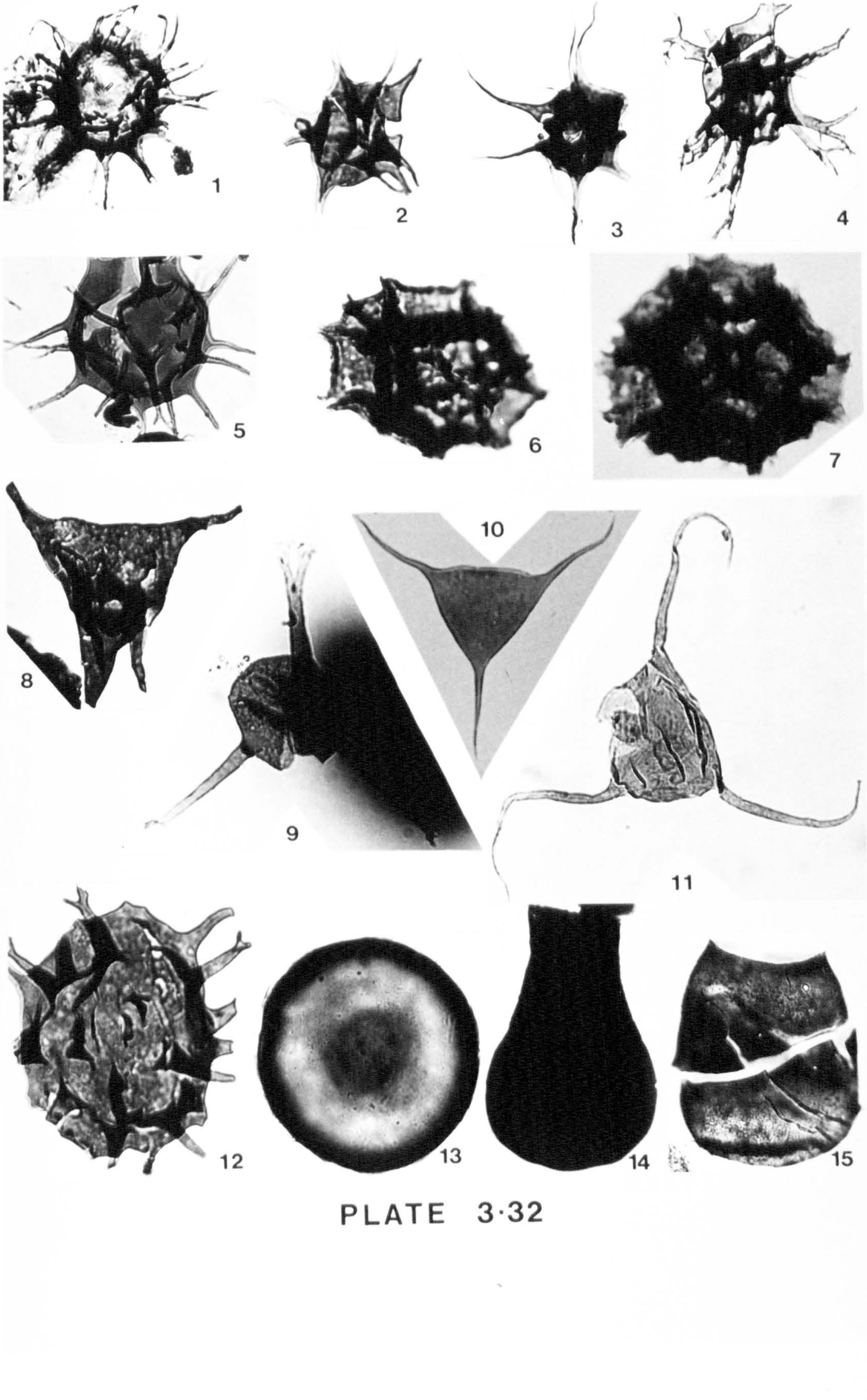


PLATE 3·32

PLATE 3.33

Plate 3.33

Chitinozoa

(all figured specimens have been oxidised and are illustrated at x400 magnification).

Fig. 1 *Ancyrochitina ?taouratinensis*; L30 (a), 149/12.3.

Fig. 2 Problematic identity; referrable either to ?*Ancyrochitina taouratinensis* or *Fungochitina ?pilosa*; CM23 (a), 149.6/20.1.

Fig. 3 *Ancyrochitina* sp. A; indicated is the remnant of an aboral process; the minute perforations on the chamber may reflect parasitic borings, or the remnants of diminutive vesicle spines; LN34 (a), 146/18.1.

Fig. 4 *Ancyrochitina* sp. A; indicated are the basal remnants of aboral processes; K44 (a), 142.2/23.

Fig. 5 *Ancyrochitina* sp. A; dissociated aboral surface; CM28 (a), 148/8.1.

Fig. 6 *Ancyrochitina* sp. B; note the process folded back into the vesicle; LN101 (a), 156.2/16.1.

Fig. 7 ?*Ancyrochitina* sp. C; LN101 (a), 147.3/9.1.

Fig. 8 *Angochitina* sp. A; indicated is the chamber ornament comprising diminutive echinae; S08 (a), 156.3/8.2.

Fig. 9 *Angochitina* sp. B; WP27 (a), 147/23.2.

Fig. 10 *Angochitina* sp. B; M40 (a), 141.5/11.2.

Fig. 11 ?*Conochitina* sp.; K44 (a), 155/6.9.

Fig. 12 *Eisenackitina castor* Jansonius, 1964, *sensu* Legault, 1973; R22 (a), 146.5/17.

Fig. 13 *Fungochitina ?pilosa* (Collinson & Scott) Taugourdeau; CM02 (a), 134.2/22.2.

Fig. 14 ?*Hoegisphaera* sp.; K52 (a), 160/12.3.

Fig. 15 *Sphaerochitina* sp.; S08 (a), 143/2.

Fig. 16 *Sphaerochitina* sp.; fragmented specimen - over oxidised revealing internal neck morphology, and subtle surface ornament; M12 (a), 145.2/20.2.

Fig. 17 Oral fragment of chitinozoan, unident; clearly delineated are transverse circular "thickenings" within the prosome; M47 (a), 140.1/17.

Fig. 18 As for Fig. 17; M47 (a), 149.2/21.

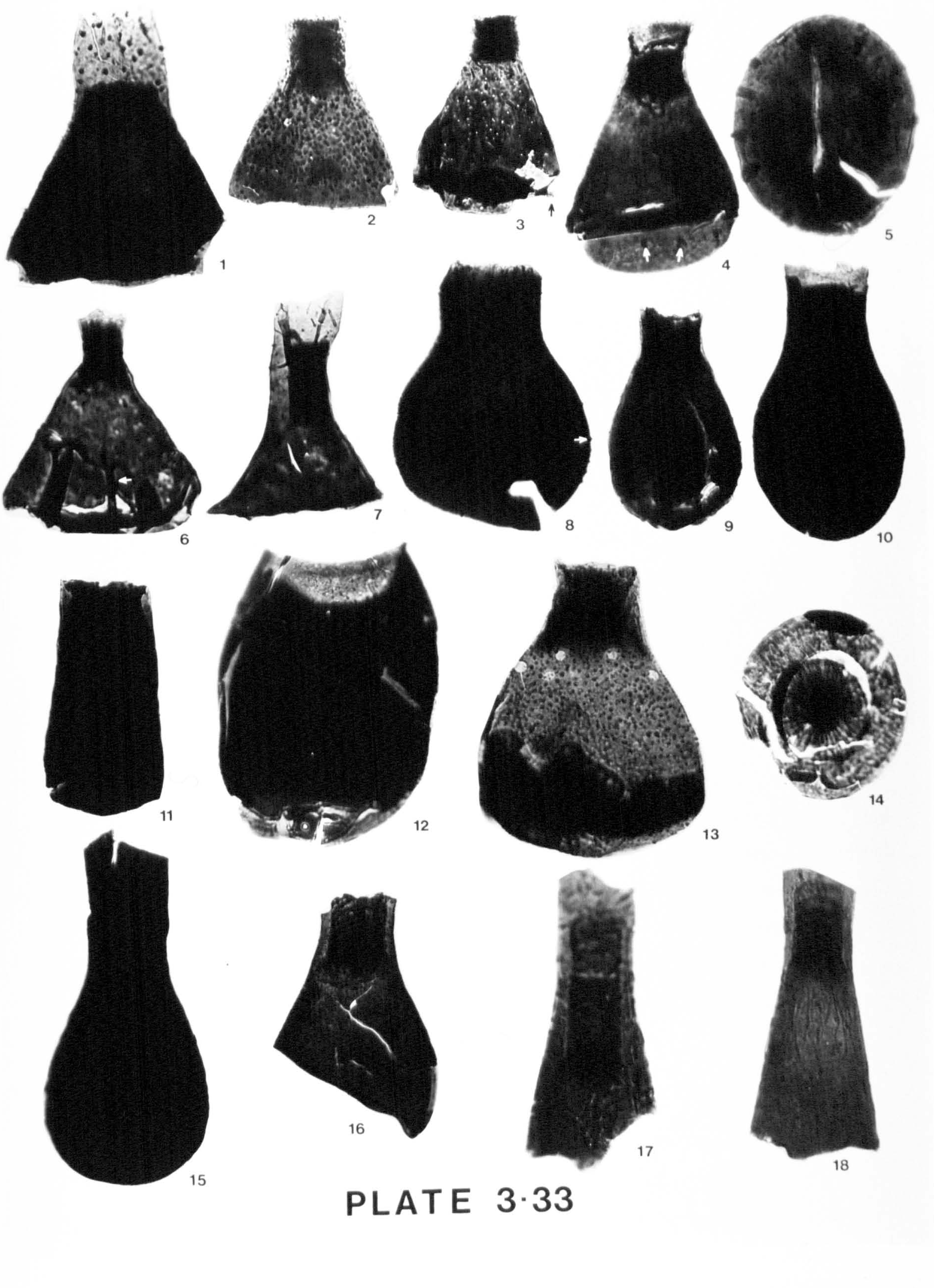


PLATE 3·33

PLATE 3.34

Plate 3.34. Scolecodonts.

Where possible, the appropriate dental formula has been calculated (adopting the approach of Jansonius & Craig, 1971; pp. 261-264). Comparisons with known species are noted below, as well as in Chapter 3. Elements have been oxidised, and are illustrated at x630 mag. unless otherwise stated.

Fig. 1 Morphotype A; coniform element; LN31 (a), 147.2/18.1.

Fig. 2 Morphotype A; coniform element; x255 magnification; LN19 (a), 152.7/8.1.

Fig. 3 Morphotype B; compound element; specimen with two pre-cuspidal denticles; 1p,2m/,3c/>6m-- ; H13 (a), 141.8/6.3.

Fig. 4 Morphotype B; compound element; x255 magnification; 1f-2p,3m...4m/>11p ; WP31 (a), 136.2/2.9.

Fig. 5 Morphotype D; compound element; 1f\-2p-<5p...11p-- ; x255 magnification; CM21 (a), 148.2/13.2.

Fig. 6 Morphotype D; compound element; ?1F\-2p...5p-6m-7p...10p ; x255 magnification; CM72 (a), 154.9/6.2.

Fig. 7 Morphotype B; compound element; dorsal fenestra well defined; 1f-2p...3p-4m/>8p; x255 magnification; LN98 (a), 135.9.24.1.

Fig. 8 Morphotype B; compound element; x1 pre-cuspidal denticle; resemblance to right dental plate of *Paulinites paranaensis* as illustrated by Lange (1949, Pl. 14, figs. 1-5) but with the ramus incomplete; 1p-2c/-3p-4m/>8p-- ; CM01 (a), 154.5/13.5.

Fig. 9 Morphotype B; compound element; resembles *Leogenys prosser* MIIs element (Frasnian), Jansonius & Craig, 1971 (Pl. 3, fig.6); 1F\-2m...6m-7m/>14p ; x255 magnification; WP26 (a), 162.1/16.9.

Fig. 10 Morphotype B; compound element; refer to Fig.9 - ?transitional to Fig.11; ?1F\-2p<5m>8p-- ;L24 (a), 157/19.8.

Fig. 11 Morphotype B; compound element; style of denticulation resembles MIs element of *Delosites* sp. ?cf. *Elleriprion demisiccus* , Jansonius & Craig, 1971 (Pl. 3, figs.12 & 13); 1F-2m>5m,6m>13p ; CM25 (a), 139.5/11.1.

Fig. 12 Morphotype B; compound element; resembles the MIId element of *Leodicites cultriformis* (Frasnian) Jansonius & Craig, 1971 (Pl.3, fig.5) 1f-2p-3m...9m/>12p ; CM23 (a), 132/6.2.

Fig. 13 Morphotype C; compound element; myocoele opening thin walled, displaying a dorsal cellular structure - resemblance to *Cheiridogenys* sp. (?MIVd, Frasnian) Jansonius & Craig, 1971 (Pl. 3, fig.2); 1m,2m>5p-- ; R21 (a), 145.1/18.2.

Fig. 14 Morphotype C; compound element; 1m...5m>8p ; K21 (a), 146.2/18.2

Fig. 15 Morphotype B; compound element; resembles the right dental plate of *Paulinites paranaensis* Lange (1949, Pl. 10, figs. 11, 12) - also refer to Fig. 12; 1f-2p-3m...6m/>12p ; CM02 (a), 149.5/18.1.

Fig. 16 Morphotype C; compound element; denticulation erect - gross morphological resemblance to *Cheiridogenys borealis* (?MIVs element; Frasnian) Jansonius & Craig, 1971 (Pl.3, fig.1); 1c,2m,3m>6p ; LN98 (a), 137.8/10.2.

Fig. 17 Morphotype C; compound element; ?cusp/falx missing - fragmented *Menogenys* sp. MIIs or MIIIs (Frasnian), Jansonius & Craig, 1971 (Pl. 3, fig. 7); ?1c\,2m>5p ;R21(a)135.1/16.1.

Fig. 18 Morphotype E; compound element; CM09 (a), 149/11.1

Fig. 19 Morphotype E; compound, bilaterally symmetrical element, x 500; R21 (a), 147/15.

PLATE 3·34

PLATE 3.35

Plate 3.35

"Wood" phytoclasts.

Fig. 1 *Plant Fragment*, Type A; LN92 (b), 132.5/16.

Fig. 2 *Plant Fragment*, Type A; LN101 (a), 146.1/8.1.

Fig. 3 *Plant Fragment*, Type A; LN101 (a), 138.5/6.1.

Fig. 4 *Plant Fragment*, Type B; LN52 (a), 150.1/7.2.

Fig. 5 *Plant Fragment*, Type B; poorly preserved specimen - "ribbing" merely preserved; LN92 (a), 140.9/11.9.

Fig. 6 *Plant Fragment*, Type B; LN92 (a), 129.1/12.1.

Fig. 7 *Plant Fragment*, Type B; H03 (a), 147.8/9.4.

Fig. 8 *Plant Fragment*, Type B; LH05 (a), 144.3/10.2.

Fig. 9 *Plant Fragment*, Type B; R21 (a), 134.9/5.1.

Fig. 10 *Plant Fragment*, Type C; S08 (a), 154.9/17.5.

Fig. 11 *Plant Fragment*, Type C; LN101 (a), 154/6.9.

Fig. 12 *Plant Fragment*, Type C; resembles the illustrations of vascular elements within the lycopsid *Bisporangiostrobus harrisii* by Chitaley & McGregor (1988, Pl. 2, figs. 4-6); K12(a) 146.5/11.5.

Fig. 13 *Plant Fragment*, Type C; S14 (a), 152.5/12.6.

Fig. 14 *Plant Fragment*, Type C; L26, scanning electron photomicrograph, x450 magnification.

Fig. 15 *Plant Fragment*, Type C; CM25, scanning electron photomicrograph, x450 magnification.

Fig. 16 *Plant Fragment*, Type C; R22, scanning electron photomicrograph, x450 magnification.

Fig. 17 *Plant Fragment*, Type C; LN101 (a), 149.2/12.3.

Fig. 18 *Plant Fragment*, Type D; K44 (a), 161.5/6.

Fig. 19 *Plant Fragment*, Type D; CM70 (a), 146/18.2.

Fig. 20 *Plant Fragment*, Type D; K12 (a), 142.6/9.2.

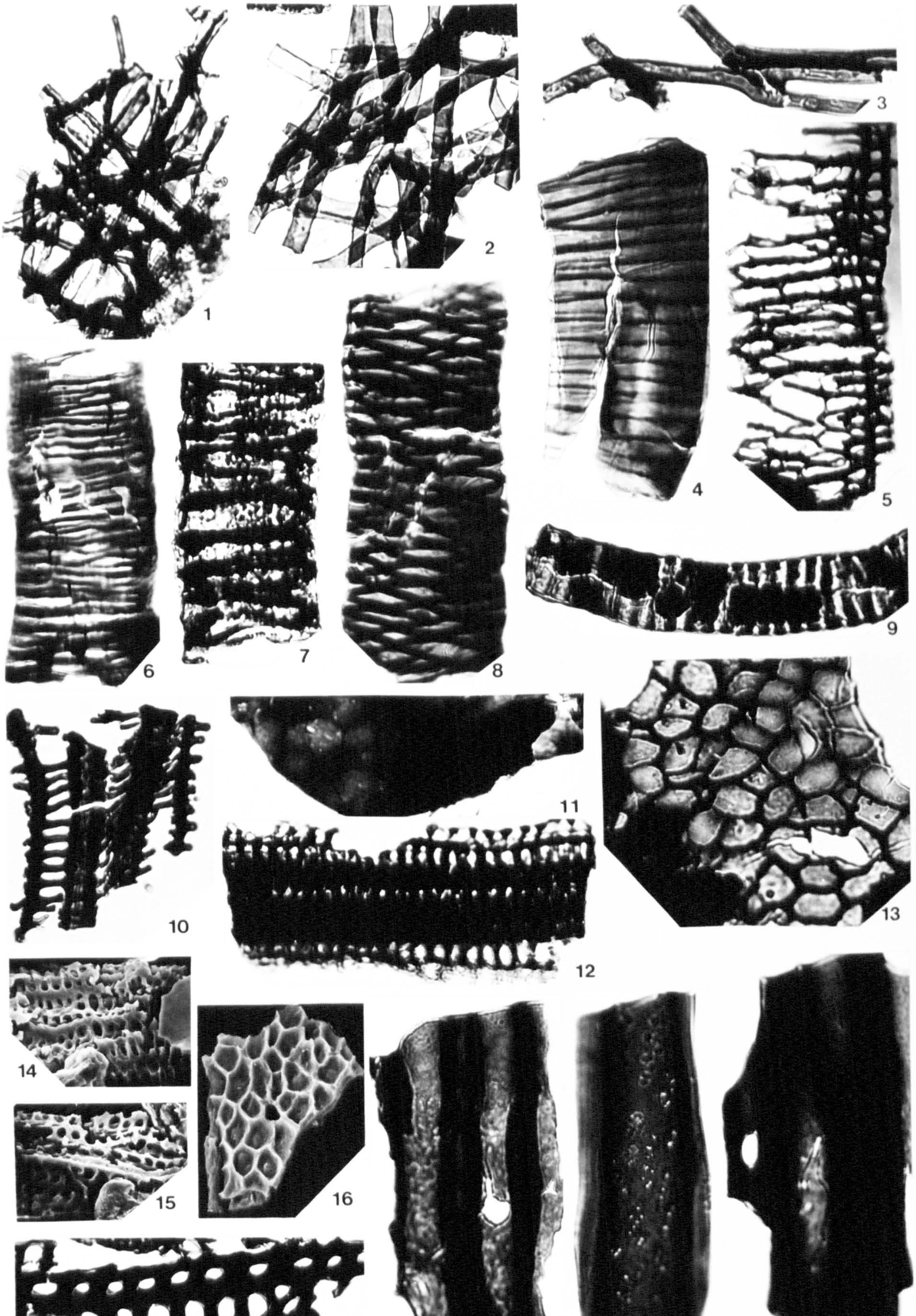


PLATE 3·35

CHAPTER 4.

BIOSTRATIGRAPHICAL SYNTHESIS

4.1 INTRODUCTION.

This chapter deals with the biostratigraphical interpretation of the various microfossil assemblages recovered from north Devon. The subsequently revised age evaluation of the sequence studied is compared with earlier assessments. Of the diverse suite of microfossils documented, conodonts and miospores provide the principal correlative indices. Other components of the microfaunal and palynofloral assemblages recovered were either so sparse, poorly preserved or of such uncertain stratigraphical distribution, that they contributed little to the overall biostratigraphical interpretation proposed herein. For clarity, the composition and related biostratigraphical implications of the conodont faunas isolated from the Lynton Formation and Ilfracombe Slates are discussed separately. Age evaluations were made by comparing the recovered faunas with both the standard conodont zonation, and the alternative *Icriodus* and *Polygnathus* zonal schemes proposed by Bultynck (1987). The biostratigraphical character of the miospore assemblages is reviewed for each major lithostratigraphical unit, and comparisons made largely with the zonal schemes proposed by Richardson & McGregor (1986) and Streel *et al.* (1987). Any speculative biostratigraphical data made available by the sparse acritarch, chitinozoa and scolecodont assemblages are discussed independent of the miospore palynostratigraphy.

Disparities are summarised between the concurrence or anomalous recovery of certain conodonts and palynomorphs detailed in the present study, with reference to known reports. A synthesis of all available biostratigraphical information for north Devon concludes the chapter. Reasons for not erecting a local, miospore-based zonational scheme are discussed.

4.2 THE CONODONT FAUNAS.

4.2.1 Introduction.

Conodonts have only been recovered from two of the four major lithostratigraphical units studied, namely the Lynton Formation and the Ilfracombe Slates. Of the calcareous horizons sampled, the Watersmeet section (of the Lynton Formation), and the Rillage, Holey, and David's Stone Limestone Members (of the Ilfracombe Slates) yielded relatively diverse and abundant faunas. Conodont faunas recovered from the Combe Martin Beach Limestone were comparatively impoverished. In general terms, faunas vary in composition from monospecific (*e.g.* CM62), to comparatively diverse (*e.g.* CM47). Abundances are also variable, ranging from <1 element kg^{-1} to corrected yields of up to 282 elements kg^{-1} (sample K53). The majority of the faunas were of low abundance and comprised 2-6 species of *Icriodus*. Sparse polygnathid faunas were exclusive to the Rillage, Combe Martin Beach and David's Stone Limestone Members, and also to sample K53. As polygnathids provide the primary index species in late Lower and Middle Devonian conodont correlations, the predominance of icriodids in north Devon was biostratigraphically unfortunate.

Problems were noted when attempting correlation between those faunas documented from north Devon, and known coeval but pelagic reference assemblages. Age assessments were therefore based on the collective biostratigraphical character of the faunas; such interpreted ages are clearly somewhat more problematical. However, despite such interpretative problems, the conodont faunas imposed a useful stratigraphical constraint upon the associated, generally more ambiguous palynostratigraphy.

Ramiform and coniform elements (by virtue of their vicarious nature), in addition to the sparse and poorly preserved tentaculitid fauna (also recovered in conodont sample preparations), did not contribute to the following age assessments.

4.2.2 The standard conodont zonational scheme for the Devonian Period.

Conodonts are one of the most biostratigraphically sensitive and useful fossil groups used for Devonian correlation. The standard conodont zonation scheme currently recognised for this System is shown, as relevant to the present study, in Fig. 4.1(a). This zonation is a synthesis of numerous conodont studies, although precise details are not discussed in this study unless of particular relevance. Conodonts have not held such a pre-eminent position in the biostratigraphical schemes devised for the Devonian of Britain as they have in other European countries. Indeed, by virtue of the nature and limited extent of marine Devonian strata within the British Isles, the scope and scale of conodont research has been severely impaired. As a consequence British faunas have made little contribution to the formulation of this globally applicable, standard conodont zonation.

A number of comparative sequences are known in Britain, with which the faunas recovered in the present study may potentially be equated (*e.g.* Matthews 1962, 1970; Kirchgasser, 1970; Hendricks *et al.*, 1971; Sadler, 1973a; Orchard 1975, 1978a, 1979; Mouravieff, 1977; Castle 1977, 1978, 1982; Drummond, 1982; Selwood *et al.*, 1984). However, in common with Owens *et al.* (1977, p. 34) and Orchard (1979), the conodont faunas detailed in the present study were compared largely with coeval assemblages reported from outside the British Isles. This was largely due to differences in faunal composition.

Klapper & Ziegler (1979) reviewed earlier biostratigraphical revisions and synoptic studies provided by, amongst others, Klapper *et al.* (1971) and Ziegler (1971). In addition they incorporate a number of refined zonal concepts into their review of a standard conodont zonation: *e.g.* the refinement of the *varcus* biozone, after Ziegler *et al.* 1976; the ten biozones established by Klapper (1977) for the Lower/Middle Devonian transitional sequences of Nevada and the Yukon Territory; the five fold zonal scheme proposed by Weddige (1977) for the Eifelian Stage, being a refinement of the 3-fold division earlier defined by Wittekindt (1966). Klapper & Ziegler (1979) also illustrate the ranges of a number of key taxa within America and Europe, relative to the zonational scheme of Klapper (1977).

From their inception within the Emsian interval, "deeper-water" polygnathids have traditionally been the favoured correlative indices, although "shallower-water" icriodids are still utilised in Lower Devonian correlation (Klapper & Ziegler, 1979). Sandberg & Dreesen (1984) and Bultynck (1987) have recently proposed alternative, Late and Middle Devonian shallow-water zonational schemes respectively (based on the temporal variation of certain Icriodontidae). These schemes allow detailed correlation between pelagic and neritic sequences. Of particular relevance to the present study was the Middle Devonian zonal scheme proposed by Bultynck (1987).

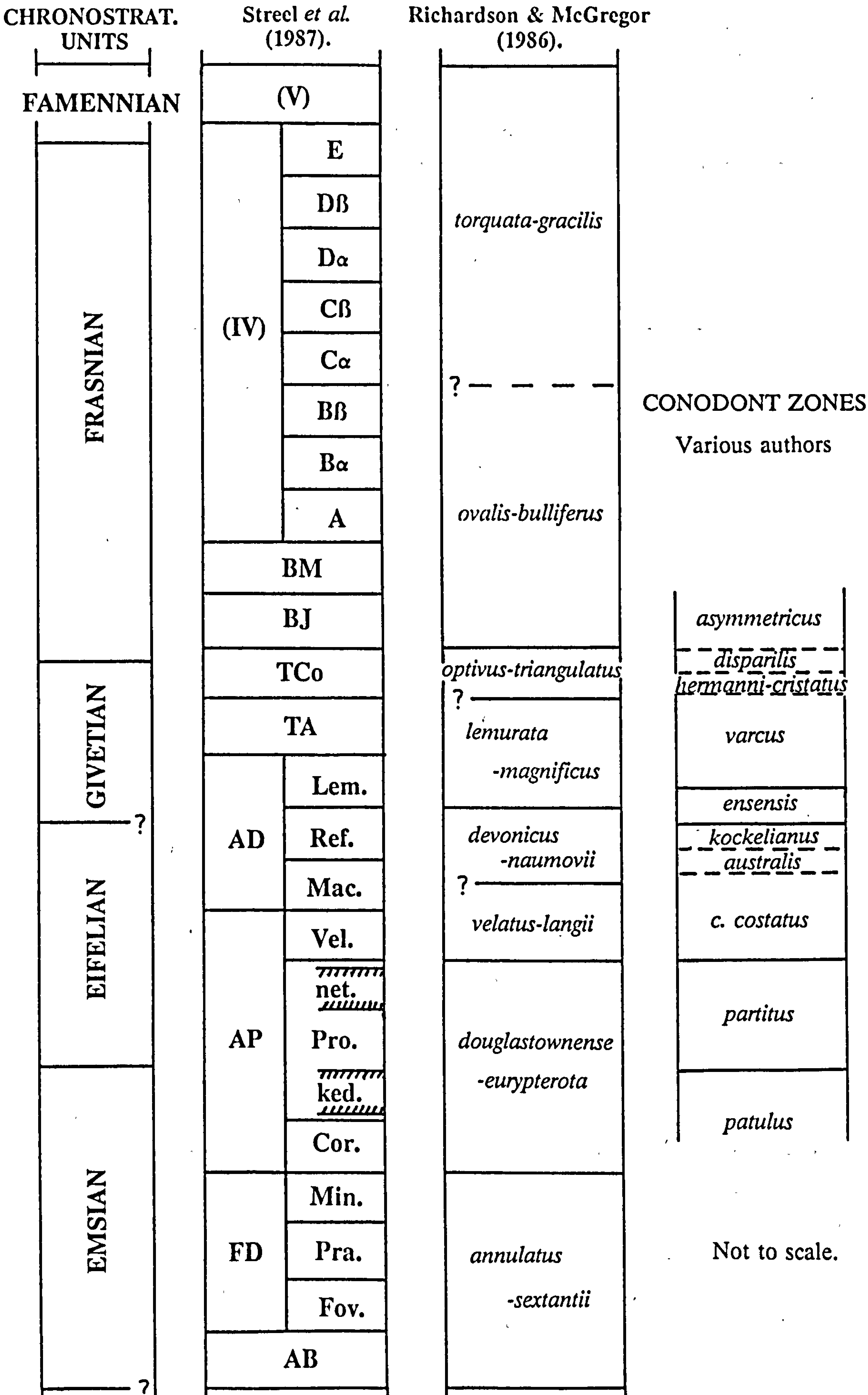


Figure 4.1(a) A comparison between the spore zones (*partim*) as proposed by Richardson & McGregor (1986) and Streel *et al.*, (1987), and the standard conodont zonation (various sources).

During the Givetian, shallow-water platform carbonates were known to be well established over a large proportion of the world (Bultynck, 1987; Tsien 1989). Within these shallow water palaeoenvironments the Icriodontidae flourished, whereas species of *Polygnathus* were invariably rare, or indeed absent. The alternative *Icriodus*-based zonation proposed by Bultynck (1987) spans the *kockelianus* Zone to the Upper *varcus* Subzone interval. Bultynck (1987) furthermore refined the standard polygnathid-based zonal scheme for the same interval (Figure 4.1(b) below).

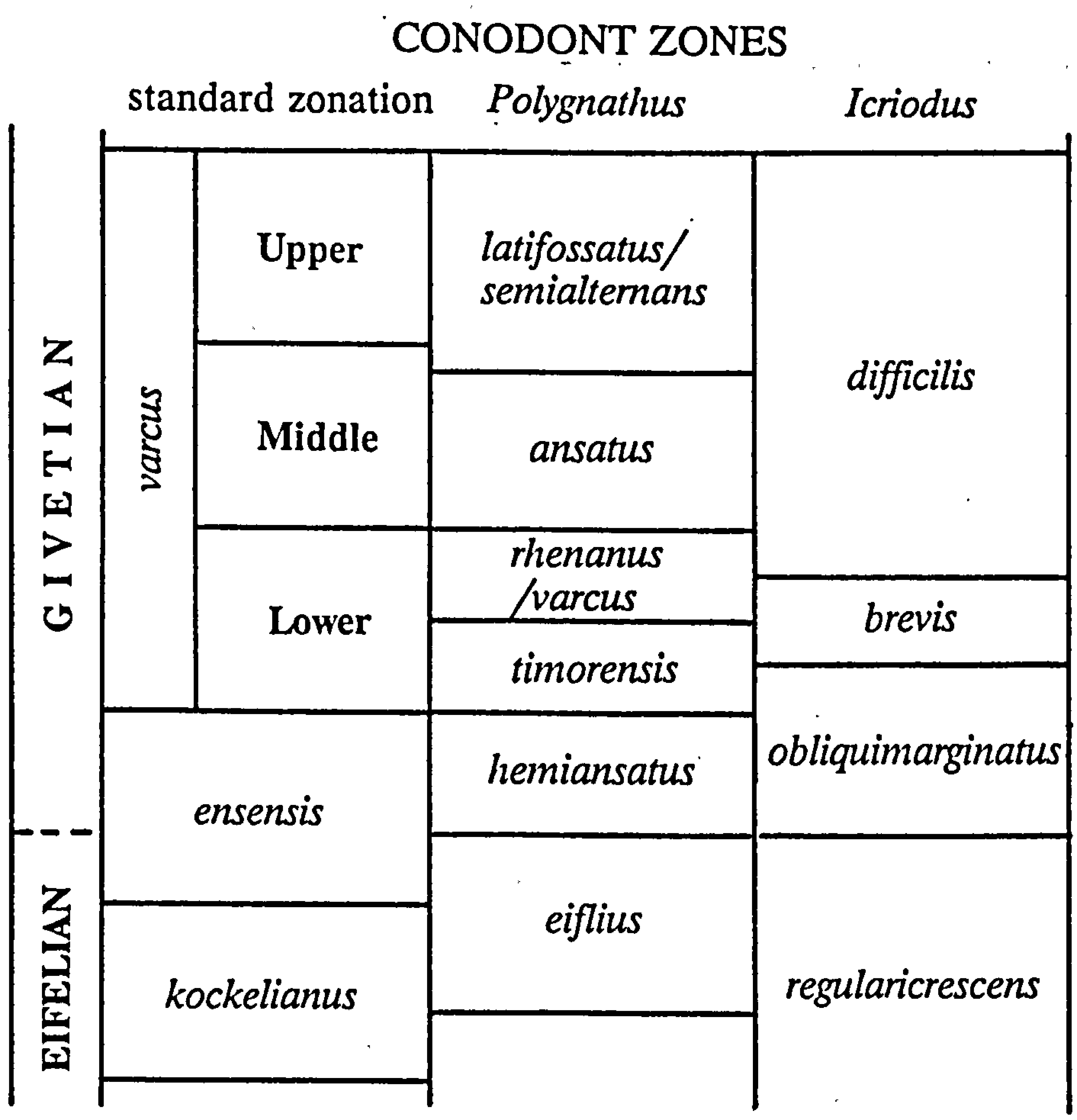


Figure 4.1(b) Alternative *Polygnathus* and *Icriodus* zonational schemes for the uppermost Eifelian and lower to middle Givetian, after Bultynck (1987). The standard conodont zonation for this interval is indicated.

In general the standard Devonian conodont zonal scheme outlined by Klapper & Ziegler (1979) was applied in the present study, supplemented by the proposals of Weddige (1982) and Ziegler & Klapper (1982). Weddige (1982) defined the *partitus* Zone, the base of which delineates the Emsian/Eifelian boundary (and thus the base of the Middle Devonian Series), and simultaneously Ziegler & Klapper (1982) established the latest Givetian *disparilis* conodont biozone - refer to Figure 4.1(a). The alternative shallow-water *Icriodus* zonation proposed by Bultynck (1987) proved useful in evaluating the age of the Ilfracombe Slates - refer to Figure 4.1(b).

4.2.3 Biostratigraphical evaluation of the conodont faunas.

The temporal distribution of conodonts through the principal carbonate units of the Devonian of north Devon is schematically shown in the accompanying figures, namely Figure 4.2 (for the Lynton Formation) and Figure 4.3 (for the Ilfracombe Slates). Appendix I(c) details the absolute number of each species per productive sample. The biostratigraphical significance of the faunas is discussed below.

4.2.3a *The conodont faunas of the Lynton Formation.*

Within the Lynton Formation, of the three localities sampled that yielded conodonts, the most varied, abundant and therefore the most biostratigraphically useful *Icriodus* fauna was recovered from the Watersmeet section (SS 746486). Consequently, the stratigraphical position and associated age of the Watersmeet section may prove central in determining the age of the entire Lynton Formation. Figure 4.2 overleaf shows the stratigraphical distribution of the five species of *Icriodus* documented through this section. The monospecific faunas recovered from the A39 road section and the Valley of the Rocks (both yielding only *Icriodus culicellus*) are of minimal biostratigraphical use.

The absence of polygnathids from this formation limits to a degree the stratigraphical significance of the conodont faunas, and may be a reflection on the palaeoenvironment (refer to the discussion in Chapter 5, Section 5.2.5a). However, despite this near exclusive recovery of icriodids, an age for the unit can be estimated. *Icriodus ?corniger corniger, I. culicellus, I. retrodepressus* and *I.* cf. *werneri* were recovered from the calcarenites exposed at Watersmeet. *Icriodus corniger corniger* (*sensu stricto*), *I. culicellus*, and *I. werneri* (*sensu stricto*) have been widely reported from Emsian and early Eifelian strata (Bultynck, 1970; Weddige 1977, 1982; Klapper & Ziegler, 1979; Bultynck, 1985). According to Weddige (1982) the inception of *Icriodus retrodepressus* coincides with the base of the *partitus* Zone [refer to Figure 4.1(a)]. The base of the *partitus* Zone is now formally recognised as defining the base of the Eifelian Stage, and thus marks the Lower/Middle Devonian Series boundary (Ziegler & Klapper, 1985, p. 105). Use of the inception of *Icriodus retrodepressus* to resolve an Eifelian age in neritic sediments is supported both by Ziegler & Klapper (1985, p.106) and Bultynck (1985, p. 263-264). In the context of north Devon, Pound (*pers. comm.*) considers the Watersmeet Section to be located within the lower third of the exposed Lynton Formation: possibly at a similar stratigraphic level to the Lee Stone Member. The combination of Pound's interpretation and the recovery of *Icriodus retrodepressus* from this section suggests that the majority of the Lynton Formation is Eifelian in age. However, the Watersmeet section is an isolated inland exposure, and despite Pound's personal communication, the precise stratigraphical position of this section has not been certainly resolved. Until this is clarified, the significance of these findings cannot be fully appreciated, although the Eifelian age interpreted (based on the conodont faunas) is compatible with the speculative age assessments provided by the palynomorph assemblages also recovered from this sequence.

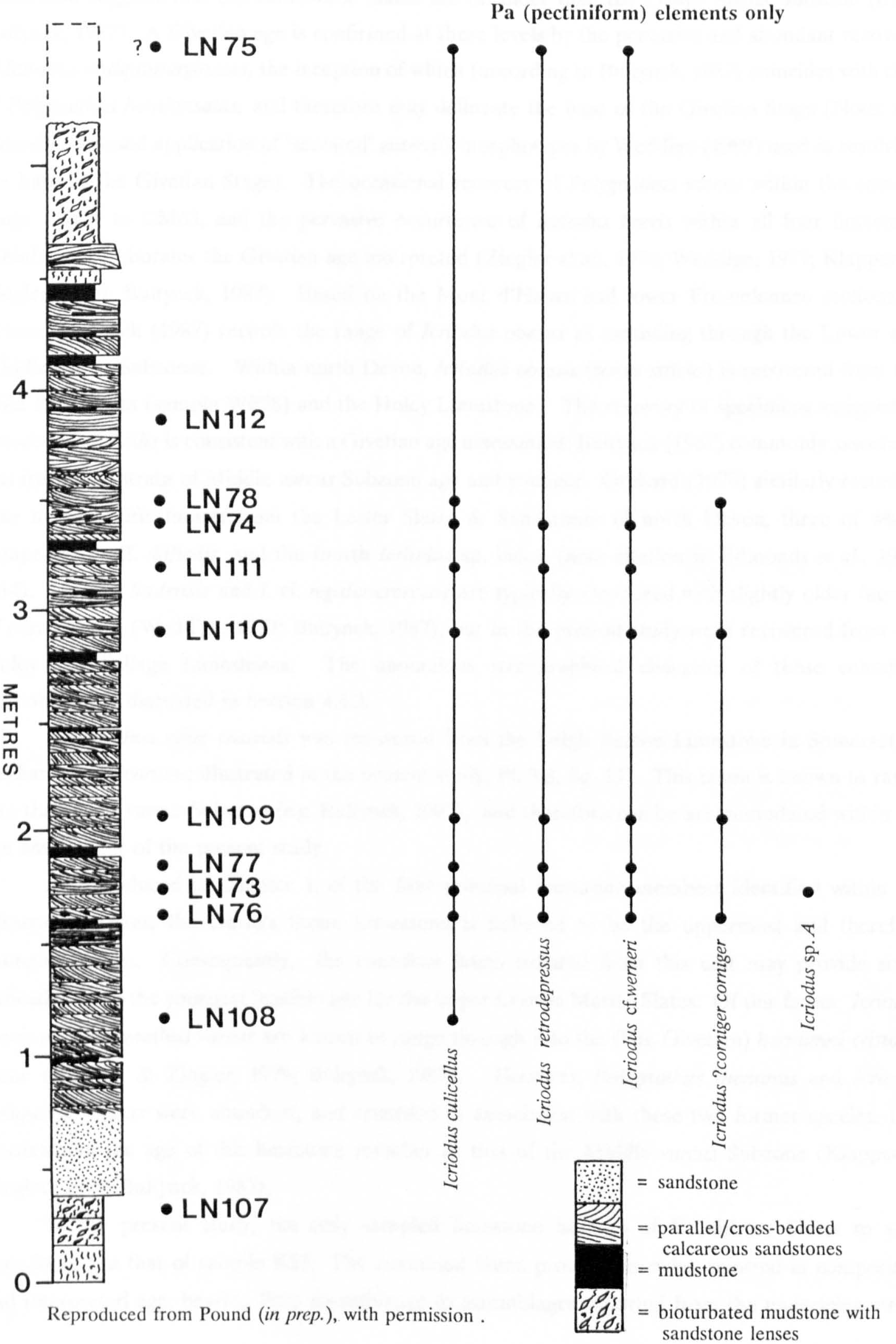
4.2.3b *The conodont faunas of the Ilfracombe Slates.*

As the relative stratigraphical position of the principal limestone members of the Ilfracombe Slates is known, the conodont-based biostratigraphical evaluation of this unit is based largely on the faunas recovered from such carbonate horizons. Faunal data are further supplemented by information collated from a few isolated calcareous horizons (*e.g.* sample K53). The temporal distribution of

FIGURE 4.2. THE TEMPORAL DISTRIBUTION OF CONODONTS THROUGH THE WATERSMEET SECTION (Lynton Formation).

WATERSMEET MEMBER Grid Ref. 7464 4866

LOG B of Pound (*in prep.*)



Reproduced from Pound (*in prep.*), with permission .

conodont taxa recovered from this lithostratigraphical unit is shown in Figure 4.3. Where appropriate, information kindly provided by Dr. M. Orchard (*pers. comm.*, 1989) is mentioned, relating to a small number of impoverished faunas recovered from the Ilfracombe Slates (exposed in Somerset).

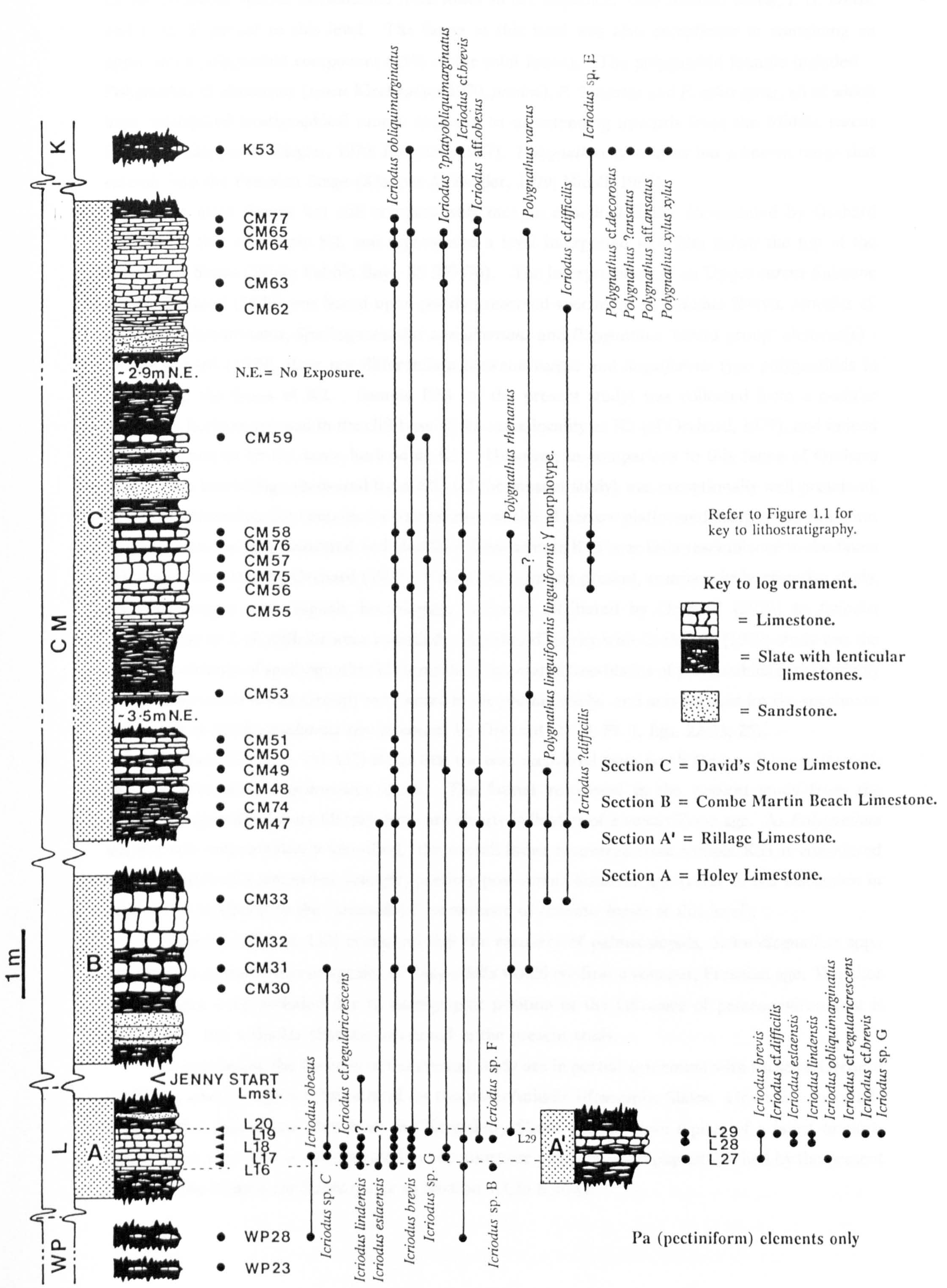
The presence of *Polygnathus rhenanus* in sample L20 of the Holey Limestone (regarded herein as a probable lateral equivalent of the Rillage Limestone, *sensu* Edmonds *et al.*, 1985), its occurrence within the overlying Combe Martin Beach Limestone, and persistence through into the David's Stone Limestone suggests that the Ilfracombe Slates are no older than the Lower *varcus* Subzone (from Bultynck, 1987). A Givetian age is confirmed at these levels by the pervasive and abundant recovery of *Icriodus obliquimarginatus,* the inception of which (according to Bultynck, 1987) coincides with that of *Polygnathus hemiansatus,* and therefore may delineate the base of the Givetian Stage (Note: the recently proposed application of "serrated" *ensensis* morphotypes by Weddige (1989) used in resolving the base of the Givetian Stage). The occasional recovery of *Polygnathus varcus* within the sample range CM31 to CM65, and the pervasive occurrence of *Icriodus brevis* within all four limestone Members corroborates the Givetian age interpreted (Ziegler *et al.*, 1976; Weddige, 1977; Klapper & Ziegler, 1979; Bultynck, 1987). Based on the Mont d'Haurs and lower Fromelennes sections in France, Bultynck (1987) records the range of *Icriodus obesus* as extending through the Lower and Middle *varcus* Subzones. Within north Devon, *Icriodus obesus* (*sensu stricto*) is recovered from the Wild Pear Slates (sample WP28) and the Holey Limestone. The recovery of specimens assigned to *Icriodus* cf. *difficilis* is consistent with a Givetian age assessment: Bultynck (1987) commonly associates this form with strata of Middle *varcus* Subzone age and younger. Orchard (1979) similarly recorded four monospecific faunas from the Lester Slates & Sandstones of north Devon, three of which comprised *I.* aff. *difficilis,* and the fourth *Icriodus* sp. indet. (note citation in Edmonds *et al.*, 1985, p.14). *Icriodus lindensis* and *I.* cf. *regularicrescens* are typically associated with slightly older faunas, of *ensensis* age (Weddige, 1977; Bultynck, 1987), but in the present study were recovered from the Holey and Rillage Limestones. The anomalous stratigraphical character of these conodont assemblages is discussed in Section 4.4.2.

