UNIVERSITY OF SOUTHAMPTON

FACULTY OF ENGINEERING, SCIENCE & MATHEMATICS
School of Ocean & Earth Sciences

The Applications of Palynostratigraphy to the Devonian of Bolivia

by

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ABSTRACT
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A continuous and unthrusted 1.2km section of ?latest Emsian to Frasnian sediments is exposed in the Rio Lajas at Bermejo, Santa Cruz Province, Bolivia. One hundred and forty-five samples were taken from this section to validate the cuttings-based Devonian subsurface palynostratigraphy. Similar palynological trends were identified in the same stratigraphic order as seen in the subsurface. A detailed study of the chitinozoan fauna was undertaken and 36 taxa were identified of which 9 are new but retained in open nomenclature pending formal description. Only 3 of the chitinozoan taxa are cosmopolitan. The palynostratigraphy from Bermejo for the first time is tied to accurate lithostratigraphy and this data was used to revise the Devonian stratigraphy at the Campo Redondo and Cha-Kjeri sections in Chiquisaca Province. Mid Devonian age assignments for the economically important Devonian Huamampampa Formation reservoir are not valid, since the new palynology indicates a mainly Early Devonian (Emsian) age.

There is sedimentological evidence in the basal Los Monos Formation for an early Eifelian marine transgression associated with the important acritarch *Evittia sommeri*. In Bolivia and South America, due to the near/effective absence of conodonts and goniatites, the Devonian Euramerican sea-level curve is relatively untested. However, a possible candidate for the Chotec Event is the basal Los Monos Formation transgression. This is the only major transgressive event during the early Eifelian. Assuming similar stratigraphic trends to Bolivia, attempts were made to find *E. sommeri* at the Chotec level in Euramerica. A total of 158 Emsian/Eifelian samples were collected and processed for palynology from the Czech Republic, Morocco, Spain and the UK with additional non-Euramerican samples from Russia. *E. sommeri* was not found. While 2 younger Devonian marine transgressions are recorded in Bolivia (mid-late Givetian and early Frasnian), the major flooding event around the Eifelian/Givetian boundary in Euramerica (Kacák Event) is notably absent. This is important since the Kacák Event has been implicated in the break-up of the high latitude, cool water Malvinokaffric Realm that included Bolivia.

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Declaration

The work presented in this thesis is my own, and was done wholly whilst in candidature for a research degree at this University. Where I have consulted or quoted from the published work of others, the source is always clearly attributed. I have acknowledged all main sources of help. None of this work has been published before submission.

Signed:

Date:

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Margarita Fieldtrip, September 2003.

CHAPTER 1 - INTRODUCTION

1.1 Background

Hydrocarbon exploration in Bolivia has increased since the late 1990s, with the Devonian Huamampampa Formation being the main subsurface target. The main Devonian outcrop occurs in the Subandean thrust belt, where thrusting and folding over the last 10Ma have complicated the stratigraphy. Since seismic data is often poor quality, resolving subsurface structure and stratigraphy has often proved problematic. Furthermore, the application of surface Devonian chronostratigraphy and lithostratigraphy to the subsurface has proved difficult resulting in conflict over formation age assignments (especially the Huamampampa Formation). Palynology was recognised by the BG Group as a potentially useful tool which could be integrated with seismic data to help refine subsurface models. A regional palynological dataset comprising 24 wells covering central/southern Bolivia and northern Argentina (many drilled in the Subandean thrust belt) was assembled by the BG Group to help address these difficulties.

In the Bolivian subsurface, a succession of distinctive marine palynomorph 'events' or epiboles (Marshall *et al.*, unpublished) were identified in the Devonian. There are five such epiboles which involve monospecific pulses in abundance (oldest to youngest) of the chitinozoan *Ramochitina magnifica*, the acritarchs *Evittia sommeri*, *Bimerga bensonii*, *Crucidia camirense* and the green alga *Petrovina connata*. Coupled with general palynological trends, these epiboles provide a means of recognising stratigraphic intervals whilst drilling. The *E. sommeri* Epibole is the most important as it occurs in the basal Los Monos Formation immediately above the Huamampampa Formation reservoir section. However, the subsurface Devonian biostratigraphy is cuttings-based and contamination by cavings is sometimes a problem which raised questions as to the validity of the subsurface palynology, especially the *E. sommeri* Epibole. The situation was further complicated by difficulties in applying accurate Devonian chronostratigraphy to the subsurface.