Polygnathus xylus ensensis was recovered from the Leigh Barton Limestone in Somerset by Orchard (*pers. comm.*; illustrated in the present study, Pl. 3.8, fig. 13). This taxon is known to range into the Lower *varcus* Subzone (*e.g.* Bultynck, 1987), and therefore can be accommodated within the age assignment of the present study.

As introduced in Chapter 1, of the four principal limestone members identified within the Ilfracombe Slates, the David's Stone Limestone is believed to be the uppermost and therefore youngest in age. Consequently, the conodont fauna isolated from this unit may provide some indication as to the youngest feasible age for the upper Combe Martin Slates. Of this fauna, *Icriodus brevis* and *Polygnathus varcus* are known to range through into the (late Givetian) *hermanni-cristatus* Zone (Klapper & Ziegler, 1979; Bultynck, 1987). However, *Polygnathus rhenanus* and *Icriodus obliquimarginatus* were abundant, and recorded in association with these two former species, thus constraining the age of this limestone member to that of the Middle *varcus* Subzone (Klapper & Ziegler, 1979; Bultynck, 1987),

In the present study, the only sampled limestone horizon of Kentisbury Slates to yield conodonts was that of sample K53. The contained fauna proved somewhat unusual in composition and interpreted age, bearing little resemblance to assemblages reported from the underlying strata.

FIGURE 4.3. THE TEMPORAL DISTRIBUTION OF CONODONTS THROUGH THE PRINCIPAL LIMESTONE HORIZONS OF THE ILFRACOMBE SLATES.



Of the conodont species documented from lower in the sequence, only *Icriodus brevis*, *I.* cf. *brevis*, and *I.* sp. E persist to this level. The fauna at this level was also exceptional in containing an appreciable polygnathid component (25% of the total fauna). The polygnathid faunule included *Polygnathus* cf. *decorosus* (*sensu* Kirchgasser 1970, *partim*), *P. ?ansatus* and *P. xylus xylus*, all of which have established stratigraphical ranges exclusive to or extending upwards from the Middle *varcus* Subzone (Klapper & Ziegler, 1979; Bultynck, 1987). *Polygnathus xylus xylus* has a known range that extends into the Frasnian Stage (Klapper & Ziegler, 1979; Nicoll, 1985).

The most diverse but still comparatively meagre conodont fauna documented by Orchard (1979) was that of sample K2, and represented a level interpreted as ≈50m below the top of the Kentisbury Slates (White Pebble Bay - SS 509476). The interpretation of an Upper *varcus* Subzone age by Orchard (1979) was based upon poorly preserved specimens of *Icriodus ?brevis, Icriodus* cf. *difficilis, I. latecarinatus*, *Spathognathodus semialternans* and *Polygnathus* "*varcus* group" element(s) - N.B. Orchard (1979), does not differentiate between *varcus* and *linguiformis* type polygnathids in quantifying the fauna of K2. Sample K53 (of the present study) was collected from a nodular carbonate horizon exposed in the cliff base at the same locality as K2 (of Orchard, 1979), and indeed was presumed to be the same horizon as K2. However, in comparison to this fauna of Orchard (1979), the assemblage recovered from K53 (of the present study) was exceptionally well preserved, and as mentioned earlier contained a comparative wealth of narrow platformed polygnathid elements. Furthermore, the taxa recovered and identified from sample K53 bear little resemblance to the fauna listed and illustrated by Orchard (1979). Furthermore in the present, comparatively extensive study, no morphotypes even vaguely homologous to forms attributed by Orchard (1979) to *Icriodus latecarinatus* or *I.* cf. *difficilis* were recorded. Another disparity with Orchard's (1979) study was the complete absence of spathognathodid elements. Dissociated free-blades of polygnathids (questionably of the *Polygnathus varcus* Group) were noted in the present study, and may account for the specimens illustrated as *Spathognathodus semialternans* by Orchard (1979; Pl. 1, figs. 22-23, 25).

Orchard (1979, p. 131-132) states that the taxa recovered from north Devon all range through into the (Frasnian) *asymmetricus* Zone. The faunas recovered in the present study from the underlying (pre-Kentisbury Slates) strata are clearly indicative of a *varcus* Zone age. As *Polygnathus ansatus* was only tentatively identified, the overall fauna recovered from sample K53 is considered representative of a somewhat younger, possibly post-*varcus* Subzone age (refer to the discussion in Section 4.4.2 relating to the "anomalous" occurrence of *Icriodus brevis* at this level).

Orchard (1979, p. 132) remarked that the recovery of palmatolepids, *Schmidtognathus* spp., *Polygnathus asymmetricus* or species of *Ancyrodella* would confirm a younger, Frasnian age. Whether these genera were excluded due to stratigraphic position or the influence of palaeoenvironment is conjecture, but a similar absence was noted in the present study.

In conclusion, the findings of the present study are in partial agreement with those of Orchard (1979), as a *varcus* age is substantiated for the lower/middle Ilfracombe Slates. However, this study suggests that faunas recorded from the Kentisbury Slates appear more typical of a latest or post-*varcus* Zone age. This is corroborated by the miospore palynostratigraphy established by the present work for the Kentisbury Slates (refer to Section 4.3.5a below).

4.3. MIOSPORES.

4.3.1 Zonal concepts.

Devonian miospore zonations of global applicability are a comparatively recent development, as faunal indices have previously been preferred. However, this is surprising, as in principle miospores are potentially ideal zonal indices, being preserved within both marine and continental facies and thus allowing correlation between these distinct sedimentary regimes. Additional biostratigraphic attributes include their abundance, high preservation potential and wide dispersal presumably by wind and water. Apart from autochthonous coals, the composition of dispersed miospore assemblages preserved in sediments is believed to represent the vegetation of the associated drainage basin (Richardson & McGregor, 1986): the source for the dispersed miospores recovered in the present study is presumed to be the flora that colonised the land area situated to the north. The prevalence of a particular parent plant onshore, the influence of proximity to the palaeoshoreline, or the simple mechanisms of sediment sorting are accepted to influence the qualitative and quantitative characteristics of an assemblage.

As is customary with other aspects of palaeontology, in palynology certain miospore taxa have been identified as biostratigraphically important. Recognition of the inception or disappearance of such forms provides the basis for local, regional or intercontinental correlation. Hughes & Moody-Stuart (1967, 1969; refer also to Hughes 1989, and references therein) departed from traditional taxonomic and biostratigraphical philosophies however, in devising the "biorecord" concept: a biorecord was designed as a conceptual taxon, having the same scope as traditional "species", but each individual biorecord may consist of a stated number of fossils from a stated unit of rock. Using this taxonomic approach, Hughes (and associates) proposed the concept of "bracket correlation" (refer to Hughes 1989, pp. 90-97), whereby "palyn-events" are correlated with a known, standard reference "event-section". This approach has, however, not been widely adopted, largely due to the inertia of traditional methodologies as favoured and applied by taxonomists and biostratigraphers. More recently, Van der Zwan (1980) and subsequently Loboziak & Streel (1981) defined a number of palynological "phases" to facilitate regional correlation. According to Van der Zwan (1980, p. 192), "phases" represent successive evolutionary steps in the gradual compositional development of palynological assemblages. Despite the biological realism of this concept, such an approach has similarly not been widely applied.

General problems associated with Devonian palynostratigraphy have been reviewed at length by several authors, including Owens & Richardson (1972), Richardson (1974) and McGregor (1979a,b). McGregor (1979a) discussed in detail the utility of spores in Devonian stratigraphical correlation, and summarised the stratigraphical variability in the dispersed miospore record as reported from a number of important Devonian reference sequences. However, it was not until 1986 that Richardson & McGregor proposed a nineteen-fold assemblage zonation for the Silurian and Devonian strata of the Old Red Sandstone Continent and adjacent regions - parts relevant to the present study are shown in Fig. 4.1(a). Prior to Richardson & McGregor (1986) there had been no unified spore zonation for this interval, which in certain respects was understandable. As McGregor (1979a) and Richardson & McGregor (1986) remarked, few studies have attempted to calibrate Devonian palynostratigraphies with more established zonations (such as those of conodonts or ammonoids). Furthermore, a large proportion of miospore biostratigraphical studies had been based upon largely barren, sparsely fossiliferous continental sequences.

In part, the zonation proposed by Richardson & McGregor (1986) incorporated zones (albeit in modified form) that had earlier been proposed for parts of the Devonian System, *e.g.* Streel (1966, and subsequent papers), Richardson (1974) and McGregor & Camfield (1976). They used the apparent instantaneity in the geographical distribution of certain taxa within a variety of sedimentary facies, as well as the co-occurrence of other characteristic species, in defining Assemblage Zones. Richardson & McGregor (1986) remark, as do others, that it is advisable to assess the stratigraphical character of an entire assemblage, rather than to rely exclusively upon one or two index taxa in age evaluation (as demonstrated by the "delayed" appearance of *Geminospora lemurata* within the Boulonnais region, France - Loboziak & Streel, 1980; 1981; 1988). Richardson & McGregor (1986) also defined the bases of some of the zones by the first manifestation of certain major morphological adaptations to spore design. These "events" (as termed by Richardson & McGregor, 1986) were considered to have greater temporal and geographical significance than the events referred to by Hughes (1975, p. 142; 1989).

Richardson & McGregor (1986, p. 4) remark that the plant megafossil zonation of Banks (1980) compares favourably in part with their proposed spore zones. Discrepancies were believed to stem from the difficulty of correlating between continental and marine strata.

Streel *et al.* (1987) subsequently synthesised over 25 years of work on the stratigraphical distribution of Devonian spores in the Ardenno-Rhenish regions (refer to Streel 1986b, for citation and comments). Their zonal scheme [shown in part in Fig. 4.1(a)] attempted to integrate spore, marine faunal and megafloral data, and comprised a number of Oppel and Interval Zones (fifty-one zones in total). The application of the Oppel Zone concept by Streel *et al.* (1987) followed the definition of Hedberg (1976, p.58) and approximates to the "assemblage zone" of the North American stratigraphic code (1983, p.863). An Oppel Zone was thus defined as "a zone characterised by an association or aggregation of selected taxa of restricted and largely concurrent range, chosen as indicative of approximate contemporaneity". Streel *et al.* (1987) also proposed Interval Zones following the definition of Hedberg (1976, p. 60 - refer to Streel *et al.*, 1987, p. 212).

Streel *et al.* (1987) was critical of the zonal scheme of Richardson & McGregor (1986), for mixing the characteristics of both Interval and Oppel Zones within their Assemblage Zones. On face value, the comments of Streel *et al.* (1987) are valid, as Richardson & McGregor's amalgamation of information (encompassing the concurrence of certain taxa, the inception of selected species and the appearance of particular morphological attributes) does seem an oversimplification of available data. By comparison, Streel *et al.*'s (1987) comprehensive fifty-one fold zonational scheme appears well founded and clearly differentiated, with Richardson & McGregor's (1986) nineteen-fold zonation appearing overly simplistic in construction. However, in the present study the applicability of parts of Streel *et al.*'s (1987) zonal scheme was found to be severely impaired, largely due to their choice of zonal taxa and the absence of these forms within the sections studied in north Devon; *e.g.* the designation by Streel *et al.* (1987) of certain taxa (for example *Corbulispora* sp.) as index species in defining the Interval Zones within Phases IV & V (spanning the ?mid Frasnian to early Famennian interval), seems completely inappropriate for purposes of regional correlation. Similar difficulties were expressed by Marshall (1988, p. 15) in evaluating the age of the Devonian miospore assemblages recovered from Papa Stour, Shetland. As a consequence, the zonation scheme of Richardson &

McGregor (1986) proved the more viable and realistic to apply to north Devon. The zonal taxa used in this scheme are readily identifiable forms, widely known within contemporaneous assemblages around the globe.

4.3.2. Miospore assemblages recovered from the Devonian strata of north Devon.

Miospores proved the most pervasive, abundant and diverse microfossils recovered from the marine-influenced sediments of north Devon. Assemblage diversity was rarely less than six distinct miospore taxa per sample, and more typically ranged between 15 and 30 taxa. As discussed in Chapter 2, sections 2.6 & 2.8, sample productivity was difficult to quantify, though qualitatively the kerogens were composed almost exclusively of terrestrially derived material.

What little comparative work has been published on the palynology of marine Devonian sediments is based almost entirely on borehole material from southern Britain. Mortimer (1967, 1969), Mortimer & Chaloner (1972), Owens *et al.* (1977), Richardson & Rasul (1978a,b), Dean (1989a,b) and Wilkinson & Knight (1989) document certain taxa which were reported in the present study, and are therefore potential correlatives. However, the lack of detailed correlation between these disjunct British sections, coupled also with the lack of documentation of miospore assemblages, necessitated reference to palynostratigraphies established outside the British Isles. Owens *et al.* (1977, p. 29) adopted a similar approach. The schemes of Richardson & McGregor (1986) and Streel *et al.* (1987) thus provide the basis of age evaluations for the miospore assemblages reported herein (refer to Fig. 4.7 for a synopsis of the principal palynological events recorded). Unlike most traditional palynological studies, the palynofloras detailed from north Devon were not compared with coeval assemblages reported from individual regions or floral provinces around the globe. Much of the information that may have been deduced from such a literature search has already been synthesised within the two zonal schemes introduced above.

The overall biostratigraphical characteristics of the miospore assemblages recorded from each major lithostratigraphical unit are discussed in the following sections. The stratigraphical distribution of miospores in the palyniferous sediments of the Lynton Formation, Hangman Sandstone Group and Ilfracombe Slates (*pars*) are detailed in Figures 4.4, 4.5 & 4.6 respectively. Samples were sequentially related to a schematic lithostratigraphical log for each unit, provided that the sedimentology of the succession was sufficiently well known (refer to remarks on sample collection in Chapter 2, Section 2.4.2). Only the productive, palyniferous samples are represented on these range charts; barren samples are merely listed in Appendix II. The overall stratigraphical evaluation of the sequence (synthesised in Section 4.8 below) is based largely on this miospore data base, irrespective of previous macropalaeontological and micropalaeontological observations.

Problems were encountered in confidently ordering samples stratigraphically through the Kentisbury and Morte Slates (refer to Chapter 2). Taxa recovered from these units are therefore recorded in simple presence/absence tables (Tables 4.1 & 4.2, respectively). Detailed structural and sedimentological remapping of the area is necessary to elucidate the relative positions of these palynological samples, and thus their associated palynology. The stratigraphical significance, of the associated acritarch, chitinozoa and scolecodont component is assessed independently.

Occasionally, the latest occurrence (disappearance) of many taxa proved uncertain. Indeed, despite the comparative wealth in species diversity, it was often difficult to gauge the influence of reworking on assemblage composition, as preservation was usually moderate to good and absolute numbers of dispersed miospores ubiquitously low.

Local palynozones are not proposed in this study, largely because of the general applicability of currently defined schemes, and also due to the lack of independent biostratigraphical evidence in north Devon provided by other faunal or floral indices. Indeed, the precise evolutionary inception or demise of a number of taxa noted in the sections studied remains unresolved. In part sedimentary facies appear to exert an influence on miospore distribution (*e.g.* the disappearance of miospores in the Hollowbrook Formation, and also the depletion in palynomorph assemblages towards the top of the Kentisbury Slates). Only for the Kentisbury and Morte Slates was there potential for defining a local zonation, as the composition and quality of the assemblages recovered from both these units limited the applicability of established zonations. However, sample locational problems and the overall ambiguity of age evaluations for these units (based on miospore data), suggested such a proposal unwise.

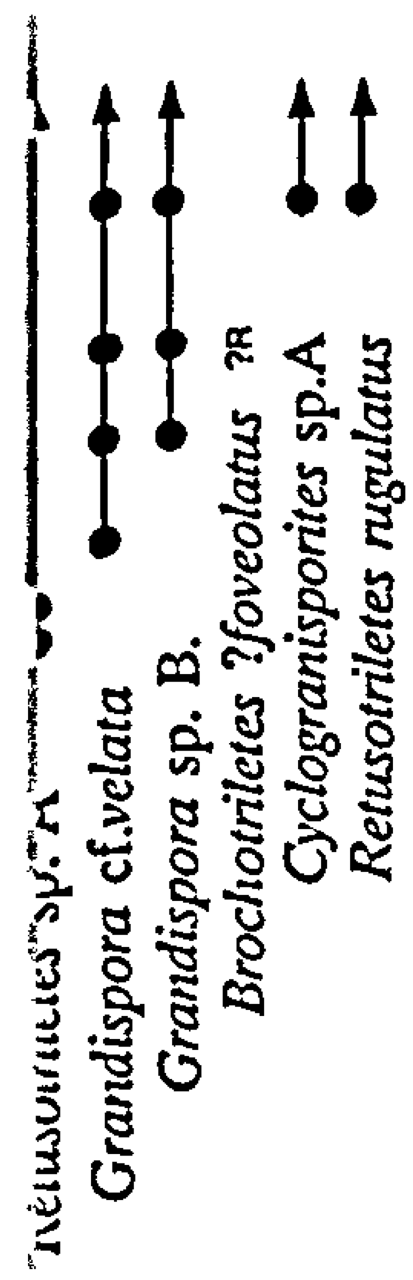
4.3.3 The Lynton Formation.

4.3.3a *The miospore palynostratigraphy of the Lynton Formation.*

The stratigraphic distribution of 60 miospore taxa recorded from the Lynton Formation is illustrated in Figure 4.4. Of this miospore population, the presence of two taxa is attributed to probable reworking, with 14 being recorded exclusive to this formation and the remaining 44 ranging through into the overlying Hangman Sandstone Group. Of the 60 taxa recorded, 22 were found pervasively through the Lynton Formation, with 31 making their first appearance within this unit. The vast majority of the miospore assemblages recovered from this unit were dominated by comparatively simplistic, acamerate miospore. Prolific numbers of *Apiculiretusispora* spp., *Emphanisporites* spp., *Dibolisporites* spp., *Retusotriletes* spp., and *Tholisporites* spp., were noted. Pseudosaccate miospores and cingulizonate forms were less common.

The occurrence of *Grandispora douglastownense* and *Ancyrospora* cf. *eurypterota* in the Lynton Formation allow resolution of the *douglastownense-eurypterota* Assemblage Zone of Richardson & McGregor (1986). The presence and comparative diversity of hystricospores and ancyrospores throughout the Lynton Formation corroborate this interpretation. In the definition of their miospore zones, Richardson & McGregor (1986) recognised a number of important morphological adaptations in spore construction. These mark important phases or "events" in the evolutionary development of dispersed miospores, and generally reflect an increase in morphological complexity and constructional diversification through the Devonian Period. During late Emsian times, and coincidental with the definition of the base of the *douglastownense-eurypterota* Zone, Richardson & McGregor (1986) identified the appearance of spores with bifurcate-tipped processes. Assemblages recorded from the base of the exposed Lynton Formation (at Yellow Stone, SS 706499) contain a profusion of bifurcate-tipped sculptured miospores (*e.g Hystricosporites ?corystus*). Within subsequent samples, "bifurcates" comprise as much as 20% of the total assemblage, although the opacity and fragmentary condition of many of these specimens restrict precise identification.

Approximately 40m above the exposed base of the Lynton Formation (*sensu* Pound, *in prep.*) the inception of *Grandispora protea* was documented (although in depleted numbers). According to Streel *et al.* (1987), and based on Riegel (1975), the base of the Eifelian Stage in the type Wetteldorf



KEY.

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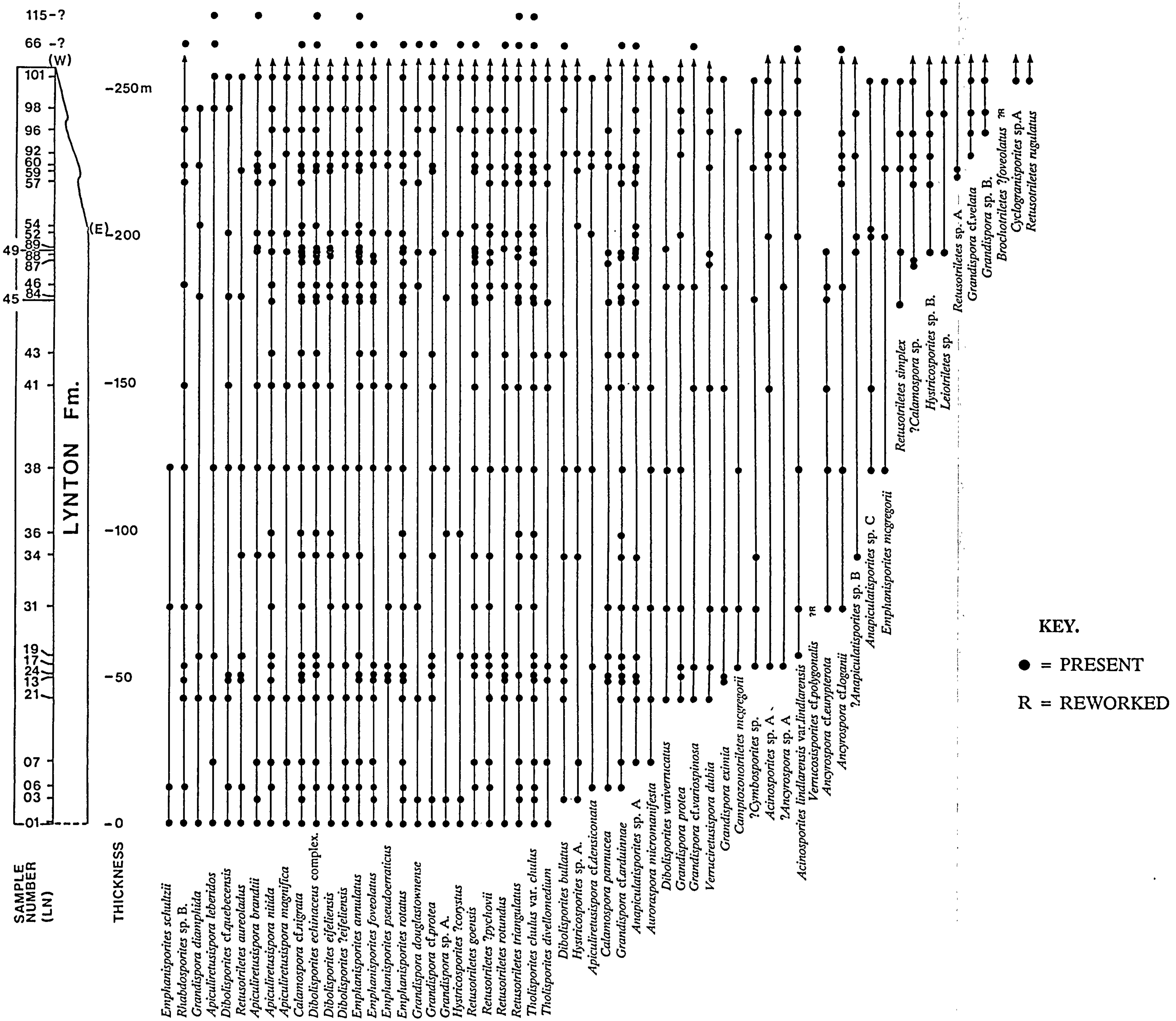
FIGURE 4.4 THE TEMPORAL DISTRIBUTION OF MIOSPORES THROUGH THE LYNTON FORMATION.



section lies within the *Pro* Interval Zone, the base of which is defined by the entry of *Grandispora protea*. According to Richardson & McGregor (1986) and Streel *et al.* (1987) the subsequent first appearance of *Grandispora velata* (*viz. Calyptosporites velatus*) can be used to indicate an early Eifelian age (note usage by Loboziak & Streel 1989, p. 193, Fig. 2). At 30.5m below the top of the Lynton Formation, and also within the conformably overlying palyniferous Hollowbrook Formation, a complex of miospores referred to *Grandispora* cf. *velata* and intergradational between *G. velata* and *G.* cf. *protea* were recorded. As discussed in Chapter 3, these aberrant forms resemble *Grandispora velata* (*sensu stricto*), but are smaller and have an occasional tendency to display more bulbous *G. protea* type" sculpture. Unfortunately, the associated palynoflora recovered from these horizons in north Devon did not contain any other zonal miospores (for example *Rhabdosporites langii*), which would thus have confirmed an early Eifelian age. However, the presence of a number of other taxa (*e.g. Retusotriletes rugulatus*) from the top of the Lynton Formation and through into the overlying Hollowbrook Formation may have some stratigraphical significance. Within the zonal scheme outlined by Richardson & McGregor (1986) the first appearance of *R. rugulatus*, for example, is defined as within the *velatus-langii* Assemblage Zone, and therefore indicative of an Eifelian age. Collectively the miospore data suggest that the Lower/Middle Devonian Series boundary is probably located somewhere within the ?middle/upper Lynton Formation (tentatively confirmed by the conodont fauna recovered from the Watersmeet Section in the present study).

Most miospore assemblages recovered from the Lynton Formation contained a diversity of *Emphanisporites*, including *E. annulatus*, *E. foveolatus* and *E. rotatus*. *Emphanisporites mcgregorii*, *E. pseudoerraticus* and *E. schultzii* were rare, with the latter species confined to the lower ≈125m of the formation. *E. annulatus* has been recorded from sediments as young as latest Devonian (Clayton *et al.*, 1977; Higgs *et al.* 1988) but its inception is biostratigraphically significant, being approximately related to the base of the Emsian Stage (*sensu* Riegel & Karathanasopoulos, 1982; Richardson & McGregor, 1986; Steemans, 1989). *E. schultzii* is predominantly associated with sediments of Emsian age. *E. foveolatus* has been used in the resolution of the Lower Emsian, having been recorded for example exclusively from the Klerf Formation of the Eifel region (Riegel, 1982, and subsequently by Streel *et al.*, 1987 - note documented occurrences listed in Section 4.5.3 below). Representatives of the *Dibolisporites* plexus were common in this unit, though of minimal biostratigraphical value. *D. echinaceus*, *D. ?eifeliensis*, *D. eifeliensis* and *D. bullatus* proved locally abundant: concords with the known proliferation of this plexus within the "Wettledorf Richtschnitt" in the Eifel Region (Riegel 1982, Table 1). According to Richardson & McGregor (1986) *Tholisporites chulus* var. *chulus* is believed to range through from Silurian into earliest Middle Devonian strata, and thus its presence within north Devon approximates to the known global demise and eventual disappearance of this taxon. *Verruciretusispora dubia* was also recovered from the Lynton Formation. Streel *et al.* (1987), after Riegel (1975), cite the occurrence of *Verruciretusispora dubia* in partial definition of the ≈mid Emsian FD (*foveolatus-dubia*) Oppel Zone, although this taxon is known to range into Middle Devonian strata (*e.g.* Richardson & McGregor, 1986).

4.3.3b *Comparisons with published reports of palynomorph assemblages from Devonian strata of Britain.*

The overall composition of the miospore assemblages recovered from the Lynton Formation does not correlate closely with published miospore data of interpreted similar age from elsewhere in the Britain Isles (*e.g.* Mortimer & Chaloner, 1972; Richardson & Rasul, 1978a,b; Dean 1989a). The youngest Lower Devonian miospore assemblages reported from the Senni Beds in South Wales are probably mid-late Pragian in age, and clearly of an earlier age relative to those of the Lynton Formation (refer to Mortimer, 1967; Richardson, 1967; Richardson & Lister, 1969).

In detail, Mortimer & Chaloner (1972) report on the palynology of concealed Devonian rocks of southern Britain, and remarked that miospore assemblages of Emsian age were noted in the Beckton, Brightling and Canvey Island Boreholes (p. 40-41, Table 6): considered of Old Red affinity, largely due to sediment colouration (refer to the remarks in Mortimer & Chaloner, 1972; p. 9). Overall, the taxa listed for each of these boreholes (Mortimer & Chaloner, 1972; p. 6-8, Table 2) bear little resemblance to the assemblages documented from either the Lynton Formation or the palyniferous lower Hangman Sandstone Group (mentioned here, as the miospore assemblages are homogeneous between these two units). The presence of *Hystricosporites* sp. A in the Brightling and Canvey Island Boreholes (Mortimer & Chaloner, 1972) suggests an age no older than late Emsian, and thus the documented assemblages are tentatively regarded as contemporaneous with those reported from the Lynton and Hollowbrook Formations. This correlation is however speculative, being based purely upon limited, published palynological evidence.

In association with reworked Tremadocian acritarchs, Richardson & Rasul (1978a,b) document comparatively diverse miospores assemblages of mid Emsian age from the Apley Barn Borehole, Witney, Oxfordshire (the age interpretation based largely upon the occurrence of *Emphanisporites annulatus*). Overall, the miospore assemblages reported by Richardson & Rasul (1978a,b) were simplistic, comprising spores of simple construction: ; acamerates dominate, with no mention made of spores with bifurcate-tipped sculpture (*i.e.* hystricospores or ancyrospores). Richardson & Rasul (1978a,b) remarked that the miospore assemblages from the Apley Barn sequence compared closely with assemblages reported by Richardson (1967) from the Strathmore Group, Perthshire and the "Basement Group" (Old Red Sandstone) of the Strathpeffer area (Richardson, 1967). By implication, these units are similarly older in age than the Lynton Formation.

Recently, Dean (1989a) has reported a probable late Emsian (possibly younger) miospore assemblage from the Bovisand Formation and Lower Staddon Grits of the Meadfoot Group, south Devon. Dean highlights a paucity of marine palynomorphs compared with spores, and notes the latter to be most abundant within the transitional beds between these two distinct lithostratigraphical units. Dean also observes that the spore assemblages are comparatively simplistic in design: "... spore taxa with elaborate and delicate ornamentation are generally absent" (Dean 1989a, p. 599). None of the taxa discussed or illustrated by Dean (1989a) are exclusive to, or truly representative of, the late Emsian. Indeed, the lack of mention by Dean of the distinctive complex of spores bearing bifurcate-tipped sculpture suggests assignment to the early to early late Emsian, *annulatus-sextantii* Assemblage Zone (*sensu* Richardson & McGregor, 1986) and not as inferred, to the *douglastownense-eurypterota* Assemblage Zone. As re-interpreted herein, the assemblages recovered from the Bovisand and Staddon Grit Formations are considered slightly older than those of the Lynton Formation.

4.3.4 The Hangman Sandstone Group.

4.3.4a *The miospore palynostratigraphy of the Hangman Sandstone Group.*

The distribution of 80 miospore taxa through the Hangman Sandstone Group is shown in Figure 4.5. The palynology reported from the Hollowbrook Formation is generally the same as that of the underlying Lynton Formation: 44 taxa span this lithostratigraphical boundary. Of the total miospore population, 27 taxa were extrapolated through the "interval of non-recovery" (see discussion below) of which 19 subsequently range into the Ilfracombe Slates. 28 forms make a first appearance within the palyniferous upper Hangman Sandstone Group (within the sample interval R21 to LH12), with reworking apparently confined to these levels and delineated by the anomalous and rare occurrence of 6 taxa. 37 taxa of the total reported at this level extend into the overlying Ilfracombe Slates.

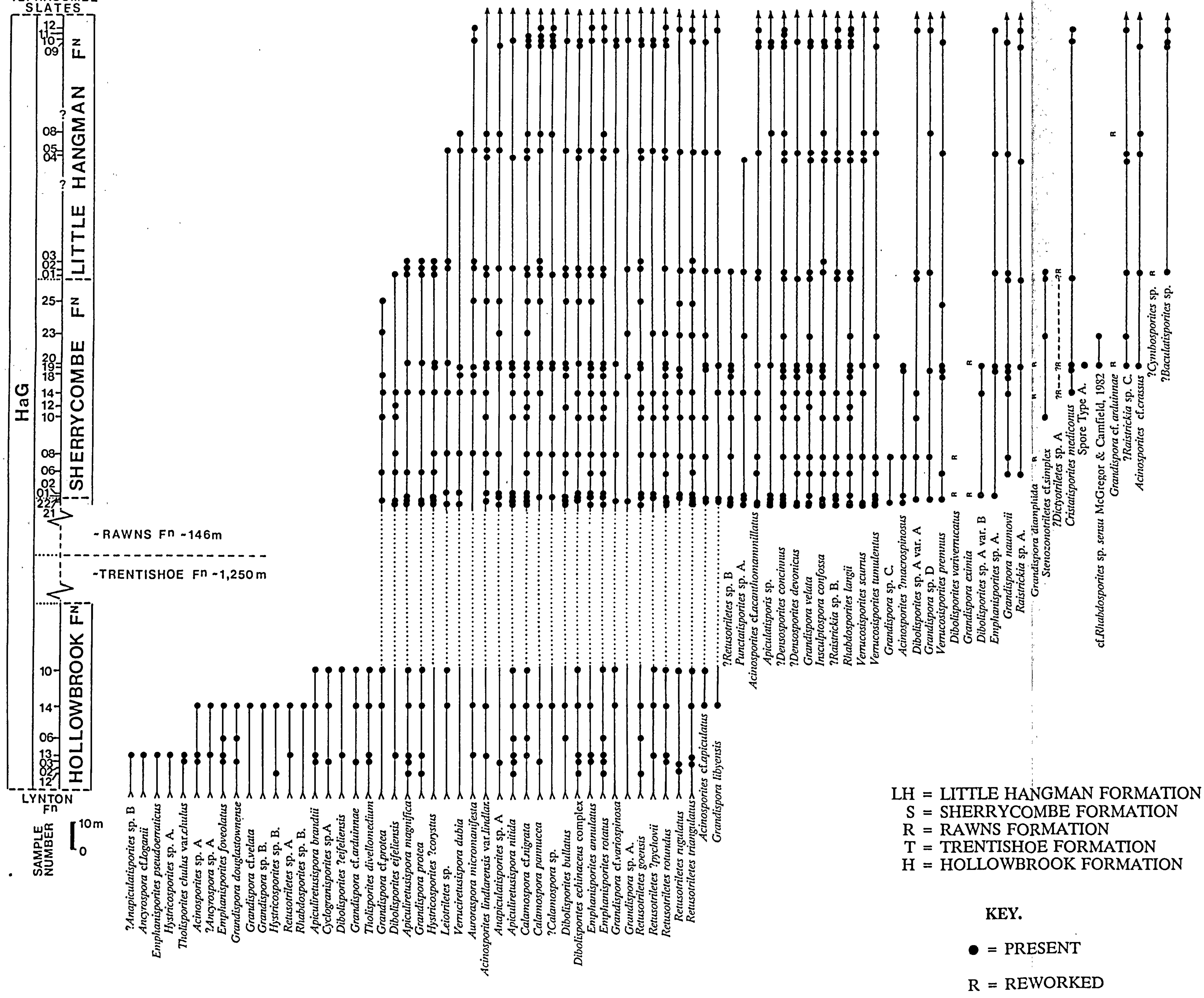
As already discussed, the collective character of the miospore assemblages recovered from the lowermost Hangman Sandstone Group (including *Grandispora* cf. *velata* and *Retusotriletes rugulatus*) suggests that these levels may be of Eifelian age, although the absence of *Rhabdosporites langii* and associated early Eifelian index taxa does not corroborate such an evaluation. In the Hollowbrook Formation, several miospore taxa have their reported last occurrence, for example *Grandispora* (al. *Spinozonotriletes*) cf. *arduinnae*. Riegel (1982) noted that *Grandispora* (al. *Spinozonotriletes*) *arduinnae* disappears in the Eifelian Nohn Formation of the Eifel region (Rheinland), with Richardson & McGregor (1986) recording the last occurrence of this taxon to be within the mid *velatus-langii* Assemblage Zone. In the present study *G.* cf. *arduinnae* was last recorded in the Hollowbrook Formation, with reworked occurrences noted in the upper palyniferous levels of the Hangman Sandstone Group and the overlying Ilfracombe Slates. In common with 18 other taxa documented from this unit, it is uncertain whether the last reported occurrence of *G.* cf. *arduinnae* in the Hollowbrook Formation reflects a true evolutionary disappearance, or is merely due to an adverse change in sedimentary facies. Most of these taxa may in fact extend somewhat higher (into the ≈1,420m "barren" interval). Similarly the disappearance of, in particular, *Emphanisporites foveolatus* and *Tholisporites chulus* var. *chulus* towards the top of the Hollowbrook Formation may represent their true biological demise, although again this is difficult to ascertain.

Palynomorphs were recovered up to approximately 45m above the base of the Hollowbrook Formation, with subsequent samples and also those collected from the Trentishoe and Rawns (*partim*) Formations proving devoid of organic matter. This interval of "non-recovery" (or "barren" interval) totals ≈1.5km of sediment, and is unfortunate as the last and/or first occurrences of a number of key Eifelian zonal taxa are consequently unresolved. It is unknown whether the numerous first appearances reported in the first palyniferous horizon subsequent to this "barren" interval (≈1.8m below the top of the Rawns Formation) reflect true evolutionary inceptions, or whether their influx is at an indeterminate level lower down in the sequence.

The palynoflora documented through the palyniferous horizons in the uppermost Rawns, Sherrycombe and Little Hangman Formations proved virtually identical, and is therefore dealt with collectively rather than separately by formation. Following the "barren" interval (described above), the first palyniferous sample (R21) contained a markedly diverse assemblage, comprising a selection of species which persist through from earlier palyniferous horizons (*e.g. Apiculiretusispora* spp., *Emphanisporites* spp., *Dibolisporites* spp., and *Retusotriletes* spp.).

FIGURE 4.5 THE TEMPORAL DISTRIBUTION OF MIOSPORES

THROUGH THE HANGMAN SANDSTONE GROUP.



In general, the palyniferous upper Hangman Sandstone Group contains a markedly diverse, exceptionally well preserved and in part prolific miospore component. Acamerate, camerate and cingulizonate miospores occur in profusion, but there appears to be a lack of forms that display bifurcate-tipped appendages (*e.g. Hystricosporites* and *Ancyrospora*). Structural complexity in spore design is a prominent feature of the assemblages, with forms recovered displaying both intexinal and elaborate exoexinal sculpture. Zonate and finely sculptured pseudosaccate spores were also common.

Of particular biostratigraphical interest at this level were the recovery of *Acinosporites* cf. *acanthomammillatus*, *?Densosporites devonicus*, *Grandispora naumovii*, *Grandispora velata (sensu stricto)* and *Rhabdosporites langii*. Notable associates include prolific numbers of *Insculptospora confossa*, *?Densosporites concinnus* and *Retusotriletes rugulatus*, coupled with a diverse complex of baculate and/or verrucate sculptured forms, attributable to the (?)*Raistrickia* or *Verrucosisporites* plexus. In the upper Hangman Sandstone Group the last occurrence of a number of species was observed, having ranged through from the Lynton Formation (*e.g. Grandispora protea*, *Hystricosporites ?corystus* and *Verruciretusispora dubia*). A small number of taxa were also recorded exclusive to the upper Hangman Sandstone Group, but had minimal biostratigraphical utility (*e.g. Dibolisporites* sp. A and *Emphanisporites* sp. A). The recovery of *Grandispora naumovii* and *?Densosporites devonicus* towards the top of the Hangman Sandstone Group identifies the *devonicus-naumovii* Assemblage Zone of Richardson & McGregor (1987): this zone approximately spans the mid Eifelian to earliest Givetian interval (by *indirect correlation, sensu* Richardson & McGregor, 1986, p.15). As mentioned earlier it is impossible to deduce whether these occurrences represent true inceptions, and therefore the exact position of the base of the *devonicus-naumovii* Assemblage Zone remains unresolved in north Devon (refer to the synoptic figure, Fig. 4.7).

Streel *et al.* (1987) cite the first occurrence of *Acinosporites macrospinosus* and *Hystricosporites reflexus* in definition of the AD Oppel Zone, which spans the Eifelian/Givetian boundary. The tentative recognition of the former species, and the absence of the latter does little to resolve the precise age of the unit at this level. Following the usage of Richardson & McGregor (1986) and Streel *et al.* (1987), the inception of *Geminospora lemurata* in the overlying upper Wild Pear Slates suggests that the uppermost Hangman Sandstone Group may feasibly be earliest Givetian in age (refer to Section 4.3.5a below). However, in light of the recent proposal of Loboziak *et al.* (1989), the upper Hangman Sandstone Group may be regarded as exclusively Eifelian in age. Indeed, when compared with the ranges of selected spores in the Middle Devonian of the Eifel region (Riegel, 1982), the concurrence of many of the taxa recovered from the upper levels of the Hangman Sandstone favours an Eifelian age interpretation.

4.3.4b *Comparisons with published reports of palynomorph assemblages from Devonian strata of Britain.*

The assemblages detailed from the palyniferous levels in the Hollowbrook Formation are similar to those of the Lynton Formation, and therefore in common with the Lynton Formation have few potential correlatives: this is based exclusively upon the miospore evidence presented herein (refer to Section 4.3.3b).

In contrast, the upper Hangman Sandstone Group can be equated with a number of isolated palyniferous sections in the British Isles. Richardson (1960) documented comparatively diverse spore assemblages from the Cromarty nodule beds of Scotland. In view of recently proposed zonal schemes, the concurrence of *Densosporites devonicus, Grandispora velata* (al. *Cosmosporites velatus*), and *Rhabdosporites langii* in the Cromarty beds suggests a pre-*lemurata*, mid-late Eifelian age (*devonicus-naumovii* Assemblage Zone of Richardson & McGregor, 1986), and therefore these beds are approximately contemporaneous with the upper Hangman Sandstone Group. Richardson (1962, 1965) subsequently described a series of four miospore assemblages from the Orcadian sediments of Orkney, Caithness and the Moray Firth area. These contained *Acinosporites acanthomammillatus, Densosporites devonicus, Grandispora naumovii* (al. *?Spinozonotriletes* cf. *naumovii*), *Grandispora velata* (al. *Calyptosporites velatus*) and *Rhabdosporites langii*, which range in part or pervasively through the Wick Flagstone Group, Achanarras Fish Beds, Thurso Flagstone Group and Eday Beds. In view of the zonations proposed by Richardson & McGregor (1986) and Streel *et al.* (1987), these associations suggest an age comparable to that of the palyniferous upper Hangman Sandstone Group.

The absence of *Geminospora lemurata* in the Harmansole Borehole, in addition to the concurrence of *Acinosporites acanthomammillatus, Grandispora* sp. cf.*Archaeozonotriletes naumovii* and *Rhabdosporites langii* suggests that the late Givetian/earliest Frasnian age interpreted by Mortimer & Chaloner (1972) is too young. The three assemblages from this borehole are re-interpreted herein, and considered more representative of a mid to late Eifelian age (*sensu* the zonal schemes of Richardson & McGregor, 1986; Streel *et al.*, 1987). This re-interpretation does not contradict the broad age evaluations provided by sparse brachiopod, fish and plant remains from this borehole (refer to Mortimer & Chaloner, 1972; pp. 15, 18).

Marshall (1988) described miospore assemblages from two localities within the Devonian sediments of Papa Stour (Shetland), which are broadly similar to the palynofloras recovered from the upper Hangman Sandstone Group. Despite the absence of *Densosporites devonicus* and *Grandispora naumovii*, Marshall (1988) interpreted an Eifelian age for the Papa Stour assemblages, assigning them to the *devonicus-naumovii* Assemblage Zone of Richardson & McGregor (1986): based largely on the occurrence of significant accessory species, namely *Verrucosisporites scurrus* and *Retispora archaeolepidophyta*. The inceptions of the latter two taxa are known to be within the *devonicus-naumovii* Assemblage Zone. Despite the anomalous recovery of *Cymbosporites magnificus* in the assemblages (indicative of an early Givetian age, *sensu* Richardson & McGregor, 1986), Marshall further refined this evaluation to a late Eifelian age, based largely on the absence of *Geminospora lemurata* in the assemblages.

In essence, the absence of *Geminospora lemurata* from all the localities listed above and the representation of established and well known Eifelian/Givetian miospores, suggests contemporaneity with the upper Hangman Sandstone Group of north Devon.

4.3.5 The Ilfracombe Slates.

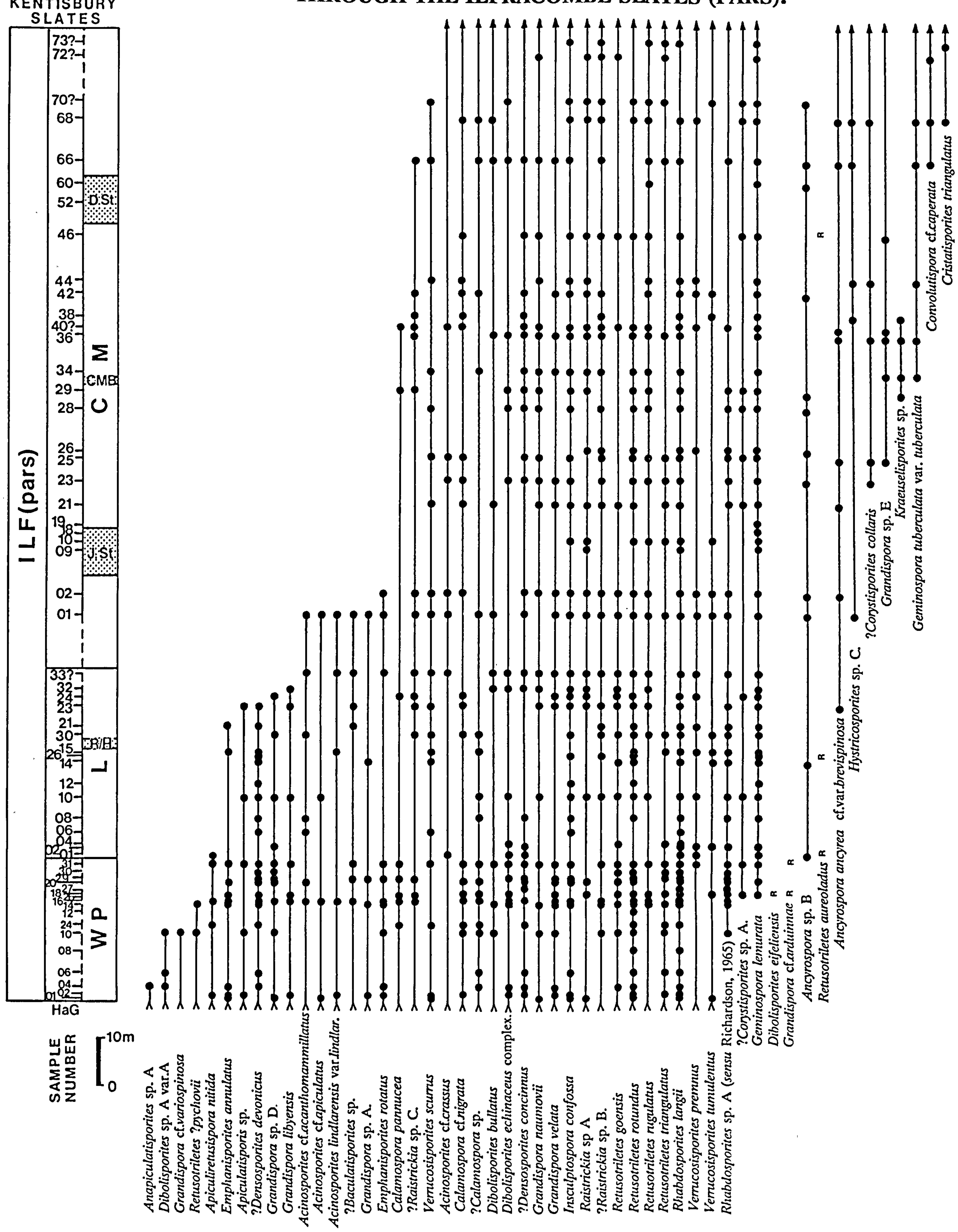
4.3.5a *The miospore palynostratigraphy of the Ilfracombe Slates.*

The temporal distribution of 52 taxa through part of the Wild Pear Slates, Lester Slates & Sandstones and Combe Martin Slates is shown in Figure 4.6. For reasons discussed in Chapter 2, assemblage composition is tabulated for the palyniferous samples of the Kentisbury Slates: 53 distinct species were recorded from this latter lithostratigraphical unit.

37 taxa documented from the palyniferous upper Hangman Sandstone Group range through into the overlying Ilfracombe Slates, of which a number first originally occurred in the Lynton

FIGURE 4.6 THE TEMPORAL DISTRIBUTION OF MIOSPORES

THROUGH THE ILFRACOMBE SLATES (PARS).



KEY.

● = PRESENT

R = REWORKED

CM = COMBE MARTIN SLATES

L = LESTER SLATES & SANDSTONES

WP = WILD PEAR SLATES

DSt = David's Stone Limestone.
CMB = Combe Martin Beach Limestone.
JSt = Jenny Start Limestone.
R/H = Rillage/Holey Limestone.

Formation (*e.g.* the *Dibolisporites echinaceus* "complex", and the *Retusotriletes rotundus* "morphon"). The occurrence of 3 taxa in the Wild Pear Slates to Combe Martin Slates interval is attributed to reworking, with 19 species disappearing in this interval, and the first appearances of 12 other taxa recorded. Overall, the palynofloras of the Ilfracombe Slates define a major transitionary period in the evolutionary record of dispersed miospores preserved in north Devon. The demise and subsequent disappearance of a number of long ranging Lower and Middle Devonian taxa (particularly large pseudosaccate spores) occurs within this unit, with the palynology of the overlying Morte Slates having greater affiliation with reported Upper Devonian assemblages.

In the Ilfracombe Slates, there is a distinct proliferation and diversification of species of camerate miospores bearing diminutive sculpture. Such forms are variously attributed to either the *Geminospora* or *Grandispora* plexuses, depending on the preferential thickening of the exoexine (geminospores bear a thickened exoexine relative to the intexinal body). Finely sculptured acamerate miospores are also common, and there is a continued abundance of miospores with irregular, predominantly verrucate or baculate sculpture (*Dibolisporites* spp., (?)*Raistrickia* spp., and *Verrucosisporites* spp.). A small population of miospores with bifurcate sculpture appear in this unit, as do forms attributed to the ?*Corystisporites* plexus. Richardson & McGregor (1986, p. 17) remarked that within their defined *lemurata-magnificus* Assemblage Zone miospores and megaspores are distinguishable. However, the present study could not confirm the timing of this palynological event, as no megaspores were recovered from this, or for that matter from any part of the Devonian sequence studied (refer to Chapter 5, Section 5.3.2d). However, megaspores have been reported by Mortimer & Chaloner (1967, 1972) from the Wyboston and Harmansole Boreholes, located to the east of the study area.

Of principal biostratigraphical significance is the inception of *Geminospora lemurata* in north Devon, which was documented in the lower Ilfracombe Slates, ≈8.5m below the top of the Wild Pear Slates. In their zonal schemes, both Richardson & McGregor (1986) and Streel *et al.*, (1987) recognised the importance of this taxon to Devonian palynostratigraphy (refer to Figure 4.7). The influx of this taxon has been widely reported around the Old Red Continent, extending from the Russian Platform (Kedo & Obukhovskaya, 1981), through Spitsbergen (Allen, 1965) to Arctic Canada (McGregor & Camfield, 1982). When studying the global distribution of *Archaeoperisaccus* around the Old Red Continent, Streel (1986a; p. 80, Fig. 4) plotted the global distribution of *Geminospora lemurata* assemblages without *Archaeoperisaccus* (for the Frasnian interval), and remarked on the widespread occurrence of *G. lemurata* (refer also to McGregor, 1979a; Text-Figs. 11 & 13). In contrast to the distribution *Geminospora lemurata,* Streel (1986a) remarked on the distribution of *Archaeoperisaccus,* preferentially to one side of the palaeoequator (*sensu* Smith *et al.*, 1980).

Richardson & McGregor (1986) defined the base of the *lemurata-magnificus* Assemblage Zone on the first occurrence of the two nominal taxa, *Geminospora lemurata* and *Cymbosporites magnificus,* and interpreted the age of this Zone as mid-Givetian (spanning the interval from the upper *ensensis* conodont Zone to the lower Upper *varcus* conodont Subzone, inclusive). Richardson & McGregor (1986, p. 16) remark significantly that the age of this Assemblage Zone is by *indirect correlation*, and therefore was not regarded as absolute in the present study. Their reference section for the base of the *lemurata-magnificus* Assemblage Zone were quoted as the uppermost beds of the Weatherall Formation, northeast of Beverley Inlet, southeastern Melville Island (McGregor & Uyeno, 1972).

The age of this section in the Canadian Arctic was loosely constrained by a single conodont date, ≈150m below the first appearance of *G. lemurata*, and which according to Uyeno (unpublished GSC report, 1980) was indicative of an age within the interval *australis* conodont Zone to *ensensis* conodont Zone (this approximates to an early/mid Eifelian to earliest Givetian age). Further to McGregor & Uyeno (1972), McGregor & Camfield (1982) investigated the temporal distribution of miospores through additional Devonian sections on Melville Island, located in the northeastern part of the island. McGregor & Camfield (1982) identified the first occurrence of *Geminospora micromanifesta* var. *minor* (synonymous with *G. lemurata*) as being within the Hecla Bay Formation (which overlies the Weatherall Formation), at sample station 8341. This inception event was located ≈1400m above a conodont productive horizon of somewhat ambiguous age (within the range from *australis* Zone to Lower *varcus* Subzone, *i.e.* early/mid Eifelian to early Givetian). Based solely on these studies, the precise timing of the first appearance of *Geminospora lemurata* must be regarded as poorly constrained.

Streel *et al.* (1987) defined the Lem. Interval Zone (being the top division of the tripartite AD Oppel Zone) based on the work of Riegel (1975), and similarly perceived the inception of *Geminospora lemurata* to occur at a level within the *ensensis* conodont Zone. Uncertainty was expressed however as to whether this event was Eifelian or Givetian in aspect (Streel, *et al.*, 1987, p.218). Previously, Loboziak & Streel (1980) had reported the influx of *G. lemurata* as being somewhat later, first appearing in the Membre de Couderousse of the Formation de Blacourt (Boulonnais, France), This member had been attributed to the TA Oppel Zone, which according to Streel *et al.* (1987) equated to the Upper *varcus* conodont Subzone. Loboziak & Streel (1988) later re-evaluated the palynofloras of the Boulonnais and recognised the inception of *G. lemurata* as being within the TCo Oppel Zone, and coincidental with the first appearance of *Chelinospora concinna* and *Cirratriradites jekhowskyi*. This re-interpretation equated the influx of *G. lemurata* to the Middle/Upper *varcus* conodont Subzones.

In palynological investigations of subsurface Devonian strata in Brazil (Loboziak *et al.*, 1988) and Libya-Tunisia (Loboziak & Streel 1989), the first occurrence of *Geminospora lemurata* has been cited to indicate the approximate base of the Givetian Stage. This application of *G. lemurata* is in spite of earlier voiced uncertainties as to the precise timing of this inception event (*sensu* Riegel, 1975 - refer to the comments under "*Range of the zone*" for the *devonicus-naumovii* Assemblage Zone, by Richardson & McGregor, 1986; p. 15). However, the recent usage by Loboziak and colleagues in equating the first appearance of *G. lemurata* to the approximate base of the Givetian Stage seems most likely to be based upon unpublished palynological and conodont work, currently in progress in the Eifel region. In a recent report submitted to the IUGS, Washington (July, 1989), Loboziak *et al.* (1989) observe the first occurrence of *Geminospora lemurata* in the Hillesheim Syncline of the Eifel region (Germany), as being ≈22m below the top of the Müllert Member of the Ahbach Formation. This inception slightly precedes the first appearance of the shallow water brachiopod *Stringocephalus*: Struve (1961) perceives the influx of this brachiopod to characterise the Wotan Member of the lowermost Loogh Formation (which overlies the Ahbach Formation), and equates to the traditional base of the Givetian Stage *sensu* Beyrich (1837). Loboziak *et al.* (1989) further correlate the inception of *G. lemurata* with the upper part of the lower *ensensis* conodont Zone (Weddige, 1977), which relates to the *ensensis-obliquimarginatus* conodont Zone (*sensu* Weddige 1984). In regards to the alternative conodont zonations of Bultynck (1987), this event lies above the base of the *obliquimarginatus Icriodus*-Zone and *hemiansatus Polygnathus*-Zone. Therefore, if the usage of Streel *et al.* (1987), Loboziak & Streel (1989) and in particular Loboziak *et al.* (1989) was adopted herein, then the appearance of *Geminospora lemurata* towards the top of the Wild Pear Slates suggests that the palyniferous levels of the upper Hangman Sandstone Group and the basal Ilfracombe Slates are latest Eifelian in age. The approach of Richardson & McGregor (1986) is more cautious and less precise and has been adopted herein, until the exact timing of the inception of *Geminospora lemurata* is formally resolved (which, in light of the recent proposals of Loboziak and associates may be imminent). Therefore, the first appearance of *G. lemurata* is taken to suggest that within north Devon, the Eifelian-Givetian boundary is positioned somewhere below the uppermost Wild Pear Slates.

The miospore assemblages documented from the Lester Slates & Sandstones and from the overlying Combe Martin Slates proved notably diverse, and generally abundant. As with the older, underlying units, assemblages recovered from these levels in the Ilfracombe Slates contained prolific numbers of *Dibolisporites* spp., and *Retusotriletes* spp.. However, several minor components of the palynoflora that ranged through from the Lynton Formation disappear within the lower Ilfracombe Slates (*e.g Acinosporites lindlarensis* var. *lindlarensis, Emphanisporites annulatus* and *E. rotatus*). Similarly, a few taxa whose first occurrence was noted within the Hangman Sandstone Group, were last recorded in these units (*e.g. Acinosporites* cf. *apiculatus, Acinosporites* cf. *acanthomammillatus, ?Densosporites devonicus, Grandispora libyensis*).

Following the influx of *Geminospora lemurata* (which is just pre-empted by the first occurrence of *Rhabdosporites* sp. A *sensu* Richardson, 1965), there are few further first occurrences noted within the remainder of the Ilfracombe Slates (*e.g.* the entry of *Ancyrospora anyrea* cf. var. *brevispinosa, ?Corystisporites collaris* and *Geminospora tuberculata* var. *tuberculata*). Indeed, the miospore populations recovered from this unit progressively appear ≈depleted in numbers and of decreasing diversity.

The next major palynological event in north Devon proved the first occurrence of *Cristatisporites triangulatus*, ≈?27m below the top of the Combe Martin Slates. Based upon a provisional reference section of the Hecla Bay Formation, Canadian Arctic, Richardson & McGregor (1986) cite this taxon as one of two nominate species that defines the *optivus-triangulatus* Assemblage Zone (also based upon the inception of *Contagisporites optivus* var. *optivus*). This Assemblage Zone spans the late Givetian to early Frasnian interval, and approximates (by *indirect correlation*) to the Upper *varcus* to Lower *asymmetricus* conodont Zones inclusively (NOTE: the recently proposed *transitans* Zone of Sandberg, Ziegler & Bultynck, 1989, is synonymous with the Lower *asymmetricus* Zone, *sensu* Ziegler, 1971).

Based on the palynostratigraphies established by Loboziak & Streel (1980, 1981) and Loboziak *et al.* (1983) for the Boulonnais region, Streel *et al.* (1987) similarly used *Cristatisporites triangulatus* in defining their mid Givetian to earliest Frasnian TA[1] and subsequent TCo Oppel Zones. The

[1] This Oppel Zone of Streel *et al.* (1987) refers to the upper part of the TLa zone as proposed by Loboziak & Streel (1980), and more recently quoted by Loboziak & Streel (1988). The TLa zone is based on the last occurrence of *Rhabdosporites langii* and the inception of *Cristatisporites triangulatus* (Note: *Rhabdosporites langii* and *R. parvulus* are differentiated by Loboziak & Streel, 1980, 1981, 1988).

former is based on the inception of *C. triangulatus* and the contemporaneous demise of *Ancyrospora ancyrea* var. *ancyrea*, whereas the latter zone is recognised by the continued presence of *C. triangulatus* coupled with the joint first occurrences of *Chelinospora concinna* and *Cirratriradites jekhowskyi*. The incompatibility of the zonal schemes of Richardson & McGregor (1986) and Streel *et al.* (1987: refer to p. 223, Fig. 13) for this late Givetian/early Frasnian interval is based fundamentally on the timing of the inception of *Cristatisporites triangulatus*, in relation to the standard conodont zonation. Unlike Richardson & McGregor (1986), Streel *et al.* (1987, p. 219) remark that this index taxon probably first occurred in or below the Middle *varcus* conodont Subzone (based upon a re-evaluation of the faunal evidence personally communicated to the authors by Bultynck, 1986), although the precise timing of the base of the TA Oppel Zone was at that time still somewhat problematical. With contributions by Bultynck, Loboziak & Streel (1988) later re-evaluated the faunal and palynofloral data from the Boulonnais and re-interpret the influx of *Cristatisporites triangulatus* as corresponding to the *ensensis* conodont Zone, and preceding the inception of *Geminospora lemurata*. If this timing of the entry of *C. triangulatus* is correct, then it is substantially earlier than has been reported elsewhere around the globe.

In north Devon, the apparent stratigraphical proximity of a conodont fauna of Middle *varcus* Subzone age (from the David's Stone Limestone) to the inception of *Cristatisporites triangulatus*, seemingly supports the definition of Streel *et al.* (1987) as to the timing of this floral event, and not that of Loboziak & Streel (1980, 1988). However, by implication this would suggest that a substantial time interval (spanning the Late *varcus* Subzone, plus *hermanni-cristatus, disparilis* and lowermost *asymmetricus* conodont Zones) is represented by a comparatively thin sedimentary sequence (≈a few 10's of metres), since the ?basal Kentisbury Slates are thought herein to be Frasnian in age. The problem is further compounded by the inability in the present study to recognise the TCo Oppel Zone of Streel *et al.*, (1987), which spans the Givetian/Frasnian boundary. The lack of resolution of this zone is due to the comparatively "rapid" and successive first appearances of *Cristatisporites triangulatus* and *Verrucosisporites bulliferus*. The zonal taxa used to identify the TCo Oppel Zone were either absent in north Devon (*e.g Cirratriradites jekhowskyi*), or as in the case of ?*Chelinospora concinna*, first occur in the Frasnian (and coincidental with the Frasnian index taxon *Verrucosisporites bulliferus*). As an alternative, in view of the rapid appearance of *Verrucosisporites bulliferus* following that of *Cristatisporites triangulatus* within the Ilfracombe Slates, it appears more feasible to regard the inception of *C. triangulatus* in north Devon as equivalent to a post-Middle *varcus* Subzone age. This interpretation is closer to that of Richardson & McGregor (1986), although in light of the described ambiguity, the precise position of the Givetian/Frasnian boundary can not be more accurately resolved.

The exact chronology of the floral events documented within the Kentisbury Slates cannot be clearly elucidated, largely due to the problem of stratigraphically ordering samples. However, a number of general observations can be made in reviewing the palynology of this unit as a whole. With reference to Table 4.1 overleaf, 53 taxa were reported from the Kentisbury Slates, of which 28 range through from the underlying strata and 13 extend up into the Morte Slates. The influence of reworking appeared to be more prevalent here than elsewhere within the succession of north Devon (12 of the 53 taxa documented were believed to be reworked:- recognised by the poor preservation,

Table 4.1 The occurrence of miospore taxa in the Kentisbury Slates.

SAMPLE No.	K01	K02	K05	K06	K08	K10	K12	K14	K16	K18	K19	K21	K23	K25	K29	K32	K34	K37	K38	K40	K41	K42	K44	K46	K48	K50	K52	K53
TAXA																												
Acinosporites acanthomammillatus				R																								
Acinosporites cf.crassus				X				X				X			X													
Acinosporites lindlarensis var. lindlarensis					R										R													
Acinosporites sp. A																R?												
Ancyrospora ancyrea cf.var. brevispinosa	?	X	?	X	?	?	X			X	?	X		X	X									?				
Ancyrospora simplex				X				X				?	?		X	X	X		X	X	X	X	?		?	X	X	
Ancyrospora sp. B				R							R				R													
Aneurospora greggsii													X				X		X		X					X		
Apiculiretusispora brandtii								R?					R?															
Calamospora cf.nigrata							X	X						X														
Calamospora pannucea																					R?							
?Calamospora sp. A							X						X		X	X			X			X			X			
?Chelinospora concinna							X									X												
Convolutispora cf.caperata				X			X					X			X	X												
?Corystisporites collaris	X	X					X	X											X									
?Corystisporites sp. A				X		X	X	X	X				X	X	X	X	X						?	X				
Cristatisporites triangulatus	?	X	X	X	X	X	X	X	X			X	X	X	X	X	X	X	X	X	X	X	X	?	X	X	X	X
?Cristatisporites sp. A *	X	X	X	X		X	X	X	X	X	X	X	X	X	X				X									
?Densosporites concinnus	X		X	X	X	X					X		X	X	X													
?Densosporites devonicus					R?																							
Dibolisporites bullatus		X	X	X	X		X			X													R			R		
Dibolisporites echinaceus "complex"			X	X	X	X	X	X						X												R		
Dibolisporites eifeliensis																				R								
Dictyotriletes sp. B							X			X																		
Emphanisporites annulatus																					R							
Emphanisporites rotatus																R	R			R			R					
Geminospora boleta		X				X							X			X			X	X	X					X	X	X
Geminospora lemurata	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Geminospora pilaformis			X				X									X				X								
Geminospora tuberculata var.tuberculata		X	X			X											X	X					X			X	X	
Grandispora aff.echinata							X				X			X	X	X			X	X		X	X				X	
Grandispora naumovii			X	X	X	X	X	X		X				X	X	X		X	X	X	X		X		X	X	X	
Grandispora protea		R		R																								
Grandispora tomentosa																				X	?					X	X	
Grandispora velata				X		?	X	X					X	X	X													
Grandispora sp. E		X		X		X	X	X				X		X	X				X				X	X			X	
Grandispora sp. F		X		X	X	X	X	X						X	?													
Grandispora sp. G	X			X	X						X		X	X	X	X			X	X	X							
Hystricosporites sp. C	X			X								X						X	X							X		
Insculptospora confossa		X	X	X	X	X	X	X		X			X	X	X	X	X		X	X	X		X			X	X	
Perotrilites ?bifurcatus		X	X	X	X	X	X	X					X	X	X						X							
Raistrickia sp. A		X	X	X	X	X		X			X	X	X				X						X					
?Raistrickia sp. B		X	X	X		X	X	X		X		X		X	X	X							X	X	X	X		X
Retusotriletes aureoladus								R																	R			R
Retusotriletes goensis				X		X	X										X								X	X		
Retusotriletes rotundus	X		X		X	X	X				X		X		X	X	X		X		X		X			X		
Retusotriletes rugulatus	X	X	X	X	X	X	X	X		X	X		X	X	X	X	X		X	X	X	X	X	X	X	X	X	X
Retusotriletes triangulatus		?	X	X	X	X	X	X		X	X	X		X	X	X	X	X		X			X		X	X	X	X
Rhabdosporites langii	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Rhabdosporites sp. A **	X	?	X		X	X	X			X					X	X	X	X	X	X	X	X	X		X	X	X	X
Verrucosisporites bulliferus		X				X	X				X				X		X		X	X	X	X				X		
Verrucosisporites premnus			X				X	X						X						?	?	X	X			?	?	
Verrucosisporites tumulentus			X										X		X	?												

* *sensu Loboziak and Streel, 1981.* ** *sensu Richardson, 1965.*

Taxa ordered alphabetically

For key to symbols refer to Table 4.2.

low abundance and stratigraphical incompatibility of certain species).

In addition to prolific numbers of *Cristatisporites triangulatus, Geminospora lemurata* and *Rhabdosporites langii, Verrucosisporites bulliferus* was documented approximately from or near to the ?base of the Kentisbury Slates. Despite the morphological similarity between certain representatives of *Geminospora boleta* and *Verrucosisporites bulliferus* (refer to the appropriate discussions of these taxa in Chapter 3), forms indisputably identified as *V. bulliferus* were noted at this stratigraphic level. Both Richardson & McGregor (1986) and Streel *et al.* (1987) cite the inception of *Verrucosisporites bulliferus* in interpreting a Frasnian age. This application of *Verrucosisporites bulliferus* is not surprising, as both zonations proposed for this interval are based on the same palynostratigraphy established for the Beaulieu Formation, Boulonnais France (Brice *et al.*, 1979; Loboziak & Streel 1980, 1981; Loboziak *et al.*, 1983).

In the zonation proposed by Richardson & McGregor (1986), the appearance of *Verrucosisporites bulliferus* approximates to the Middle *asymmetricus* conodont Zone, and is one of two nominate species used to define the (*Archaeoperisaccus*) *ovalis* - *bulliferus* Assemblage Zone. The base of the BJ Oppel Zone (Streel *et al.*, 1987) is based on the first occurrence of *Verrucosisporites bulliferus* and *Hystricosporites multifurcatus*; the BJ Oppel Zone is somewhat older than the *ovalis-bulliferus* Assemblage Zone, the former equated with the Lower/Middle *asymmetricus* conodont Zone (refer to Loboziak & Streel, 1988, p. 73). Despite this disparity, both zonal schemes accept that the inception of *Verrucosisporites bulliferus* indicates a Frasnian age. The absence in north Devon of all other taxa recognised by Streel *et al.* (1987) as important zonal forms in their succeeding BM Oppel Zone, and IV and V Phases, limits further refinement of the age for the Kentisbury Slates.

Richardson & McGregor (1986, p.18) remark that zonate/pseudosaccate monolete spores are prevalent within Frasnian assemblages. Apart from a small population of aberrant, monolete *Geminospora lemurata* recovered from the Kentisbury Slates, no singularly monolete-camerate taxa (*e.g.* referrable to *Archaeoperisaccus* Naumova, 1953) were recorded from north Devon. This absence may reflect the presumed palaeolatitude of Britain for the Devonian Period, being located outside of the floral province currently interpreted for the *Archaeoperisaccus*-producing parent plant (*sensu* McGregor, 1979a; Streel 1986a).

Towards the top of the Kentisbury Slates, the decline and eventual disappearance of the a number of large, sculptured camerate miospores was noted (*e.g. Grandispora naumovii* and *Rhabdosporites langii*). This may be in response to a change in palaeoenvironment (as reflected in the sedimentary facies), with the transition from the Kentisbury to more ?distal sediments of the lower Morte Slates. Alternatively, these last occurrences may reflect true evolutionary disappearances. A comparable demise in large spores was noted by Richardson & McGregor (1986, p. 18) in the Frasnian *ovalis-bulliferus* Assemblage Zone.

As discussed in detail earlier, the TA and TCo Oppel Zones of Streel *et al.* (1987), and the *optivus-triangulatus* Assemblage Zone of Richardson & McGregor (1986) are ill-defined in the Ilfracombe Slates of north Devon. This is partly due to the absence of *Ancyrospora ancyrea* var. *ancyrea* and *Cirratriradites jekhowskyi* within the studied section, coupled with the described, rapid and successive appearance of *Cristatisporites triangulatus* and *Verrucosisporites bulliferus.* Of further interest is the ?limited thickness of sediment (≈10's of metres), which as interpreted by the present study, equates to quite a substantial time interval (according to the conodont zonation; see earlier). A number of explanations may account for this anomaly. The inception of *Verrucosisporites bulliferus* in north Devon may have been somewhat earlier than is previously defined: the Frasnian age interpretation is made with the proviso that the appearance of *V. bulliferus* is synchronous with its influx within the Beaulieu Formation of the Boulonnais region, France (refer to the discussion above for references). Alternatively, slow sedimentation rates or inaccurate sample location may account for the described poor resolution of the TA and TCo Oppel Zones of Streel *et al.* (1987). The latter is made more likely, as samples collected from the eastern outcrop of the Kentisbury Slates are only arbitrarily located at or near the ?base of this unit (due to structural complexity and poor sedimentological control). With future detailed structural mapping and accurate placement of those samples listed herein, the associated assemblages may prove to have come from a higher level in the Kentisbury Slates.

4.3.5b *Comparisons with published reports of palynomorph assemblages from Devonian strata of Britain.*

A number of assemblages recovered from concealed Devonian rocks in southern Britain were interpreted by Mortimer & Chaloner (1972) as Givetian in age. Taking into account the recently proposed zonational schemes for the Devonian System, the assemblages recovered from the Bolney Borehole are re-interpreted (herein) as early to mid Givetian in age, and thus approximate correlatives with the Lester Slates & Sandstones or Combe Martin Slates of north Devon. Similarly, the assemblages detailed from the Bushey and Tatsfield Boreholes are clearly indicative of a slightly younger, latest Givetian age, based on the co-occurrence of *Cristatisporites* (al. *Samarisporites*) *triangulatus* and *Geminospora lemurata*. *Chelinospora concinna* is also present in the Tatsfield Borehole. Mortimer & Chaloner (1972) make no mention of *Verrucosisporites bulliferus* (and associated Frasnian zonal taxa as now recognised after Richardson & McGregor, 1986, and Streel *et al.*, 1987), implying that the assemblages recovered by Mortimer & Chaloner (1972) are older than the Frasnian Stage, and therefore comparable to the uppermost Combe Martin Slates or ?lowermost Kentisbury Slates. However, Mortimer & Chaloner (1972, p. 13, Table 3) do list the occurrence of "*Geminospora* sp. (with distal verrucae)". This record most probably refers to specimens of *Geminospora boleta*, which have been recorded herein from the Frasnian Kentisbury Slates of north Devon.

The recovery of *Densosporites devonicus*, *Grandispora velata* and *Rhabdosporites langii* through the palyniferous horizons of the Ward Hill, Observatory and Bu Ness Groups of Fair Isle, suggested to Marshall & Allen (1982) the possible equivalence of these groups to the Eday Beds, *sensu* Richardson (1965). This age evaluation was reinforced by an abundance of *Ancyrospora ancyrea* cf. var. *brevispinosa* and an interpreted inception(?) of *Grandispora ?naumovii*. However, the occurrence of *Geminospora lemurata* (al. *Geminospora tuberculata*) in Fair Isle confirms an early/mid Givetian age for these assemblages, and furthermore suggests a probable correlation with either the Lester Slates & Sandstones or Combe Martin Slates. The absence of *Cristatisporites triangulatus* (and *Contagisporites optivus* var. *optivus*) in the Fair Isle material rules out comparison with the palynology of the Kentisbury Slates.

Marshall (1988) remarked upon the concurrence of *Ancyrospora langii*, *Cristatisporites triangulatus*, *Contagisporites optivus* and *Geminospora lemurata* in the Old Red Sandstone sequences of the Walls Group (Marshall, *in press*) and SE Shetland (Allen & Marshall, 1981). In part the concurrence of these taxa clearly reflects a late Givetian if not younger age, and may equate with the uppermost Combe Martin Slates or lowermost Kentisbury Slates.

4.3.6 The Morte Slates.

4.3.6a *The miospore palynostratigraphy of the Morte Slates.*

In common with the Kentisbury Slates, the palaeontology reported from the Morte Slates lacked detailed structural and sedimentological constraints. Consequently, palynological information is tabulated (refer to Table 4.2 overleaf), with the hope that in the future, these assemblages may be more correctly ordered as a consequence of a detailed, integrated sedimentological and structural study. In collecting from the Morte Slates, a number of samples were taken from what was believed to approximate to the base of the unit, some from towards the ?middle of the succession, and similarly some from the top. Broad variations in the stratigraphical character of the palynomorph assemblages were thus noted.

Of the 33 taxa documented from the Morte Slates, 13 range through from the Kentisbury Slates, with 6 other taxa considered reworked and the remaining 14 exclusive to this unit. Of the 41 taxa reported *in situ* within the Kentisbury Slates, only 13 persist through into the Morte Slates (see remarks in Section 4.3.5a, and discussion below). Clearly, a major change in the composition and abundance of the palynoflora can be resolved across the Kentisbury/Morte Slates boundary.

Despite the apparent simplicity of the spore assemblages recovered from the Morte Slates and also the absence of important zonal taxa, reasonably substantiated age evaluations have been made. In the eastern outcrop of the Morte Slates, sediments of this unit are presumed to conformably overly the Kentisbury Slates (Edmonds *et al.*, 1985). The transition between these two units is not delineated by an abrupt megascopic contrast in sedimentary facies. As remarked in Section 4.3.5a, the miospores assemblages from these two units are however strikingly different, with a marked reduction in species diversity and assemblage abundance. Whether this contrast in the palynofloras is attributable to a subtle change in palaeoenvironment, or is a reflection of stratigraphic position is uncertain. Richardson & McGregor (1986, p. 18) remark that within the Frasnian *ovalis-bulliferus* Assemblage Zone most large, sculptured, zonate-pseudosaccate miospores dwindle in numbers and disappear. The recovery of simplistic palynofloras from the Morte Slates and the last occurrence in the Kentisbury Slates of large pseudosaccate spores (*e.g Rhabdosporites langii* and *Grandispora naumovii*), concurs with this observation.

Despite the continuation into the Morte Slates of a number of taxa through from the underlying Kentisbury Slates (*e.g. Aneurospora greggsii, Ancyrospora simplex* and *Geminospora lemurata*), in general terms the stratigraphic character of the palynofloras recovered from the Morte Slates is considered different to that of the Kentisbury Slates. Almost 50% of the total taxa listed for the Morte Slates were exclusive to this unit: the first occurrences of these species can only be traced spatially from east to west, and not chronologically. Despite the depletion in assemblage composition at the Kentisbury/Morte Slates boundary, the persistence of certain important zonal forms, such as *Cristatisporites triangulatus, Geminospora lemurata* and *Verrucosisporites bulliferus*, into the Morte Slates suggests affiliation with the *ovalis-bulliferus* Assemblage Zone (Richardson & McGregor, 1986). The absence at this level of any late Frasnian/earliest Famennian zonal taxa (such

Table 4.2 The occurrence of miospore taxa in the Morte Slates.

SAMPLE No.	M01	M02	M03	M04	M05	M07	M10	M12	M15	M18	M20	M22	M24	M26	M28	M31	M33	M35	M37	M38	M40	M41	M42	M43	M44	M45	M46	M47
TAXA •																												
Ancyrospora langii							X										X				X		X		X			
Ancyrospora simplex	X	X		X	X	X	X	X	X		X	X	X	X	X	X	X	X		X	X	X	X	X	X	X		
Aneurospora greggsii	X	X						X			X							X			X		X					
Auroraspora cf. torquata																							X		X			
Calamospora pannucea																							?R					
?Calamospora sp. A				X					X	X		X	X		X	X	X	X					X		X			
Convolutispora cf. subtilis						X				X					X			X		X					X			
Convolutispora sp. A						X		X	X		?	X		X	X													
Crassispora catenata								X			X	cf.		X				X			X	X	X	X	X		?	X
Cristatisporites triangulatus	?			X				X	X	X	?	X	?		X			X			?	X	X	?	X			
?Cyclogranisporites sp. B								X		X										X								
Diaphanospora reticulata				X	X	X	X	X	X	X	X	X	X	X	X			X		X	X	X	X	X	X	X	X	X
Geminospora boleta						X			X	X		X	X	X				X			X	X	X	X	X	X	X	X
Geminospora lemurata	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Geminospora ?spinosa						X				X		X	X	X	X			X		X					X	X	X	
Geminospora tuberculata var. micrornata																	X						X					
Geminospora tuberculata var. tuberculata						X	X													X		X						
Grandispora aff. echinata	?										X							X					X					
Grandispora saetosa																							X		X			
Grandispora tomentosa									X		X			X				X			X		X		X			
Grandispora sp. D.																									R			
Grandispora sp. E					?R							?R								?R								
Insculptospora confossa							X	X	X					X				X					X				X	
Punctatisporites planus			?			X			X				?					X		X				X				
Retusotriletes rugulatus	X	X																										
Retusotriletes triangulatus				X	X	X	X	X		X		?		X	X			X			X		X					
Rhabdosporites langii								R					R		R								R					
Rugospora sp.							X	X		X	X											X	X		X		X	
Verrucosisporites bulliferus	X									X		X			X			X				X	X					
Verrucosisporites scurrus												R						R										
Spore Type B		X																X					X	X				
Spore Type C						X			X	X													X					
?hystricospores, unident.										R			R															

• taxa ordered alphabetically.

KEY.
X = present
R = reworked
? = identity questioned
?R = questionably reworked

as *Auroraspora torquata* or *Grandispora gracilis*), supports this interpretation. The near ubiquitous recovery of *Diaphanospora reticulata* through the Morte Slates corroborates a Frasnian age, as according to Richardson & McGregor (1986, p. 18) this taxon is a common constituent of the Frasnian *ovalis-bulliferus* Assemblage Zone.

Streel *et al.* (1987) and Streel & Vanguestaine (1989) remarked that the limit between the *ovalis-bulliferus* and *torquata-gracilis* Assemblage Zones of Richardson & McGregor (1986) is poorly defined. Furthermore, Streel & Vanguestaine (1989) comment that most of the species assumed to first occur contemporaneously within the Hanover Shale Formation, western New York State, U.S.A., (the reference section of the *torquata-gracilis* Assemblage Zone), have in fact been reported in the Boulonnais region of northern France across five successive Interval Zones that transgress the Frasnian-Famennian boundary. However, as mentioned in Sections 4.3.1 and 4.3.5a, the zones defined by Streel *et al.* (1987) for the middle/upper Frasnian (based on the palynology of the Boulonnais: Loboziak & Streel, 1980, 1981; Loboziak *et al.*, 1983) were effectively unresolved in the present study. Apart from *Verrucosisporites bulliferus*, the absence of all the zonal taxa cited by Streel *et al.* (1987) for this Frasnian interval not only limits a detailed evaluation of the age of the Kentisbury Slates, but similarly also for the overlying Morte Slates. In comparison, the broader zonal concepts as proposed by Richardson & McGregor (1986) proved more applicable when interpreting ages for these units.

Due to the uncertainty in sample ordering, the precise stratigraphical ranges of taxa through the Morte Slates remains problematical. However, the recovery first of *Crassispora catenata* from within the ?middle of this unit, followed by *Auroraspora* cf. *torquata* from towards the ?top are of biostratigraphical significance. Richardson & McGregor (1986) remarked that the inception of the former species is associated with the latest Frasnian, and thus established the *torquata-gracilis* Assemblage Zone (delineated by the inception of *Auroraspora torquata* and *Grandispora gracilis*, and which spans the latest Frasnian to early late Famennian interval). Based on this evidence, it seems plausible that the ?middle-upper Morte Slates are latest Frasnian in age, with the topmost levels possibly of earliest Famennian age.

4.3.6b *Comparisons with published reports of palynomorph assemblages from Devonian strata of Britain.*

By and large the assemblages recovered from the Morte Slates do not compare favourably with most published reports of Frasnian assemblages from the British Isles, largely due to the apparent simplicity, low diversity and low abundance of the Morte Slates assemblages. Based on palynological evidence, Mortimer & Chaloner (1967, 1972) remarked that rocks of Frasnian age were encountered in the Stonebridge Park, Tottenham Court Road and Wyboston Boreholes. Of these three borehole assemblages, those of the Wyboston Borehole are closest in composition to those of the Morte Slates. *Ancyrospora langii, Ancyrospora simplex, Cristatisporites triangulatus, Grandispora tomentosa* and *Geminospora lemurata* are common to both. *Hystricosporites multifurcatus* is now recognised by Streel *et al.* (1987) as a key zonal form, with its inception defining the base of the Frasnian BJ (*bulliferus-jekhowskyi*) Oppel Zone. This taxon and the associated megaspore assemblage recorded from the Wyboston Borehole were unfortunately not reported from north Devon. Despite the presence of *Rhabdosporites langii* in the Wyboston Borehole, the palynological data collated for this borehole confirms a tentative correlation with the Morte Slates.

The palynomorph assemblages reported by Owens *et al.* (1977) from the Devonian of the

Steeple Aston Borehole bear little resemblance to those detailed from the Frasnian sediments of north Devon. *Ancyrospora simplex, Geminospora lemurata* and *Verruciretusispora* sp (re-allocated in the present study to *Geminospora boleta*) are the only taxa clearly common to both sequences. Although of comparable age, the Frasnian palynomorph assemblages described by Le Gall *et al.,* (1985) from the Gramscatho Group, South Cornwall, bear little resemblance to those recovered herein from the Morte Slates.

Although outside the British Isles, the proximity and favourable comparability of the two miospore assemblages reported by Clayton & Graham (1974) with those of the Morte Slates merits mention. Clayton & Graham (1974) recovered a Givetian/Frasnian aged assemblage from the Sherkin Formation, of south-west County Cork (Ireland), which included *Cristatisporites triangulatus* and *Grandispora saetosa.* These species were similarly reported from the Morte Slates. Higgs & Russell (1981) documented a miospore assemblage of probable Frasnian age from the Green Sandstone Formation, Moll's Gap Quarry (County Kerry), that contained a number of taxa also found during the course of the present study in the Morte Slates [*e.g Ancyrospora simplex, Cristatisporites triangulatus, Geminospora boleta* and *?Rhabdosporites parvulus* (= *Diaphanospora reticulata*, of the present study)].

The Famennian miospore assemblages reported by Dolby (1970b), Dolby & Neves (1970) Utting & Neves (1970) and Mitchell *et al.* (1982) are distinct in composition, compared with those listed herein from the Morte Slates (Note: re-evaluation by Higgs *et al.,* 1988).

4.4. THE BIOSTRATIGRAPHIC UTILITY OF THE MICROPLANKTON, CHITINOZOA, SCOLECODONT AND "WOOD" COMPONENT RECOVERED FROM NORTH DEVON.

4.4.1 Introduction.

Few publications systematically record or illustrate marine palynomorphs from the Devonian strata of the British Isles (Owens *et al.,* 1977; Richardson & Rasul, 1978a,b; Dean 1989b: Wilkinson & Knight, 1989). In view of the isolated occurrence of such palynomorphs in north Devon and the obvious lack of reference literature, any non-miospore age evaluations are based on comparisons with coeval assemblages reported from outside the British Isles. An additional limitation is that the precise temporal distribution through the Devonian System of certain taxa, or indeed whole microfossil groups (*e.g* scolecodonts), is still poorly understood.

As will be discussed further in Chapter 5, the general absence of acritarchs and chitinozoa within certain parts of the sequence may be the result of palaeoenvironmental exclusion (rather than a reflection of stratigraphic position). The regional occurrence of acritarchs and chitinozoa within the Devonian sediments of north Devon is plotted on Table 4.3, overleaf. Reworking is not indicated. Any disparity between the noted occurrence of acritarchs and chitinozoa within Appendix II and Table 4.3 implies that although acritarch or chitinozoa fragments were present within a particular sample, they could not be satisfactorily assigned to any genus. In this study, scolecodont taxa have only superficially been differentiated (refer to Chapter 3): their occurrence is merely indicated in Appendix II.

SAMPLE No.	LN17	LN34	LN52	LN88	LN92	LN96	LN98	LN101	H06	H13	R21	R22	S01	S02	S08	S10	S12	S14	S18	S20	S25	LH01	LH04	LH05	LH08	LH09	LH10	LH11	LH12
TAXA																													
ACRITARCHS																													
Cymatiosphaera reticulosum											X							X							X				
Cymatiosphaera cf. reticulosum							X			X																			
Dateriocradus sp.											X																		
Dictyotidium cf. cohora						X	X		X		X		X	X	X		X	X	X	X	X		X	X		X	X	X	X
Dictyotidium cf. polygonium																		X											
Dictyotidium sp. A			X		X																X								
?Dictyotidium sp. B											X			X															
Dictyotidium sp. C											X					X													
Diexallophasis denticulata					X	X	X													X									
Diexallophasis remota	X		X		X	X	X				X			X		X			X	X	X	X							
Diexallophasis simplex																X													
Leiosphaeridia sp.						X	X						X	X															
Micrhystridium sp. A											X									X	X								
Micrhystridium sp. B					X		X				X																		
Multiplicisphaeridium ramusculosum						X					X		?	X	X			X		X	?						X		
Multiplicisphaeridium sp. A			X		X	X	X																						
?Oppilatala sp.																X													
Veryhachium trispinosum "complex"			X	X			X							X	X		X												
?Veryhachium sp.							X																						
Vulcanisphaera sp.						X	X									X			X										
Acritarch Type A																			X										
CHITINOZOA																													
Ancyrochitina sp. A		X																											
Ancyrochitina sp. B								X																					
?Ancyrochitina sp. C								X																					
Angochitina sp. A							X								X				X	X									
Eisenackitina castor											X	X			X										X				
Fungochitina ?pilosa																			X		X		X	X		X			
Sphaerochitina sp.							X			X					X	?				X									

SAMPLE No.	WP02	WP10	WP12	WP14	WP16	WP20	WP26	WP27	WP31	L10	L15	L23	L30	CM01	CM02	CM23	CM28	CM66	K12	K29	K32	K42	K44	K52	M05	M12	M35	M40	M41	M42	M44	M46
TAXA																																
ACRITARCHS																																
Cymatiosphaera reticulosum	X			X			X							X													X		X			
Cymatiosphaera sp. A																							X	X								
Dictyotidium cf. cohora			X		X	X	X		X	X	X	?								X	X	X	X	X						X		
Dictyotidium sp. A		X												X					X													
Diexallophasis remota	X					X													X													
Gorgonisphaeridium sp.																				X	X											
Maranites gallicus																										X		X		X	X	X
Maranhites perplexus																									X	X	X			X	X	X
Micrhystridium sp. C			X		X		X																									
Multiplicisphaeridium ramusculosum	X	X																														
Multiplicisphaeridium sp. A		X		X					X																							
?Ovnia desertica																											X					
Polyedryxium decorum																					X		X									
?Veryhachium europaeum		X																														
Veryhachium trispinosum "complex"																						?										
CHITINOZOA																																
?Ancyrochitina toouratinensis													X	X		X		X														
Ancyrochitina sp. A																	X						X									
Angochitina sp. A						X	X						X				X									X						
Angochitina sp. B						X		X																				X				
?Conochitina sp.																		?					X									
Fungochitina ?pilosa			X		X		X	X				X			X	X	X							X								
?Hoegisphaera sp.																							X	X								
Sphaerochitina sp.												X														X	X			X		

Table 4.3. The occurrence of acritarch and chitinozoa taxa within the Devonian of north Devon.

4.4.2 The contribution of the Acritarcha to age evaluations.

The recovery of certain species of acritarch (*e.g. Vulcanisphaera* sp.) suggests the occasional influence of reworking on assemblage composition, with a probable provenance from ≈Silurian (or older) strata (in ?south Wales). In a study of the mid Emsian strata in the Apley Barn Borehole (Oxfordshire), Richardson & Rasul (1978a,b) reported extensive reworking of Lower Palaeozoic acritarchs and chitinozoa into the miospores assemblages. Hassan (1982) noted a similar feature in a study of the palynology of the Lower Devonian Red Marl Group (south Wales).

In north Devon, only some of the microplankton were considered truly contemporaneous with the encasing sediment, despite many of the forms documented having quite extensive stratigraphical ranges which can accommodate their occurrence in north Devon. As an illustration, *Diexallophasis remota* and *Multiplicisphaeridium ramusculosum* may feasibly be reworked into north Devon, although their occurrence in this sequence is compatible with the known range of these species: *Diexallophasis remota* has been reported from Silurian strata (*e.g.* Jardiné *et al.,* 1974; Steemans, 1989) and throughout the Devonian (*e.g.* Riegel 1974; Playford, 1977; Deunff, 1980; Wicander & Wood, 1981; Wicander 1984; Streel *et al.,* 1988; Steemans 1989), and *Multiplicisphaeridium ramusculosum* is a widely known cosmopolitan form, ranging from the Upper Ordovician to Upper Devonian (Wicander & Lu Li-Chang, 1988, p. 125). The broad stratigraphical range of such species limits their potential stratigraphic utility.

Conversely, the occurrence of a few selected species corroborate age evaluations provided largely by the miospore assemblages. *Diexallophasis simplex* was formally described from the Givetian Silica Formation, Ohio, U.S.A. (Wicander & Wood, 1981). This form has been subsequently reported from other Middle Devonian sediments by Wicander & Wright (1983; Columbus and Delaware Limestone, Ohio), Wicander (1984; resumé of North American acritarch biostratigraphy) and Wood & Clendening (1985; Boyle Dolomite of Kentucky). This species was recovered from the Sherrycombe Formation (north Devon) in the present study, which according to miospore data is referrable to the ?mid/late Eifelian (to ?earliest Givetian) interval. A further illustration is provided by the recovery of *Maranhites perplexus* from the Morte Slates, which confirmed the Upper Devonian spore-based age interpreted for this unit. *M. perplexus* was first described by Wicander & Playford (1985) from upper Frasnian material of the Lime Creek Formation, Iowa, U.S.A. Recently, Wilkinson & Knight (1989) report this species from the late Famennian strata that crops out at Loe Bar, south Cornwall.

For further examples, refer to the acritarch systematics in Chapter 3, where the known geologic range of acritarchs identified to species level is provided.

4.4.3 The contribution of the chitinozoa faunule to age evaluations.

As with the acritarch population, in isolated examples the chitinozoa assemblages contributed to or confirmed age evaluations which were based largely on the miospore assemblages. Unfortunately, many of the chitinozoa recorded in this study could not be assigned with confidence to known species, mainly due to their fragmentary form.

In north Devon, *Eisenackitina castor* was recorded from the Rawns, Sherrycombe and Little Hangman Formations of the upper Hangman Sandstone Group (?mid/late Eifelian - ?earliest Givetian interval). Jansonius (1964) remarked that *E. castor* ranged from the Upper Silurian to Middle Devonian (Givetian). Legault (1973) reported on the abundance of this species from the Bell, Rockport Quarry and Arkona Members of the Givetian Hamilton Formation, of southwestern Ontario, Canada. Wood (1974) subsequently documented *E. castor* from the Givetian Silica Formation of Ohio, and more recently Streel *et al.* (1988) have reported this form from subsurface Devonian strata in Northeast Libya. The recovery of *E. castor* from north Devon is compatible these reports (also refer to Jenkins & Legault 1979, p. 255, Text-Figure 6).

Fungochitina (al. *Sphaerochitina*) *pilosa* was originally diagnosed by Collinson & Scott (1958) from the Cedar Valley Formation (Middle Devonian), N.W. Illinois, U.S.A. Subsequent studies of this formation also reported *F. pilosa* (Dunn, 1959; Urban, 1972). Urban & Newport (1973) later described this taxon from the Middle Devonian Wapsipinicon Formation, Iowa. Based on Jenkins & Legault (1979, p. 255, Text-fig. 6), *Fungochitina* (al. *Sphaerochitina*) *pilosa* spans the Givetian to late Frasnian interval. Paris (1980) documented *F. pilosa* from the Mariposas Formation, Spain, with Wood & Clendening (1985) subsequently recorded this form from the Boyle Dolomite of Kentucky. Recently, Paris (in Streel et al., 1988) reports this species from subsurface Devonian strata of Northeastern Libya. The occurrence of *Fungochitina ?pilosa* in the palyniferous upper Hangman Sandstone Group and the Wild Pear Slates, Lester Slates & Sandstones and the Combe Martin Slates concurs with previous ages assessments; these units are collectively Middle Devonian in age. The rarity and poor preservation of specimens referrable to *F. ?pilosa* in the Kentisbury Slates (sample K52) is believed to reflect reworking (although the occurrence at this level is compatible with the Givetian to Frasnian range as defined by Jenkins & Legault, 1979; p. 255, Text-Figure 6).

4.4.4 The contribution of scolecodonts and "wood" to age evaluations.

Little research has been undertaken to investigate the precise temporal variability of scolecodonts through the Devonian Period. Forms recorded in the present study were attributed to one of five broadly defined morphotypes, largely because of the chaotic state of current scolecodont taxonomy. The stratigraphic ranges of specific forms was not assessed. However, forms described and illustrated herein are compared with a selection of known Devonian elements. A number of these compare favourably with reported species of Frasnian scolecodonts, *sensu* Jansonius & Craig, 1971 (refer to Chapter 3 of the present study, and the description of Plate 3.34).