1.2 Objectives

This project was devised in order to resolve the above stratigraphic issues. The aims of this study were:

1) Validate the subsurface Devonian palynostratigraphy by comparing the subsurface data derived by the BG Group (Marshall *et al.*, unpublished) with a detailed study of a continuous, unthrusted surface section (Bermejo).
2) Assess the validity of the *E. sommeri* Epibole.
3) Refine the Devonian chronostratigraphy and constrain the age of the Huamampampa Formation.

4) Complete a detailed study of the chitinozoa at Bermejo with a view to assessing their correlative value.
5) Study the palynostratigraphy and relate this to palaeoenvironment.
6) If possible, place the palynological events and sedimentological trends in global context by studying similar aged sections elsewhere in the world.

To achieve these objectives, three field seasons were completed in Bolivia during 2002-2004. In addition, fieldwork was also carried out in Spain (2003-4), UK (2003), Morocco (2004), Siberia (2005) and the Czech Republic (2005). Over 600 samples were collected for palynology and/or geochemistry during these expeditions and these are listed in **Appendix 1**. The palynological data produced in this study has already been applied successfully during the drilling of the Margarita-4 appraisal well in southern Bolivia during 2004.

1.3 Regional setting

This study concentrates on the Devonian of the southern Subandean thrust belt of Bolivia (**Fig. 1.1-1.2**). The southern Subandean is an active thin-skinned thrust and fold belt extending 600km from just west of Santa Cruz southwards into NW Argentina and formed in response to continued subduction along the western margin of South America. Deformation propagated into the Subandean at around 10Ma (Schmitz & Kley, 1997) along dècollement surfaces in Silurian and Devonian strata. The amount of tectonic shortening varies along strike with published values between 50-150km (Echiavarria *et al*., 2003 and references therein). The region is characterised by NNE-SSW trending anticlines developed over west-dipping listric faults with Devonian strata commonly exposed within the cores of these anticlines (**Fig. 1.3**).

1.4 Devonian lithostratigraphy in the Subandean

The Devonian sediments in the Subandean region (**Figs. 1.1-1.2**) comprise a clastic dominated sequence with an unthrusted thickness of approximately 2.5km. There are five major formations in the Devonian (youngest to oldest): Iquiri (White, 1925), Los Monos (Mather, 1922), Huamampampa (Steinmann *in* Ulrich, 1892), Icla (Kozlowski, 1923) and Santa Rosa (Ahlfeld & Branisa, 1960). These are all mainly shallow marine deposits spanning the Lochkovian to Frasnian interval. The overlying Itacua Formation comprises diamictites and has occasionally been assigned to the latest Devonian (Famennian) but this has yet to be proved in the southern Subandean and the formation is not considered further herein. There are two informal divisions in the subsurface: the ‘Terrestrial Los Monos’ (‘TLM’) and the ‘Huamampampa Sucio’ (Dirty or Silty Huamampampa). The validity of these informal divisions is discussed in **Chapter 3.**