The stratigraphical variation in dispersed "wood" phytoclasts is similarly poorly understood. Of interest to the current study is the work of Burgess (1987) and the synoptic report of Edwards & Burgess (1990), where the terrestrialization of plants is discussed and the known temporal range of certain plant-derived phytoclasts recorded. In these studies, certain cuticular fragments were recorded through Siluro-Devonian times, being considered analogous to vascular plant cuticles, but differed in lacking stomata and also in usually being imperforate. Burgess (1987) looked in detail at the spatial and temporal distribution of plant-derived phytoclasts in the Silurian and Lower Devonian sediments of the classic Anglo-Welsh Basin, and traced the evolution of adaptive characteristics as displayed by primordial land-plants. Burgess recognised at least three phases of land plant development, defined initially by the establishment of cryptospore-producing plants, followed by the appearance and diversification of thalloid non-vascular plants referable to the Nematophytales (Lang), and finally marked by the radiation of upright, dichotomising pteridophytes, or non-vascular but similar plants. Subsequently, Edwards & Burgess (1990, p. 61-62, Fig. 1) remarked that most ornamented types of cuticle appeared in Wenlock times and extend through into Devonian strata.

In the present study, types of "wood" were differentiated into four, heterogeneous categories. The widespread stratigraphical occurrence of many of these plant fragments within north Devon precludes their utility as zonal indices for detailed correlation. Furthermore, the simplicity of the dispersed "wood" assemblages (?)suggests that the parent plants may well have been anatomically and phylogenetically conservative. However, in broad terms two assemblage-types may be defined. Types A and B are homologous at least in part to *Laevitubus, Filomata, Porcatatubus* and *Torotubus, sensu* Burgess (1987): in north Devon these are confined largely to the Lynton Formation and the Hangman Sandstone Group (refer to Chapter 5, Fig. 5.1). In view of the age evaluations presented herein, these two dispersed "wood"-types are interpreted to range into ?mid/late Eifelian to ?earliest Givetian times. The sporadic occurrence of these two forms in overlying strata are probably reworked. In contrast, Types C and D were found pervasively throughout the studied sequence.

4.5. BIOSTRATIGRAPHICAL ANOMALIES.

4.5.1 Introduction.

The perceived total stratigraphical ranges of most microfossil taxa are not necessarily absolute. Indeed, the timing of a number of important micropalaeontological events across the Old Red Sandstone Continent may prove to have been diachronous, and not, as is currently presumed, contemporaneous (*e.g.* note Loboziak & Streel, 1980; comments in McGregor, 1981). In general the precision of stratigraphical ranges is often diluted by the inaccurate assessments of total assemblage age, misidentifications and unrecognised reworking. With these points in mind, the following section discusses extensions to currently interpreted stratigraphical ranges of a few selected taxa, and the anomalous concurrence of certain other forms. Taxa are discussed stratigraphically as they occur in the Devonian strata of north Devon, rather than alphabetically by genus. Occasionally it proved difficult to discriminate between reworking and real extensions to the stratigraphical ranges of palynomorphs. In most palynological studies, low specimen abundance and/or poor preservation have informally been used in the recognition of reworking. However, because palynomorph abundance was relatively low throughout the studied section, and also because oxidised specimen preservation was usually moderate to good, such criteria were deemed unreliable for identifying reworking in north Devon.

4.5.2 Conodonts.

Disparities were noted between the temporal distribution or isolated occurrence of conodonts in north Devon, relative to the known stratigraphical ranges of such taxa as defined outside the British Isles. The sporadic and generally low conodont yields reported herein limit a complete assessment of the extent of reworking on assemblage composition. Indeed, although plausible extensions to the stratigraphical ranges of certain conodont taxa are recognised these are not formally proposed, by virtue of the paucity of the data base.

Faunas from the Rillage and Holey Limestones are dominated by icriodids, a number of which are commonly perceived to be mutually exclusive (*e.g. Icriodus* cf. *regularicrescens* and *I. brevis:* from Weddige 1977, Bultynck 1987). In the Rillage Limestone, specimens attributed to *I.* cf. *difficilis* concur anomalously with forms of *I. lindensis* (from Weddige, 1977; Bultynck, 1987). However, *I. lindensis* occurs in abundance, which suggests reworking is unlikely (although this process may explain the rare presence of *I.* cf. *regularicrescens* at this level). The occurrence of one specimen identified as *I. ?fusiformis* (from sample 86.055) is interpreted as reworked, as *I. fusiformis* (*sensu stricto*) is more commonly associated with Lower Devonian faunas (*sensu* Weddige, 1977). *I. brevis* is pervasive throughout the conodont-productive carbonates of the Ilfracombe Slates, including sample K53 of the Kentisbury Slates. According to Weddige (1977), this taxon is not found above the *varcus* Zone, although Klapper & Ziegler (1979) and more recently Bultynck (1987) have illustrated its range as extending beyond this biozone. According to Klapper & Ziegler (1979) this form is restricted to the Givetian Stage, and thus its occurrence in the Kentisbury Slates may be reworked, or alternatively an extension to the known range of this species.

The polygnathid faunas (comprising *Polygnathus linguiformis linguiformis*, *P. rhenanus*, and *P. varcus*) recovered from the Combe Martin Beach and David's Stone Limestones are compatible with reported Givetian associations (*e.g* Ziegler *et al.*, 1976; Weddige, 1977; Bultynck, 1987). Presuming the Frasnian age interpreted for the Kentisbury Slates to be correct, then the *Polygnathus* assemblage recorded from sample K53 is somewhat unusual in containing forms tentatively assigned to *P. ansatus*. According to Ziegler *et al.* (1976), Weddige (1977), Klapper & Ziegler (1979) and Bultynck (1987), *Polygnathus ansatus* (*sensu stricto*) spans the Middle *varcus* Subzone, and is confined to the Givetian interval. Reworking may account for the recovery of this taxon from the Kentisbury Slates.

4.5.3 Miospores

Current miospore biozonations are not intended to be absolute statements, but simply embody evolving concepts. Therefore, zonal schemes are susceptible to refinement and larger scale modification, subsequent to new discoveries. Therefore, the palynostratigraphy established for north Devon may have some bearing on future revisions to the zonal schemes previously proposed by Richardson & McGregor (1986) and Streel *et al.* (1987).

In a few instances, the poor preservation and ineffective oxidation of palynomorphs recovered from north Devon limited accurate identification: reworking occasionally proved difficult to assess. Problems were further compounded by the uncertain stratigraphical location of some sample stations. Irrespective of these factors, a detailed palynostratigraphy has been constructed, and significant anomalies identified. A small, representative selection of the more significant biostratigraphical anomalies are discussed below, according to their lithostratigraphical occurrence: from the Lynton Formation through to the Morte Slates.

Emphanisporites foveolatus has been widely reported from strata of Emsian age (Schultz, 1968; Lanninger, 1968; Riegel 1975, 1982; Riegel & Karathanasopoulus, 1982; Turnau 1986). Streel *et al.* (1987) recognised the biostratigraphical importance of this taxon, using the joint first occurrence of *E. foveolatus* and *Verruciretusispora dubia* to delineate the base of the FD Oppel Zone and therefore indicating a lower Emsian age. Lanninger (1968) recorded *Emphanisporites foveolatus* through the Klerfer Schichten and Wetteldorfer Sandstein, S.W. Eifel, although Riegel (1982) later restricted the range of this taxon to the Klerf Formation, perceiving it to be exclusive to lower Emsian strata. More recently Turnau (1986) reported *E. foveolatus* from near the top of the Zwolen Formation of Pionki, Poland, in an undifferentiated marine sequence spanning the *annulatus-sextantii* and *douglastownense-eurypterota* Assemblage Zones of Richardson & McGregor (1986). Steemans (1989) notes this taxon from Siegerland, Germany, reporting its stratigraphical range as spanning the late Pragian to Emsian interval (attributable to the AB Biozone). In the present study, *E. foveolatus* formed a prolific component of assemblages documented from the Lynton and Hollowbrook Formations (as much as 15% of the total miospore population). Clearly, the recovery of *E. foveolatus* from north Devon substantially extends the range of this taxon well into the late Emsian, as these units are referred to the *douglastownense-eurypterota* Assemblage Zone of Richardson & McGregor (1986) - if not higher (see Section 4.3.4a earlier).

Species of *Dibolisporites* are prolific in the lower part of the studied sequence, with the genus becoming increasingly infrequent and of lower diversity through the Hangman Sandstone Group and into the Ilfracombe Slates. *Dibolisporites* (al. *Anapiculatisporites*) *eifeliensis* was originally described from the Emsian Grès de Wetteldorf of the Rheinisches Schiefergebirge, S.W. Eifel (Lanninger, 1968), and has subsequently been reported from Emsian and Eifelian strata of eastern Gaspé, Canada (McGregor 1973, 1974, 1977) and from Emsian sediments of the Moose River Basin, Ontario (McGregor & Camfield (1976). Moreau-Benoit (1976) and Le Herissé (1983) recorded this form from ?Lochkovian to Emsian strata of Brittany, France. Massa & Moreau-Benoit (1976) and subsequently Moreau-Benoit (1979) document *D. eifeliensis* from the Rhadamès Basin, Libya, with Richardson (in Paris *et al.*, 1985) also noting it within Emsian assemblages from Libyan borehole material. Turnau (1986) subsequently recorded this form in the Emsian strata of the undivided marine Zwolen Formation, Pionki, Poland. Recently Ravn & Benson (1988) report *D. eifeliensis* from an unnamed subsurface Devonian unit of probable Emsian/Eifelian age in southwestern Georgia (U.S.A.), whilst Steemans (1989) documents this species from the Lower Devonian of Belgium, reporting its range as spanning the Lochkovian to Emsian (BZ to AB Oppel Zones of Streel *et al.*, 1987). According to the synoptic range charts of Richardson & McGregor (1986), this taxon just extends into the Eifelian *velatus-langii* Assemblage Zone. In the present study, *Dibolisporites eifeliensis* was recorded pervasively throughout the Lynton Formation, extending through the Hollowbrook Formation, and appearing in numbers in the palyniferous levels of the upper Hangman Sandstone Group. Initially, the concurrence of *D. eifeliensis* with *?Densosporites devonicus* and *Grandispora naumovii* was attributed to reworking, but the former taxon was recovered in such numbers that this explanation seemed improbable. In view of the overall age interpreted herein for the miospore assemblages of the upper Hangman Sandstone Group, the stratigraphical range of *Dibolisporites eifeliensis* is considered to extend well into ?mid/late Eifelian times.

By comparison with the reports of Richardson & McGregor (1986), *Acinosporites* cf. *apiculatus* and *Acinosporites lindlarensis* var. *lindlarensis* in the Lynton Formation have a somewhat delayed entry. Richardson & McGregor (1986), for example, specify the first occurrence of *A. lindlarensis* var. *lindlarensis* as within the *annulatus-sextantii* Assemblage Zone. In north Devon, this taxon appears at a somewhat higher (younger) level, ≈60m above the exposed base of the Lynton Formation and following the first appearance of *Grandispora protea.*

The stratigraphical range of *Grandispora libyensis* was stated by Moreau-Benoit (1980) to span approximately the Emsian to Frasnian interval (based on a taxonomic re-evaluation of assemblages described by Massa & Moreau-Benoit, 1976). Riegel (in Paris *et al.*, 1985) reported this species from subsurface Middle Devonian strata in northeast Libya. Loboziak *et al.* (1988, p. 360, Table 1) and Loboziak & Streel (1989, p. 193, Figure 2) have plotted the range of this taxon from the Givetian to

Frasnian Stages, with Coquel & Latreche (1989) and also Coquel & Moreau-Benoit (1989) subsequently recording this taxon from Famennian and Lower Carboniferous strata of North Africa. In the present study, the stratigraphical range of *G. libyensis* proved more restricted, being confined to the ?early Eifelian Hollowbrook Formation and extending through into the early/?mid Givetian Lester Slates & Sandstones.

Verrucosisporites tumulentus was first described from the Givetian/Frasnian Sherkin Formation (Clayton and Graham, 1974). This study concurs with the findings of McGregor & Camfield (1982) in recording this species from sediments as old as ?mid/late Eifelian in age (the Rawns, Sherrycombe and Little Hangman Formations of north Devon). This species ranges into the Frasnian strata of the Kentisbury Slates.

Geminospora lemurata was first described by Balme (1962) from the Frasnian Gneudna Formation of the Carnarvon Basin in Western Australia, and has since been widely reported from the late Middle Devonian to pre-Famennian, Late Devonian interval in both northern and southern hemispheres. The first appearance of *G. lemurata* in lower Givetian strata is well established[2] (Playford, 1983; Richardson & McGregor, 1986; Streel *et al.*, 1987; and references therein). The influx of this taxon in the Membre de Couderousse (of the upper part of the Formation de Blacourt, Boulonnais, France) is acknowledged to be slightly delayed (Loboziak & Streel, 1980; 1981; 1988). However, the last occurrence of this taxon is less clearly understood (refer to Playford, 1983, p. 321-322). In a continuation of their studies of the Late Devonian palynology of the Boulonnais, northern France, Loboziak & Streel (1981, p. 55) remarked that *G. lemurata* was present in the uppermost levels of the Formation d'Hydrequent, which were possibly as young as early Famennian. According to Richardson & McGregor (1986) this taxon was believed to range only part way into the Frasnian *ovalis-bulliferus* Assemblage Zone, with a possible extension into the Famennian Stage. Chitaley & McGregor (1988) subsequently remarked on the homology between the dispersed spores of the late Famennian lycopsid *Bisporangiostrobus harrisii* and the dispersed miospore taxon *Geminospora lemurata*; the spores of *B. harrisii* differ in being proximally tripapillate. In a study of the subsurface Silurian and Devonian palynology of the Illizi Basin (Algerian Sahara), Boumendjel *et al.* (1988, p. 333, Fig. 2) trace *G. lemurata* from the lower Givetian Alrar Formation, extending through into the Famennian (Fa2c) upper Gazelle Formation. With seeming contradiction, however, Boumendjel *et al.* (1988, p. 335) make no mention of the occurrence of this taxon in the discussion of the latter Famennian palynoflora. Loboziak *et al.* (1988, p. 360, Table 1) and Loboziak & Streel (1989, p. 193, Fig. 2) recently report *G. lemurata* from subsurface strata as young as the (Frasnian) IV Phase zone in the Parana Basin (Brazil) and the Ghadamis Basin (Tunisia-Libya) respectively. In the present study, prolific numbers of *Geminospora lemurata* occur in association with *Crassispora catenata* and *Auroraspora* cf. *torquata* from the ?uppermost Morte Slates. The concurrence of the two latter taxa suggests a latest Frasnian, ?earliest Famennian age at this level (refer to the discussion in Section 4.3.6a). Consequently, the findings of the present research suggest that the range of *Geminospora lemurata* extends through at least until latest Frasnian (or younger) times.

The stratigraphical range of ?*Corystisporites collaris* in north Devon is slightly anomalous when compared with previous reports. Tiwari & Schaarschmidt (1975) first diagnosed this taxon based on

[2] Independent of the findings of Loboziak *et al.* (1989) - awaiting formal publication of their results.

material recorded from the Middle Devonian strata of the Prüm Syncline, Eifel, Germany. McGregor & Camfield (1982) later reported this taxon from the Middle Devonian of the Canadian Arctic. In north Devon, ?*C. collaris* was traced through from the Combe Martin Slates into the Kentisbury Slates, thus allowing the range of this taxon to be extended into the Frasnian Stage.

Based on occurrences in the Ilfracombe Slates, the stratigraphical range of a number of taxa are upwardly extended. The demise of *Rhabdosporites langii* is widely acknowledged as approximating to the Givetian/Frasnian boundary (note: Loboziak & Streel 1988, and usage in Loboziak & Streel 1989). However, based on the stratigraphic interpretations proposed in the present study and the persistence of this taxon throughout most of the Kentisbury Slates, the range of *R. langii* is extended into the Frasnian Stage. Reworking is considered an unlikely influence, as this species was recovered from the Kentisbury Slates in comparatively large numbers: Richardson & McGregor (1986) tentatively suggested that *R. langii* may range into Frasnian strata (as illustrated by the dashed extension to the stratigraphical range of this taxon into the *ovalis-bulliferus* Assemblage Zone). The present study confirms their observation. Similarly, *Grandispora naumovii* was shown in the synoptic range charts of Richardson & McGregor (1986) as exclusive to the Middle Devonian interval. In the miospore assemblages recovered from the Kentisbury Slates, *G. naumovii* was prolific in numbers, found in association with *Cristatisporites triangulatus* and *Verrucosisporites bulliferus*. This association indicates that the range of *Grandispora naumovii* should likewise be extended into the Frasnian Stage.

Verrucosisporites premnus has been widely reported from Middle Devonian strata (Richardson, 1965; McGregor & Camfield, 1982; Paris *et al.*, 1985). Richardson & McGregor (1986) relate the disappearance of this species as within the *optivus-triangulatus* Assemblage Zone. However, *V. premnus* was reported (albeit intermittently) through the Kentisbury Slates and thus a component of Frasnian assemblages. This report is compatible with the observations of Loboziak *et al.* (1988), who recorded this species from the Upper Devonian Ponta Grossa Formation, Brazil.

According to Richardson & McGregor (1986) *Cristatisporites triangulatus* does not extend into the latest Frasnian/Famennian *torquata-gracilis* Assemblage Zone. However, within the ?top Morte Slates (samples M42 & M44) *Cristatisporites triangulatus* was found in numbers in association with *Auroraspora* cf. *torquata*. This concurrence suggests that the range of *Cristatisporites triangulatus* may be extended at least into the latest Frasnian interval. This extension is compatible with the top of the range of this species as reported by Loboziak & Streel (1981): *C. triangulatus* was recorded from the ?Famennian part of the Hydrequent Formation in the Boulonnais region, France.

4.6. THE MICROPALAEONTOLOGICAL CORRELATION OF SECTIONS CONSIDERED LATERALLY EQUIVALENT.

4.6.1. Introduction.

In north Devon, there are a number of Devonian sections that are presumed to be contemporaneous: the overall sparsity and poor preservation of macrofossils unfortunately precludes their use in confirming the contemporaneity of these sections (except for the work of Holwill, 1965, on the coral faunas). With the notable exception of the coralliferous limestone members of the Ilfracombe Slates (by which Webby, 1966b, related the Ilfracombe Slates of Somerset with the coastal Devonian strata of north Devon), isolated sections have in the past been correlated largely upon sedimentology. The quality and quantity of the micropalaeontology documented herein suggests an immediate (and ?ambitious) application of this study: to test the contemporaneity of selected, discrete sections. Three individual test cases are outlined below.

4.6.2. Intraformational correlation.

The sediments exposed at Little Burland (SS 661485) and Great Burland (SS 662495), west of Lynton, are reported to straddle the Lynton/Hollowbrook formational boundary (after Pound *in prep.*, and Tunbridge, 1978 respectively). These sequences are separated by less than ≈200m, but exact correlation between the two has proved problematical. Each section was therefore sampled systematically, and the palynology subsequently documented.

The palynomorph assemblages recorded from these sites were comparable. In particular they comprised prolific numbers of *Dibolisporites* spp., *Emphanisporites* spp., and *Retusotriletes* spp.: qualitatively yields were very similar. The taxa recorded from these two localities were however not unique to these sections. Indeed, the majority of species recorded in these formational boundary beds occur within the overlying palyniferous Hollowbrook Formation and extend to some extent down into the Lynton Formation (except for *Acinosporites* cf. *apiculatus* and *Grandispora libyensis*).

No palynological evidence was collated to suggest that these two sections are not lateral equivalents. However, the palynofloras recorded were not unique to these levels.

4.6.3. The utility of conodont faunas in local correlation.

Edmonds *et al.* (1985, p.13-14) suggested that the Rillage Limestone (SS 543486) and Holey Limestone (SS 576474) of the Ilfracombe Slates are lateral equivalents. In the present study, conodont samples were collected systematically from both units in an attempt to clarify their relationship. The faunas recovered from each unit are virtually identical in composition, comprising almost exclusively icriodids: *Icriodus brevis, I.* cf. *brevis. I. eslaensis, I. lindensis, I. obliquimarginatus, I.* cf. *regularicrescens* and *Icriodus* sp. G. Apart from *Icriodus* cf. *regularicrescens*, all the listed species were recovered from overlying younger strata (of the Combe Martin Slates). The only significant disparity between the two limestone members was the recovery of *Polygnathus rhenanus* from the Rillage Limestone. The occurrence of this polygnathid merely confirms the Lower/Middle *varcus* Zone age interpreted for this stratigraphic level.

As with the palynology of the "Burland's" (Section 4.6.2) the microfossil assemblages recovered from the Rillage and Holey Limestones are broadly comparable. However, the species reported for each unit were not unique to these horizons, and therefore cannot confirm a definitive correlation. The general comparability of the faunas does, however, suggest that the two limestones are approximately of the same stratigraphic age.

4.6.4. Regional correlation - to test the proposed diachroneity of the top of the Lynton Formation (after Pound, *in prep.*).

Pound (*in prep.*) reports that the top of the Lynton Formation is diachronous: the transition between the Lynton Formation and Hangman Sandstone Group exposed in the east of the study area (*e.g.* at Oxen Tor, SS 729490) can be correlated with the marine succession of the Lynton Formation exposed west of Crock Point (SS 687494 to 686492), which is ≈50m below the interpreted top of the Lynton Formation.

The palynofloras reported for Oxen Tor and west Crock Point are comparatively simple, and precise correlation is limited for reasons similar to those outlined earlier. Furthermore, comparison of the two sections is hampered by the paucity of the palynomorph assemblages recorded from within and stratigraphically adjacent to the "anoxia" event (*sensu*, Pound *in prep.*), west of Crock Point (SS 687493: approximates to the position of sample LN52).

4.6.5 Conclusions.

In spite of high species diversity and reasonable specimen abundance (on a regional scale), the microfossils documented from the Devonian strata of north Devon proved insufficient to resolve more local-scale correlative problems. Many inception events or true disappearances of taxa are unresolved, largely due to changes in sedimentary facies and the associated non-recovery of palynomorphs. Interpretative problems are compounded by the predominance of simplistic, stratigraphically long ranging forms in many assemblages. Furthermore, the inapplicability of established zonal schemes to certain levels in the studied sequence also restricted correlation on a finite scale. Despite these observations, a more comprehensive knowledge of the sedimentology (if combined with the findings of the present study) may help clarify relationships in certain parts of the studied sequence.

4.7. THE RESOLUTION OF CHRONOSTRATIGRAPHIC UNITS AS DEFINED BY THE PRESENT STUDY AND THEIR COMPARABILITY WITH PREVIOUS SYNOPTIC STUDIES.

Despite the documentation of a diverse suite of fossils (encompassing conodonts, spores, plants, invertebrates and vertebrates) from a variety of discrete sections within the Orcadian, Caledonian and Anglo-Welsh basins, few Devonian Series boundaries have been recognised with confidence. House *et al.* (1977) comprehensively detailed the geographical and temporal distribution of surface and subsurface Devonian sediments within the British Isles, and concluded that in places the Devonian is still poorly understood. House & Dineley (1985) later reported on developments in resolving Devonian Series boundaries in the marine strata of Britain, and noted that for north Devon the overall picture is still one of uncertainty.

The resolution by House *et al.* (1977) of stage boundaries in the Devonian strata of north Devon was briefly mentioned in Chapter 1 (Section 1.5), and schematically shown in Figure 1.4, as too were the subsequent revisions discussed by House & Dineley (1985). The revised age evaluations of the Devonian strata studied in north Devon (proposed herein) are compared solely with these two previous synoptic reports, rather than comparisons with individual, contemporaneous Devonian outcrops in the Southwest.

In general, the present research and the findings of House *et al.* (1977) appear broadly compatible. The two interpretations differ primarily in the resolution of the Lower/Middle Devonian boundary. Traditionally this datum approximates to the level where the transitional, shallowest marine sediments of the Lynton Formation are succeeded by the terrigenous clastics of the Hangman Sandstone Group (House & Selwood, 1966). However, according to Simpson (1964) the macrofossils, and in particular the brachiopods from the Lynton Formation suggested a late Emsian or possible early Eifelian age (refer to House *et al.*, 1977). Recent studies by Evans (1980; 1983 - refer to the synopsis in House & Dineley, 1985, p. 304) favoured a late Emsian age, although an earliest Eifelian age for the uppermost levels of this unit could not be discounted. Based on conodont and palynological evidence presented herein, the precise position of the Lower/Middle Devonian boundary is still somewhat problematical. From palynological evidence, an Eifelian age does appear most likely for the uppermost Lynton Formation. With formal clarification of the exact stratigraphic position of the Watersmeet section (and associated conodont fauna), substantially more of the Lynton Formation may be regarded as Eifelian in age (Pound is confident that the Watersmeet section is located in the lower third of the exposed Lynton Formation, *pers. comm.* 1989).

The top of the Hangman Sandstone Group was formally referred to the Givetian Stage based on the occurrence of supposed *Stringocephalus,* but Lane (1965) reinterpreted these to be deformed *Myalina* valves. Currently, there is no convincing evidence for the positioning of the Givetian-Frasnian boundary (House *et al.,* 1977, p. 12). The palynofloras recorded in the present study from the uppermost Rawns Formation, Sherrycombe and Little Hangman Formations proved broadly similar to those documented from the lower/?middle Wild Pear Slates. Collectively, these assemblages suggest a ?mid/late Eifelian, possibly earliest Givetian age. Until the data of Loboziak *et al.* (1989) is formally published (see Section 4.3.5 herein), the Eifelian/Givetian boundary cannot be resolved with any greater precision, using miospore zonal schemes as they currently stand.

Holwill *et al.* (1969, and earlier papers of Holwill) regarded the cyrtospiriferid and coral faunas preserved in the Combe Martin Slates as indicative of a lower Upper Devonian age. Webby (1966b: confirmed by Scrutton, 1975) viewed these coral faunas as more Givetian in aspect (refer to House *et al.,* 1977 and Section 1.4.2c herein). Orchard (1979) recovered a conodont fauna of Upper *varcus* Subzone age from a thin limestone horizon believed situated ≈50m below the top of the Kentisbury Slates, and following the zonal usage at that time referred these sediments to the Upper Devonian. Following the recommendations of the Devonian Subcommission, this conodont Zone (and associated faunas) was attributed to the Givetian Stage. Thus in the context of north Devon, fauna K2 has subsequently been re-assigned to the Givetian, which by implication suggests that the Middle/Upper Devonian Series boundary is located at an ("as yet") indeterminate level within the Morte Slates (House & Dineley, 1985 - refer also to Chapter 1, Figure 1.4 of the present study).

Conodont faunas recovered from the Lester Slates and Sandstones and the Combe Martin Slates are indicative of the Lower/Middle *varcus* Subzones, but the fauna recovered from sample K53 comprised somewhat anomalous forms that show little resemblance to those reported from lower down in the sequence. The palynology permits slightly more refined age evaluations, with the inception of *Geminospora lemurata* within the Wild Pear Slates confirming a Givetian age. The appearance of *Cristatisporites triangulatus* in the upper Combe Martin Slates is followed somewhat rapidly by the inception of *Verrucosisporites bulliferus* within the ?lower Kentisbury Slates. The concurrence of these two taxa suggests a Frasnian age for the Kentisbury Slates, and thus identifies the Middle/Upper Devonian boundary as approximating to the Combe Martin Slates/Kentisbury Slates boundary. This evaluation is more in keeping with the original interpretation of House *et al.* (1977), rather than with that of House & Dineley (1985, based on Orchard, 1979), the latter placing the boundary at a higher stratigraphic level.

House *et al.* (1977) did not consider a Famennian age for the top of the Morte Slates. The palynology of the ?lower part of this unit proved comparatively simplistic, containing forms typical of the Frasnian Stage. In the ?upper Morte Slates, the recovery of *Auroraspora* cf. *torquata* and associates suggests a latest Frasnian age (*sensu* Richardson & McGregor, 1986). The top of this unit may feasibly be of earliest Famennian age, although there is no direct evidence to confirm this supposition.

4.8. SUMMARY.

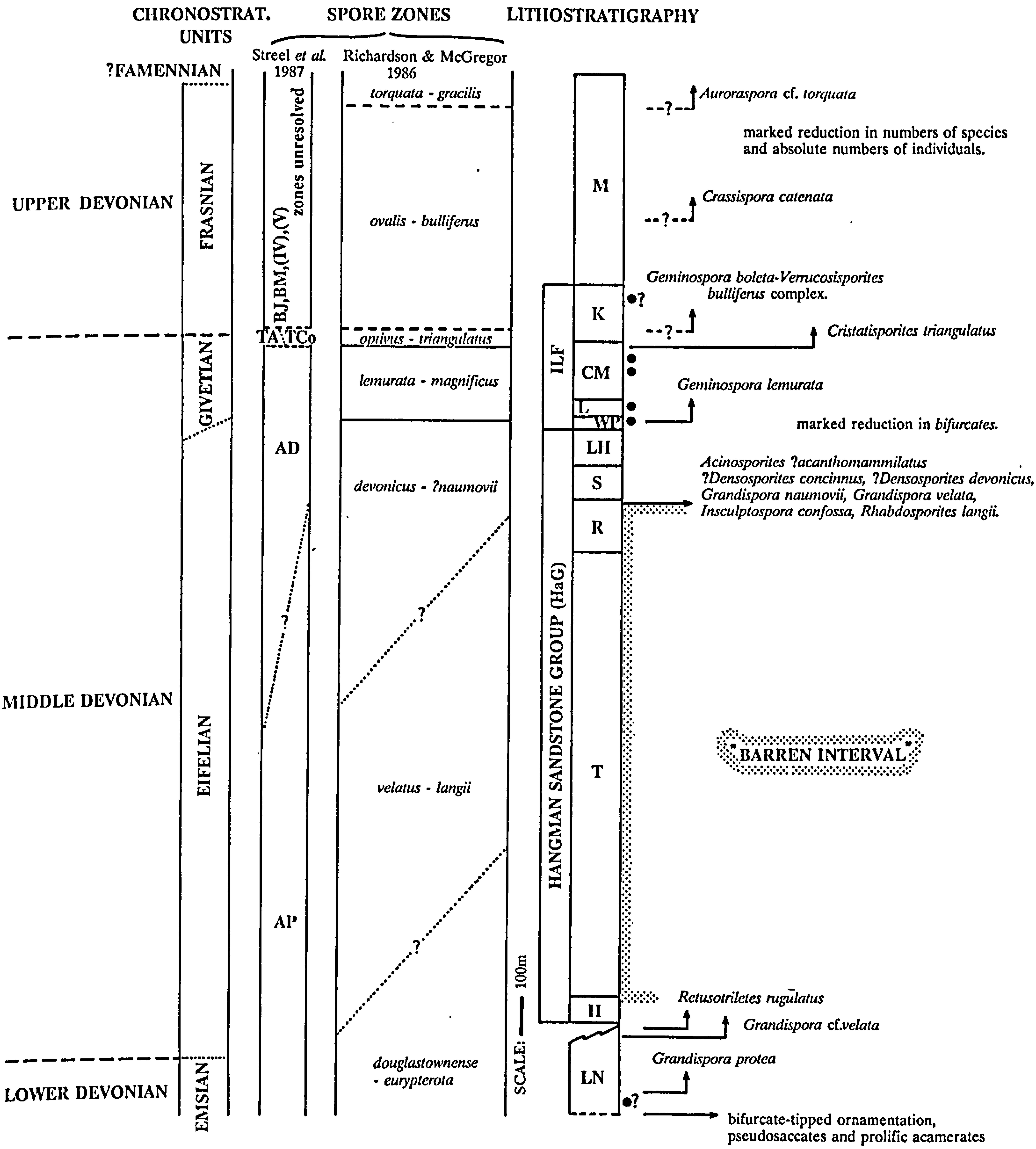
Marine and terrestrial palynomorphs proved the most pervasive and abundant microfossils in the studied sequence, with conodonts restricted to a number of isolated horizons. For the sequence as a whole, age evaluations are based largely on the temporal distribution of miospores. Marine palynomorphs were considered by and large reworked: those believed *in situ* corroborated biostratigraphical interpretations provided by other microfossil indices.

Figure 4.7 summarises the principal palynological events traced through the Devonian strata (*partim*) of north Devon, and schematically shows the full extent of the interval of non-recovery (marked as "barren interval"). Where appropriate, the approximate stratigraphical positions of the key conodont faunas (as discussed earlier) are given. In addition, the relationship between the lithostratigraphy of north Devon and established Devonian spore zonational schemes is indicated (after Richardson & McGregor, 1986; Streel *et al.*, 1987; as well as consideration of the findings of Loboziak *et al.*, 1989). The following biostratigraphical overview refers largely to the events depicted in Figure 4.7.

The recovery of miospores with bifurcate-tipped processes from palyniferous samples collected as close to the exposed base of the Lynton Formation as possible, suggests an age for this level no older than the late Emsian Stage (*sensu* the "floral event" of Richardson & McGregor, 1986). Pseudosaccate, patinate and prolific numbers of acamerate miospores were pervasive throughout the Lynton Formation, with acritarchs, chitinozoa and scolecodonts rare. A late Emsian age is confirmed by the recovery of the two nominate taxa of Richardson & McGregor 's (1986) *douglastownense-eurypterota* Assemblage Zone: tentatively corroborated by the presence of *Hystricosporites ?corystus*. Approximately 42.5m above the exposed base of the Lynton Formation, the first appearance of *Grandispora protea* was recorded. According to Streel *et al.* (1987; based on the study of Riegel, 1975), the inception of *Grandispora protea* defines the base of the *Pro* Interval Zone, within which the base of the Eifelian Stage reportedly occurs (in the Heisdorf/Lauch Formation limit in the type Wetteldorf section; Riegel 1975). Forms attributed to *Grandispora* cf. *velata* were recorded towards the top of the Lynton Formation, in association with a variety of taxa commonly affiliated with Eifelian assemblages (*e.g Retusotriletes rugulatus*). An Eifelian age for the upper Lynton Formation cannot be unequivocally confirmed, based exclusively on palynological evidence, due to the absence at this level of *Grandispora velata* (*sensu stricto*) and associated Eifelian zonal taxa (*e.g. Rhabdosporites langii*). A conodont fauna of Eifelian aspect was however recorded from an isolated inland exposure at Watersmeet. Unfortunately, the precise stratigraphical position of this section requires clarification before the age interpreted for this fauna can be fully appreciated: according to (Pound, *pers. comm.*, 1989) the Watersmeet exposure is almost certainly sited within the lower third of the exposed Lynton Formation. Collectively, the miospore and conodont evidence collated for the Lynton Formation suggests that this unit comprises, in part, sediments of late Emsian to early Eifelian age. At present the Lower/Middle Devonian Series boundary is tentatively placed towards the top

FIGURE 4.7

THE PRINCIPAL PALYNOLOGICAL EVENTS DETAILED FROM THE DEVONIAN OF NORTH DEVON.



KEY
M = Morte Slates
ILF = Ilfracombe Slates
HaG = Hangman Sandstone Group
LN = Lynton Formation

● = Conodont fauna

refer to Figure 1.1 for additional key.

of this unit, based solely on the distribution of miospores. The present study broadly agrees with the age evaluation of House *et al.* (1977), and contradicts the near exclusive Emsian age interpreted by Evans (1983) for this formation.

The homogeneity in the palynoflora, through from the Lynton Formation into the Hollowbrook Formation suggests that these two units are of comparable age. Palynologically, there is no justification for placing the Lower/Middle Devonian Series boundary coincidental with a change in sedimentary facies (where the Lynton and Hollowbrook Formations are juxtaposed). It is uncertain whether the apparent disappearance of certain taxa in the Hollowbrook Formation is truly representative of an evolutionary extinction, or is in fact facies-related.

Following an interval of "non-recovery" that encompasses ≈1500m of continental sediments, the first palyniferous horizon was identified ≈1.8m below the top of the Rawns Formation. The palynomorph assemblages recovered from this level were remarkably diverse, and dominated by miospores (of variable structural complexity and design). Spores with bifurcate-tipped sculpture were notably rare. Subordinate numbers of acritarchs, chitinozoa and scolecodonts were also reported. An assortment of miospore zonal taxa were present at this level. The recovery of *Acinosporites* cf. *acanthomammillatus, ?Densosporites devonicus, Grandispora naumovii, Grandispora velata* (*sensu stricto*) and *Rhabdosporites langii* confirms an age no older than mid-Eifelian. The *devonicus-naumovii* Assemblage Zone (of Richardson & McGregor, 1986) and the AD Oppel Zone (of Streel *et al.*, 1987) are resolved at this level; both zones span the Eifelian/Givetian boundary. Based exclusively on the palynology documented in the present study, and the miospore zonations as currently defined (excluding the recent proposal of Loboziak *et al.*, 1989), refined resolution of the Eifelian/Givetian boundary in north Devon is impossible. An earliest Givetian age for the uppermost Hangman Sandstone Group is possible. Alternatively, based on the findings of Loboziak *et al.* (1989) the upper Hangman Sandstone and lowermost Ilfracombe Slates may be regarded as Eifelian in age.

The inception of *Geminospora lemurata* defines the base of the *lemurata-magnificus* Assemblage Zone (Richardson & McGregor, 1986) or the Lem. Interval Zone (Streel *et al.*, 1987; topmost division of the tripartite AD Oppel Zone). The base of these zones approximate with the *ensensis* conodont Zone, and thus the timing of this floral event is interpreted as within the latest Eifelian to earliest Givetian interval (excluding the recent proposal of Loboziak *et al.*, 1989). In north Devon, the first appearance of *Geminospora lemurata* was recorded within the Wild Pear Slates. Following the influx of *Geminospora lemurata*, conodont faunas of Lower/Middle *varcus* Subzone age were reported from the Lester Slates & Sandstones and Combe Martin Slates. Collectively, the micropalaeontology reported from these levels within the Ilfracombe Slates indicates a Givetian age.

Within the uppermost horizons of the Combe Martin Slates, and subsequent to the Middle *varcus* conodont fauna recovered from the David's Stone Limestone Member, the inception of *Cristatisporites triangulatus* was recorded. According to Richardson & McGregor (1986) the entry of *C. triangulatus* (coupled with *Contagisporites optivus* var. *optivus*) is indicative of a late Givetian age. In the zonal scheme of Streel *et al.* (1987), the mid/late Givetian TA Oppel Zone is also defined on the first occurrence of this taxon, in conjunction with the demise of *Ancyrospora ancyrea* var. *ancyrea* (Note: earlier comments in Section 4.3.5a, relating to the TLa Oppel Zone of Loboziak & Streel, 1980; 1988). The TCo Oppel Zone of Streel *et al.* (1987) was unresolved in north Devon. *Verrucosisporites bulliferus* is a widely recognised important zonal taxon, and forms the basis of

Frasnian age determinations within the zonal schemes of both Richardson & McGregor (1986) and Streel *et al.* (1987). The appearance of *Verrucosisporites bulliferus* in the ?lower Kentisbury Slates rapidly followed the first occurrence of *Cristatisporites triangulatus*, and suggests that the Middle/Upper Devonian Series boundary is located in the uppermost Combe Martin Slates to ?lower Kentisbury Slates interval. Unfortunately, the BM Oppel Zone and subdivisions of the IV and V Phase zones of Streel *et al.* (1987) were unresolved in north Devon. The palynology and the conodont fauna recovered from the same locality as the K2 limestone of Orchard (1979) raises questions concerning the Upper *varcus* Zone age evaluated by Orchard for this level. According to the findings of the present study, the Kentisbury Slates are considerably younger than the suggestion of Orchard (1979).

Despite an abrupt depletion in the palynofloras at the top of the Kentisbury Slates (which may be facies related), the miospore assemblages of the ?lower Morte Slates proved moderately diverse. In common with the Kentisbury Slates, the Interval Zones of Phases IV and V (of Streel *et al.*, 1987) could not be recognised. The recovery of *Crassispora catenata* and *Auroraspora* cf. *torquata* from the ?middle/top of the Morte Slates is stratigraphically significant. The base of the *torquata-gracilis* Assemblage Zone of Richardson & McGregor (1986) is of latest Frasnian age, and is defined by the first occurrence of *Auroraspora torquata* and *Grandispora gracilis*. According to Richardson & McGregor (1986), the inception of *Crassispora catenata* occurs in the late Frasnian and ranges to the top of the Strunian (*sensu* Higgs and Streel, 1984). Therefore, despite the depauperated palynology of the Morte Slates, the recovery of *Crassispora catenata* and *Auroraspora* cf. *torquata* suggests an age no older than late Frasnian for the ?top of this unit. An ?earliest Famennian age is plausible.

As exemplified by the present work, and based on the miospore zonational schemes of both Richardson & McGregor (1986) and Streel *et al.* (1987), it is virtually impossible at present to resolve Devonian Stage and Series boundaries with precision. Furthermore, the infrequent occurrence or absence of certain zonal taxa limited the utility and applicability of these two schemes in certain areas of the present study. Despite such limitations, north Devon may clearly prove to be an invaluable reference section for Devonian palynostratigraphy.

CHAPTER 5.

PALAEOENVIRONMENTAL EVALUATION.

5.1 INTRODUCTION.

It is now widely accepted that the distribution of many microfossils was influenced by ecological and geographical factors (*e.g.* Klapper & Johnson, 1980; Sweet, 1988). Unlike other aspects of micropalaeontology (*e.g.* quaternary palynology, foraminifera or ostracod studies), in conodont research or Palaeozoic palynology there has been little detailed work into the presumed interaction between organism and palaeoenvironment. In the past, the effects of facies dependency were often overlooked, and the realisation that, for example, the distribution of conodonts were often restricted to quite specific palaeoenvironments is comparatively recent (*e.g.* Sweet 1988, p. 149). Indeed, analogy with the modern biosphere shows that the biota may be severely influenced by the environment. With extrapolation back through geological time, environment may have dictated assemblage composition, and thus would impose restrictions on present day biostratigraphical evaluations.

The influence of palaeoenvironment on the micropalaeontology of north Devon is discussed below. However, the conclusions reached are limited by the low numbers of conodonts and indigenous marine palynomorphs documented, and also by the current fragmentary knowledge of the sedimentology of the Devonian strata of north Devon.

5.2 CONODONTS.

5.2.1 Introduction.

Until the mid seventies conodont research was orientated largely towards stratigraphical correlation and the establishment of biozonational schemes (Seddon & Sweet, 1971), and the environmental tolerances of specific conodont taxa were largely unknown. Biofacies studies have recently gained impetus with an increased awareness of the ramifications that conodont animal palaeoecology has on biostratigraphy. Such research has been enhanced by the discovery of exceptionally well preserved soft-bodied specimens from Granton and Wisconsin (Briggs *et al.* 1983, Mikulic *et al.* 1985, Aldridge *et al.* 1986; Smith *et al.*, 1987). Even before these finds, there had been a gradual acceptance that the spatial distribution of conodonts was in part dependent on sedimentary facies, and several broadscale ecological models were suggested (*e.g.* Seddon & Sweet, 1971; Barnes & Fåhræus, 1975). To early workers the widespread occurrence of conodonts in a variety of contemporaneous marine sediments suggested a pelagic life habit. Seddon (1970), and Seddon & Sweet (1971) suggested an active pelagic mode of existence for the conodont animal, with different species occupying horizontal, depth-stratified zones. According to such bathymetric models, death assemblages would become increasingly diverse in deeper water. This was however not always the case. Druce (1973) postulated that distance from the shore was the principal controlling factor, and mooted a horizontal-segregation model.

Druce (1970), Barnes *et al.* (1973a) and Barnes & Fåhræus (1975) conversely favoured a nektobenthonic or benthic life habit. Barnes & Fåhræus (1975, p.145) also postulated that certain conodonts may have had pelagic larval stages. However Klapper & Barrick (1978) subsequently demonstrated that no conclusive explanation of life habit could be inferred from the study of death assemblage distribution patterns. Based on a comparative study of the distribution of modern benthic and pelagic (planktic) marine organisms (chaetognaths, forams, and isopods) they concluded the death assemblage patterns produced by either ecological group to be indistinguishable, with some pelagic organisms exhibiting death assemblage patterns commonly associated with benthic organisms, and *vice versa*.

Clark (1981) recently postulated that the conodont animal probably occupied both pelagic and benthic environments, from living just off the sea floor to well within the water column. Indeed, the conodont animal must have formed a notable component of the Palaeozoic shallow marine biota, with the majority of species, according to Clark (1981), occurring in normal marine stenohaline conditions. Austin & Higgins (1985 p. 22) suggest that at least some species were capable of tolerating low salinities. Barnes & Fåhræus (1975) considered conodonts to be euryhaline, whilst von Bitter (1976) proposed some species as having adapted to hypersaline conditions.

Austin & Higgins (1985, p. 22) remarked that temperature may well have affected conodont distribution, but as yet this has not been fully investigated. Of interest, however, is the summary of global Devonian conodont distribution provided by Klapper & Johnson (1980). They concluded that Devonian conodonts were restricted to tropical latitudes, and within this climatic realm, probable endemic *Icriodus* faunas may have been established during the Lower and Middle Devonian (producing distinct conodont provinces). Klapper & Johnson (1980) also considered the influence of ocean currents in the possible dispersal of conodont larvae: due to the configuration of landmasses at the time circum-equatorial currents prevailed. In the Late Devonian, conodonts continued to be confined to a low-latitude belt. The near global applicability of the biozonal scheme devised by Ziegler (1962) attests to the wide geographic distribution of Late Devonian conodont species and the lack of well defined conodont provincialism.

Conodont life habit may also have been influenced by trophic activity and/or energy of the palaeoenvironment (*e.g.* as demonstrated by the Middle Devonian studies of Sparling, 1984). In a study of Permian conodont palaeoecology, based upon the Lamar Limestone of the Delaware Basin (Texas, U.S.A.), Babcock (1976) suggested that decreasing food supply basinwards may have restricted the abundance and diversity of conodonts in such deeper water environments, irrespective of mode of life.

5.2.2 Devonian conodont biofacies.

In the study of this extinct group, preferred life habits can only be deduced from the association of fossils and sediments. Such an indirect method of study is likely to provoke much debate and require constant revision (Sweet, 1988). Thus, many of the early models proposed to explain conodont distribution are now regarded as acute over simplifications, particularly in relation to the complex distribution patterns now interpreted to have existed across Upper Palaeozoic shelf environments (see for example Nicoll, 1984; Sweet, 1988, p.149). The following section traces the more recent developments in the ideas put forward to explain Devonian conodont biofacies.

Davis (1975) interpreted the distribution of *Polygnathus* and *Icriodus* in the Tully Limestone of New York State as consistent by and large with the depth-stratification model of Seddon & Sweet (1971). By equating coeval conodont distribution to palaeoenvironment, Bultynck (1976), Chatterton (1976), Sandberg (1976), Schumacher (1976) and Weddige & Ziegler (1976) simultaneously either confirmed earlier Devonian conodont ecostratigraphies or proposed alternative models. In these studies biofacies were defined on conodont diversity, abundance or faunal associations.

Chatterton (1976) realised the influence of temperature and variations in salinity on faunal composition, based upon Eifelian and early Givetian faunas from Canada, recognising four distinct Middle Devonian biofacies (refer to Table 5.1(a)). The most offshore (basin or slope) biofacies was dominated by *Polygnathus*. Further inshore (shallow open marine conditions) this plexus was found in association with *Icriodus* and/or *Pelekysgnathus* and/or *Belodella*. Chatterton considered *Icriodus* to be excluded from shallow, slightly restricted environments, which were occupied instead exclusively by coniform-bearing animals such as *Panderodus*. Weddige & Ziegler (1976) thought environmental energy to be a primary control on the distribution of the *Icriodus* and *Polygnathus* animal in the neritic facies of the Lower/Middle Devonian in the Eifel area (Rhenish Slate Mountains, Germany). The habitats of the two genera were differentiated vertically in quiet water, with the *Icriodus* niche more extensive and densely populated in high-energy shallow water. Such changes in facies were marked by changes in carbonate content, and equated with the associated conodont fauna. High carbonate content (reef-detritus) was believed to indicate higher-energy facies, and was reflected in an abundance of *Icriodus* relative to low numbers of *Polygnathus*.

In the same Conodont Paleoecology volume (Barnes 1976, ed.) Sandberg (1976) proposed five coeval conodont biofacies based on percentages of platform genera, in a variety of palaeoecological and palaeotectonic scenarios for the Lower *expansa* Zone (formerly the Upper *styriacus* Zone) in the Western United States [shown in Table 5.1(b)]. To recognise specific biofacies, at least 65% of the total platform population had to be of the nominate platform genera. According to Sandberg's (1976) model, the distribution of genera such as *Palmatolepis* accord with the bathymetric model of Seddon & Sweet (1971), although the occurrence of the *Polygnathus* animal could not be accommodated within this model. Sandberg (1976) believed this disparity reflected the ability of the *Polygnathus* animal to tolerate a diversity of palaeoenvironmental conditions. Of specific interest to this study is the polygnathid-icriodid biofacies of Sandberg, which was identified in outer cratonic platform environments.

Schumacher (1976) recognised three distinctive conodont biofacies in central Missouri that retained their ecological integrity from the Givetian through to the Frasnian, despite the species composition of the biofacies changing with time. An *Icriodus*-dominated biofacies was confined to shallow subtidal facies, with narrow-platformed polygnathids bearing simple ornamentation similarly preferring shallow subtidal marine conditions. Schumacher noted that the latter category ranged into deeper water, although the interpreted palaeoenvironment was still close to wave base. He defined a third biofacies, the *Ancyrodella*-*Polygnathus asymmetricus* biofacies, that was typified by taxa with broad platforms and was restricted to the deeper subtidal facies. Weddige (1977) mentioned the ecological factors that influenced the distribution of *Polygnathus* and *Icriodus* in the Lower and Middle Devonian habitats of the type Eifelian, with Weddige & Ziegler (1979) subsequently remarking that ecology was a major influence on the neritic distribution of *Icriodus* evolutionary lineages. They perceived the complex phylogeny of icriodids in the Middle Devonian to be dependent upon a

CONODONT BIOFACIES:	BIOFACIES III	BIOFACIES II	BIOFACIES IA	BIOFACIES I	
CHARACTERISTIC FORMS:	*Polygnathus*	*Polygnathus and Icriodus and/or Pelekysgnathus and/or Belodella*	*Polygnathus and Belodella and/or Coelocerodontus*	*Panderodus and/or Coelocerodontus*	
ENVIRONMENT:	basin or slope	shallow open marine	shallow slightly restricted:	semirestricted	restricted
TEMPERATURE:	normal marine	normal marine	slightly above normal	above normal	above normal
SALINITY:	normal marine	normal marine	slightly above normal	above normal	above normal
LITHOLOGY:	calc. shale	limestone and calc. shale	limestone	limestone & dolomite	dolomite & evaporites
ENERGY OF SUBSTRATE:	low	low to high	moderate to low	low	low
CONODONT ABUNDANCE:	low to high	moderate to high	low	very low	absent
MACROFAUNA DIVERISTY :	low	high	moderate	low	very low
CONODONT FAUNAL DIVERISTY:	moderate to high	high	moderate	low	-

Table 5.1(a) The probable environmental conditions and generic compositions of the Middle Devonian conodont biofacies recognised in Western and Northwestern Canada. Modified from Chatterton (1976).

PALAEO-TECTONIC SETTING	OFFSHORE	NEARSHORE	"BACKSHORE"						
	MUDDY OUTER SHELF	SANDY INNER SHELF	SHOAL	BACK-MOUND	TIDAL FLAT	BARRIER	TIDAL LAGOON	SABKHA	COASTAL PLAIN
CONODONT BIOFACIES	I Palmatolepid	II Palmatolepid-polygnathid	III Polygnathid-"icriodid"	IV Polygnathid-pelekysgnathid		VI, VII, ? Scaphignathid, pandorinellinid, +?			
ICRIODONTID FAUNA	Rare Icriodus	Both types of Pelekysgnathus (transported)	Triple-row Pelekys-gnathus	Both types of Pelekysgnathus (indigenous)		Single-row Pelekys-gnathus		UNKNOWN	

Table 5.1(b) A biofacies model for a Famennian regressive megacycle sequence across the Dinant Nappe, Belgium - incorporates an alternative Icriodontid biofacies model. Modified from Sandberg & Dreesen (1984).

complicated interplay of ecological, adaptive and facies influences.

Sandberg & Ziegler (1979) supplemented the earlier findings of Sandberg (1976) by defining three further biofacies for the nearshore palaeoenvironment (namely the scaphignathid (VI), pandorinellinid (VII) and patrognathid (VIII) biofacies). They noted that certain shallow-water forms exhibit unique evolutionary patterns within these unusual environments, despite having common ancestry from the early Frasnian form *Pandorinellina insita* (Stauffer). These supplementary biofacies were comparable to the clydagnathid (V) biofacies of Sandberg (1976), but differed in the interpreted levels of salinity, the nature of the bottom sediments, and the degree of aeration, amongst other factors. Klapper and Ziegler (1979) remarked upon the prolific number and diversity of polygnathids in relatively deep water Middle Devonian environments, with the rapid evolutionary rates of this plexus allowing them to serve as ideal biostratigraphical indices.

Sandberg & Dreesen (1983, 1984) further supplemented the original biofacies model of Sandberg (1976), defining a ninth anthognathid (IX) biofacies as recognised in the hypersaline environments of the Upper *postera* Zone of Utah. Sandberg & Dreesen also identified the habitat, apparatus and ranges of Late Devonian *Icriodus*, *"Icriodus"* and *Pelekysgnathus* to be sufficiently distinct to justify refinement of the earlier polygnathacean-based biofacies model. Thus they formulated an alternative Icriodontidae zonal scheme (Sandberg & Ziegler, 1984) and biofacies model [refer to Table 5.1(b)]. A detailed study of Late Devonian mud-mound tracts in Belgium and the partly contemporaneous basinal Kellwasser Limestones of West Germany (Dreesen & Thorez, 1980; Dreesen, 1984; Sandberg & Dreesen, 1984) allowed the correlation of this shallow-water zonation with the deeper water *Palmatolepis*-based standard zonal scheme. Upper Devonian icriodids were interpreted as euryhaline, ranging from near-shore to pelagic biofacies and later replaced by the mesohaline (possibly nektobenthonic) *Pelekysgnathus* complex.

At about the same time, Sparling (1983) remarked that the spatial distribution of polygnathids in the lower Middle Devonian strata of north-central Ohio suggested that the host animals were sensitive to energy levels and substrate texture. In a subsequent, detailed study, Sparling (1984) remarked that *Icriodus* and *Polygnathus* ratios in the Middle Devonian of the same area were consistent with the observations of Weddige & Ziegler (1976), itself based upon the earlier bathymetric model of Seddon and Sweet (1971). According to Sparling (1984, p.115-117, Fig.2), the distribution of *Icriodus* was consistent with a depth stratified habit, although pronounced segregation in cosmopolitan species of *Polygnathus* suggested a benthic habit for part of this fauna. In his study, Sparling recorded a reduction in the total number of elements per kilogram of rock processed, with a transect from open marine conditions (below wave base), through shoal and into lagoonal sediments. The decrease in abundance was accompanied by *Icriodus* becoming dominant over *Polygnathus*.

Nicoll (1984) analysed the distribution of conodonts in the steeply-dipping marginal slope facies of the Upper Devonian reef complex in the Canning Basin. He concluded that the patterns recorded did not indicate any clear depth segregation of conodont species, nor correspond with the biofacies recognised by Seddon (1970), or by Druce (1969, 1973, 1976).

Klapper & Lane (1985) subsequently discussed Upper Devonian (Frasnian) conodonts of the *Polygnathus* biofacies in the Northwest Territories (N.W.T.), Canada. They remarked on the difficulty of detailed biostratigraphical evaluation, being only possible when there were minor incursions of species of *Palmatolepis*, *Ancyrodella* or *Ancryognathus* (characterising the *Palmatolepis* biofacies).

Outside of the N.W.T, specific variants of these three genera form the basis of the standard conodont zonation for the Frasnian Stage, although this has not been inter-correlated with the usual constituents of the *Polygnathus* biofacies.

Dreesen *et al.* (1986, p. 31) synthesised their earlier ecostratigraphic studies, and defined the optimal habitats of some important platform conodonts in the Late Devonian. They suggested *Icriodus* to be a euphotic genus that lived in most environments, including the pelagic realm. The distribution of *Polygnathus* was believed to be more complex. Representatives of the *P. nodocostatus* group occurred in more offshore and/or deeper water, whereas the *P. semicostatus* group were seemingly associated with shallower water, and/or nearshore environments. Furthermore, due to the stratigraphic and palaeoenvironmental sensitivity of conodonts, Dreesen *et al.* (1986) remarked that this fossil group is of immense value in resolving eustatic changes and epeirogenic events during the Middle Devonian to Late Mississippian interval (refer to Dreesen 1982, 1984).

Recently, Weddige & Ziegler (1987) have recognised that in association with conodont faunas, a variety of lithic facies indicators may also be preserved. Based upon a study of pelagic upper Lower Devonian sediments in the Barrandian, CSSR, Weddige & Ziegler (1987) resolved shifts in facies according to changes in the relative ratios of five lithic or faunistic indices, namely; tentaculites to crinodal stems, pyrite to ironstones, clay to carbonate content, the genus *Latericriodus* to *Polygnathus*, and *Polygnathus* taxa of the *linguiformis* to *costatus* branches. Weddige & Ziegler (1987, p. 339) considered the associations established by their study to substantiate earlier findings of Weddige & Ziegler (1976, 1979) and Sparling (1984). Drawing collectively upon these studies, Weddige & Ziegler (1987) synthesised an overall *Icriodus-Polygnathus-Latericriodus* facies range from shallow-water neritic to deeper pelagic environments. In the same volume, Matya (1987) recognised six conodont biofacies within the Famennian strata of Pomerania, northwestern Poland, and subsequently confirmed known worldwide transgressive and regressive events (*e.g.* Johnson *et al.*, 1986) by their recognition in Poland.

Bultynck (1987) appreciated the difficulty of direct and accurate correlation between late Eifelian to late Givetian neritic faunas and the standard conodont zonation. For this interval, the conodont zonation is based on *Polygnathus* faunas associated with pelagic facies. A subsequent study of the pelagic and neritic conodont successions within the Givetian sediments of the pre-Sahara Morocco allowed Bultynck (1987) to define an alternative shallow-water *Icriodus*-based zonational scheme (as outlined in Chapter 4, Section 4.2.2).

5.2.3 Conodont biofacies recognition in the marine Devonian strata of Southwest England.

Austin *et al.* (1985, p. 128) commented that few publications relating to British Devonian conodont faunas provide the relative abundances of specific conodont genera. Nevertheless, the presence of *Icriodus* biofacies can be recognised within certain Lower, Middle and Upper Devonian strata of Devon and Cornwall. For example, Sadler (1973a) reported the predominance of *Icriodus* (98%+ of the total fauna) over *Spathognathodus* and *Polygnathus* in Lower Devonian sediments of Cornwall. A detailed study of the conodont faunas of the Plymouth Limestone by Orchard (1978a) was used to elucidate the development of the carbonate complex from Middle through to Late Devonian times. Differences in the composition of coeval faunas (*e.g* in late Givetian and early Frasnian strata) were attributed to variations in palaeoenvironment. Orchard (1978a) noted considerable temporal variation in the abundance of icriodids within the Plymouth Limestone, with a marked abundance of simple cones in the Eifelian faunas and a virtual absence of icriodids in the Givetian limestones of the western Plymouth Limestone outcrop. He interpreted this exclusion to be palaeoenvironmentally induced. In a study of late Givetian/Frasnian faunas from the Marble Cliffs (north Cornwall), Kirchgasser (1970) noted *Icriodus* to be extremely sparse, although remarking that in general sorting and reworking does influence faunal composition. Stewart (1981a) refined a number of lithostratigraphical interpretations for the Famennian sediments of north Cornwall through the recognition of conodont biofacies.

5.2.4 Taphonomy and the conodont faunas of north Devon.

As introduced in Chapter 2 (Section 2.6.1) the conodont faunas recovered from north Devon show a marked imbalance not only in generic composition, but also in the representation of known multielement associations. As mentioned in Chapter 3, Klapper and Philip (1971, 1972), amongst others, proposed a number of multielement configurations that related the biostratigraphically useful pectiniform (Pa) elements to vicarious ramiform-types. Amongst others, Nicoll (1983, 1985) suggested emendations to the composition of some of these apparatuses. Of relevance to this study are the interpreted components of the septimembrate icriodid (*Icriodus expansus*) and polygnathid (*Polygnathus xylus xylus*) apparatuses (Nicoll 1983, 1985 respectively). The known multielement composition for each species is shown in Table 5.2(a) overleaf, coupled with details of the recovery of each different element-type from the principal carbonate horizons studied [Table 5.2(b)]. Specific details are further provided for the David's Stone Limestone [Table 5.2(c)], as the recovered fauna proved the most diverse and abundant. By comparing the data presented in Tables 5.2(b/c) with those of 5.2(a), a pervasive imbalance in the faunal composition is obvious. Amongst others, Bultynck (1972) and Ziegler (1974) documented icriodid assemblages with a comparable structure, and deduced independently that such associations reflect the unsorted natural apparatuses of host *Icriodus* animals. More judicious interpretations of similar phenomena identify mechanical sorting as the most probable cause of such faunal imbalance. McGoff & Briggs (1988; *pers.comm.*, 1989) recently assessed the hydrodynamic properties of different types of conodont element, and concluded that appreciable winnowing of the less dense and robust elements (*e.g.* S, M and coniform elements) may occur in comparatively low flow regimes. Pectiniform "lags" composed almost exclusively of the more robust, higher density pectiniform elements thus accumulate. In studying the settling and entrainment velocities of various shapes and sizes of conodonts in an artificial environment, and then based on faunal compositions noted for lag-deposits from the Dinantian Barry Harbour Limestone, McGoff (*pers. comm.*) further remarks that faunal composition may be greatly influenced. By implication, this has severe ramifications to current analytical (statistical) methods applied in determining apparatus composition, based upon dissociated element associations. In view of the findings of McGoff, the "imbalanced" Pa-dominated faunas documented from north Devon are interpreted as pectiniform lags, and the probable result of sedimentary sorting. Only in exceptional cases (?less turbulent conditions) were ramiform or coniform elements recovered, although in appreciably reduced numbers (*e.g.* sample CM47).

Polygnathus		Icriodus	
Element type	No. of elements	Element type	No. of elements
M	2	I (Pa)	2
Sa	1	Ca	
Sc	4	Cb	
Sb	2	Cc	140+
Sd	2	Cd	
Pb	2	Ce	
Pa	2	Cf	
7 types	15 elements per apparatus (x2 Pa elements per animal)	7 types	142+ elements per apparatus (x2 Pa elements per animal)

Table 5.2(a) The multielement composition of the *Icriodus* and *Polygnathus* apparatuses (refer to Chapter 3 for discussion and Nicoll, 1983, 1985). The different element-types and their relative numbers are indicated.

Limestone Member or principal conodont-productive horizon/unit	No. of conodont-productive samples (of total sampled)	General faunal composition *			
		Icriodus Pa elements	*Polygnathus* Pa elements	non-Pa polygnathid elements (Pb, S, M)	coniform elements (undifferentiated)
K53	1 (3)	67% (49)	25% (18)	8% (6)	-
David's Stone	17 (19)	84% (320)	6%+ (25)	9% (33)	<1% (?4)
Jenny Start	1 (10)	100% (2)	-	-	-
Combe Martin Beach	3 (4)	72% (23)	19% (6)	9% (3)	-
Rillage	3 (3)	99%+ (135)	<1% (1)	-	-
Holey	5 (5)	100% (181)	-	-	-
Wild Pear Slates	2 (2)	100% (4)	-	-	-
Lynton Formation	12 (17)	99%+ (162)	-	-	<1% (1)

Table 5.2(b) The relative numbers of different element-types from the principal conodont-productive units/horizons of north Devon. The relative number of fossiliferous samples, of the total analysed per unit, is indicated. The relative proportion (and absolute numbers) of each element-type is listed (for the fauna as a whole); differentiated into icriodid and polygnathid Pa elements, non-Pa (presumed) polygnathacean elements and coniform elements (undifferentiated).

Sample No.	Icriodus (Pa)	Polygnathus (Pa)	non-Pa polygnathid elements	coniform elements
CM77	100% (2)	-	-	-
CM65	84% (36)	7% (3)	7% (3)	2% (1)
CM64	74% (14)	5% (1)	16% (3)	5 % (1)
CM63	100% (5)	-	-	-
CM62	100% (1)	-	-	-
CM59	66% (2)	34% (1)	-	-
CM58	90% (56)	2% (1)	8% (5)	-
CM76	100% (8)	-	-	-
CM57	95% (20)	5% (1)	-	-
CM75	100% (3)	-	-	-
CM56	91% (73)	5% (4)	3% (2)	1% (1)
CM53	75% (6)	25% (2)	-	-
CM51	86% (6)	-	-	14% (1)
CM50	100% (17)	-	-	-
CM49	79% (22)	14% (4)	7% (2)	-
CM48	84% (11)	8% (1)	8% (1)	-
CM47	61% (38)	11% (7)	28% (17)	-

Table 5.2(c) As for Table 5.2(b), but dealing specifically with the David's Stone Limestone. Although the faunas recovered from this unit proved notably diverse and abundant, there is still a pervasive predominance of icriodids. The under-representation of vicarious non-Pa elements confirms a pectiniform lag interpretation.

5.2.5 Palaeoenvironmental interpretations.

Where calculable the ratio of *Icriodus* to *Polygnathus* elements recovered from each sampled horizon is listed in Appendix I. Irrespective of stratigraphic position icriodids dominate the conodont assemblages documented from north Devon, and as discussed in Section 5.2.4 post-mortem sorting appears to have been a severe influence upon the representation of certain element-types. Currently, conodont biofacies analyses rely principally on the spatial distribution of Pa (pectiniform) elements. Therefore, despite the noted imbalance, the faunal data collated does allow some speculation as to the nature of the palaeoenvironment that prevailed at certain times during the Devonian Period in north Devon.

5.2.5a *The Lynton Formation.*

According to Pound (*pers.comm.*) the sediments that constitute the Watersmeet Member were deposited in approximately 10 metres water depth. The comparatively diverse icriodid faunas documented from this section lack presumed associated acodinan elements: only one coniform element was recovered. The A39 road section (SS 731490) interpreted by Pound (*pers.comm.*) as having been deposited in less than 5m of water: this section yielded a solitary specimen of *Icriodus culicellus*. Depositional water depths envisaged for the sediments exposed along the northern flank of the Valley of the Rocks (SS 708499) are problematical (these horizons yielded a small fauna comprising solely *Icriodus culicellus*).

Weddige & Ziegler (1979, p. 163) related palaeoenvironment to the occurrence of the certain groups of *Icriodus* species. In their study, Weddige & Ziegler equated the ecophenotypic "*regularicrescens*-branch" group with *Icriodus culicellus*, and noted that these two icriodid complexes were commonly associated with crinoidal or coralliferous limestones (representative of deposition in weakly agitated to turbulent shallow waters). Weddige & Ziegler (1979) also defined a *werneri*-branch which was considered representative of quieter, shallower water conditions. *Icriodus retrodepressus*, a member of the *corniger* group (*sensu* Weddige & Ziegler 1979, Fig. 3, p. 163) was also perceived to be indicative of such conditions. The recovery of *Icriodus culicellus* from the Valley of the Rocks and from the A39 road cutting tentatively suggests shallow, possibly agitated water conditions (according to the observations of Weddige & Ziegler, 1979). The diverse *Icriodus* fauna documented from the Watersmeet Member includes *I.* cf.*werneri*, *I. culicellus* and *I. retrodepressus*, and again by citing the principles defined by Weddige & Ziegler (1979), the association of these morphotypes is indicative of quiet, shallow water conditions. However, the pervasive development of cross-lamination in these sandy calcarenites suggests some degree of current activity. Furthermore, the "imbalance" in the element composition (as marked by the virtual absence of coniform elements) confirms the likelihood that these faunas were current sorted. It therefore seems reasonable to suggest that the icriodid fauna preserved at Watersmeet was probably derived from a somewhat quieter palaeoenvironmental setting, and transported a ?short distance (based upon preservation) after death, into the current recovery site.

5.2.5b *The Ilfracombe Slates.*

Despite the numerical paucity of the faunas recovered from this unit, a few observations can be made in relation to conodont biofacies. The water depths interpreted for the Ilfracombe Slates vary through the sequence, but are considered to be less than ≈50m (Pound, *pers.comm.*). Icriodids predominate, with 61% of the conodont-productive horizons yielding exclusively *Icriodus*. Polygnathids occur sporadically throughout the sequence [refer to Tables 5.2(b/c)].

In detail, the exclusive recovery of icriodids, or a predominance of this plexus over an associated (but depleted) polygnathid fauna was observed for all the conodont faunas recovered from the Rillage, Holey, Combe Martin Beach, and David's Stone Limestone Members, and from sample sites WP23, WP28 (of the Wild Pear Slates) and K53 (of the Kentisbury Slates). This equates to the shallow, open marine Biofacies II defined by Chatterton (1976). Similarly, a tentative analogy can be drawn with the Upper Devonian polygnathid-icriodid biofacies (III) of Sandberg (1976; and subsequent publications), suggesting moderately shallow marine conditions (on an outer cratonic platform, *sensu* Sandberg 1976). However, the application of this model to the present data is questionable, being originally defined for Late Devonian conodont assemblages.

According to Schumacher (1976) *Icriodus*-dominated faunas are confined to shallow subtidal conditions. In view of Schumacher (1976), the predominance or exclusive occurrence of *Icriodus* within the limestones of north Devon further corroborates an interpretation of shallow subtidal marine conditions. According to Schumacher (1976), a fauna typified by narrow platformed polygnathids may be associated with both shallow and deeper subtidal facies, although usually indicative of the former. Based on the observations of Weddige & Ziegler (1987), the recovery in the present study (albeit rare) of broader-platformed, Middle Devonian *linguiformis* polygnathids from the Combe Martin Beach Limestone and from the base of the David's Stone Limestone suggests that possible "deeper-water" conditions prevailed at the times of deposition of these horizons. For the Combe Martin Beach Limestone, this concurs with the palaeoenvironmental interpretation proposed by Webby (1966b, p. 38). Webby (1966b) considered the maximum deepening of the sea in north Devon (and perhaps the maximum northerly extent of the Middle Devonian marine transgression in this area) was attained during the accumulation of the Combe Martin Beach Limestone member.

As outlined earlier, Weddige & Ziegler (1979) defined three main Middle Devonian, *Icriodus* ecophenotypic groups, based upon evolutionary lineages. With reference to Weddige & Ziegler (1979) the principal *Icriodus* taxa documented from the Ilfracombe Slates (namely *Icriodus regularicrescens, I. obliquimarginatus, I. lindensis* and *I. brevis*) are components of the *regularicrescens*-branch. According to Weddige & Ziegler (1979), these morphotypes occur in weakly agitated to turbulent shallow waters. In addition, Weddige and Ziegler (1979) assigned *Icriodus difficilis* to their *struvei*-branch, interpreting this ecophenotypic group as capable of tolerating both quiet and turbulent shallow water conditions. Based upon the observations of Weddige & Ziegler (1979), the predominance of *Icriodus* in the Ilfracombe Slates further confirms the probability of shallow water conditions. Furthermore, at certain levels within the sequence, the faunas appear to encompass both quiet and turbulent water ecomorphotypes.

Of particular interest is the comparability between the conodont yields of the present study, with those documented for the A and B associations of the Lucas-Columbus transgression by Sparling (1983, 1984). In his study, Sparling recognised three distinctive sedimentary settings, with the A & B sedimentary associations reflecting warm, quiet marine to lagoonal conditions, with coralline biostromes and shoal/intershoal palaeoenvironments interpreted (high to low energy levels, respectively). In both these environmental scenarios icriodids were low in absolute numbers, but predominated over polygnathacean taxa. A similar faunal structure was recorded for the Ilfracombe

Slates in the present work.

The virtual absence of conodonts from the Jenny Start Limestone is noteworthy. Of the ten samples processed from this member only one sample (CM13) yielded conodonts (two *Icriodus lindensis*), which on reflection may have been reworked from the older the Rillage/Holey Limestones. If, however, these elements are autochthonous, then the virtual absence of conodonts in this unit may be attributable to adverse palaeoenvironmental conditions. Although conducive to prolific coral growth, the environment that prevailed during the deposition of these limestones may have been inhospitable to the conodont animal. For analogy, Nicoll (1984) remarked on a distinct contrast in conodont faunal abundance between the reef and bioherm core of Upper Devonian carbonate complexes in the Canning Basin, Australia. The reef facies were impoverished with respect to conodonts, with 50% of the samples proving barren. For the Jenny Start Limestone, 90% of the samples proved unproductive (see Section 5.4).

5.3. PALYNOMORPHS.

5.3.1. Introduction.

This section synthesises observations relating to the spatial distribution of marine and terrestrial palynomorphs preserved in the Devonian strata studied. The following section briefly reviews the literature relating to palynomorph palaeoecology in Palaeozoic marine sediments (including dispersed, land-derived spores).

5.3.1a *Acritarchs.*

The Acritarcha are believed to have been planktonic organisms and affiliated to the plant Kingdom. It therefore seems feasible to assume that their distribution in Palaeozoic oceans was controlled by the availability of light, in addition to water-depth, water circulatory patterns and salinity/temperature levels (Jacobson, 1979; Colbath, 1980; Dorning, 1981a). In general there is minimal literature available dealing specifically with the spatial distribution of acritarchs in such Palaeozoic palaeoenvironments.

Staplin (1961) related an increase in acritarch diversity to increasing distance from a reef complex in the Upper Devonian Duvernay facies of Alberta Canada. Staplin was able to recognise an association between the occurrence of certain morphotypes and particular distances from the reef, noting a predominance of sphaeromorphs within reef or reef-associated sediments. Forms with simple processes (*e.g Micrhystridium*) were commonly recovered proximal to the reef, whilst forms with branched processes (*e.g Multiplicisphaeridium*) occurred in large numbers further offshore. Gray & Boucot (1972) confirmed that over a wide area in Ohio sphaeromorphs dominate the nearshore environment, with Bell (1973) similarly equating reef development with sphaeromorph abundance.

Subsequently, a number of papers have either suggested or detailed a relationship between microplankton diversity, morphology, distance from shore and water depth (*inter alia,* Downie 1963; Riegel 1974; Cramer *et al.,* 1972; Wall *et al.,* 1977; Wicander & Playford 1985; Dorning 1986). Of particular interest are the observations of Dorning (1981a) and Dorning & Bell (1986), who defined qualitatively and quantitatively a number of distinct acritarch associations relative to increasing water depth and distance from the palaeoshore, for the Wenlock and Ludlow of the Welsh Basin. High percentages of *Micrhystridium* and *Multiplicisphaeridium* were noted to occur preferentially in assemblages representative of open-marine shallow shelf to deeper-water areas respectively, irrespective of reef development. Thus the relative abundance of the *Micrhystridium*-plexus compared with multiplicisphaerid acritarchs may act as a gauge in recognising slightly shallower or deeper-water biofacies in open marine shelf environments. On a broader scale, Dorning & Bell (1986) outlined three generalised palaeoenvironmental scenarios that may be identified using palynomorph assemblage composition and abundance. Reef limestones may be recognised by their very high percentage of *Leiosphaeridia*, very low acritarch abundance, absence of chitinozoa and scolecodonts, and very low amounts of organic debris. Limestones deposited in shallow, restricted circulatory conditions may be diagnosed by their high percentage of sphaeromorphs, rare chitinozoans and scolecodonts, and significant amounts of organic debris. Open-marine limestones and mudstones contain diverse acritarch assemblages, with chitinozoans and scolecodonts, and some organic debris.

5.3.1b *Chitinozoa.*

Few detailed palaeoecological studies have been undertaken for the Chitinozoa, although Urban & Kline (1970) and later Laufeld (1974, p. 121) remarked that the distribution of this heterogeneous group of organisms is facies-controlled. Chitinozoa are geographically widespread (Laufeld, 1979), and also occur within most sedimentary facies, except reefs and high-energy, shallow-water environments. In a study of Wenlock Chitinozoa of Gotland, Laufeld (1974) remarked that chitinozoa were absent in reef limestones, with reef-associated bioclastic carbonates containing depauperated assemblages: an increase in chitinozoa abundance was observed seaward of biohermal limestones. Laufeld (1974) also remarked that flask-shaped varieties with short spines (*e.g. Sphaerochitina*) were more commonly recorded in shallow-water areas. Wright (1978) believed salinity to be a prime influence upon the distribution of Middle Devonian chitinozoa in the Midwestern United States, with Dorning (1981b) corroborating the earlier findings of Laufeld (1974) in a study of the distribution of chitinozoans within the type Wenlock and Ludlow areas. Further to Laufeld (1974, p. 119-121), Dorning & Bell (1986) have commented that the abundance of both chitinozoa and scolecodonts may be inversely proportional to carbonate percentage in open marine sediments.

Attributes such as mondial distribution and variable facies association have led several authors to propose the Chitinozoa to be planktonic, and to support this hypothesis, a number of morphological features displayed by members of this group have been interpreted as buoyancy structures (*e.g.* the "gas-bag" appendage terminations of *Ancyrochitina fragilis*, Chaiffetz, 1972). However, some have argued that the larger heavier forms (*e.g Rhabdochitina* or *Conochitina*) must have adopted a benthic habit (Koslowski, 1963; Urban & Kline, 1970; Urban, 1972). A pseudoplanktonic life-mode has also been suggested by Jansonius (1964) and Laufeld (1967), whereby spinose chitinozoa were attached to floating objects.

5.3.1c *Scolecodonts.*

Very little is known of the palaeoecology of scolecodonts, except that they were exclusive to the marine environment. In a recent appraisal of Silurian paulinitid polychaetes from Gotland, Bergman (1989) attempted to equate scolecodont distribution with lithotype. Although a number of broad associations were documented, with certain genera recovered preferentially from certain facies, the sedimentary facies interpreted by Bergman (1989) appear somewhat vague. Furthermore no estimates of palaeodepth were suggested.

5.3.1d *Miospores.*

The empirical inverse relationship between land-derived, dispersed spores and pollen *vs.* marine microplankton is well established, and is a widely accepted qualitative means of assessing proximity to palaeoshoreline (see amongst others, Upshaw 1964; Gray and Boucot 1972; Wicander & Playford, 1985 - refer to Chapter 1, Section 1.7.2).

In general, palynological data such as spore to acritarch diversity, general spore abundance and the concurrence of certain morphotypes have allowed reasoned speculation of palaeoenvironment.

5.3.2 Observations.

5.3.2a *Introduction.*

The Devonian of north Devon has the potential of providing an ideal setting for tracing the variation in the composition of fossil palynomorph assemblages, through regressive and transgressive sedimentary cycles. An appraisal of the relationship between palaeoenvironment and palynology is however limited for a variety of reasons. Relatively little detail is known of the relationship between the spatial distribution of fossil palynomorphs and marine sedimentary facies. In the context of north Devon and irrespective of sedimentary facies, the palynofloras documented contained abundant and diverse, terrestrially-derived organic matter. Microplankton, chitinozoa and scolecodont were infrequent, scarce and of lower diversity and abundance (refer to Chapter 2, Section 2.6.2). In virtually all palyniferous samples, marine palynomorphs form less than 1% of the total palynoflora documented. Only in a few assemblages recovered from the Morte Slates did the acritarch and chitinozoa component comprise as much as 5%. These relative estimates are included simply to convey the paucity of the marine palynomorphs, as a detailed palynofacies study was considered unviable (refer to Chapter 2, Section 2.8).

Correia (1967) and Cramer (1972) noted the effect of high temperatures on the preservability of various palynomorph groups, remarking that at high temperatures (*e.g.* above 150°C) acritarchs, chitinozoa and miospores tend to lose sculpture. With an increase in temperature, such palynomorphs may "shatter". Although palynomorph preservation was noted to be variable in the present study, it is questionable whether regional metamorphism has preferentially had such a deleterious effect solely on the acritarchs and chitinozoa, and thus accounting for their low numbers. As discussed in Chapter 2 (Section 2.4), with careful oxidation well preserved palynomorphs were recovered. Therefore, the paucity in marine palynomorphs is believed a primary characteristic of the palynofloras, and relates to palaeoenvironmental influences rather than preservation potential.

Generalised kerogen characteristics for the studied section are summarised in Figure 5.1, together with the broadscale distribution of "woody" phytoclasts and scolecodonts (reworking is not indicated). Table 5.3 relates the productivity of the total sample set (for each lithostratigraphic unit) according to the occurrence of the seven major phytoclast categories, as defined in Appendix II. The influence of reworking was similarly not considered in the compilation of this table.

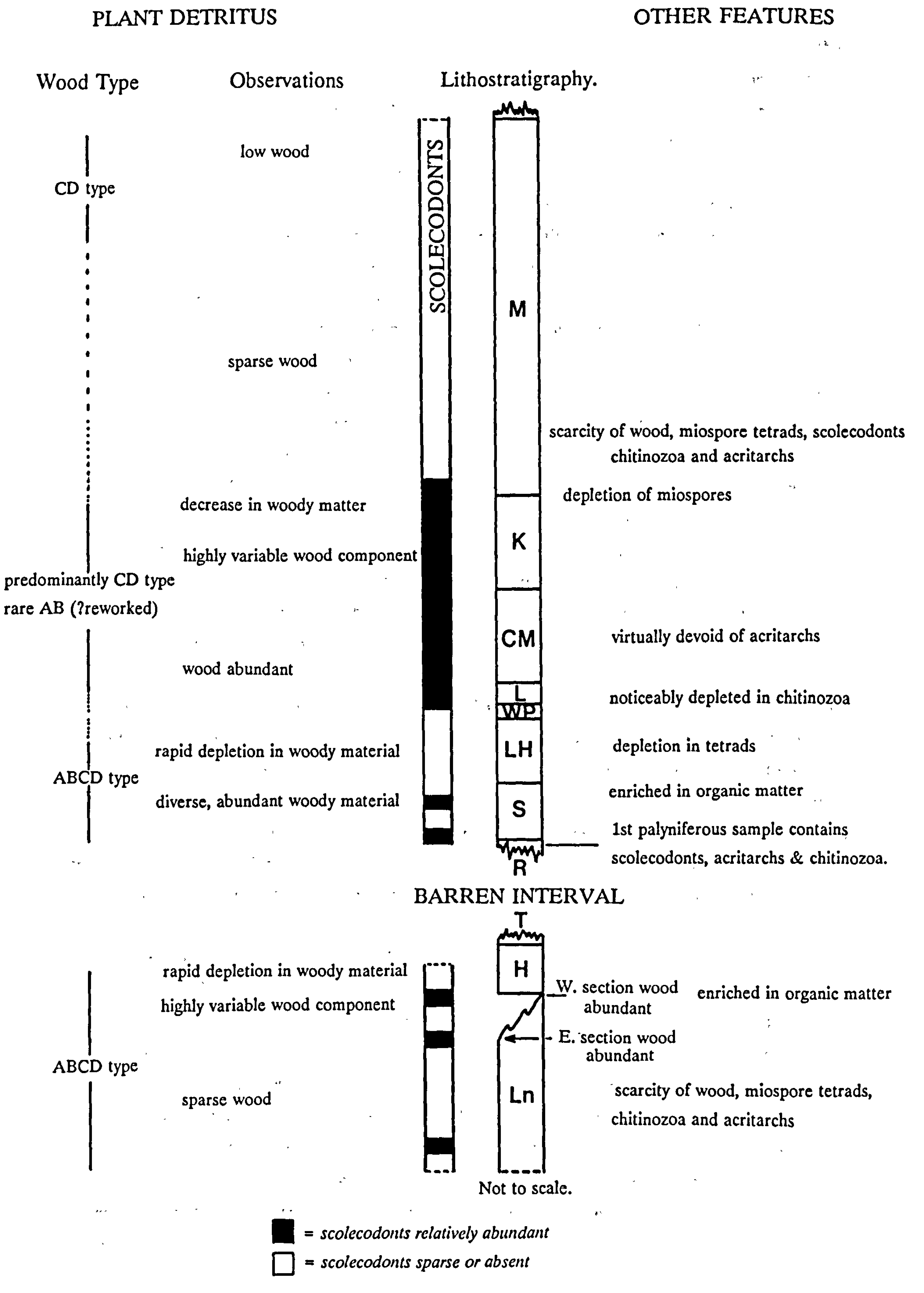
Lithostratigraphic unit	Total number of samples	% Miospores	% Tetrads	% Acritarchs	% Chitinozoa	% Scolecodonts
M	28	100%	36%	29%	36%	4%
K	30	93%	77%	27%	50%	80%
CM	33	76%	58%	3%	48%	73%
L	18	89%	44%	17%	22%	78%
WP	20	90%	30%	40%	70%	30%
LH	12	83%	25%	75%	67%	33%
S	15	80%	67%	67%	33%	40%
R	11	18%	18%	9%	18%	18%
T	18	-	-	-	-	-
H	11	54%	18%	9%	27%	18%
LN	42	76%	40%	14%	26%	48%

Table 5.3. Generalised sample productivity of the various lithostratigraphical units studied (% of samples yielding various phytoclast types) - categories as defined in Appendix II.

Apart from confirming the regional predominance of terrestrially-derived phytoclasts, in general no clear relationship is apparent between the occurrence of the other major palynomorph groups and sedimentary facies. There does, however, appear to be a broad correlation between acritarch occurrence and the absence of scolecodonts (and *visa versa*). To illustrate this, note the high scolecodont recovery from the Lester Slates & Sandstones, the Combe Martin Slates and the Kentisbury Slates, relative to the rare acritarch component: conversely the near absence of scolecodonts from the "distal" Morte Slates. One should note that microfossil presence or absence was assessed in an entire lithostratigraphic unit (and therefore a broad facies-type), rather than within individual assemblages.

As mentioned, the diversity and abundance of terrestrially-derived phytoclasts far exceeds that of the associated acritarch and chitinozoa assemblages. Consequently, when terrestrial and marine palynomorphs concur, the presence of the latter groups is usually obscured by the land-derived palynoflora. Furthermore, unlike the observations of Dorning (1981a), and Dorning & Bell (1986), the composition of the impoverished marine palynomorph assemblages reported from north Devon appear to show little dependency on sedimentary facies: a number of stratigraphically long ranging taxa (*e.g. Diexallophasis remota*) were recovered from a variety of lithostratigraphical units. In view of their exceedingly low numbers, it is conceivable that many of the marine palynomorphs recovered are allochthonous. This is confirmed by the very rare recovery of certain acritarchs (*e.g. Vulcanisphaera* sp.), being commonly associated with much older, pre-Devonian strata. Where marine palynofloras are conceivably contemporaneous with the encasing sediment (*e.g.* in the Morte Slates), the low abundance and low species diversity may be a reflection of adverse palaeoenvironmental conditions (*e.g.* restricted marine conditions or extremes in salinity and/or temperature). However, the known sedimentology for the area does not support such a hypothesis. Consequently, the recovery of acritarchs, chitinozoa, and/or scolecodonts in the present study was used simply to indicate probable marine-influenced sedimentation, but only then when reworking had been discounted.

Figure 5.1 Generalised kerogen characteristics.



5.3.2b *Acritarchs and chitinozoa.*

Of the 177 palyniferous samples reported in this study, 31% yielded acritarchs and 49% chitinozoa. As introduced in Section 4.5, there are few comparative marine Devonian sections in the British Isles which have yielded microplankton and chitinozoa. Hypothetically, if one assumes that the majority of these assemblages are autochthonous rather than reworked, then the comparatively low species diversity and low abundance of the palynofloras broadly equates to the nearshore biofacies as defined by Dorning (1981c). However, within north Devon multiplicisphaerid and *Micrhystridium* acritarchs co-occur in near-shore environments in approximately equal numbers, as well as relatively abundant species of *Dictyotidium, Diexallophasis, Micrhystridium, Multiplicisphaeridium,* and *Veryhachium*. What is unusual, considering the transect through transgressive and regressive sediments in north Devon, is the widespread depletion or absence of sphaeromorphs (contrary to the observations of Staplin, 1961 - see Section 5.3.1).

The recovery of a *Maranhites* spp. complex from the Morte Slates provides the most convincing evidence that at least a few of the microplankton assemblages recovered from this sequence are truly contemporaneous (refer to Chapter 4, Section 4.5.2). In illustration, *Maranhites perplexus* Wicander & Playford (1985) was first described from the upper Frasnian Lime Creek Formation, Iowa (U.S.A.), and is reported herein from the Morte Slates of north Devon. Wicander & Playford (1985) believed the palynomorph assemblages documented from the Lime Creek Formation indicated a nearshore normal marine environment. To interpret a similar palaeoenvironmental scenario for the Morte Slates based solely upon the presence of is taxon is somewhat tenuous, but worth consideration.

Based on the observations of Laufeld (1974), the recovery of short-spined chitinozoa (*e.g. Fungochitina ?pilosa*) from part of the Devonian strata of north Devon is compatible with the interpreted shallow-water marine conditions.

In conclusion, the low abundance of marine palynomorphs is difficult to interpret, considering all palyniferous sediments identified by the present study were influenced in part or entirely by marine conditions. Marine palynomorphs may have been depleted in the north Devon area, due to adverse palaeoenvironmental conditions during the Devonian Period: this is difficult to ascertain based upon current sedimentological knowledge. Pound (*in prep.*) recognised an "anoxia" within the Lynton Formation based upon sedimentology and trace fossil assemblages, although from a palynological view point, the lack of amorphous organic matter within this section does not substantiate such a claim.

5.3.2c *Scolecodonts.*

43% of the 238 palynological samples studied contained scolecodonts. With the exception of parts of the Lynton Formation, Hangman Sandstone Group, Wild Pear Slates and the majority of the Morte Slates, scolecodonts were recorded pervasively throughout the studied section (refer to Figure 5.1). As mentioned in Section 5.3.2a an inverse relationship was noted between acritarch and scolecodont occurrence in interpreted marginal/shallow marine facies (assuming that the presence/exclusion of these microfossils was not influenced by stratigraphic position or reworking). Strata considered to be more distal in aspect (*e.g.* the Morte Slates, or the most basinwards facies of the Lynton Formation - exposed west of Crock Point, Pound *pers.comm.*) proved notably devoid of scolecodonts.

5.3.2d *Miospores and plant detritus.*

Few publications deal specifically with the spatial distribution of different morphotypes of fossil miospore (refer to McGregor, 1979a; Streel & Bless, 1980; Streel 1986a). Land-derived plant matter (spores and plant fragments) are normally most abundant in continental and neritic facies, with the greatest concentrations being noted in the inner neritic zone (Dorning 1986; Richardson & McGregor, 1986). In a palynological study of the Recent sediments of the Orinoco Delta and associated shelf area, Müller (1959) considered fluvial transport to be the principle mechanism for the dispersal of spores and pollen into lacustrine, lagoonal and marine deposits (refer also to Peck, 1973, regarding localised modern pollen transportation). Recently Richelot & Streel (1985) addressed the interplay between fluvial and aerial pollen grain dispersal in sediments at Calvi, Corsica, and noted the former to be a significant influence.

For the Devonian Period, Dorning (1986, p.263, fig. 14.6) outlines superficial spatial distribution patterns of selected miospore taxa for the Givetian of North America (*Retusotriletes, Acinosporites* and *Grandispora*). In his schematic model Dorning illustrates acamerate miospores to be distributed far offshore, preserved within the more distal facies. In north Devon, there appeared no strict, simple relationship between sedimentary facies and the occurrence of different miospore morphotypes. Camerates, acamerates, densospores and cingulate spores were comparatively widespread, with their occurrence appearing controlled more by stratigraphic position than by palaeoenvironmental conditions. For example the inception and proliferation of the miospore *Geminospora lemurata* within the Ilfracombe Slates, is presumed to reflect the evolution of the progymnosperms in the Middle Devonian (Allen, 1980), and not as a response to changes in local palaeoenvironment. No megaspores were reported from any part of the studied sequence (even from within the most proximal facies), unlike occurrences noted from further to the east, in central and southern England (from the Wyboston Borehole; Mortimer & Chaloner 1967).

Qualitatively, of the 177 palyniferous samples recorded, there appeared to be a generalised inverse relationship between the abundance of land-derived phytoclasts and interpreted distance from the palaeoshore. With increasing proximity to land (for example, towards the top of the Lynton Formation), the extracted kerogens were usually enriched in discrete miospores and miospore-tetrads, in addition to a high "wood" component. Conversely, the more distal sediments tended to yield sparser palynomorph assemblages. Amongst others, Clayton & Graham (1974, p. 586) have used the recovery of intact spore tetrads to suggest minimal transportation, as in general these are easily mechanically disaggregated. Using this principal, 56% of all palynomorph assemblages detailed from north Devon may have been subjected to minimal transportation. An approximate, positive correlation was recognised between the "more proximal" sediments and the recovery of complete tetrad.

Parts of the Lynton and Little Hangman Formations, Wild Pear, Kentisbury and Morte Slates yielded exceptionally sparse palynomorph assemblages. Localised fluctuations in water depth & sedimentation rates (refer to Streel & Vanguestaine, 1989), the variable preservation potential of organic matter, or simply the degree of bioturbation may account for such subtle variations. Overall, kerogen yields were very low, with no apparent relationship discernible between sedimentary facies and variations in total organic carbon (T.O.C) content (refer to Section 2.6 and Fig. 2.5: based on 12 samples T.O.C varies between ≈0.1-0.3%, with the higher values not necessarily related to the more proximal sedimentary facies).

For the palyniferous strata of north Devon, the marked diversity in the dispersed miospore record suggests that the local land macroflora (from which these phytoclasts were presumably sourced), was similarly diverse (even if parent-plant sporangia contained more than one miospore morphotype, *sensu* Moore, 1946). Furthermore, not only was the proximal land flora well established during the deposition of the oldest lithostratigraphical unit exposed in the area (namely the Lynton Formation), but this macroflora was clearly evolving, as gauged by the changing composition of the dispersed miospore assemblages. With the passage of time through the Devonian Period, the miospore assemblages in north Devon became increasingly diverse and complex, reaching an acme in morphological innovation and assemblage composition during latest Eifelian/Givetian times (contemporaneous with the deposition of the upper Hangman Sandstone Group and the Ilfracombe Slates). Subsequently, miospore design became more conservative towards the top of the studied sequence (*i.e.* in the Frasnian strata). From what is known of the palaeolatitude for this area suggests that the terrestrial palaeoenvironment was semi-arid (Allen, 1974ab, 1979). Therefore, the associated land-flora had clearly adapted to the presumably harsh palaeoenvironmental conditions that prevailed over this area, having overcome problems of dehydration.

5.4 LITHOLOGICAL VARIABILITY AND MICROFOSSIL COMPOSITION.

Lithotype is presumed to be an important determinate of microfossil yield and associated assemblage composition. The micropalaeontology of carbonates as opposed to silicates has been shown to vary quite markedly (*e.g.* Weddige & Ziegler, 1976, 1987; Nicoll, 1984; Dorning, 1986; Dorning & Bell, 1986). In this study, a diverse suite of carbonates were processed for conodonts, but few specific relationships established between sediment productivity and petrography. Bioclastic limestones with a moderate to rich macrofaunal content generally yielded the most diverse faunas. The low-yield conodont faunas recovered from the calcarenites of the Lynton Formation may have been diluted by the high terrigenous clastic input. Limestones enriched in disarticulated crinoid ossicles (*e.g.* carbonates of the Wild Pear Slates) as well as highly coralliferous limestones (*e.g.* the Jenny Start Limestone; refer to Section 5.2.5b) yielded negligible numbers of conodonts, or proved barren. The virtual absence of conodonts from the coralliferous Jenny Start Limestone is interpreted as analogous to the low reef-productivity noted by Nicoll (1984) in the Canning Basin.

Dark blue/grey silicate lithotypes were preferentially sampled for palynomorphs (refer to Chapter 2, Section 2.4.2). In addition, twenty limestones samples were collected from the Ilfracombe Slates and prepared for palynological analysis. Of the twenty processed, eighteen contained negligible ?organic matter, whereas the remaining two (from the Jenny Start Limestone) yielded abundant "wood". These cursory studies tentatively confirm the absence or depletion of palynomorphs in certain Palaeozoic limestones, as remarked on by Dorning (1981a, 1986).

5.5 SUMMARY.

The indigenous marine microfossil assemblages reported from the Devonian strata of north Devon are difficult to equate to palaeoenvironment. The sparse data-base and uncertain extent of reworking limit precise interpretation. For parts of the Lynton Formation and Ilfracombe Slates, the character of the conodont faunas suggests normal, nearshore open-marine conditions. However, post-mortem sorting of the faunas is apparent, as the majority represent pectiniform-lag deposits.

In general, palynomorph diversity and sediment productivity qualitatively decrease with increasing distance from the palaeoshoreline. Kerogen isolates were dominated by terrestrially derived organic matter, although subtle variations in sediment yield were observed. In general, the relationship between distance from the palaeoshore and the composition of the marine palynomorph assemblages proved uncertain. Problems of interpretation were further limited as a high proportion of the microplankton and chitinozoa recorded in this study may well have been reworked. An apparent correlation was however noted between scolecodont abundance and the "more proximal", shallow-marine facies. Cursory T.O.C. studies indicate that irrespective of sedimentary facies, the organic content of the sediments is very low.

Overall, the character of the conodont and palynomorph assemblages indicates that shallow-marine, nearshore conditions prevailed during times of deposition of parts of the Lynton Formation and Ilfracombe Slates. The microplankton assemblages recovered from the Morte Slates differ conspicuously from the rest of the sequence, and by direct analogy with the upper Frasnian strata of Iowa (Wicander & Playford, 1985), may conceivably represent slightly more open marine conditions. The microplankton reported from this unit may however be unique purely for stratigraphic rather than palaeoenvironmental reasons.

The diversity in the dispersed miospore record reported from north Devon suggests that the presumed proximal land-flora was well established and diverse during the Devonian Period, having adapted to the semi-arid palaeoenvironment interpreted for the land area to the north.

CHAPTER 6.

GEOTHERMOMETRY.

6.1 INTRODUCTION.

The discipline of geothermometry has by tradition been dominated by the petrologist or organic geochemist, largely because data acquisition relied upon optical or geochemical techniques. Within the last two decades, research into certain aspects of sedimentology and micropalaeontology has revolutionised this specialist discipline, inviting a much wider audience to address and resolve palaeothermometry problems. Previously, the principal utility of microfossils had been in stratigraphical evaluation. Their application as geothermometric indices has been a comparatively recent departure (*inter alia*, Staplin 1969: Thermal Alteration Index (TAI); Epstein *et al.*, 1977: conodont Colour Alteration Index (C.A.I.); Heroux *et al.*, 1979: acritarch and chitinozoa reflectivity; Legall *et al.*, 1981: Acritarch Alteration Index (AAI); Goodarzi & Higgins 1987: scolecodont reflectivity). Studies on the organic reflectance of microfossils (*inter alia* Goodarzi, 1985a; Bertrand & Heroux, 1987) demonstrated their suitability as thermal maturity indicators. Through the combination of the rapid thin-section technique devised by Hillier & Marshall (1988) and conventional reflectance method, such potential is now being widely recognised. Thus through either the quantitative or qualitative estimation of palaeotemperatures indexed by microfossils, one may speculate the degree of regional or burial metamorphism, and associated depth of burial and/or related rates of subsidence. Such phenomena are routinely evaluated using either vitrinite reflectivity, or alternatively palynomorph colouration.

Literature on the correlation between the various organic thermal maturation indices, as well as organic and inorganic indices is still comparatively sparse. Robinson *et al.* (1987), for example, compared clay mineralogy with conodont C.A.I. and vitrinite reflectance studies for the Lower Palaeozoic Welsh Basin and the Upper Palaeozoic rocks of the Alston Block and Northumberland Trough in Northern England. Nowlan & Barnes (1987) equate C.A.I to vitrinite reflectance and palynomorph translucency (refer to Table 11.1 therein), and review the potential application of conodont colour alteration to regional and economic geology. Similarly, Kovacs & Arkai (1987) equated conodont alteration with carbonate texture, illite crystallinity and vitrinite reflectance, based upon material collected from metamorphosed limestones in northern Hungary. Hillier & Clayton (1989) recently equated illite/smectite diagenesis to vitrinite reflectivity for the Devonian lacustrine mudrocks of the Orcadian Basin, Scotland.

The integrated theme adopted by the current research programme allowed correlation between two distinct organic thermal maturation indices; namely vitrinite reflectance and the conodont Colour Alteration Index (C.A.I.).

6.2 CONODONT COLOUR ALTERATION INDICES (C.A.I.) AND TEXTURAL CHARACTERISTICS FOR THE DEVONIAN CONODONT FAUNAS OF NORTH DEVON.

6.2.1 Introduction.

Variation in the colour of conodont elements was apparent to a number of early researchers, although no explanation was forthcoming. Ellison (1944) documented the dehydration and associated darkening of conodonts when heated, which Lindström (1964) subsequently attributed to coalification. Through a detailed systematic study, Epstein *et al.* (1977) recognised the potential utility of conodonts as semi-quantitative thermal indices, and established an index to gauge colour alteration in conodonts. Their research incorporated the regional mapping of conodont colour relative to burial depth, the experimentally controlled open-air pyrolysis of elements (thereby reproducing the sequence of colour changes noted in naturally altered conodonts), and the correlation of conodont C.A.I. with traditional thermal indices (as standardly applied in hydrocarbon exploration: T.A.I and vitrinite reflectance). Rejebian *et al.* (1987) extended this index by calibrating the temperature ranges of conodont C.A.I. values from 5 to 8 (above ≈300°C), and equated distinct textural alteration characters with different geological processes. The conodont Colour Alteration Index (C.A.I.) and its equivalents are outlined in Table 6.1 - after Epstein *et al.* (1977) and Rejebian *et al.* (1987).

6.2.2 Methodology.

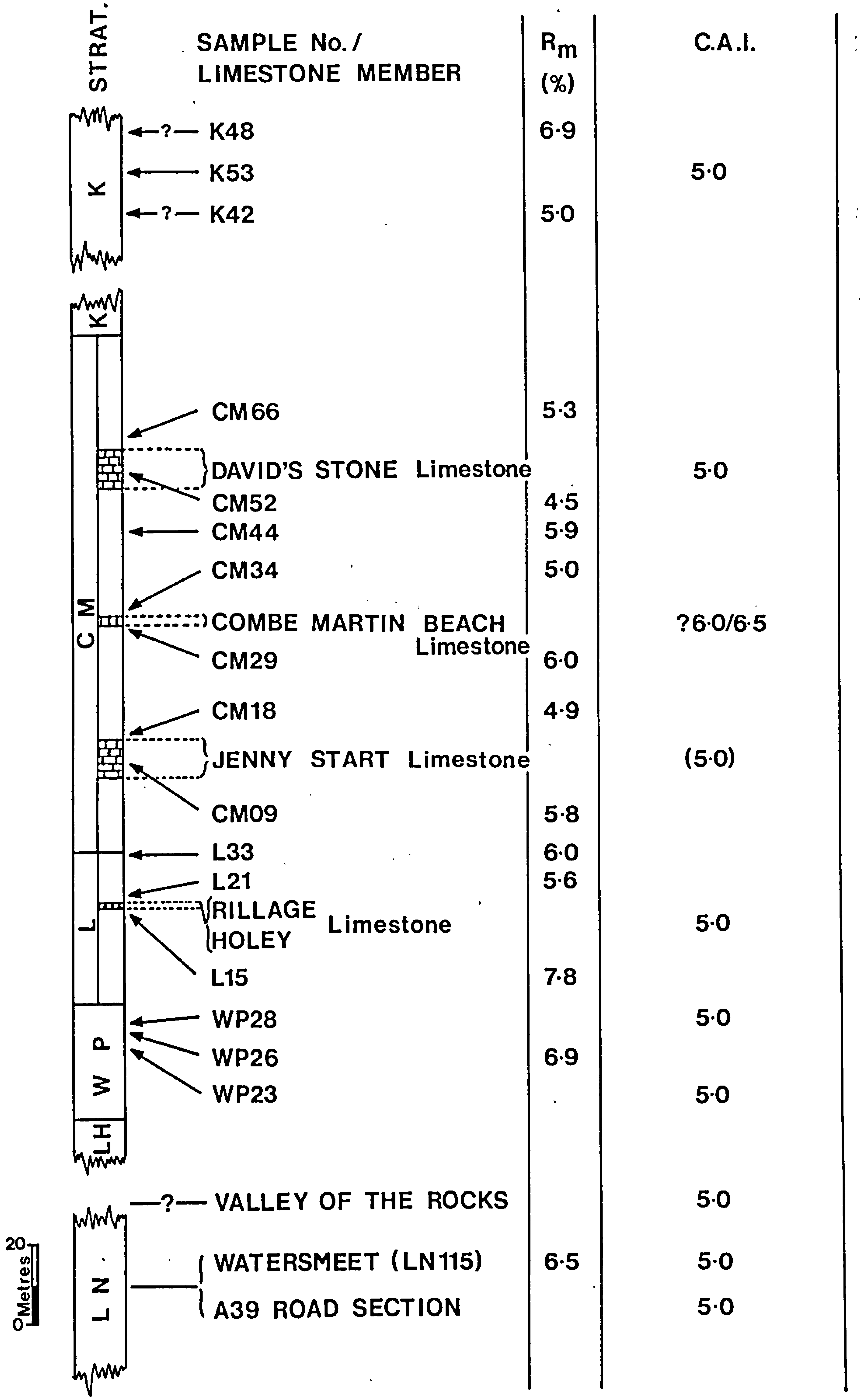
To evaluate the C.A.I., the colouration of conodont elements, deemed representative of the fauna studied, is compared with standards of known conodont C.A.I. Although this visual evaluation is subjective, relying on the ability of the researcher to estimate C.A.I., direct comparison with known standards can minimise error. In the present study, conodont C.A.I. standards were made available by Dr. R. Burnett (University College, Dublin). To ensure the compatibility of data, *Icriodus* elements provide the basis of all C.A.I. estimates herein; conodont colour has been known to vary both within an individual element and between different morphotypes of a fauna. The rarity of ramiform elements and the restricted recovery of polygnathids eliminated them as viable candidates, although their indices were noted during the course of C.A.I. evaluations.

6.2.3 Results

6.2.3(a) Conodont colour.

The stratigraphical distribution of conodont C.A.I. values are shown on Figure 6.1, and their comparability with established indices indicated on Table 6.1. The colour of conodont elements recovered from the studied carbonate lithotypes, except for the Combe Martin Beach Limestone Member, consistently equate to a high C.A.I. value of 5+. From Epstein *et al.* (1977) these values indicate high rank, and relate to a high temperature interval of 300-400 °C (Greenschist metamorphic grade). Rejebian *et al.* (1987) expanded the 5 index temperature range, spanning 300-480 °C. In comparison, conodonts examined from the Combe Martin Beach Limestone exhibit unusually high indices (6-6½, ≈equivalent to 360-610 °C, after Rejebian *et al.*, 1987) and in contrast to the regional trend outlined. Intense localised deformation, mineralisation and extreme diagenetic influences may collectively or in isolation account for this disparity. Indeed, the intense mineralisation of the Combe Martin Beach Limestone (reflected in the ferruginous appearance of this unit, as remarked upon by Evans 1922, and Edmonds *et al.*, 1985, p. 15) may explain the anomalously high C.A.I. values recorded

FIGURE 6.1 THE COMPARABILITY OF VITRINITE REFLECTIVITY (Rm %) WITH C.A.I VALUES FOR THE DEVONIAN OF NORTH DEVON.



Index	Colour Alteration (Munsell colour)	Temperature range (°C)	Vitrinite Reflectance (%)	This Study		
				C.A.I	Rm	Temp. °C *
1	pale yellow 2.5 Y7/4 to 8/4	<50-50°C	<0.8			
1.5	very pale brown 10 YR7/3 to 10YR8/4	50-90°C	0.7-0.85			
2	brown to dark brown 10 YR4/2 to 7.5 YR3/2	60-140°C	0.85-1.3			
3	increasingly dark brown, 5 YR2.5/2 to 10 YR2.5/1	110-200°C	1.4-1.95			
4	Black 5 YR2.5/1 to 10 YR2.5/1	190-300°C	1.95-3.6			
5	Black 7.5' to 2.5' YR2.5/0	300°C+	+3.6	*	4.1%+	293°C-360°C
(after Epstein et al., 1977)						
5	Black (N1)	300-400°C	no details	*	"	"
6	Medium dark grey to Medium grey, N4-N5	360-550°C	"	?*		
6.5	Medium light grey to light grey, N6-N7	440-610°C	"			
7	Very light grey to white, N8-N9	490-720°C	"			
8	colourless/crystal clear	>600°C	"			
(after Rejebian et al., 1987)						

Table 6.1. The Conodont Alteration Index, after Epstein *et al.* (1977) and Rejebian *et al.* (1987). Indicated are equivalents in terms of the Munsell colour chart (Goddard *et al.*, 1951), with calibrated temperature ranges and related vitrinite reflectance values indicated.

for this limestone member. Significantly, sparse miscellaneous microfossil assemblages (including ostracod carapaces, bryozoa and gastropod steinkerns) were recovered from this unit displaying a pigmentation similar to that of conodont faunas. This suggests that the anomalously high C.A.I. values collated for the Combe Martin Beach Limestone may be attributable to diagenetic discolouration, and not primarily induced through thermal alteration.

The conodont C.A.I. temperature estimate of 360 °C+ for the Combe Martin Beach Limestone (by applying the principles of Rejebian *et al.*, 1987) differs from the lower, vitrinite-based values recorded in the present study for the same stratigraphic section (313-332 °C). Kelm (1986) noted the lack of biotite in clay mineral assemblages from the Devonian sediments of this region, which tends to (arbitrarily) confirm that the regional thermal regime was less than 425 °C.

6.2.3(b) Textural alteration.

The S.E.M. proved extremely useful in analyzing ultrastructural detail. As already remarked (refer to Chapter 2), the overall condition of the conodonts recovered from north Devon was poor. Orchard (1979, p. 130) similarly commented on the overall poor preservation of conodonts recovered from north Devon. Texturally unaltered specimens were rare. The faunas showed highly variable degrees of preservation, including element corrosion, deformation and fracturing, which collectively limit detailed taxonomy. C.A.I. values documented (Section 6.2.3a) are consistent with an interpretation of chlorite-grade metamorphism, and element preservation noted for the faunas from north Devon comparable to that associated by Rejebian *et al.*, (1987; fig. 1, p. 472), with regional metamorphic alteration. A number of elements also display subtle remnants of diagenetic alteration, which was only resolved at high magnification under the SEM. The photomicrograph of *Icriodus brevis* (Pl. 6.7, fig.9, the present study) clearly shows cubic crystal growths between the denticles on the upper surface. This and other such specimens resemble the diagenetically altered elements described and illustrated by Rejebian *et al.* (1987; fig. 1).

6.3 VITRINITE REFLECTANCE.

6.3.1 Introduction

A variety of geochemical and optical techniques are available for assessing the thermal maturity of organic matter preserved within sediments. Teichmüller (1987) reviews the microscopic methods currently applied in rank evaluation ("coalification" studies), and provides a useful companion to any preliminary appraisal of the current techniques routinely employed.

The optical assessment of organic rank may encompass reflectance, fluorescence or an investigation of colour in white light. At low temperatures, the various maceral types respond differently to coalification, in relation to chemical and physical modification. Naturally, the methodology adopted depends largely upon the nature of the material studied. Vitrinite phytoclasts are the commonly preferred subject in assessing the degree of organic metamorphism, largely because they are the most widely occurring maceral group. Indeed, vitrinite reflectance is an accepted indicator of thermal maturation and favoured to other procedures, as measurements can be made on clastic rocks with a finely dispersed vitrinite component. However vitrinite reflectance does have limited application, with the qualitative technique of palynomorph colour assessment considered far more sensitive in low temperature evaluations. Vitrinite reflectance is preferentially applied at higher rank (refer to the discussion below).

The general absence of vitrinite ("*sensu stricto*") in pre-Devonian sequences, the unreliability of vitrinite measurement below ≈0.3 %, and the possibility of misidentification or analysis of reworked phytoclasts, restricts the widespread applicability of vitrinite reflectance studies. Furthermore, vitrinite reflectivity may be modified by oxidation (Creaney, 1977), the character of the host lithotype (Jones *et al.* 1971), or by association with other kerogen types (*inter alia*, Price & Barker 1985). In pre-Devonian sediments, graptolites (Goodarzi, 1985b), chitinozoa or acritarchs (Heroux *et al.*, 1979; Goodarzi, 1985a) provide the basis of reflectance studies (see also, *inter alia*, Kemp *et al.* 1985). Ottenjann *et al.*, (1974), viewed sporinite fluorescence more reliable for determining levels of organic metamorphism at very low rank (<0.3 % reflectance). However, sporinite fluorescence decreases with increasing temperature, and thus cannot be successfully applied above reflectivities of 1.3 % (Jacob, 1964; Van Gijzel, 1967, 1971, 1975, 1981; Ottenjann *et al.*, 1975; Hart, 1986; McPhilemy, 1988).

Palynomorphs are known to change in colour from yellow through to black with increasing temperature. Amongst others Staplin (1969) and Barnard *et al.* (1976), devised spore colour indexes: the Thermal Alteration Index (T.A.I) and Spore Colour Index (S.C.I.) respectively. Numerous similar schemes are currently available, with attempts of standardising spore colour assessment unfortunately not overcoming the inherent subjectivity of the technique. This is particularly true when discriminating between shades of brown and black. The diversity and incompatibility of these various colour index schemes also limits the comparability of such data, although recent research into the quantification of spore colour may prove instrumental in synthesing a unified spore colour index (Marshall, *in press*). According to Heroux *et al.*, (1979) a black spore colour (T.A.I.= 5; S.C.I.= 10) equates to a vitrinite reflectance value of ≈3 %, and is inapplicable in high maturation studies. Exactly how spore colour equates to reflectivity is still highly debated (for example see Teichmüller 1987, Fig. 22 p. 146).

Hoffman & Jenkner (1932) first reported on the increase in the reflectance of organic macerals with increasing temperature. Initial studies considered the relationship to be stepped (*inter alia*, Seyler, 1943; Shaw 1953), but subsequent research has proven the increase in reflectance with rank to be continuous (Broadbent & Shaw, 1955). Temperature, pressure (tectonic stress &/or depth of burial) and time have independently or collectively been the suggested mechanisms for coalification processes. Price (1983) recently questioned the influence of burial time in organic metamorphism, considering vitrinite reflectance an absolute time-independent parameter for geothermometry (correlating vitrinite reflectance and maximum temperature). He contested the widely accepted theories of Karweil (1956) and Lopatin (1971) for organic catagenesis, which were based on first order reaction kinetics. Robert (1985) and Teichmüller (1987) further advocate the time independency of vitrinite reflectance, with temperature principally responsible for coalification reactions. It is however often difficult to definitively evaluate the strictly empirical relationship between vitrinite reflectance and temperature.

Temperature resolution now available from vitrinite studies (Price, 1983; Barker & Pawlewicz, 1986), coupled with the palynological bias to the current research, favours the assessment of vitrinite reflectance in preference to other organic or inorganic investigative means (eg. clay mineralogy) available for quantifying rank. Vitrinite reflectance studies were initiated to quantitatively assess the degree of organic metamorphism of the host Devonian sediments, as well as to corroborate the more subjective C.A.I. evaluations of temperature discussed earlier in Section 6.2. Durand *et al.* (1986) view vitrinite reflectivity only to be a suitable and reliable index in estimating palaeotemperatures for the vitrinites of coal beds. However, Durand *et al.* (1986) do concede that the technique may be applied to samples with a low, dispersed organic component, but only then with greater inaccuracy.

A general characteristic of low rank maturities (Rm <≈1.5%) is the distinct variation in reflectivity, largely as a result of primary differences in maceral-type (refer to Teichmüller 1987, Fig. 25, p. 147). At higher temperatures maceral-types cannot readily be differentiated simply according to degree of reflectivity, as their reflectance signatures become increasing compatible (Teichmüller 1987, p. 129-130). Gross morphology may be the only means of identifying maceral-type, though the degree of birefringence and enhanced particle relief in polished section may facilitate identification (Cornford *et al.*, 1987).

As remarked in Chapter 1 (Section 1.6.3), previous palynological pilot studies in the study area have proved largely inconclusive, with the Devonian sediments yielding only negligible organic material. Only coalified hystricospores have previously been reported from the sequence (Owens, in Edmonds *et al.*, 1985, p. 6; refer also to Richardson & Hassan *pers.comm.*, in Pound, 1984; Pound *in prep.*). However apart from the prolific and diverse palynomorphs documented within this study, an associated "woody" component (vitrinite) forms a variable but usually prolific component of the kerogen isolates. There appears a generalised relationship between hypothetical proximity to land, and an enrichment in "woody" palynodebris (refer to Chapter 5), with the uppermost Lynton Formation, and the palyniferous horizons within the Hollowbrook, Rawns and Sherrycombe Formations yielding remarkably high levels of "vitrinite[1]".

The described abundance of "vitrinite" thus allowed an investigation of vitrinite reflectivity in north Devon. The only previous vitrinite reflectivity study in this area is that of Cornford *et al.* (1987), who investigated the vitrinite reflectance profile through the Culm (Carboniferous) strata of north Devon and north Cornwall.

6.3.2 Materials and Methods.

When viewed in transmitted light, all organic matter isolated from the studied sequence appears opaque, which in itself suggests that the succession as a whole has been influenced by high temperatures (refer to Section 2.7.2b). "Whole rock" reflectance determinations proved unviable, as the organic constituent within the sediments is consistently low and widely dispersed. An investigation of the T.O.C. content of twelve representative samples revealed organic carbon concentrations of between 0.1% and 0.3% (refer to Chapter 2, Figure 2.5). Hillier & Marshall (1988) outline a preparatory technique allowing the determination of rank for rocks with a low kerogen content, such as those recovered herein. Organic isolates were therefore analysed using this polished thin-section method, which was considered far more advantageous than traditional procedures as a substantially lower quantity of kerogen is required, and also the material may be viewed simultaneously in both transmitted and incident light.

The organic component within samples was isolated using normal palynological procedures,

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[1] the precise definition of vitrinite as applied to low rank material (refer to Robert, 1985, p. 81, 102) is used to reference the opaque, but morphologically distinctive fibrous, cellular and tubular debris of plants found in the present study.

as discussed in Chapter 2 (reference Phipps & Playford, 1984). The bulk of the kerogens were oxidised and detailed systematically, with a small unoxidised proportion prepared for S.E.M analysis and/or vitrinite reflectance measurement. A Zeiss UMSP 50 (microspectrophotometer) microscope equipped with a x40 antiflex objective and calibrated using a diamond standard (of 5.23% reflectivity) was used in all reflectance measurements. Values were recorded on an IBM PC driven by the reflectance programme "Slap", written by S.J. Hillier (Southampton University). Measurements were made under oil (R.I. 1.515) at 546nm, illuminated in white light. The reflectivity of vitrinite particles was preferentially measured, and the mean random reflectivity (Rm) calculated (usually based upon 50 measurements on different vitrinite grains - refer to the discussion below). At elevated temperatures organic matter behaves anisotropically. Thus R_{max} and R_{min} values were recorded in the present study for a limited suite of kerogen-rich samples: the anisotropic, particulate phytoclasts were first orientated in crossed-polars, allowing recognition of the optimum R_{max} and R_{min} positions. Anisotropy measurements were similarly based on ≈50 measurements for each sample. Piller & Gehlen (1964) and Creaney (1977) detail measuring procedures and possible sources of error in reflectance measurements, concluding that instrumentation error is extremely small (± 0.5-1 % of the reflectance value) - also refer to Davis (1978). Mackowsky (1975) considered a standard deviation of <0.1% when measuring the reflectance of vitrinite in coals. At low rank, Stach *et al.*, (1982) anticipated the standard deviation as being 10% of the measured mean random reflectance value, with Teichmüller (1987, p. 130) considering Rm a good rank parameter in studies of up to 4% reflectivity.

According to Robert (1985, p. 102) the statistical determination of vitrinite reflectivity requires a minimum of 30 to 50 measurements, with values spread over more than 1% VR_o (vitrinite reflectance in oil) discounted. As will be discussed, the high rank and subsequent influence of anisotropy makes this error margin impractical. Over 100 individual measurements per sample are the usual norm when dealing with organic rich sediments (Stach *et al.*, 1982). According to Stach *et al.*, (1982), there is however little point in increasing the number of measurements above 100 as the accuracy parallels the square root of the number of determinations. Distinctions in vitrinite, liptinite and inertinite reflectivity so apparent at low maturities become academic at high rank, thus validating the measurement of identifiable palynomorphs in the present study. In "wood"-deficient samples, such measurements supplemented "true" vitrinite reflectance data. In the present study, an average of 50 measurements on different vitrinite/"liptinite" particles were collated for each sample. The resulting reflectance values, individually expressed as a percentage of the incident light intensity, were plotted as relative frequency histograms (measurements were normalised to allow for direct comparison between different samples). Extreme values were edited from the final data set to minimise the deviation of the calculated mean from the "true". In all cases the arithmetic mean and standard deviation were computed for the edited and unedited data set (refer to Appendix III for sample reflectivity profile). Care was taken to attempt to discriminate between reworked vitrinite, and an indigenous "wood" population (after Stach *et al.*, 1982). Well rounded vitrinite particles were treated as derived (following Cornford *et al.*, 1987).

6.3.3 Results and discussion.

6.3.3a *Introduction.*

Table 6.2 summarises the results of over 3,500 measurements on 76 samples, with interpreted palaeotemperatures also provided. The geographical and stratigraphical distribution of vitrinite reflectivity is shown in Fig. 6.2. Details of the numerical basis of Fig. 6.2 are provided in Appendix III, itemising the quantitative and qualitative (visual) characteristics for each sample. A selection of histogram plots (Figure 6.3, Figure 6.4i,ii) and the graphical relationship between Rm and the related standard deviation (Figure 6.4 iii) are also provided. The results of organic anisotropy for 14 samples is shown in Figure 6.5. Where possible, values of Rm for vitrinites and palynomorphs were differentiated, to test whether maceral-type influences reflectance even at such elevated rank levels. Reflectance values were converted to temperature estimates using the two time-independent conversion formulae of both Price (1983) and Barker & Pawlewicz (1986).

The extracted kerogens contained quite varied "wood" and palynomorph components as viewed in incident light. Dispersed vitrinites ranged in size from <25 μm to the more typical dimensions of 50-110 μm+ (rarely exceeding 200 μm), and displayed quite variable morphologies (refer to Plate 6.1, figures 1-9, 11-13; see also the systematic description of "wood" phytoclasts in Chapter 3). The palynomorph constituent also appeared highly variable in incident light (refer to Section 6.3.4). Amorphous organic matter (A.O.M.) was absent from the entire Devonian sequence studied. The significance of this is discussed in relation to hydrocarbon potential (Section 6.3.6).

Lithostratigraphical Unit	Number of Samples	Rm	Tmax * °C	Tmax ** °C
Morte Slates	12	5.6	414	325
Kentisbury Slates	7	7.0	443	349
Combe Martin Slates	13	5.5	412	323
Lester Sl. & Sst.	7	6.0	423	332
Wild Pear Slates	5	6.4	432	339
Little Hangman Fn	4	7.3	449	353
Sherrycombe Fn	7	6.4	432	339
Rawns Formation	2	5.8	419	329
Hollowbrook Fn	3	6.5	434	341
Lynton Formation	14	6.0	423	332

Table 6.2. The averaged value of Rm (mean random reflectivity in oil) per lithostratigraphic unit. Temperature conversions are according to: * Price (1983), and ** Barker & Pawlewicz (1986).

6.3.3b *Mean random reflectivity (Rm).*

Vitrinite values (Rm) were recorded across a 4.0% - 7.8% interval (Figure 6.2), and are clearly indicative of meta-anthracite rank. As summarised in the above Table 6.2, according to Barker & Pawlewicz (1986) the average palaeotemperatures exceed 320°C throughout the region. The mean random reflectivities recorded are consistently high, with no apparent dependency of Rm values upon stratigraphical position, through the ≈3 km sequence. Within north Devon, there is questionably some slight decrease in reflectivity towards the top of the section (*i.e.* within the Morte Slates), with an associated subtle increase eastward (towards the closure of the Lynton Anticline). Teichmüller & Teichmüller (1979) remarked upon the sympathetic variability in vitrinite reflectance and illite crystallinity (after Kasig & Späth, 1975) within the Palaeozoic rocks of the Venn (Stavelot) anticline, with the higher values recorded from or towards the fold closure, and throughout the southeastern limb of this regional structure. The variation in Rm noted by Teichmüller & Teichüller (1979; ≈4%) is however far greater than that recognised in the present study (≈1%).

Within north Devon, two distinct sedimentary facies associations are recognisable (after Edmonds *et al.*, 1985): argillite-dominated successions (*e.g* the Morte Slates) and sandstone-dominated sequences (*e.g.* the Hangman Sandstone Group). For obvious reasons (different levels of competency and absolute viscosity), sequences dominated by finer grained lithologies were visually more intensely deformed, relative to those comprising predominantly more sandier units (Edmonds *et al.*, 1985, p. 58). In the present study, there appeared no discernible pattern between lithology and the associated vitrinite reflectance signature (*i.e* the argillaceous-dominated sequences exhibit comparable vitrinite reflectivities to those with a predominance of sandy material).

A representative selection of reflectance histogram plots are provided in Fig. 6.3. The distributions are largely unimodal, though in a limited number of cases (not illustrated on Fig.6.3) the spread appeared bimodal. This prompted an investigation to elucidate whether maceral-type controls reflectivity, even at such high rank: refer to Figures 6.4i and 6.4ii. The various kerogen types analysed from sample H12 (Fig.6.4i) may superficially be differentiated based upon reflectivity (40 specimens measurements). The vitrinite population [plot H12(A)] exhibited a consistently lower reflectance signature, in comparison to that of the palynomorphs [plot H12(B)], the latter being displaced somewhat towards Rm ≈10%. By tentative extrapolation of the coalification tracks associated with the different maceral groups, depicted by Teichmüller (1987, Fig. 25, p. 147; modified after Smith & Cook 1980), the trend described herein does seem feasible. However, and as exemplified by sample LH12 (Fig.6.4ii), other samples did not display such clearly differentiated reflectance signatures, with both palynomorph and vitrinite populations exhibiting comparable reflectivities. Therefore, no definitive distinction can be proposed for such high rank material, in light of such conflicting evidence.

Figure 6.4iii shows the graphical relationship between standard deviation (σ) and Rm for all 76 samples studied. The spread in data illustrates the known variability in Rm values, being further corroborated by anisotropy studies. Standard deviations are consistently greater than 10% Rm (note comments made earlier in relation to the accuracy of data).

FIGURE 6.2 THE STRATIGRAPHICAL DISTRIBUTION OF Rm THROUGH THE DEVONIAN OF NORTH DEVON.

(samples are located both geographically and stratigraphically).

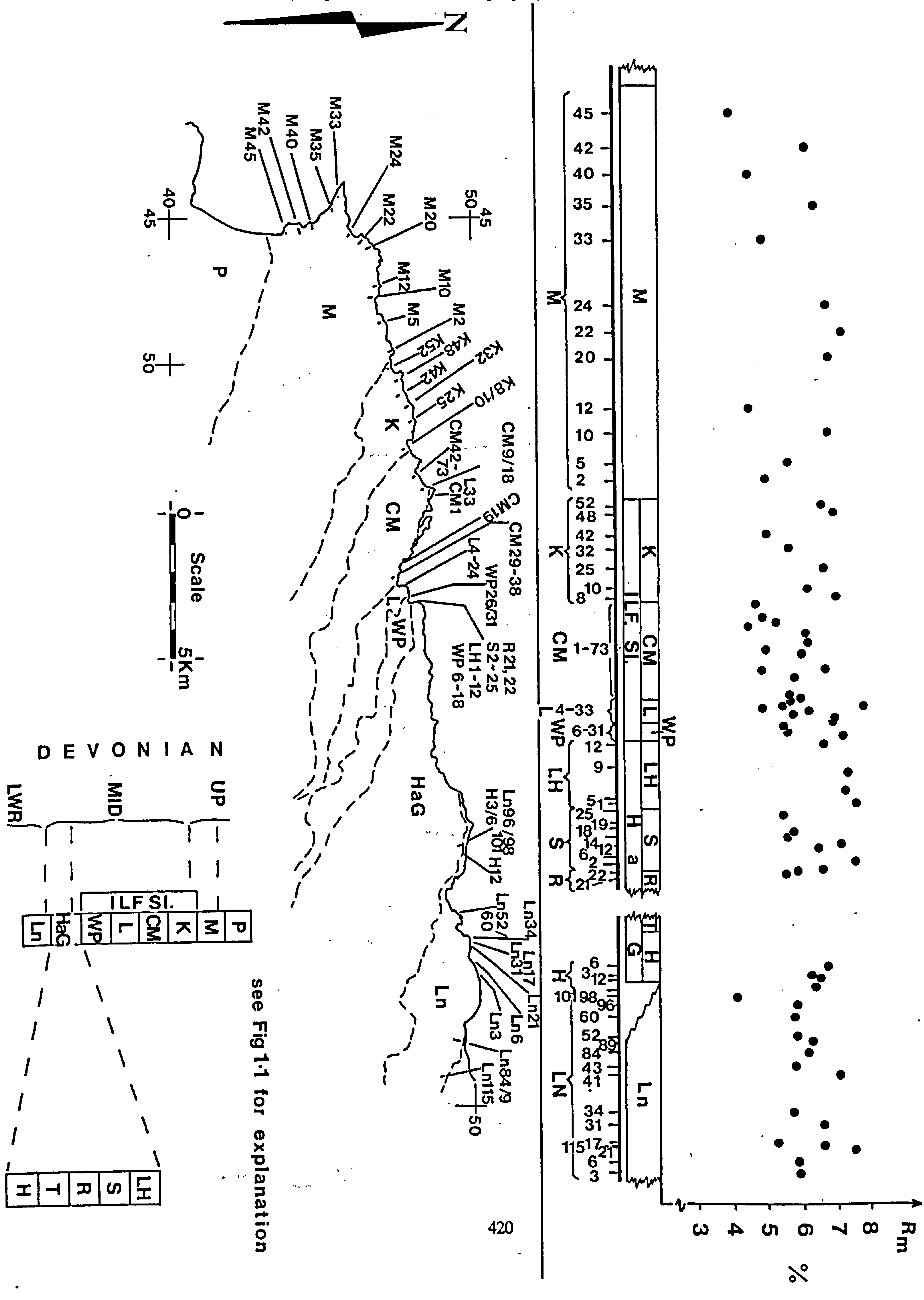


FIGURE 6.3 VITRINITE REFLECTANCE HISTOGRAM PLOTS REPRESENTATIVE OF THE DEVONIAN OF NORTH DEVON.

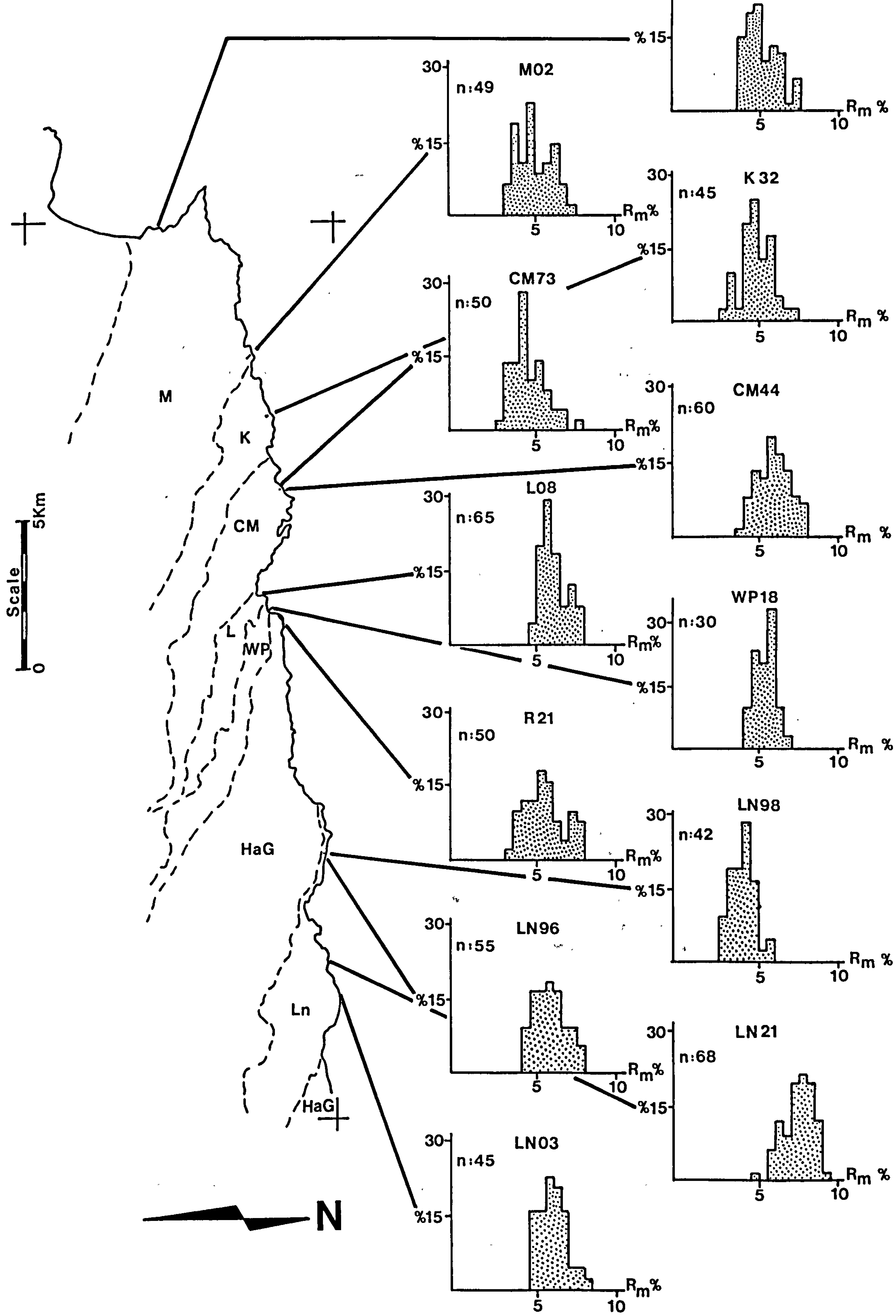
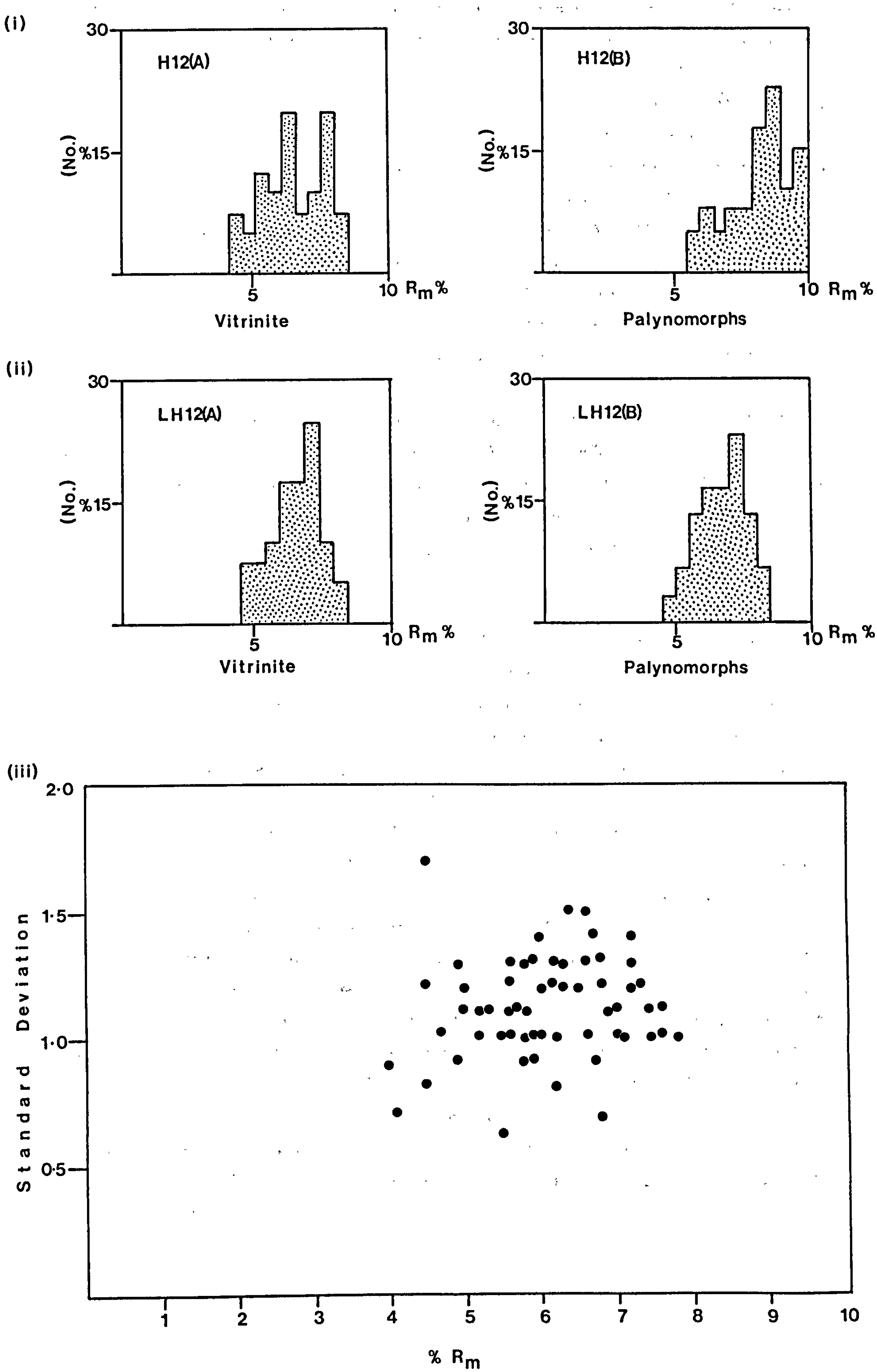


FIGURE 6.4



(i)
30
H12(A)
(No.) %15
5
10 Rm %
Vitrinite
30
H12(B)
(No.) %15
5
10 Rm %
Palynomorphs
(ii)
30
LH12(A)
(No.) %15
5
10 Rm %
Vitrinite
30
LH12(B)
(No.) %15
5
10 Rm %
Palynomorphs
(iii)
2·0
1·5
1·0
0·5
Standard Deviation
1
2
3
4
5
6
7
8
9
10
% Rm

The only previous vitrinite reflectance study undertaken in north Devon is that of Cornford *et al.* (1987): they studied the regional variation in vitrinite reflectivity through the coastal outcrops of the Culm sediments, and also for the inland Culm exposures adjacent to the Dartmoor Granite, north Devon. In general, reflectance values (the present study) compare favourably with the regional data documented by Cornford *et al.* (1987), the only disparity being the anomalously low values recorded by Cornford *et al.* (1987) at Westward Ho! On a regional scale, the sediments that crop out at Westward Ho! are believed to be tectonically unique, juxtaposed into their current position through thrusting (refer to the discussion below, Section 6.3.3c). The indiscriminate and stratigraphically unconstrained distribution in organic reflectance revealed by this study was similarly remarked upon by Cornford *et al.* (1987) for part of the (Carboniferous) Crackington and Bude Formations. However, values of vitrinite reflectance reported by Cornford *et al.* (1987) were not as consistently high as evidenced by the present study; this may simply be attributable to the less extensive data base of Cornford *et al.* (1987).

The vitrinite reflectance "profile" established herein for north Devon is comparable to data recently published by Clayton (1989), who recorded similarly high reflectivities (Rm = 4.06-5.21%) for the Upper Devonian-Carboniferous succession in the Kinsale Harbour - Old Head of Kinsale region, southern Ireland. Clayton (1989) remarked upon the lack of correlation between vitrinite reflectance and stratigraphic position, through approximately 2 km of sediment (see Section 6.3.6).

6.3.3c *The Westward Ho! Paradox.*

The unique structure and sedimentology of the Westward Ho! nappe (or "allochthon") that crops out in the Bideford area (north Devon), has been remarked upon by deRaaf *et al.* (1965) and Elliott (1976). Kelm (1986) also defined an area of lower maturity ("diagenetic zone") centred on Westward Ho!. According to Cornford *et al.* (1987), the Carboniferous strata of the Bideford and underlying Crackington Formation exposed in the Bideford area (centred on Westward Ho!), north Devon, are of a shallower burial history (1-5-2.67%R) in comparison to the contiguous Crackington and Bude Formation sediments exposed at Hartland through to Crackington Haven (4.41-5.67%). Cornford *et al.* (1987) interpreted this disparity (in vitrinite reflectivity) as indicating these two areas to have been influenced by quite different thermal regimes during the Carboniferous Variscan orogeny. Based upon the anomalously low vitrinite values recorded from the Bideford area, Cornford *et al.* (1987) suggested that folding clearly post-dated maturation, and subsequently used this data to propose a regional geothermal gradient of 40°C/km during the Variscan tectonic episode for north Devon. However, as shown by the present study, and in part by Cornford *et al.* (1987), the Devonian sediments and the bulk of the Carboniferous strata that outcrop in north Devon display uniformly high vitrinite reflectivities. This suggests that for the majority of these units, organic metamorphism in north Devon was in fact syn-orogenic (refer to Section 6.3.5). This data questions the validity of establishing a Variscan geothermal gradient for the region, based upon the "anomalous" sedimentary sequence (and associated vitrinite reflectance profile) exposed at Westward Ho! (Cornford *et al.*, 1987).

6.3.3d *Anisotropy.*

At low rank Davis (1978) remarked that vitrinite is optically isotropic, behaving as uniaxial (negative) material. However at high rank anisotropy, expressed as the difference between maximum and minimum reflectance (R_{max} - R_{min}), becomes increasingly influential. Robert (1985) considers vitrinite to behave anisotropically above 2% vitrinite reflectivity. The considerable variability in reflectance measurements noted within the vitrinite populations of north Devon are believed a consequence of this phenomenon (refer to Figure 6.5). The identification of pleochroic vitrinite laths (Pl. 6.1, figs. 8a, 8b) and palynomorphs (Pl. 6.1, figs. 10a, 10b) confirmed this anisotropic property.

The position of the optical axes within high rank "biaxial" vitrinites (Stone & Cook, 1979; Teichmüller & Teichmüller, 1979) is believed to be controlled by overburden pressure and on a millimetric scale, by diagonally directed stress transmitted through minerals compressed against the organic particle (Teichmüller, 1987). Specimen orientation, and thus the disposition of the optical axes, may be a primary influence on the measurement of reflectance at high rank. Therefore, in making a number of measurements on high rank organic isolates, one may anticipate that the orientation of the extracted organic matter on the cover-slip may be variable, and similarly the associated reflectivity (as indicated by the large standard deviations - refer to Fig. 6.4 and Appendix III). In low rank determinations, Robert (1985) considers values spread over more than 1% VRo (vitrinite reflectance in oil) should be discounted. In the present study, at high rank anisotropy makes this error margin impractical.

Recently the validity of using anisotropy in assessing rank has been questioned (Teichmüller 1987, p.130). She demonstrated the constant or decreasing trend in a regional Rm against anisotropy plot for the Federal Republic of Germany, over the meta-anthracite spectrum (between 4-6% R_{max}). In view of such findings, anisotropy measurements for north Devon were made simply to demonstrate the variability in reflectance measurements in the vitrinite population. Fourteen samples were therefore analysed, and the results are graphically summarised in Figure 6.5. The determination of R_{max} and R_{min} followed the guidelines of Stone & Cook (1979) and Teichmüller (1987), whereby only 10% of the maximum and minimum values collated were subsequently averaged. R_{max}(av) was also calculated (refer to Fig. 6.5), being the average R_{max} index for the entire data set. This illustrates the suppression of R_{max} if the entire data set are averaged, and not just the appropriate 10-20% proportion. From Fig. 6.5, the variability in reflectance within one individual sample is obvious, and in a few cases, anisotropy may therefore account for anomalously low or high reflectivities. In illustration, the Rm value for LN98 appears exceptionally low, but the anisotropy plot (on Fig. 6.5) clearly allows for a much wider spectrum in reflectivity.

To illustrate the pleochroic nature of many organic particles, a vitrinite lath and palynomorph are shown on Plate 6.1 (figs. 8ab, & 10ab, respectively). The grains were photographed in the (a)R_{min} and (b)R_{max} position, being separated by a 90 rotation. The difference in brightness is striking. In the current work, pleochroism in spores was usually associated with an equatorial (lateral) section (Pl. 6.1, fig. 10). Polar sections of spores (*i.e.* proximal or distal) invariably appeared non-pleochroic, with the related Rm measurement tending towards the R_{max} reflectance value. Ting (1981) noted that in "normally" coalified vitrinites vertical loading alone causes minimum reflectance to be orientated in a vertical position, with the maximum lying perpendicular to this directed stress. The orientation of R_{max} and R_{min} outlined may reflect the influence of lateral tectonic stresses, or

FIGURE 6.5 ANISOTROPY PLOTS: Rmax, Rm, Rmin.

(samples located geographically)

conversely simple normal loading. Unfortunately, the precise mechanism chiefly responsible was not identified, due to the scarcity of suitable material in orientated blocks.

6.3.4 Phytoclast identification in high rank assemblages.

An unexpected benefit of assessing the vitrinite reflectance of the organic isolates from north Devon proved to be the collation of assemblage and taxonomic data. A consequence of applying the preparatory technique outlined by Hillier & Marshall (1988) is that a thin veneer of kerogen can be scanned, with proximo-distally flattened palynomorphs recorded. In incident light microscopy, the pre-oxidised opacity of the palynoflora allowed the recognition of certain palynomorph morphotypes, some being diagnostic of the Devonian Period. Fine structure is commonly diffuse, and overall resolution is limited by the variable attitude of individual specimens within the mounting medium (phytoclasts commonly set in a variable plane of focus). However, the gross morphology of most of the particulate organic matter was discernible and allowed reasoned speculation as to the generic and occasionally specific identity of certain specimens.

Plates 6.1, 6.2, and 6.3 illustrate a selection of phytoclasts photographed in incident light. "Plant debris" (Pl. 6.1, figs. 1-9, 11-13), miospores (Pl. 6.1, fig. 10; Pl. 6.2, figs. 1-21; Pl. 6.3, figs. 1-8), tetrads (Pl. 6.1, figs. 15, 16), acritarchs (Pl. 6.3, figs. 9-11), chitinozoa (Pl. 6.3, figs. 12-19) and scolecodonts (Pl. 6.1, fig. 14) are illustrated. ?Tracheids (Pl. 6.1, fig. 1) and cellular (?*Nematothallus* "type") plant fragments (Pl. 6.1, fig. 12) were common in most of the samples analysed. Acritarchs and chitinozoa were less prevalent and scolecodonts rare, corroborating transmitted light observations. The latter two microfossil groups were usually fragmented, and commonly only the chambers of chitinozoa tests were observed (*e.g.* Pl. 6.3, figs 12, 13).

Miospores formed an appreciable percentage of virtually all samples, as noted in transmitted light microscopy. *Emphanisporites* is an easily recognisable form genus in normal transmitted light studies, and similarly proved an easily recognisable constituent of assemblages in incident light microscopy (Pl. 6.2, figs. 1-4; Pl. 6.3, figs. 5-7). The specimen illustrated on Plate 6.2, figure 11, is most probably the distal surface of *Emphanisporites foveolatus*; from transmitted light microscopy *E. foveolatus* is known to occur in abundance within the Lynton Formation. *Retusotriletes* (Pl. 6.2; figs. 9, 10, 13) and *Apiculiretusispora* (Pl. 6.2, figs. 5-8) were also readily identified. *Tholisporites chulus* var. *chulus* (Pl. 6.2, fig, 14) was tentatively identified; such specimens may represent forms of *Retusotriletes pychovii* (a species known to display pronounced curvaturate ridges and suppressed contact areas). The densospore complex was also well represented; proximal views (Pl. 6.2, figs. 16, 17, 19, 20; Pl. 6.3, fig. 4) tend to suggest a bizonate ("annulate") construction to the "equatorial flange" (*sensu* McGregor & Camfield, 1982) and thus favours a *Densosporites* identification. Distal views (Pl. 6.2, figs. 12, 18, 21; Pl. 6.3, figs. 2) show the conate/spinose sculpture on the specimens to be partially confluent at their base. Such cristate sculpture is commonly associated with *Cristatisporites*, although is also considered typical of the *Acinosporites* plexus. Large specimens of *Rhabdosporites langii* were rare (Pl. 6.3, fig. 1). Occasionally, assemblages contained a predominance of finely apiculate miospores (Pl. 6.3, fig. 8) and "laevigate" miospores (?*Punctatisporites*), both types of problematic identity.

Despite certain limitations, assemblage composition was documented with remarkable precision, whilst assessing vitrinite reflectance (refer to Appendix III). These observations provided corroborative evidence for transmitted light microscopy of the same assemblages. The technique may in future prove of interest as the dimensions of high rank palynomorphs can be assessed in unoxidised kerogen isolates; organic particles are believed to swell substantially when oxidised (Smith & Butterworth, 1967; Johnson, 1985), although conversely, sporopollenin has been reported to contract as a result of coalification (Pierart, 1974, 1975, 1978, 1981).

6.3.5 The timing of coalification.

The high vitrinite reflectance values pervasive throughout the studied sequence, coupled with the lack of dependence of maturation level on stratigraphic position, suggests coalification was syn-orogenic and attributable to Hercynian crustal thickening. Any pre-existing primary variation in organic reflectance (induced through burial metamorphism), has clearly been overprinted. Regional metamorphic heating is the mechanism believed responsible for these high reflectance values: elevated temperatures are considered the combined product of heating through the decay of radioactive isotope elements within the sediments, coupled with the stratigraphic (burial) and/or tectonic thickening of the crust.

Dodson & Rex (1971) obtained potassium-argon whole-rock isotopic dates for the Devonian and Culm sediments in north Devon, and interpreted these as dating uplift and cooling at 312 ± 32m.y. (which approximates to the Namurian-Westphalian boundary, from Harland *et al.*, 1982). They were however uncertain as to which precise tectonic phase this value equated to: indeed the substantial error margin renders this whole rock date virtually meaningless.

Igneous activity in the study area is minimal. Lloyd *et al.*, (1973) describe a dolerite dyke from the Horseshoe Rocks, which crop-out beneath the Bristol Channel 6.4 Km N.W. of Ilfracombe: the outcrop of this intrusion along strike of the Devonian sediments of north Devon, coupled with its sheared morphology led the authors to ascribe a Variscan date to this dyke. A keratophyric tuff, the Bittadon felsite, defines the base of the Pickwell Down Sandstones (Edmonds *et al.*, 1985, p. 33), and an autolytic kersantite lamprophyre dyke is reported to intrude the Pilton Shales north of Fremington (Edmonds *et al.*, 1985, p. 57). A dyke of doleritic composition and possibly of early Variscan age (based upon field relationships) is reported to cut the Lynton Formation sediments exposed at Ramsey Beach (SS 646494; Pound, *in prep.*). Clearly, such localised, small scale igneous activity cannot account for the high and widespread values of vitrinite reflectance. Furthermore, a heat source at depth is considered unlikely. Geophysical studies have indicated a Bouger gravity anomaly below north Devon, with values decreasing northwards across Exmoor (see review in Edmonds *et al.*, 1985). An unexposed granite may account for the size but not the shape of this anomaly: Bott *et al.*, (1958) interpreted the steady gradients and shape of the contours to be atypical of subsurface granitoid bodies. The granitic intrusion of Dartmoor, to the south of the study area, is considered to have had minimal, if any, influence on the coalification of organic matter preserved within the coastal Devonian strata of north Devon.

Brooks *et al.*, (1988) evaluated recently acquired seismic data for the Bristol Channel, and interpreted a major southerly-dipping Late Palaeozoic Variscan thrust; provides a thin-skinned link between the South Wales foreland deformation and the orogenic hinterland in S.W. England. A recent appraisal of the structure of this Variscan foreland in south Wales (Gayer & Jones, 1989) corroborates the evaluation of Brooks *et al.*, (1988), interpreting the Bristol Channel structure to be a thrust rather than a complex strike-slip fault zone (*sensu* Tunbridge, 1986).

The model proposed by Gayer & Jones (1989; refer to Figure 6.6, herein) predicts the coalification history for the area, and may be differentiated into four "distinct" evolutionary phases outlined below:

Phase 1: Deposition of the Devonian sediments of north Devon; schematically shown by Fig. 6.6a for the Early Carboniferous. An increasing vitrinite reflectance profile (with depth - not shown) is presumed to have developed through burial and an associated increase in overburden pressure. This is speculative, based merely on analogy with other studied sequences (*e.g.* Cope 1986; Teichmüller & Teichmüller, 1986), and is not directly evidenced by the data collated in the present study. Such a profile has clearly been overprinted.

Faulting in the Bristol Channel influenced Mid-Devonian sedimentation.

Phase 2: Hercynian deformation and related tectonic crustal thickening during Westphalian A/B (Fig. 6.6b): thrusting (reactivation of earlier extensional faults) in the Bristol Channel area. Thermal gradient increases, and induces the coalification of organic matter. Elevation of the sedimentary sequence of north Devon ("Bristol Channel Landmass"). This becomes a primary clastic source for the prograding Bideford Delta in the south, and the fluvial coal basin to the north. Regional scale coalification was independent of igneous activity.

Based on the present study, tectonic crustal thickening may have been in the region of ≈?10km (refer to Section 6.3.6 below).

Phase 3: Continued, post-Westphalian Variscan crustal shortening, inverting the Culm Basin (Fig. 6.6c). Erosion of the thrust sheet in the north Devon area (that had constituted the Bristol Channel Landmass), contemporaneous with continued Variscan thrust stacking and related to the northward progradation of a detachment beneath the Culm basin sediments. Back-thrusting at the northern and southern margin of the Culm Basin.

Phase 4: (Not shown in Fig 6.6) Subsequent uplift and planation, revealing the distribution in vitrinite reflectance currently observed: no dependency between stratigraphic position and Rm.

For the studied sequence the coalification (Rm ≈4%+) of particulate organic matter is interpreted as having been syn-orogenic, and related to Phases 2 and 3 outlined above.

To the south, Pamplin (1988) collated inorganic thermal maturation data (clay mineral indices) for the Devonian strata of north Cornwall, and interpreted peak metamorphism to be synchronous with the early ductile phase of second deformation (S_2); he considered the isograd pattern may in part be a reflection of uplift in the core of the Davidstow Anticline. Further to the south, where the influence of D_2 is weak, the metamorphic signature is either attributable to syn-D_1 tectonism or reflects the geothermal gradient associated with burial in the Trevone Basin. Although the structure may be different in north Devon, in principle the pattern of metamorphic overprinting shown by

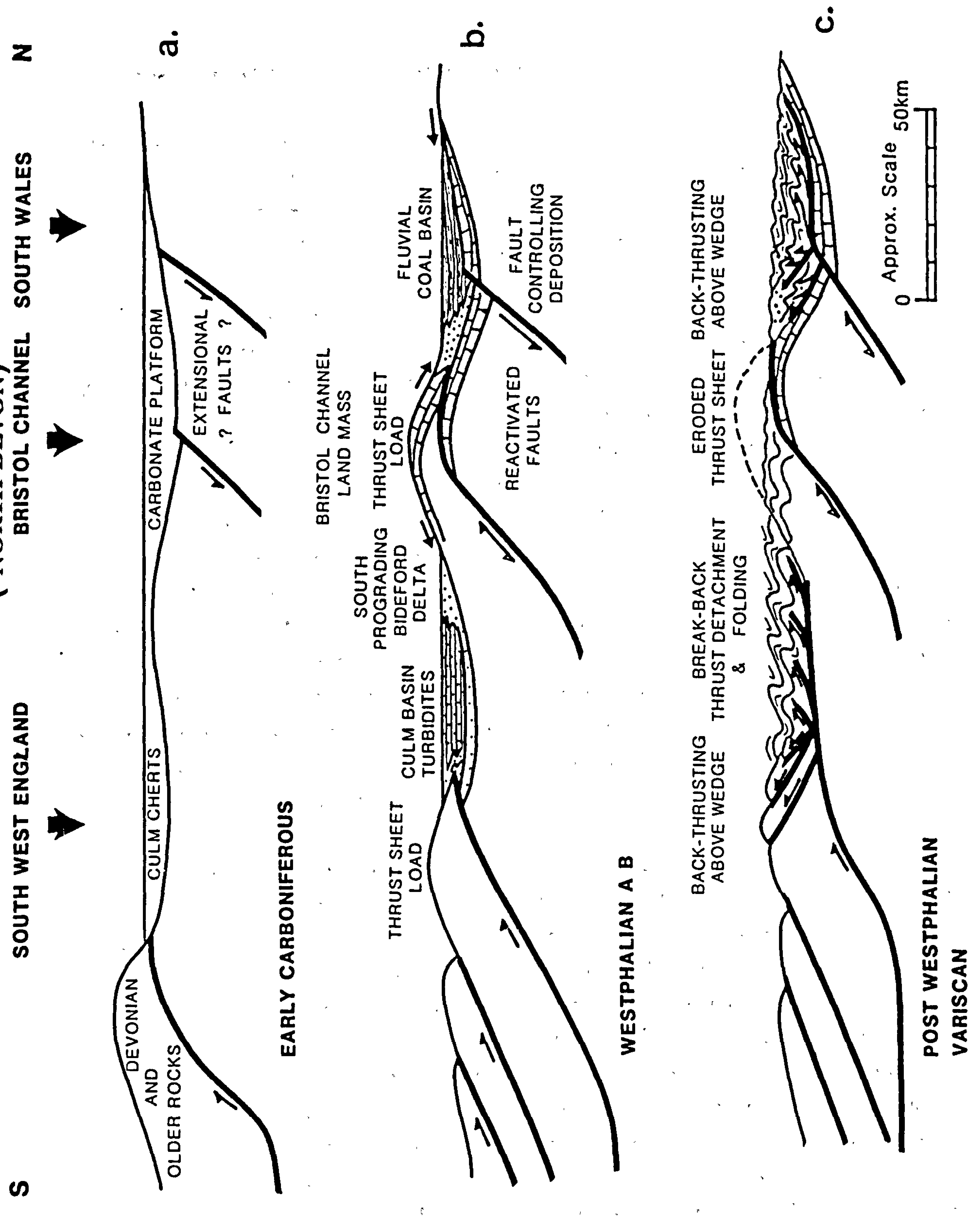


FIGURE 6.6 Diagrammatic cross-sections across the northern Variscan margin in southwest Britain, showing the stages in the development of the South Wales coalfield foreland basin and related structures to the south - after Gayer & Jones (1989; Figure 2, p. 178).

organic and inorganic thermal maturation indices is similar to that noted in part by Pamplin (1988) for north Cornwall, and related to tectonic crustal thickening.

6.3.6 Hydrocarbon potential and overburden estimates.

The visual assessment and categorisation ("Typing") of kerogen constituents allows speculation of the hydrocarbon potential of a given sediment body (*e.g.* Dow, 1977; Masran & Pocock, 1981). Oil-prone kerogen-types comprise amorphous organic matter (A.O.M), spores and cuticles, whereas gas-prone kerogens contain "woody" detritus and fusains (*e.g.* Brooks 1981). Kerogens recovered from north Devon are dominated by "woody" material and palynomorphs, and unlike many of the organic-rich laminites reported from the Orcadian Basin, Scotland (Marshall *et al.*, 1985), the sediments are devoid of A.O.M. Pound (*pers.comm.*, 1988) identified an anoxia within the Lynton Formation (west of Crock Point) based upon trace fossil assemblages and sedimentological evidence: by implication suggests a stratified water column with an oxygen deficient basal layer. The absence of A.O.M. in samples collected from this section does not palynologically substantiate this claim. Hypothetically, the predominance of "wood" and miospores within the Devonian strata of north Devon does suggest that these sediments have the capability of producing a mixed hydrocarbon product.

According to the correlation of Techmüller (1987, Fig.22, p.146) the opacity of the organic particles recovered from north Devon indicates a potential for wet gas or late catagenetic methane, although the high reflectivities suggest the sole possibility of the latter. Using the relationships expressed in Nowlan & Barnes (1987; Fig.11.1, p. 193) the high conodont C.A.I. values suggest the potential for dry gas or a barren source. The high conodont C.A.I.'s and elevated vitrinite reflectance values outlined earlier are indicative of a supramature organic metamorphic facies. Furthermore, the combination of low T.O.C. (refer to Chapter 2, Section 2.6.2; Fig. 2.5), high rank (coalified organics) and the lack of A.O.M. minimalises, if not precludes the hydrocarbon source potential of the Devonian strata of north Devon.

Reflectance-depth trends have been determined at other European localities along the Variscan Front (Teichmüller & Teichmüller, 1979, 1986; Stach *et al.*, 1982; Robert 1985; Muchez *et al.*, 1987; Teichmüller, 1987). Using reflectance gradients established in West Germany (Teichmüller & Teichmüller, 1986) and from the Southern North Sea (Cope, 1986), Cornford *et al.* (1987) interpreted the reflectance profile for the Culm sediments at Westward Ho!, and proposed a geothermal gradient of 40°C/km (refer to Section 6.3.3c). By direct comparison, the maximum burial depth for the Devonian sediments of north Devon may be estimated: comparison of the averaged Rm values for north Devon (Table 6.2 herein) with these source references suggests that the Devonian sediments of north Devon may have been buried to depths in excess of 6-7 km. Even if one allows for abnormally high geothermal gradients during Carboniferous times, several kilometres of sediment overlying the studied sequence would have been necessary to account for the observed maturation levels. Taking a generalised geothermal gradient of 30°C/km, and assuming a layer-cake stratigraphy for the Devonian of north Devon, the averaged Rm values for the region (refer to Table 6.2) equates to a potential overburden thickness in excess of $\approx$10 km for the entire studied sequence. According to Cornford (*pers. comm.*) less than 2km of Carboniferous strata is currently exposed immediately south of the Devonian sediments of north Devon, and has itself been buried to depths of between

5/8km by thrust slices. Clearly, the majority of data collated for north Devon (Cornford *et al.*, 1987, and the present study) suggest that substantial tectonic crustal thickening (?thrust stacking[2]), followed by considerable erosion between the Hercynian and the present day, is necessary to explain the currently observed, elevated vitrinite reflectance values. Based largely upon fluid inclusion data, Wilkinson (1990) similarly estimated 10 km of overburden to have overlain the Devonian strata presently exposed at Porthleven (south Cornwall): this has subsequently been removed through post-Hercynian erosion.

Clayton (1989) reported comparable, high vitrinite reflectance data from the Upper Devonian-Carboniferous strata of the Kinsale Harbour-Old Head of Kinsale area, southern Ireland (as mentioned in Section 6.3.3b). Although Clayton proposed a number of explanations to account for such elevated values (including a substantial thickness of Silesian cover and/or thrust stacking), he was uncertain as to how much of the subsequent uplift and erosion was attributable to basin inversion or was in fact in response to regional uplift (as a consequence of Variscan deformation). Similar interpretative problems are noted for north Devon.

6.4 SUMMARY.

The sediments of north Devon have been subjected to a high (metamorphic) thermal regime, which produced temperatures in excess of 300°C (323-353°C; Table 6.2), as alluded to by subjective conodont C.A.I. determinations and quantified by vitrinite reflectance studies. Kelm (1986) argued that the Morte Slates reached an upper temperature limit of less than 425/450°C, as gauged by the absence of biotite in clay mineral assemblages. The present study corroborates the work of Kelm, but also provides a more refined approximation for this thermal value: 323-353°C (refer to the converted temperatures, *sensu* Barker & Pawlewicz, 1986 - Table 6.2 herein). Regional temperature estimates determined using the approach of Price (1983; 412-449°C) are considered excessively high and unrepresentative, largely due to this described absence of biotite (Kelm 1986).

The timing of coalification is considered to have been syn-orogenic. Due to the lack or dependency of Rm on stratigraphical position through the ≈3km sequence, no reasoned estimates of stratigraphic burial depth are available, although tectonic thickening may have been as great as ≈10km. Indeed, any precise estimates of burial depth and associated geothermal gradients, based solely on vitrinite reflectance values for the Hercynides of north Devon, are herein, and contrary to Cornford *et al.* (1987), deemed unreliable. This is largely due to the described lack of dependency of Rm to stratigraphic position, with ambiguity further compounded by the influence of anisotropy on Rm determinations (refer to Section 6.3.3c).

Although both oil and gas prone organics are present within the Devonian sediments of north Devon, the sequence is precluded from being a potential hydrocarbon source due to high rank and extremely low levels of T.O.C.

[2] predominantly during the Westphalian A B phase of Variscan orogensis - refer to Gayer & Jones (1989) and Section 6.3.5 herein.

PLATE 6.1

Plate 6.1

All phytoclasts are illustrated at x510 magnification, in incident light.
Sample codes are recorded after each description.

Plant debris, pleochroic phytoclasts, miospore tetrads and scolecodonts.

Fig. 1 plant fragment; internally banded ?tube, *Plant Fragment* Type ?B/C, LN96.

Fig. 2 field view with individual phytoclast reflectivities indicated, M42.
P = palynomorph, V = vitrinite.

Fig. 3 plant fragment; vitrinite lath, *Plant Fragment* Type D, R22.

Fig. 4 plant fragment; irregular, broad vitrinite particle with distinct pyrite growth (bright, sub-polygonal inclusions) LN84.

Fig. 5 plant fragment; vitrinite lath, *Plant Fragment* Type B, LN03.

Fig. 6 plant fragment; vitrinite lath, *Plant Fragment* Type ?D, H12.

Fig. 7 plant fragment; ?tracheid lath with distinct, bright pyrite inclusions, R22.

Fig. 8 pleochroic vitrinite lath; Fig. 8a, R_{min} ; Fig. 8b, R_{max}, H12.

Fig. 9 plant fragment; ?tracheid clast, CM38.

Fig. 10 pleochroic palynomorph, oblique polar section ; Fig. 10a, R_{min} ; Fig. 10b, R_{max}, R22.

Fig. 11 plant fragment, ?cuticle particle; *Plant Fragment* Type C, R22.

Fig. 12 plant debris, cuticle particle; *Plant Fragment* Type C, LH01.

Fig. 13 plant fragment, LN96.

Fig. 14 scolecodont; longitudinal section, M02.

Fig. 15 spore tetrad, intact, CM42.

Fig. 16 complete spore tetrad, WP31.

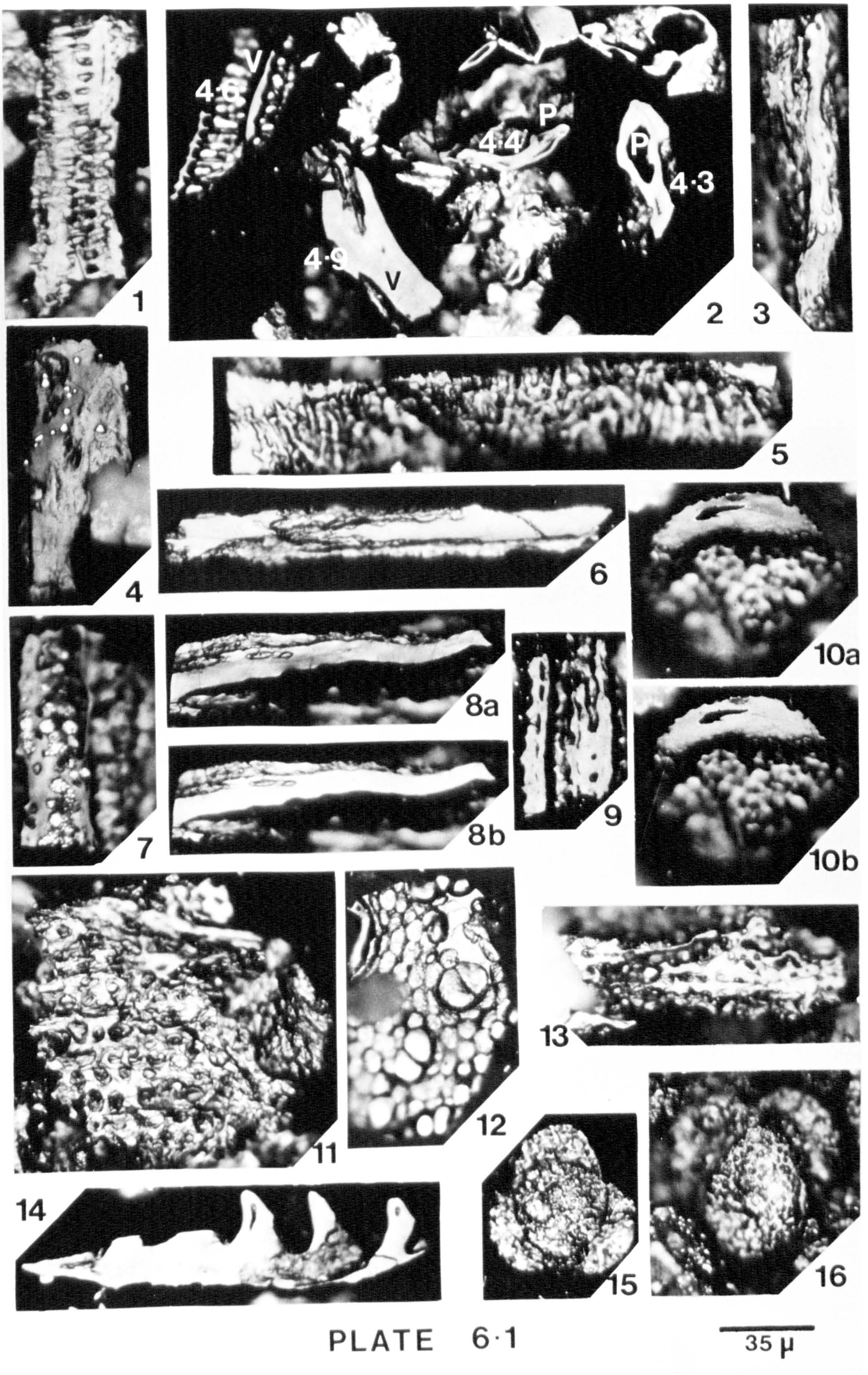


PLATE 6·1

PLATE 6.2

Plate 6.2

All phytoclasts are illustrated at x510 magnification, in incident light.
Sample codes are noted after each description.

Miospores.

Fig. 1 *Emphanisporites* sp., probable *rotatus* (McGregor) McGregor, 1973 (based upon transmitted light observations). Proximal surface; S19.

Fig. 2 *Emphanisporites* sp., probable *rotatus* (McGregor) McGregor, 1973 (based upon transmitted light observations). Proximal surface; LH12.

Fig. 3 *Emphanisporites* sp., possible *rotatus* (McGregor) McGregor, 1973; proximal surface;WP31.

Fig. 4 *Emphanisporites* sp., possible *rotatus* (McGregor) McGregor, 1973; proximal surface;LN21.

Fig. 5 *Apiculiretusispora (?nitida),* Owens, 1971; proximal surface; WP31.

Fig. 6 *Apiculiretusispora (?nitida),* Owens, 1971; proximal surface; S02.

Fig. 7 *Apiculiretusispora (?nitida),* Owens, 1971; proximal surface; H12.

Fig. 8 *Apiculiretusispora (?nitida),* Owens, 1971; proximal surface; WP31.

Fig. 9 *Retusotriletes* sp., unident., proximal surface; R22.

Fig. 10 *Retusotriletes* sp., unident., proximal surface; S14.

Fig. 11 distal pole, *Emphanisporites foveolatus* Schultz, 1968; LN21.

Fig. 12 ?densospore complex, distal surface (*?Densosporites concinnus*); WP31.

Fig. 13 *Retusotriletes* sp., unident., proximal surface; CM34.

Fig. 14 *?Tholisporites chulus* (Cramer) McGregor var. *chulus*, proximal surface; LN84.

Fig. 15 ?foveolate - microreticulate palynomorph, unident., (*?Brochotriletes* spp.); S25.

Fig. 16 ?densospore complex (*?Densosporites concinnus*); proximal surface; S06.

Fig. 17 ??densospore complex, gradational to *Grandispora* spp., proximal surface; LH05

Fig. 18 ?densospore complex, distal surface; S19.

Fig. 19 ?densospore complex, proximal surface with "bizonate" construction apparent; WP31.

Fig. 20 ?densospore complex, proximal surface with "bizonate" construction apparent; LH05.

Fig. 21 ?densospore complex, distal surface; S19.

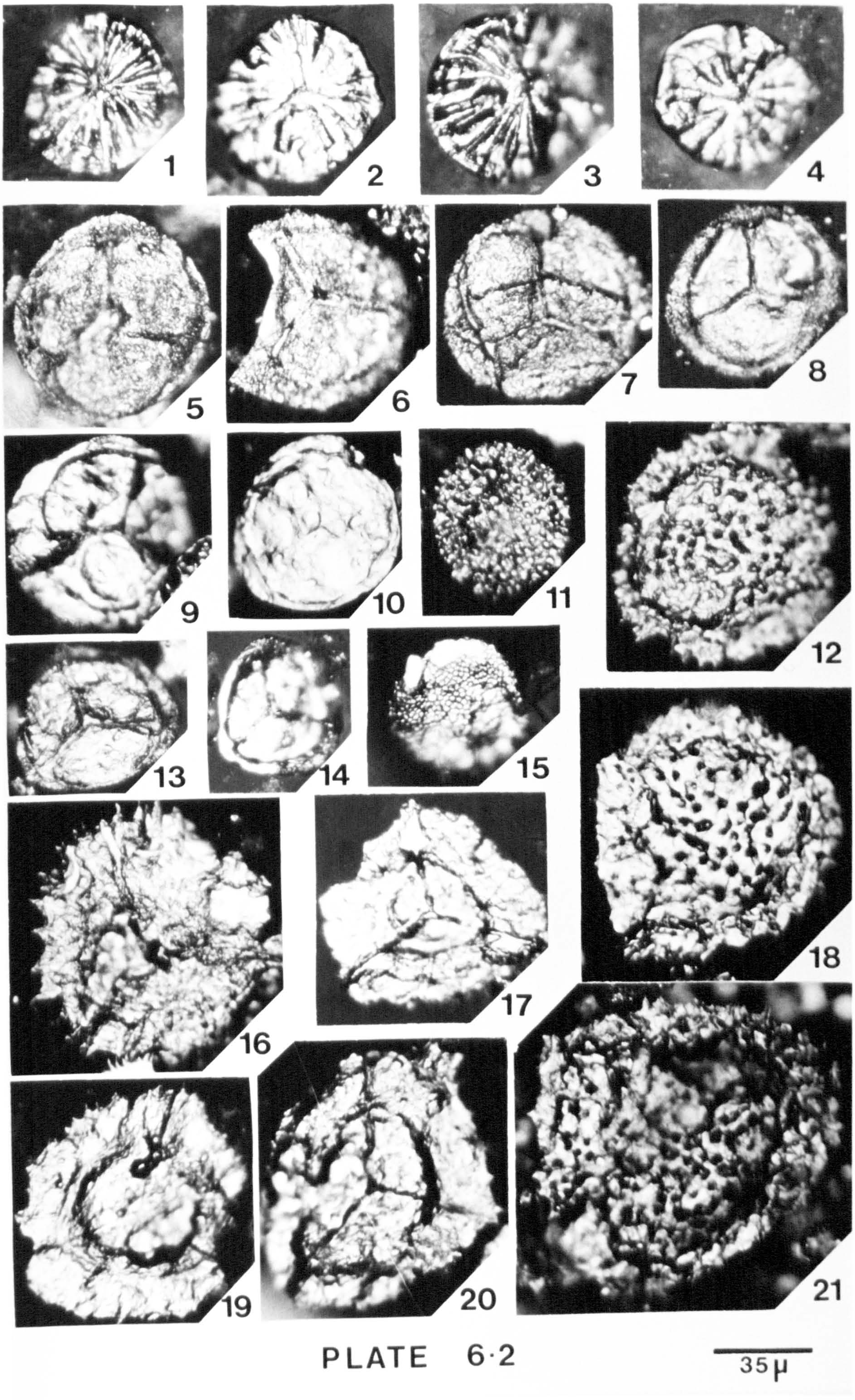


PLATE 6·2

PLATE 6.3

Plate 6.3

All phytoclasts are illustrated at x510 magnification, in incident light.
Sample codes are noted after each description.

Miospores, acritarchs and chitinozoa.

Miospores.

Fig. 1 *Rhabdosporites langii* Richardson, 1960; proximal surface; LH05.

Fig. 2 ?densospore complex, distal pole; R22.

Fig. 3 apiculate miospore (*?Geminospora lemurata*), proximal surface; M42.

Fig. 4 ?proximal surface of densospore complex; WP31.

Fig. 5 *Emphanisporites* sp., probable *rotatus,* (McGregor) McGregor, 1973; proximal surface; LN21.

Fig. 6 *Emphanisporites* sp., probable *rotatus,* (McGregor) McGregor, 1973; proximal surface; LN84.

Fig. 7 *Emphanisporites* sp., probable *rotatus,* (McGregor) McGregor, 1973; proximal surface; LN41.

Fig. 8 finely apiculate miospore, unident; LH05

Acritarchs.

Fig. 9 *Dictyotidium* cf. *cohora* Wicander & Wood, 1981; LH05.

Fig. 10 *Dictyotidium* cf. *cohora* Wicander & Wood, 1981; LH05.

Fig. 11 *Cymatiosphaera reticulosa* (Kirjanov) Colbath, 1983; WP12.

Chitinozoa.

Fig. 12 fragmented chitinozoan chamber; M40.

Fig. 13 fragmented chitinozoan chamber; CM44.

Fig. 14 *Fungochitina ?pilosa;* CM38.

Fig. 15 *?Sphaerochitina* sp; LH09.

Fig. 16 chitinozoan, unident.; M40.

Fig. 17 chitinozoan, unident.; M40.

Fig. 18 *Fungochitina ?pilosa*; LH05.

Fig. 19 finely ornamented chitinozoan lacking aboral surface, unident; CM44.

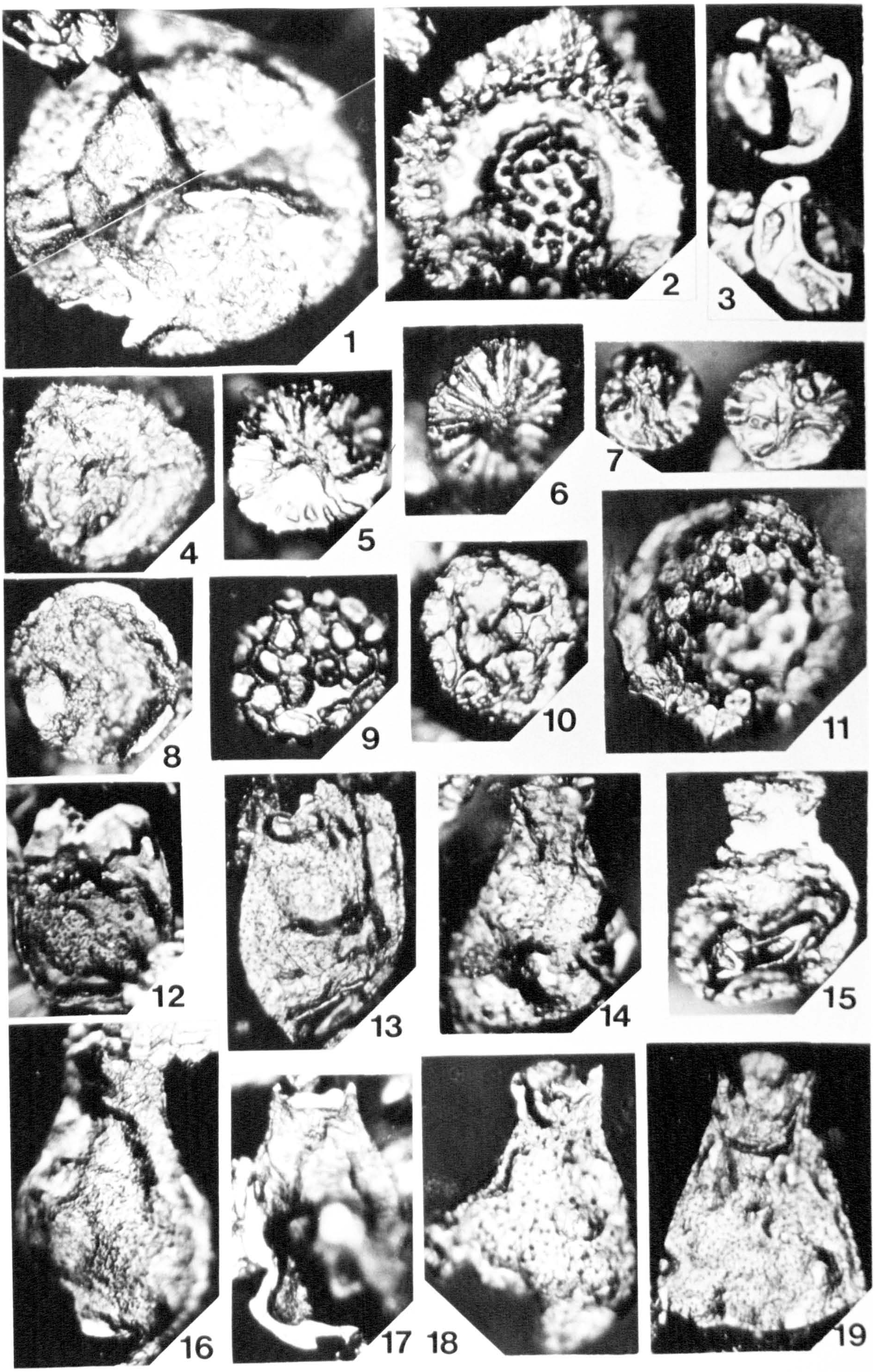


PLATE 6·3

35μ

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APPENDICES

Contents.

Appendix I.

Conodont sample characteristics and faunal data.

Within the Ilfracombe Slates, the principal limestone members, (namely the Rillage/Holey, Jenny Start, Combe Martin Beach and David's Stone) were preferentially sampled for conodonts, in addition to a number of isolated carbonate horizons. A few selected sites within the Lynton Formation were also sampled.

The following appendix is subdivided into three parts, and includes details of the reconnaissance sampling:

Appendix II(a) provides generalised details of location with hand-specimen/field descriptions for each sampled horizon/lithotype. Also detailed is information relating to sample processing and the subsequent microfossils extracted: initial mass processed and final residue retained, and the general faunal recovery (total number of elements recovered, & corrected yield).

A key to the macropalaeontology noted during sample preparation is provided:

= bivalves
= brachiopods
= bryozoa
= corals (colonial)
= corals (solitary)
= crinoid ossicles
= gastropods
= shelly fauna (fragments, unident.)

S_0 refers to bed thickness.

Appendix II(b) lists bulk faunal composition; numbers of icriodids, polygnathids and ramiforms were collated independently, and where possible an arbitrary indication of *Icriodus* (Ic) : *Polygnathus* (Po) ratios provided. The recovery of miscellaneous microfossils (*e.g.* coniform (S_2) & ramiform elements) is also indicated. A key to the characters used is provided below:

= gastropod steinkerns.

= ichthyodonts (comprising teeth, spines and irregular ?bone matter).

= bryozoa (aggregates or dissociated).

= tentaculites (usually pyritised).

= ostracod carapaces.

Appendix II(c) The precise conodont faunal composition is detailed.

Conodont elements recovered during reconnaissance sampling of the area are also listed.

Samples processed for conodonts representative of the limestones within the Ilfracombe Slates.

Limestone Member / Formation	Sample Number	Grid.Ref.	Lithology	Initial Mass (kg)	Residue % undissolved	Conodonts	Corrected Yield (el/kg)
			Sample Characteristics				
Kentisbury Slates	K 53	SS 54 NW 5087 4755	9cm nodular laterally discontinuous crinoidal limestone, @ cliff base	0.360	28%	73	282
	K 35		So: 8cm, crinoidal biosparite 2/5 mm bioclasts; slaty	1.757	55%	-	-
	K 33	5147 4787	So: 6cm, crinoidal-rich biosparite slaty wisps	2.832	45%	-	-
Total:	3		Total :	4.949		73	
David's Stone Limestone Member	CM 77	SS 54 NW 5367 4802	So: 3cm, poorly washed micrite	2.610	5%	2	<1
	CM 65		So: 9cm, poorly washed micrite granular; rare ?	1.228	7%	43	38
	CM 64		So: 12cm, poorly washed micrite faunau isolated ?	5.545	3%	19	4
	CM 63		So: 14cm, micrite, slate partings poorly fossiliferous rare	1.932	-	5	3
	CM 62		So: 15cm, Packstone spary rare bio' "schistose" granular texture	7.410	21%	1	<1
	CM 59		So: 11cm, biosparite fe+ staining rare bio' clast <2mm ?	2.400	2%	3	1
	CM 58		So: 12cm, wavy bedded micrite, // lam. grey/blue unfossilerous ?	1.825	8%	62	37
	CM 76		So: 8cm, sparite "ganular" ? fossils	2.850	1%	8	3
	CM 57		So: 13cm, ferruginous micrite wavy So; rare macro' ?	6.190	13%	21	4
	CM 75		So: 27cm. sampled base of bed sparite	4.975	11%	3	<1
	CM 56		So: 13cm, bio' rare, micritic isolated ?	3.014	54%	80	58
	CM 55		So: 18cm, poorly washed sparite macro' rare, <5 mm fragmented	1.755	4%	-	-
	CM 53		So: 6cm, lenticular micrite mud drapes; rare ?	1.640	7%	8	5
	CM 51		So: 5cm, biomicrite, mud drapes rare macro'	1.347	4%	7	5
	CM 50		So: 9cm, bio'-rich isolated ?	2.194	9%	17	9
	CM 49		So: 12cm, dk blue/grey micrite slaty wisps; isolated	2.245	3%	28	13
	CM 48		So: 12cm, wavy/lenticular sparite patchy micrite, ferruginous	2.137	2%	13	6
	CM 74		So: 31cm, sampled through bed nodular micrite in slate matrix	3.200	58%	-	-
	CM 47	5365 4785 SS 54 NW	So: 4cm, lenticular biosparite poorly washed; isolated bio' 4/6mm	2.147	25%	62	39
Total:	19		Total :	56.644		382	
Combe Martin Beach Limestone Member	CM 33	SS 54 NE 5730 4737	So: 27cm, biosparite,pyrite green/purple colour fe+ bio'	2.978	11%	19	7
	CM 32		So: 23cm, biosparite pyrite bioclasts 2/4mm;cleaved;fe+;	4.197	7%	-	-
	CM 31		So: 24cm,biosparite green/fe+ stain pyritised; bio rich	2.605	4%	12	5
	CM 30		So: 17cm, biosparite uncleaved pyritised, bio	5.030	9%	1	<1
Total:	4		Total :	14.810		32	
Jenny Start Limestone Member	CM 17	SS 54 NW 5430 4845	So: 15cm, sparite, slaty wisps bio. rare. ?	4.215	1%	-	-
	CM 16		So: 10cm, poorly washed micrite slaty wisps; bio.	5.892	2%	-	-
	CM 15		Top 45cm So; poorly washed sparite bio.	2.420	8%	-	-
	CM 14		So: 25cm; wavy bedded biosparite bio.	3.073	10%	-	-
	CM 13		So: 20cm, poorly washed sparite wavy So; ?bio.	2.402	-	2	<1
	CM 12		So: 10cm, ? biosparite, slaty wisps; bio.	2.470	2%	-	-
	CM 11		So: 5-10cm (wavy bedded),poorly washed biomicrite,fe+ stain; 2/3mm	2.315	3%	-	-
	CM 08		So: 5cm, poorly washed biomicrite macro'	1.978	-	-	-
	CM 07		So: 10cm, poorly washed micrite bio rare.	2.575	-	-	-
	CM 06		So: 8cm, finely laminated micrite fe+ stained; rare bio	1.750	-	-	-
Total:	10		Total :	29.090		2	

APPENDIX I(a) CONODONT SAMPLE PROFILE.

Samples processed for conodonts representative of the limestones within the Ilfracombe Slates.

Limestone Member / Formation	Sample Number	Grid.Ref.	Lithology	Initial Mass (kg)	Residue % undissolved	Conodonts	Corrected Yield (el/kg)
Rillage Limestone Member	L 29	SS 54 NW 5432 4855	So: 12cm, biosparite, bio 3/5 mm bioclasts; slaty wisps.	2.354	6%	79	36
	L 28		So: 12cm, biosparite, bio 3/5 mm bioclasts.	1.888	6%	15	8
	L 27		So: 13cm, sparite. macro' rare fragmented	2.425	8%	42	19
Total:	3		Total :	6.667		136	
Holey Limestone Member	L 20	SS 54 NE 5762 4744	So: 8cm, sparite, slaty wisps bioclasts fragmented <4mm,	2.473	11%	25	11
	L 19		So: 13cm, poorly washed sparite crinoid rich, bioclasts <4mm	3.039	14%	19	7
	L 18		So: 17cm, sparite, fe+ stained, slaty wisps	2.608	10%	40	17
	L 17		So: 13cm, sparite slate wisps. bio.	2.905	10%	49	19
	L 16		So: 15cm, coarse biosparite <1.5cm richly fossiliferous,	2.333	13%	48	24
Total:	5		Total :	13.358		181	
"Crinoidal limestones within the Wild Pear slates	WP 28	SS 54 NE 5799 4763	So: 5cm, nodular crinoidal lmst. bio'<5mm wavy/planar So,blue/grey	2.590	45%	3	2
	WP 23	5800 4767	So: 7cm, nodular crinoidal lmst. wavy So,?bioclasts, principally	2.512	53%	1	<1
Total:	2		Total :	5.102		4	
Overall Total:	46		Total :	130.62 kg		810 conodont elemen	

Reconnaissance sampling, 1986
('86 prefix - tentatively ordered stratigraphically)

Sample No.	Grid Ref.	Initial Mass kg	Residue (%)	Conodonts	Yield el/kg
86 055	5685 4740	3.002	4%	31	11
86 024	5360 4800	7.010	27%	-	-
86 026	5360 4800	7.807	37%	-	-
86 058	5685 4740	2.790	9%	-	-
86 057	5685 4740	2.378	57%	-	-
86 056	5685 4740	2.560	70%	8	10
86 053	5700 4745	2.680	20%	1	<1
86 014	5730 4740	6.165	37%	66	17
86 016	5730 4741	5.798	54%	-	-
86 050	5745 4735	2.424	66%	-	-
86 072	5470 4835	1.912	51%	2	2
86 071	5470 4835	3.356	6%	-	-
86 067	5515 4845	1.240	12%	87	80
86 065	5625 4780	6.039	74%	3	2
86 063	5610 4800	1.990	51%	-	-
86 023	5660 4770	6.716	26%	9	2
86 019	5660 4770	7.280	33%	9	2
86 039	5820 4790	0.759	59%	-	-
86 037	5820 4790	1.990	37%	-	-
Total: 19		73.896		216 conodont elements	

CONODONT SAMPLE AND FAUNAL PROFILE FOR THE LYNTON FORMATION.

Samples processed for conodonts representative of the Lynton Formation.

	Sample Number	Grid.Ref.	Lithology	Initial Mass (kg)	Residue % undissolved	Conodonts (total)	Corrected Yield (e/kg)	Ic	S_2	Misc.
Valley of the Rocks	LN114	4992 7076	Calcarenite	1.620	6%	12	8	12	-	
A39 (Road Section)	LN113	7310 4900	Calcarenite	4.740	82%	1	1	1	-	
Watersmeet Member	LN75 (A)	7464 4866	Calcarenite	2.460	21%	17	9	17	-	
	LN112		Calcarenite	2.550	9%	-	-	-	-	
	LN78 (C)		Calcarenite	2.887	56%	8	6	8	-	
	LN74 (A)		Calcarenite	2.740	46%	7	5	7	-	
	LN111		Calcarenite	2.280	33%	5	3	5	-	
	LN110		Calcarenite	3.240	13%	30	11	30	-	
	LN109		Calcarenite	2.090	11%	19	10	19	-	
	LN77 (C)		Calcarenite	2.160	43%	22	18	22	-	
	LN73 (A)		Calcarenite	2.420	49%	20	16	20	-	
	LN76 (C)		Calcarenite	2.725	43%	16	10	16	-	
	LN108		Calcarenite	1.365	45%	6	8	5	1	
	LN107		Calcarenite	1.850	81%	-	-	-	-	
East Lynmouth Beach	LN29	7275 4963	?micrite rare bioclasts	0.540	16%	-	-	-	-	
Lee Stone Member	LN11	6947 4970	?Calcarenite	5.810	83%	-	-	-	-	
	LN10		?Calcarenite	3.850	84%	-	-	-	-	
Total:	17 samples			45.327 kg		163 conodont elements				

Total number of samples processed: 82

Total mass of rock processed: 249.843 kg

Total number of conodonts recovered: 1,189

APPENDIX I(b). FAUNAL COMPOSITION.

The Ilfracombe Slates.

Sample Number	Ic	Po	rami.	other	Ic : Po	Misc.
K 53	49	18	6	-	3 : 1	
K 35	-	-	-	-	-	
K 33	-	-	-	-	-	
CM 77	2	-	-	-	-	
CM 65	36	3	2	1?Pb 1 coni	12 : 1	
CM 64	14	1	3	1 ?coni	14 : 1	
CM 63	5	-	-	-	-	
CM 62	1	-	-	-	-	
CM 59	2	1	-	-	2 : 1	
CM 58	56	1	5	-	56 : 1	
CM 76	8	-	-	-	-	
CM 57	20	1	-	-	-	
CM 75	3	-	-	-	-	
CM 56	73	3	2	1 coni 1?Po.blade	24 : 1	
CM 55	-	-	-	-	-	
CM 53	6	2	-	-	3 : 1	
CM 51	6	-	-	1 ?coni	-	
CM 50	17	-	-	-	-	
CM 49	22	3	2	1?Po.blade	7 : 1	
CM 48	11	-	1	1?Po.blade	-	
CM 74	-	-	-	-	-	
CM 47	38	7	16	1 Pb	5 : 1	
CM 33	13	3	3	-	4 : 1	
CM 32	-	-	-	-	-	
CM 31	9	3	-	-	3 : 1	
CM 30	1	-	-	-	-	
CM 17	-	-	-	-	-	
CM 16	-	-	-	-	-	
CM 15	-	-	-	-	-	
CM 14	-	-	-	-	-	
CM 13	2	-	-	-	-	
CM 12	-	-	-	-	-	
CM 11	-	-	-	-	-	
CM 08	-	-	-	-	-	
CM 07	-	-	-	-	-	
CM 06	-	-	-	-	-	
L 29	78	1	-	-	78 : 1	
L 28	15	-	-	-	-	
L 27	42	-	-	-	-	
L 20	25	-	-	-	-	
L 19	19	-	-	-	-	
L 18	40	-	-	-	-	
L 17	49	-	-	-	-	
L 16	48	-	-	-	-	
WP 28	3	-	-	-	-	
WP 23	1	-	-	-	-	
Subtotal :	714	47	40	9		

Reconnaissance sampling, 1986

Sample Number	Ic	Po	rami.	other	Ic : Po	Misc.
86 055	26	1	1	2 Pb 1?Po.blade	26 : 1	
86 024	-	-	-	-	-	
86 026	-	-	-	-	-	
86 058	-	-	-	-	-	
86 057	-	-	-	-	-	
86 056	7	1	-	-	7 : 1	
86 053	1	-	-	-	-	
86 014	66	-	-	-	-	
86 016	-	-	-	-	-	
86 050	-	-	-	-	-	
86 072	2	-	-	-	-	
86 071	-	-	-	-	-	
86 067	87	-	-	-	-	
86 065	3	-	-	-	-	
86 063	-	-	-	-	-	
86 023	9	-	-	-	-	
86 019	7	2	-	-	-	
86 039	-	-	-	-	-	
86 037	-	-	-	-	-	
Subtotal :	208	4	1	3		
Lynton Formation conodonts :	162			1		
OVERALL TOTAL :	1,084	51	41	13		

1,189 conodonts recovered.

Sample No.*	LN108	LN76	LN73	LN77	LN109	LN110	LN111	LN74	LN78	LN75	LN113	LN114
Taxa												
Icriodus ?corniger corniger		1				2			1			
Icriodus culicellus	2	8	5	9	7	9	2	1	3	4	1	6
Icriodus retrodepressus		1	1	1	4	2	2	1		1		
Icriodus cf. werneri		3	1	1	2	2	1	1		9		
Icriodus sp. A.			4									
coniform element.	1											
icriodids, unident.	3	3	9	11	6	15		4	4	7		6

* samples ordered stratigraphically

APPENDIX Ic. Absolute numbers of species per individual fauna - The Lynton Formation.

Sample No. *	86.019	86.023	86.065	86.067	86.072	86.014	86.053	86.056	86.055
Taxa									
Icriodus ?arkonensis				1					
Icriodus brevis		2		3	1	4			1?
Icriodus cf. brevis	3	1		2					
Icriodus cf. difficilis			1	4		1			
Icriodus ?fusiformis									1
Icriodus lindensis				3					1?
Icriodus obliquimarginatus				4				1	
Icriodus ?platyobliquimarginatus		1		1					1
Icriodus sp. C				1					
Icriodus sp. D						1			
Icriodus sp. E				1		1		1	
Icriodus sp. G							1		
Polygnathus varcus								1	
icriodids, unident.	4	5	2	67	1	59		5	22
polygnathids, unident.									2
ramiforms, undifferentiated	2								1
pectiniforms (non-Pa)									2

* samples ordered ca. stratigraphically

APPENDIX Ic. Absolute numbers of species per individual fauna - Reconnaissance Sampling, 1986.

Sample No.* / Taxa	WP23	WP28	L16	L17	L18	L19	L20	L27	L28	L29	CM13	CM30	CM31
Icriodus brevis			5	3	3	3	4	4		20			1
Icriodus cf. brevis		2	1			1				3			
Icriodus cf. difficilis										2			
Icriodus ?difficilis													
Icriodus eslaensis			1				1 ?		1	3			
Icriodus lindensis			2	3	3	1 ?	2		5	7	1		
Icriodus obesus		1		1									
Icriodus aff. obesus						1							
Icriodus obliquimarginatus			9	3	3	2	1	4					1 ?
Icriodus ?platyobliquimarginatus				2	4								
Icriodus cf. regularicrescens			3	1	1					1			
Icriodus sp. B			4										
Icriodus sp. C				1	1								1
Icriodus sp. D													
Icriodus sp. E													
Icriodus sp. F						1							
Icriodus sp. G										1			
Polygnathus ?ansatus													
Polygnathus aff. ansatus **													
Polygnathus cf. decorosus													
Polygnathus l. linguiformis													
Polygnathus rhenanus										1			1
Polygnathus varcus													1
Polygnathus xylus xylus													
icriodids, unident.	1		23	36	23	10	17	34	9	41	1	1	
polygnathids, ("varcus" Gp) unident.													1
polygnathids, (linguiformis), unident													
coniform elements, unident													
ramiforms, undifferentiated.													
non-Pa pectiniforms													

Sample No.* / Taxa	CM33	CM47	CM48	CM49	CM50	CM51	CM53	CM56	CM75	CM57	CM76	CM58	CM59	CM62	CM63	CM64	CM65	CM77	K53
Icriodus brevis		11	3					10				7	1			7			17
Icriodus cf. brevis		1						2	1			6							5
Icriodus cf. difficilis	1	1												1					
Icriodus ?difficilis		1																	
Icriodus eslaensis		1																	
Icriodus lindensis																			
Icriodus obesus																			
Icriodus aff. obesus		1		1													1	1	
Icriodus obliquimarginatus	2	6	3	10	14	5	3	4		1		6			1	9	13	1	
Icriodus ?platyobliquimarginatus				4											3	1	1		
Icriodus cf. regularicrescens																			
Icriodus sp. B																			
Icriodus sp. C																			
Icriodus sp. D																			
Icriodus sp. E								18		3	2	5							8
Icriodus sp. F																			
Icriodus sp. G										2			1						
Polygnathus ?ansatus																			3
Polygnathus aff. ansatus **																			1
Polygnathus cf. decorosus																			11
Polygnathus l. linguiformis	3	1		1															
Polygnathus rhenanus		2										1							
Polygnathus varcus		2					1	1		1 ?							2		
Polygnathus xylus xylus																			3
icriodids, unident.	10	10	5	7	3	1	3	39	2	14	6	32			1	4	15		19
polygnathids, ("varcus" Gp) unident.		1	1	3				3					1			1	1		
polygnathids, (linguiformis), unident		1					1												
coniform elements, unident						1 ?		1								1 ?	1		
ramiforms, undifferentiated.	3	15	1	2				2				5				3	2		6
non-Pa pectiniforms		1															1 ?		

* samples ordered stratigraphically

** sensu Bultynck (1987)

APPENDIX Ic. Absolute numbers of species per individual fauna - The Ilfracombe Slates.

Appendix II.

Palynological sample characteristics and extracted palynofloral composition.

Brief details of sample location (6 figure grid reference), carbonate content (subjectively gauged by the degree of sample effervescence in industrial grade HCl⁺), colouration⁺⁺ & texture (*i.e.* visual silt component) and duration of oxidation are provided (to the left of the spread sheet).

Details of approximate or exact stratigraphical/geographical position are provided.

a.b. = refers to *above base* of a particular section.
b.t. = refers to *below top* of a particular section.

"...of T log", or (T) refers to sedimentological logs complied by Tunbridge (1978a and subsequent publications)
"...of CP log", or (CP) refers to sedimentological logs complied by Pound (*in prep.*).

Some of the details of exact sample position appear vague (*e.g* those collected from the Trentishoe Formation). In such cases there were few or no field marker horizons to which those levels sampled for palynology could be referenced - furthermore these samples proved barren. In other instances (*e.g.* the Wild Pear Slates), structural complexity and sedimentological monotony limit the accurate location of palyniferous horizons.

If a detailed resampling programme is to be undertaken, the reader is advised to refer to Tunbridge (1978a, and subsequent papers) in regards to the sedimentology of the Hangman Sandstone Group, and Pound (*in prep.*, at time of submission of this thesis) for the Lynton Formation. Sedimentological logs presented within these studies are not replicated herein; palyniferous horizons simply described with reference to these logs. Schematic, composite logs are illustrated in Chapter 4.

To the right of the spread sheet, a basic listing is provided of the palynoflora constituents. For simplicity, seven broad categories were defined and their presence indicated by an asterix. Absolute specimen counts were considered unviable (refer to Chapter 2). Reworking is not indicated. Those samples analysed for vitrinite reflectance are indicated (refer to Appendix IV).

The six classes of phytoclast differentiated are: dispersed miospores, miospore tetrads (including partially fragmented tetrads), acritarchs, chitinozoa, scolecodonts, and wood debris. These categories are undifferentiated, apart from the woody component, under which the four morphotypes defined in Chapter 3 are identified. Samples which did not yield any organic material are referred to as barren. Details of barren samples are provided to guide future palynological studies in this area.

\+ * = minimal effervescence.
** = moderate effervescence.
*** = strong effervescence.

++ Sample colouration was quantified according to the Munsell rock colour chart, Goddard *et al.*, (1951).

APPENDIX II. PALYNOLOGICAL SAMPLE PROFILE.

	Sample characteristics.					Palynology						
Sample	Grid ref.	Colour (silt)	CO_3	Duration of Oxidation (minutes)	Sample station location / position above section base (unless specified)	Vit. refl.	Miosp.	Tetrads	Acrit.	Chitin.	Scolec.	Wood.
LN01	70604993	(s)N5	**	25 min.	Yellow Stone		*	*			*	BD
LN02	"	(s)5G5/2	-	-	Yellow Stone, 2.0m above LN01		Barren					
LN03	"	N3	-	38 min.	Yellow Stone, 9.3m above LN01	*	*	*				ABC
LN06	70254975	(s)N4	*	55 min.	Wringcliff Bay 5.85m a.b.(CP)	*	* CD					
LN07	"	N5	-	30 min.	Wringcliff Bay 12.75m a.b.(CP)		*	*		*	*	ABCD
LN08	69484968	N6	*	-	W.Lee Stone 2.8m a.b.(CP)		Barren					
LN13	"	(s)N5	-	30 min.	W.Lee Stone 9.7m a.b.C(P)		*			*	*	AB
LN17	"	N5	-	25 min.	W.Lee Stone 14.25m a.b.(CP)	*	*		*	*	*	ABCD
LN18	"	N5	-	-	W.Lee Stone 15.50m a.b.(CP)		Barren					
LN19	"	(s)N4	-	35 min.	W.Lee Stone 17.20m a.b.(CP)		*	*		*	*	ABCD
LN21	69534970	(s)N5	-	25 min.	E.Lee Stone 2.7m a.b.(CP)	*	*	*		*	*	ABCD
LN24	"	N4	-	35 min.	E.Lee Stone 9.8m a.b.(CP)		*	*			*	ABCD
LN31	69534966	N4	-	35 min.	Outcrop above Lee Stone @ 0.8m(CP)	*	*				*	ABCD
LN34	69474963	N4	-	35 min.	Duty Point 2.55m a.b.(CP)	*	*			*	*	AB
LN35	"	N4	-	-	Duty Point 6.35m a.b.(CP)		Barren					
LN36	"	N4	-	45 min.	Duty Point 10.1m a.b.(CP)		*			*	*	B
LN38	68684935	(s)N4	-	23 min.	W.Crock Point 21.70m a.b.(CP)		*	*				BCD
LN40	"	N4	-	-	W.Crock Point 35.75m a.b.(CP)		Barren					
LN41	"	N5	-	38 min.	W.Crock Point 48.85m a.b.(CP)	*	*	*				B
LN43	"	(s)N5	-	35 min.	W.Crock Point 60.67m a.b.(CP)	*	*					BCD
LN44	2	N4	-	-	W.Crock Point 67.25m a.b.(CP).		Barren					
LN45	"	N5	*	35 min.	W.Crock Point 78.70m a.b.(CP)		*	*				ACD
LN46	"	(s)N4	*	35 min.	W.Crock Point 83.05m a.b.(CP)		*					ABC
LN49	"	N3	**	55 min.	W.Crock Point 94.90m a.b.(CP)		*			?	*	AB
LN52	"	N3	*	35 min.	W.Crock Point 101.10m a.b.(CP)	*	*	*	*	?		BCD
LN54	"	N4	*	30 min.	W.Crock Point 103m a.b.(CP)		Barren					
LN57	"	N5	*	30 min.	W.Crock Point 118.20m a.b.(CP)		*	*		?	*	CD
LN59	"	(s)N5	*	30 min.	W.Crock Point 121.84m a.b.(CP)		*	*				AND
LN60	"	N4	*	30 min.	W.Crock Point 123.1m a.b.(CP)	*	*	*			*	AND
LN66	67704903	(s)N5	*	50 min.	Woody Bay @ 13.82m a.b.(CP).		*					CD
LN83	72954900	N5	*	-	Oxen Tor 23.4m below LN/HaG jn.		Barren					
LN84	"	5Y4/1	**	50 min.	Oxen Tor 21.3m below LN/HaG jn.	*	*	*				ABD
LN85	"	(s)N5	-	-	Oxen Tor 17m below the LN/HaG jn.		Barren					
LN86	"	(s)5Y4/1	-	-	Oxen Tor 11m below the LN/HaG jn.		Barren					
LN87	"	(s)5Y4/1	*	55 min.	Oxen Tor 8.4m below LN/HaG jn.(CP).		*			?	*	ABCD
LN88	"	(s)5Y4/1	-	60 min.	Oxen Tor 6.6m below LN/HaG jn.(CP).		*		*	*	*	AD
LN89	"	(s)N5	*	50 min.	Oxen Tor 4.8m below LN/HaG jn.(CP).	*	*	*		?	*	ABCD
LN92	66154950	(s)N4	*	35 min.	30.50m below LN/HaG boundary (CP).		*		*	*		ABCD
LN96	"	N4	*	50 min.	21.20m below LN/HaG boundary (CP).	*	*		*		*	ABCD
LN98	"	N5	-	50 min.	14.70m below LN/HaG boundary (CP).	*	*		*	*	*	ABCD
LN101	"	(s)N4	-	55 min.	3.35m below LN/HaG boundary (CP).		*	*		*	*	ABCD
LN115	74644866	(s)N6	*	30 min.	Watersmeet, mudstone @ 3.32m a.b.(CP)	*	*	*			*	BD
H02	66154850	(s)N4	*	60 min.	Little Burland (CP) @ 8.40m a.b.		?					
H03	"	(s)5B5/1	-	35 min.	Little Burland (CP) @ 10.75m a.b.	*	*	*				BCD
H06	"	(s)N4	-	55 min.	Little Burland (CP) @ 19.30m a.b.	*	*		*			CD
H08	"	(s)N5	*	-	Little Burland (CP) @ 33.60m a.b.		Barren					
H09	"	(s)5GY6/1	-	-	Little Burland (CP) @ 38m a.b.		Barren					
H10	"	(s)N6	-	45 min.	Little Burland (CP) @ 45 m a.b.		*			*	*	ACD
H12	66244948	(s)N5	-	60 min.	Great Burland (T) @ 6.2m a.b	*	*			*		CD
H13	"	(s)5YR4/1	-	60 min.	Great Burland (T) @ 13 m a.b.		*	*		*	*	ABCD
H14	"	(s)N6	-	50 min.	Great Burland (T) @ 31.5 m a.b.		*			?		ABCD
H15	"	(s)5YR4/1	-	-	Great Burland (T) @ 34m a.b.		Barren					
H16	"	(s)N6	-	-	Great Burland (T) @ 37m a.b.		Barren					
T03	64504915	(s)10YR6/2	-	-	Lymcove Beach.		Barren					
T05	"	(s)10YR5/4	-	-	Lymcove Beach, 6m above T03.		Barren					
T07	"	(s)10YR4/1	-	-	Lymcove Beach, 14m above T03.		Barren					
T09	"	5YR6/4	-	-	Lymcove Beach, 17.5m above T03.		Barren					
T12	"	(s)10YR4/1	-	-	Ltmcove Beach, 22m above T03.		Barren					
T14	64004871	(s)10YR5/4	-	-	East Bonsley Cut.		Barren					
T16	63204850	(s)5YR6/4	-	-	East Neck Wood.		Barren					
T17	"	(s)10YR4/1	-	-	East Neck Wood, 3m above T16.		Barren					
T19	"	5YR5/2	-	-	East Neck Wood, 5.5m above T16.		Barren					
T23	"	10YR6/2	-	-	West Neck Wood.		Barren					
T25	"	(s)5YR5/2	-	-	West Neck Wood.		Barren					
T30	62104865	5YR4/4	-	-	West of Mare & Colt.		Barren					
T31	61704852	(s)5YR4/4	-	-	East Red Cleave.		Barren					
T32	"	(s)10YR6/2	-	-	East Red Cleave, 3.5m above T31.		Barren					
T33	60804840	(s)5YR5/2	-	-	Sherrycombe Beach.		Barren					
T34	"	5YR5/2	-	-	Sherrycombe Beach, 4m above T34.		Barren					
T35	60204855	(s)10YR6/2	-	-	West Blackstone Point.		Barren					
T37	"	(s)5YR6/4	-	-	West Blackstone Point.		Barren					
R03	58404827	(s)5Y8/1	-	-	74m b.t. (of T log)		Barren					
R05		(s)5Y8/1	-	-	60m b.t. (of T log)		Barren					
R07		(s)N6	-	-	52.0m b.t. (of T log)		Barren					
R08		(s)N5	-	-	36m b.t. (of T log)		Barren					
R09		(s)N5	-	-	27.5m b.t. (of T log)		Barren					
R15		5Y8/1	-	-	17.0m b.t. (of T log)		Barren					
R16		(s)5Y8/1	-	-	16.0m b.t. (of T log)		Barren					
R17		(s)5Y8/1	-	-	14.5m b.t. (of T log)		Barren					

Sample	Grid ref.	Colour	CO_3	Oxidation	Sample position	Vit. refl.	Miosp.	Tetrads	Acrit.	Chitin.	Scolc.	Wood
R18		(s)5Y8/1	*	-	14.0m b.t. (of T log)		Barren					
R21		5Y2/1	*	45 min.	1.8m b.t. (of T log)	*	*		*	*	*	ABCD
R22	58174807	N4	*	50 min.	0.4m b.t. (of T log)	*	*			*	*	ABCD
S01	58174807	5Y2/1	*	50 min.	0.2m a.b.(of T log)		*		*		*	ACD
S02		N3	**	50 min.	1.0m a.b (of T log)	*	*	*	*		*	ABCD
S06		N4	**	50 min.	11.6m a.b (of T log)	*	*	*				ABCD
S08		(s)5Y2/1	*	50 min.	16.9m a.b (of T log)		*	*	*	*		ABCD
S10		5Y2/1	-	55 min.	31.0m a.b (of T log)		*	*	*	?		ABD
S11		N4	*	-	32.75m a.b (of T log)		Barren					
S12		N2	*	60 min.	35.0m a.b (of T log)	*	*	*	*		*	BCD
S14		5Y2/1	**	60 min.	39.4m a.b (of T log)	*	*	*	*	*	*	ABCD
S17		N5	*	-	43.5m a.b (of T log)		Barren					
S18		N3	*	60 min.	47.3m a.b (of T log)	*	*	*	*	*		BCD
S19		N3	**	65 min.	49.1m a.b (of T log)	*	*	*	*		*	CD
S20		5Y2/1	*	45 min.	50.9m a.b (of T log)		*	*	*	*	*	CD
S21		5Y2/1	-	-	55m a.b (of T log)		Barren					
S23		N4	-	50 min.	62.5m a.b (of T log)		*	*				BCD
S25	58204788	N2	***	50 min.	74.3m a.b (of T log)	*	*		*	*		BCD
LH01	58204788	(s)N5	*	55 min.	1.1m a.b (of T log)	*	*	*	*	*	*	BCD
LH02	"	N5	-	90 min.	3.0m a.b (of T log)		*	*	*	*		BCD
LH03	"	(s)N7	-	90 min.	6.3m a.b (of T log)		*					D
LH04	58164787	N5	-	95 min.	3.8m a.b.of anticlinal base; uncertain.		*		*	*		D
LH05	"	N4	**	60 min.	1.0m above LH04	*	*		*	*	*	ABD
LH06	"	N7	*	-	5.5m above LH04		Barren					
LH07	"	(s)N5	-	-	7m above LH04		Barren					
LH08	"	N4	-	90 min.	9.4m above LH04		*		*	*		CD
LH09	58204784	(s)5B5/1	*	65 min.	10.6m b.t (of T log)	*	*	*	*	*	*	ABCD
LH10	"	N5	-	80 min.	9.2m b.t (of T log)		*		*	*	*	ABCD
LH11	"	(s)5B5/1	-	95 min.	7.6m b.t (of T log)		*		*			AD
LH12	"	(s)N5	*	50 min.	6.8m b.t (of T log)	*	*		*	*		D
WP01	58224786	N4	**	-	0.2m a.b.		*			*		BCD
WP02	"	N4	*	90 min.	1.2m a.b.		*		*	*		CD
WP04	"	(s)5Y6/1	*	70 min.	3.2m a.b.		*			*		ACD
WP05												
WP06	"	N4	*	95 min.	5.6m a.b.	*	*			*		CD
WP08	"	N4	-	80 min.	?10.3m a.b. wavecut platform;		*			*		D
WP09	"	N4	*	-	?12m a.b.		Barren					
WP10	"	5B5/1	-	100 min.	?14.1m a.b. sequence intensely		*		*	*		CD
WP12	"	(s)5B5/1	-	95 min.	?18.70 a.b.	*	*		*	*		D
WP14	"	N4	*	100 min.	?20.5m a.b. deformed		*		*		*	D
WP16	"	N4	**	90 min.	?21m a.b.		*		*	*		ABCD
WP18	"	N4	-	100 min.	?22.5m a.b.	*	*	*				ABCD
WP19	"	N5	-	-	?23.75m a.b.		Barren					
WP20	"	N4	-	95 min.	?25.0m a.b.		*		*	*	*	BCD
WP24	58004767	N6	-	90 min.	West Wild Pear Beach, ?13.6m b.t		*			*		CD
WP26		N4	**	100 min.	?8.5m b.t	*	*	*	*	*	*	BCD
WP27		(s)5B5/1	**	95 min.	?6.8m b.t		*	*		*	*	CD
WP29		N4	-	100 min.	?4.2m b.t		*	*		*		CD
WP30		5B5/1	*	105 min.	2.6m b.t		*	*			*	BCD
WP31	57994763	5B5/1	-	90 min.	1.0m b.t. (predominance of sandstones)	*	*	*	*	*	*	BCD
L01	57994763	5B5/1	-	90 min.	?1.0m a.b., 475m E. of Lester Point.		*				*	C
L02	"	N4	*	90 min.	2.2m a.b.		*	*			*	CD
L03	"	N5	-	-	3.75m a.b.		Barren					
L04	57604746	5B5/1	-	90 min.	20.7m below base of Holey Limestone.	*	*				*	CD
L06	(200m 150 from	5B5/1	-	90 min.	17.9m below base of Holey Limestone.		*				*	CD
L08	Lester Point)	N4	***	95 min.	14.8m below base of Holey Limestone.	*	*			*	*	CD
L09		N3	*	-	12.75m below base of Holey Limestone.		Barren					
L10		N4	-	95 min.	10.4m below base of Holey Limestone.	*	*	*	*		*	CD
L12		(s)N4	**	105 min.	7.2m below base of Holey Limestone.		*				*	CD
L14		N3	-	100 min.	2.65m below base of Holey Limestone.		*	*				D
L15		(s)N5	*	100 min.	0.6m below base of Holey Limestone.	*	*		*		*	BD
L21		(s)N4	*	105 min.	2.7m above top of Holey Limestone.	*	*				*	BCD
L23		N6	*	90 min.	7.2m top of Holey Limestone.		*	*	*		*	BCD
L24	57624744	N4	**	110 min.	9.2m top of Holey Limestone.	*	*	*	?		*	BCD
L26	54324855	(s)N6	*	120 min.	0.8m below base of Rillage Limestone.		*					CD
L30		(s)N5	*	90 min.	0.95m above base of Rillage Limestone.		*	*		*	*	CD
L32		(s)N5	*	90 min.	10.8m above base of Rillage Limestone.		*	*		*	*	CD
L33	54354853	N4	*	120 min.	14m ? above base of Rillage Limestone.	*	*	*		*	*	ACD
CM01	54454848	(s)N5	*	95 min.	?8.4m below base Jenny Start Limestone.	*	*	*	*	*	*	BCD
CM02	"	N5	**	140 min.	?4.0m below base Jenny Start Limestone.		*	*		*	*	BCD
CM03	"	N4	**	-	2.5m below base Jenny Start Limstone.		Barren					
CM05	54304845	(s)N6	**	-	1.4m below base Jenny Start Limestone.		Barren					
CM09	"	N5	***	145 min.	5.8m above base Jenny Start Limestone.	*	*			?	*	D
CM10	"	N5	**	95 min.	8.3m above base Jenny Start Limestone.		*			*	*	CD
CM18	"	5YR2/1	***	90 min.	1.4m ?below top Jenny Start Limestone.	*	*				*	D
CM19	56754752	, N3	***	90 min.	0.8m above top Jenny Start Limestone.	*						D
CM21	"	(s)N6	*	95 min.	4.9m above top Jenny Start Limestone.		*	*		*	*	CD
CM23	"	(s)N5	*	95 min.	10m above top Jenny Start Limestone.		*	*		*	*	BCD
CM25	"	N5	*	95 min.	?15m above top Jenny Start Limestone.		*	*		*	*	CD
CM26	57304737	(s)5Y5/1	*	120 min.	?13.9m below base Combe Martin Beach Lst.		*	*		*	*	D
CM28	"	(s)5YR6/1	*	120 min.	5.1m below base Combe Martin Beach Lst.		*	*		*	*	CD
CM29	"	5YR6/1	*	95 min.	1.2m below base Combe Martin Beach LSt.	*	*	*		*	*	CD

Sample	Grid ref.	Colour	CO_3	Oxidation	Sample position	Vit. refl.	Miosp.	Tetrads	Acrit.	Chitin.	Scolec.	Wood
CM34	"	N6	*	120 min.	0.9m above top Combe Martin Beach Lst.	*	*	•		•	•	CD
CM36	"	(s)N5	*	125 min.	8.8m above top Combe Martin Beach Lst.		*	•			•	CD
CM37	"	(s)N5	-	-	?11m above top Combe Martin Beach Lst.		Barren					
CM38	"	(s)N5	*	115 min.	?12.6m above top Combe Martin Beach Lst.	*	*	•		•	•	CD
CM40	53654802	(s)N5	*	125 min.	?25.4m below base of David's Stone Lst.		*	•			•	CD
CM42		N6	*	120 min.	?14.5m below base of David's Stone Lst.	*	*	•			•	CD
CM43		(s)N4	-	-	?12.9m below base of David's Stone Lst.		Barren					
CM44		N5	**	90 min.	?11.6m below base of David's Stone Lst.	*	*	•		•		ACD
CM46		N5	*	130 min.	1.7m below base of David's Stone Lmst.		*	•			•	CD
CM52		(s)N4	*	130 min.	4.75m above base of David's Stone Lmst.	*	*				•	CD
CM60		(s)N6	*	140 min.	8.95m above base of David's Stone Lmst.		*			?	•	NCD
CM66		N6	*	120 min.	3.6m above top of David's Stone Lmst.	*	*	•		•	•	CD
CM67		(s)N5	-	-	7.5m above top of David's Stone Lmst.		Barren					
CM68		N5	*	120 min.	12.2m above top of David's Stone Lmst.		*			•	•	CD
CM69		N5	*	-	14.25m above top of David's Stone Lst.		Barren					
CM70		5B5/1	*	120 min.	16.4m above top of David's Stone Lmst.	*	*	•		•	•	CD
CM71		(s)N5	*	-	?18.75m above top of David's Stone Lst.		Barren					
CM72		(s)N6	**	130 min.	?25.7m above top of David's Stone Lmst.		*	•		?	•	ACD
CM73	53654788	N4	*	135 min.	?28.5m above top of David's Stone Lmst.	*	*	•		•	•	CD
K01	52954775	(s)N4	*	130 min.	Raparee Cove; E. section, cliff base.		*				•	NCD
K02	"	N5	-	130 min.	2.7m above K01.		*		•	•	•	CD
K05	"	N6	*	130 min.	7m above K01.		*	•			•	CD
K06	"	(s)N6	*	135 min.	Foreshore exposure,6.1m below base main.sst.		*	•			•	CD
K08	"	N6	-	140 min.	7.7m above K06.	*	*	•	•		•	ACD
K10	"	(s)5B5/1	*	110 min.	17.75 above K06.	*	*	•		?	•	CD
K12	"	(s)N6	-	115 min.	W.section,cliff base;1.8m below main sst.unit		*	•	•	?	•	CD
K14	"	(s)N5	-	110 min.	7.2m above K10, 2.2m below top of sst.unit		*	•		•		CD
K16	52664770	(s)5YR4/1	*	120 min.	Larkstone Beach, adjacent to access path		*				•	CD
K18	"	5B5/1	**	120 min.	7m above K16.		*	•		•	•	CD
K19	51924797	(s)5B5/1	*	140 min.	0.8m above base of anticline,in road section.		*			•	•	CD
K21		(s)N6	*	130 min.	7.0m above K19.		*	•			•	CD
K23		N6	-	135 min.	18.6m above K19.		*	•			?	NCD
K25		N6	-	120 min.	?30.3m above K19.	*	*	•				CD
K29	51954790	(s)N4	*	145 min.	0.6m above fault, road cutting.		*	•	•		•	CD
K32	51474787	N5	*	145 min.	Tunnels Beach.	*	*	•	•	•	•	ACD
K34	51434780	5B5/1	*	120 min.	Tunnels Beach.		*	•		•	•	CD
K37	51364773	(s)N5	-	110 min.	Tunnels Beach.		*	•			•	CD
K38	"	N5	-	115 min.	Tunnels Beach, 7m above K37.		*	•		•		CD
K40	51124765	(s)N5	*	115 min.	Ridge Rocks.		*	•		•	•	D
K41	"	(s)N4	-	120 min.	Ridge Rocks, 2.5m above K40.		*	•		•	•	BCD
K42	"	(s)N5	**	120 min.	Ridge Rocks, ?15.5m above K40.	*	*	•	•	•	•	CD
K44	50904765	(s)N5	*	120 min.	Torrs Point.		*	•	•	•	•	CD
K46	50854755	(s)N6	*	115 min.	White Pebble Bay		*	•		•	•	CD
K48	50404740	(s)N5	**	115 min.	S. of Breackneck Point.	*	*	•		•	•	CD
K49	50324733	(s)N5	-	-	Hazel Bushes Bay.		Barren					
K50	50274729	N4	*	120 min.	Hazel Bushes Bay.		*	•		•	•	NC
K51	50214720	N5	*	-	Hazel Bushes Bay.		Barren					
K52	50074717	(s)N5	*	140 min.	Hazel Bushes Bay.	*	*	•	•	•	•	CD
K53	50854755	(s)N6	**	110 min.	White Pebble Bay.		*				•	CD
M01	49954715	(s)N5	**	100 min.	? @Ilfracombe Sl./Morte Sl. boundary		*				?	?CD
M02	"	N6	*	100 min.		*	*				•	CD
M03	49554707	5YR8/1	-	105 min.			*					?CD
M04	49284700	(s)N6	-	105 min.	Freshwater Bay.		*					D
M05	48704097	(s)5G5/2	*	105 min.	Shag Point.	*	*		•			D
M07	48354668	(s)5BG5/2	-	95 min.	Broadoar Bay.		*					D
M10	47754665	5G6/1	-	95 min.	Lee Bay.	*	*					D
M12	47434680	N6	-	95 min.	S.E. of Pensport Rock.	*	*		•	•		CD
M15	46954675	(s)5G5/2	*	100 min.	S.W. of Damagehue Rock.		*	•		•		CD
M18	46354683	(s)5B7/1	-	100 min.	Bull Point.		*			?		CD
M20	46054658	5G5/2	*	90 min.		*	*	•		•		D
M22	45804632	N5	-	90 min.	NNE of Rockham Beach.	*	*					CD
M24	45724598	5B7/1	*	90 min.	Rockham Bay.	*	*	•				D
M26	45384577	5B7/1	-	105 min.	Oreweed Cove.		*					CD
M28	44974576	N4	*	105 min.			*	•				CD
M31	44424568	(s)N5	-	90 min.			*					CD
M33	44244550	(s)N5	-	90 min.	Morte Point.	*	*					D
M35	44634532	N5	-	90 min.		*	*	•	•	•		CD
M37	45004513	(s)N4	**	95 min.			*			•		CD
M38	45154500	N5	**	95 min.			*	•				D
M40	45384457	N3	*	110 min.		*	*		•	•		D
M41	45524442	(s)5Y2/1	*	110 min.			*	•	•	•		D
M42	45394437	N3	**	60 min.		*	*	•	•	•		CD
M43	45304420	5Y2/1	**	100 min.	Barricane Beach		*			•		D
M44	45374402	N3	*	65 min.			*	•	•			CD
M45	45484384	N3	*	100 min.	Woolacombe Beach	*	*	•				CD
M46	45584381	5GY4/1	*	95 min.			*		•			CD
M47	45584381	(s)5Y4/1	-	95 min.			*			•		CD

For the precise geographical location of samples collected from the Kentisbury and Morte Slates, refer to Text-figures 2.2 & 2.3.

Appendix III.

Vitrinite reflectivity sample profile.

This appendix outlines the results of vitrinite reflectivity studies used in the evaluation of organic metamorphism. The table has been divided into four parts. Corresponding to each sample code, the number of individual measurements are noted, in addition to two groups of figures which refer to edited and unedited data sets. All interpretations and conclusions in relation to thermal evolution and phytoclast rank are based upon the edited data set, with extreme (and therefore considered unrepresentative) values edited out. The edited and unedited data sets are provided to demonstrate that the character of the data-base was not markedly corrupted through selective editing. The mean random reflectivity *(Rm)* in oil, and the standard deviation are provided. The temperature estimates listed were calculated according to the time independent conversion formulae of Barker & Pawlewicz (1986) and not that of Price *et al.* (1983), as the former relationship was considered far more realistic (in the present study). Observations of the extracted kerogen in incident light, coincidental to rank assessment, are also provided. Genera or morphotypes identified in reflected light are abbreviated under "comments" (a key is provided).

Sample No	No.of measure-ments	(edited) Mean Rm	Standard Deviation	Temp.+ °C	No.of measure-ments	(unedited) Mean Rm	Standard Deviation	Temp.+ °C	Comments (observations in reflected light)
LN03	45	5.9	0.9	330.7	60	5.8	1.5	329.4	wood/Palyno. present.
LN06	50	5.9	1.3	330.5	51	6.0	1.3	331.7	Palyno; Apr,Em,?P.
LN17	50	5.2	1.1	317.6	53	5.3	1.3	319.6	wood-rich, unstructured.
LN21	68	7.5	1.0	355.3	100	7.6	1.3	356.8	organic rich; Ap, Em.
LN31	50	6.6	1.0	343.0	65	6.7	1.4	344.5	Palyno.rare; Wood rich.
LN34	50	5.7	1.1	328.0	52	5.8	1.2	328.2	Palyno; Apr,Em.
LN41	45	7.1	1.0	350.3	60	6.9	1.4	346.9	Palyno. rare; Em.
LN43	50	5.8	1.1	328.7	53	5.9	1.3	330.1	Palyno; Ap,Em.
LN52	70	5.9	1.3	331.5	78	6.3	1.7	336.7	wood abundant; Ap.
LN60	44	5.8	1.3	328.6	46	5.8	1.4	328.7	Palyno; Apr,Em.
LN84	50	6.2	1.2	336.2	53	6.3	1.3	337.1	wood/Palyno.; Ap,Em.
LN89	50	6.3	1.2	338.2	52	6.4	1.2	339.4	Palyno.present; Ap.
LN96	55	5.9	1.0	330.7	60	5.9	1.0	331.1	Palyno.rare
LN98	42	4.1	0.7	292.8	67	4.5	1.6	301.3	wood/Palyno; ?An,Ap,Em.
LN101	75	6.4	1.1	338.5	90	6.5	1.4	341.2	Palyno.rare; Ap,Dib,H,Tetrad.
LN115	30	6.5	1.2	341.2	43	6.1	2.0	334.2	Wood rare; ?Palyno.,Ch.
H03	55	6.3	1.3	337.3	73	6.3	1.7	337.4	wood/Palyno; Ap,?An,H.
H06	50	6.8	1.2	345.4	65	6.9	1.5	346.8	Paly rare; ?Dib.
H12	40	6.5	1.2	340.8	46	6.7	1.5	344.0	wood/paly; ?An,Ap,?G,H,R.
R21	50	5.6	1.2	325.8	55	5.5	1.4	323.9	wood rare/Palyno; Ap.
R22	53	6.0	1.2	331.6	57	5.9	1.4	331.0	Palyno; Ch, Ap,D,?Di,G,R.
S02	25	6.6	1.5	342.9	28	6.5	1.8	341.1	wood/Palyno.rare; Ac, Ap.
S06	55	7.6	1.0	357.4	76	7.6	1.5	356.9	Palyno; Ap, Em, ?G.
S12	50	6.5	1.2	340.8	56	6.8	1.5	345.6	wood rich/Palyno; ?An,Ap,Em.
S14	65	7.2	1.2	350.9	86	7.3	1.6	353.3	wood abundant; Palyno; R.
S18	46	5.6	1.3	325.7	53	5.6	1.6	325.8	Palyno rare; Ap.
S19	32	5.8	1.1	329.2	38	5.8	1.3	328.9	Palyno.rich; Ap,?D,Em,?H.
S25	50	5.5	1.0	324.2	55	5.5	1.2	323.3	Palyno.rich; Ac,Ap,Apr,?C/D.
LH01	50	7.6	1.1	357.2	65	7.6	1.4	357.7	Palyno.rich; Ap,C,Ch,D.
LH05	70	7.3	1.2	352.3	82	7.2	1.3	351.4	wood rich; Ac,Ap,Ch,D,?Dib,Rh.
LH09	55	7.4	1.1	354.1	70	7.5	1.3	355.8	wood/Palyno; Ap,C,Ch,D.
LH12	40	6.7	0.9	344.0	43	6.8	1.0	345.5	wood/Palyno; ?Ac,Ap,Ch,D,Em.
WP06	51	7.2	1.3	351.1	61	7.1	1.6	350.5	Palyno.; Ap.
WP12	52	5.6	1.0	326.0	58	5.6	1.2	324.9	wood-rich;Ac,An,Ap,Ch,?C/D,?Con,Di,Em,?Rh
WP18	30	5.5	0.6	322.8	41	5.8	1.3	329.4	Palyno.rare; Ap,C,Em.
WP26	40	6.9	1.1	347.0	60	7.0	1.7	348.5	Palyno.rich; Apr,D,?C,Ch.
WP31	55	7.0	1.1	348.8	68	7.0	1.4	349.1	Palyno.rich; Apr,Ap,?C,Em,Tetrad.
L04	50	5.8	1.0	328.1	54	5.7	1.2	326.4	Palyno; Ap,?P,C.
L08	65	6.2	0.8	336.3	85	6.2	1.2	335.5	rare Palyno; wood-rich
L10	8	4.9	1.3	311.5	63	5.8	1.3	329.2	wood/Palyno. rare; Ap.
L15	50	7.8	1.0	359.8	54	7.9	1.1	361.1	wood/Palyno. present
L21	85	5.6	1.0	326.1	94	5.5	1.1	323.4	rare Palyno. wood-rich.
L24	60	5.7	1.1	327.7	64	6.0	1.4	332.2	wood/Palyno. rich; P.
L33	50	6.0	1.4	331.7	56	6.0	1.6	332.5	rare wood; Ap.
CM01	55	5.7	1.1	326.7	60	5.8	1.3	328.0	wood/Palyno. rich; Ap.
CM09	50	5.8	0.9	328.1	58	5.6	1.1	324.6	wood/Palyno.rare; Ap,?Ch
CM18	50	4.9	0.9	311.2	63	4.8	1.3	309.3	?exclusively wood.
CM19	55	6.7	1.4	344.5	65	6.7	1.9	343.2	?exclusively wood
CM29	22	6.0	1.0	332.6	28	6.3	1.4	336.8	Palyno. rare.
CM34	25	5.0	1.1	314.4	28	5.1	1.3	315.2	wood/palyno; Ac,Ch.,Tetrad.
CM38	65	6.2	1.0	335.9	85	6.2	1.3	335.3	wood/Palyno.present; Ch.
CM42	35	6.2	1.3	336.0	38	6.3	1.5	337.4	Palyno.rich; Ap,?C,H,Tetrad
CM44	60	5.9	1.0	331.4	72	6.3	1.4	337.9	wood rare; Ch-rich, Ap.
CM52	50	4.5	0.8	302.6	54	4.5	1.0	302.6	wood/Palyno. present
CM66	20	5.3	1.1	320.0	26	5.4	1.5	320.6	wood/Palyno. rare
CM70	32	5.0	1.1	313.0	39	4.8	1.3	308.4	pyrite growth in vit.
CM73	50	4.7	1.0	307.3	53	4.7	1.2	306.9	Palyno; Ap.
K08	60	7.0	1.0	348.5	74	6.9	1.3	347.1	Palyno. present; Ap.
K10	50	6.2	1.2	336.0	52	6.2	1.3	335.9	wood/Palyno.; Ap.
K25	65	6.6	1.0	343.1	80	6.8	1.4	345.4	Palyno; Ap,P,Tetrad.
K32	45	5.6	1.1	325.3	55	5.4	1.4	321.5	Palyno.rare; Ap,Apr,?Dib.
K42	54	5.0	1.2	313.2	58	4.8	1.3	309.8	wood/Palyno. present.
K48	50	6.9	1.1	346.8	76	7.3	1.5	352.6	wood/Palyno.rare; Ap.
K52	50	6.6	1.3	341.7	54	6.6	1.5	342.8	Palyno; Apr,?C/D.
M02	49	5.0	1.1	313.6	57	5.1	1.3	316.2	Palyno; Ap.
M05	12	5.6	1.1	325.4	15	5.0	1.5	314.3	pyrite rich; Palyno.rare
M10	10	6.8	0.7	345.7	14	7.1	1.4	350.1	wood/Palyno.rare; Con.
M12	40	4.5	1.2	303.5	44	4.7	1.6	306.5	wood/Palyno.rare; Ap.
M20	35	6.8	1.2	346.2	64	7.3	2.0	352.5	wood/Palyno.rare; Ap.
M22	35	7.2	1.4	351.0	42	7.4	1.8	354.8	Palyno.rare; Ap.
M24	25	6.8	1.3	345.5	40	7.1	2.1	349.4	Palyno.rare.
M33	25	4.9	1.3	310.4	30	4.8	1.6	309.4	Palyno.rare; Ap, ?P
M35	35	6.4	1.5	338.5	73	6.5	2.6	341.3	?wood/Palyno.rare; Ap.
M40	60	4.5	1.7	302.8	68	4.8	2.1	308.7	wood rare; Ch-rich.
M42	60	5.2	1.0	317.4	86	5.1	1.7	316.4	Palyno.abundant; Ap.
M45	55	4.0	0.9	289.0	61	3.9	1.1	287.1	wood/Palyno.rare.
Total:	3590				4401				
Mean:	47.2	6.0	1.1	332.2	57.9	6.1	1.4	333.1	

76 samples.

Abbreviations : Palyno.= Palynomorphs; Ac.= Acritarch; An.= Ancyrospora; Ap.= Apiculate spore; Apr.= Apiculiretusispora; C.= Cristatisporites ("densospore complex"); Ch.= Chitinozoa; Con.= Convolutispora; D.= Densosporites ("densospore complex"); Dib.= Dibolisporites; Em.= Emphanisporites; G.= Grandispora; H.= Hystricosporites; P.= Punctatisporites; R.= Retusotriletes; Rh. = Rhabdosporites.

Appendix IV.

Total Organic Carbon (T.O.C.) determinations.

The methodology used in assessing the T.O.C. content of 12 representative, indurated sediment samples from north Devon is outlined.

A Carlo Erba Instruments CHNS-O, EA 1108 Elemental Analyser, run with the programme *EAGER* was used. The stability and error of the system was assessed using a Sulphanilamide standard ($C_6H_8N_2O_2S$), that has a known carbon content of 41.84% (lowest available).

Twelve samples were chosen at random (considered representative of the sampled section). One to two samples from each palyniferous lithostratigraphical unit were tested. Once crushed to a fine powder, using a pestle and mortar, samples were prepared by one of two means:

1. Initial treatment with industrial grade hydrochloric acid (to remove mineralic carbonate), and subsequently washed to neutral with distilled water.
2. Samples left untreated.

Once thoroughly dried, approximately 2mg of either the treated (*decalcified*) or untreated sediment were weighed out and "sealed" within a tin capsule. These pellets were loaded into an automated loading carousel. Numerical and histogram records were retained.

Logistical information.

Individual sample run time 900 seconds.
Furnace temperature $\approx$ 1000°C
Filament temperature = 190°C

For such low elemental traces, the manual documents the error margin as $\pm$10% of the measured value.

Refer to the Carl Erba Instruments Instruction Manual for additional information.