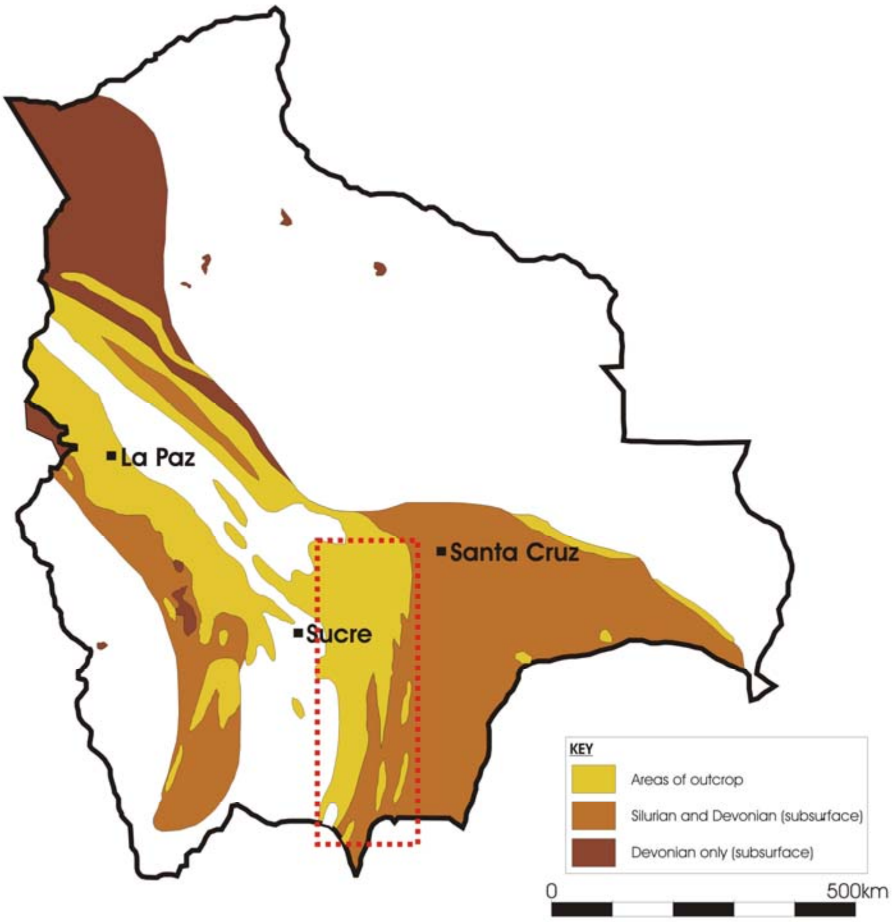


Figure 1.1. Siluro-Devonian outcrop in Bolivia (BG Group). The southern Subandean thrust belt is highlighted.

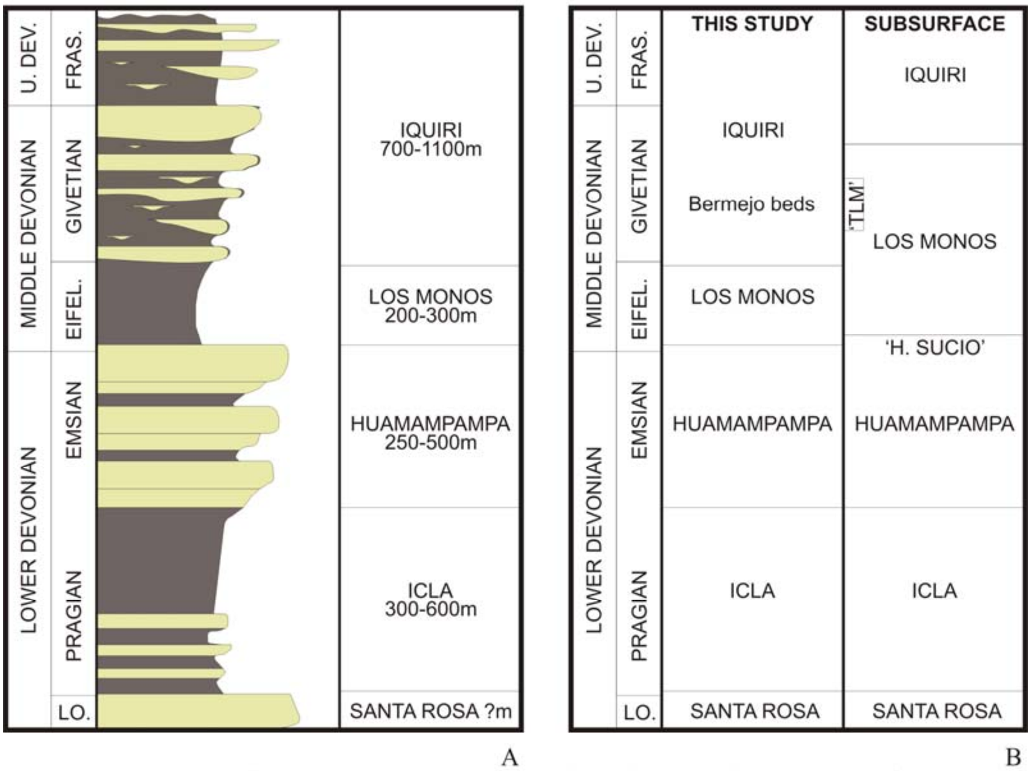


Figure 1.2. (A) Generalised Devonian stratigraphy in the Subandean (thicknesses are from BG Group). A comparison of surface (this study) and subsurface stratigraphies is shown in (B). 'TLM'='Terrestrial Los Monos'.

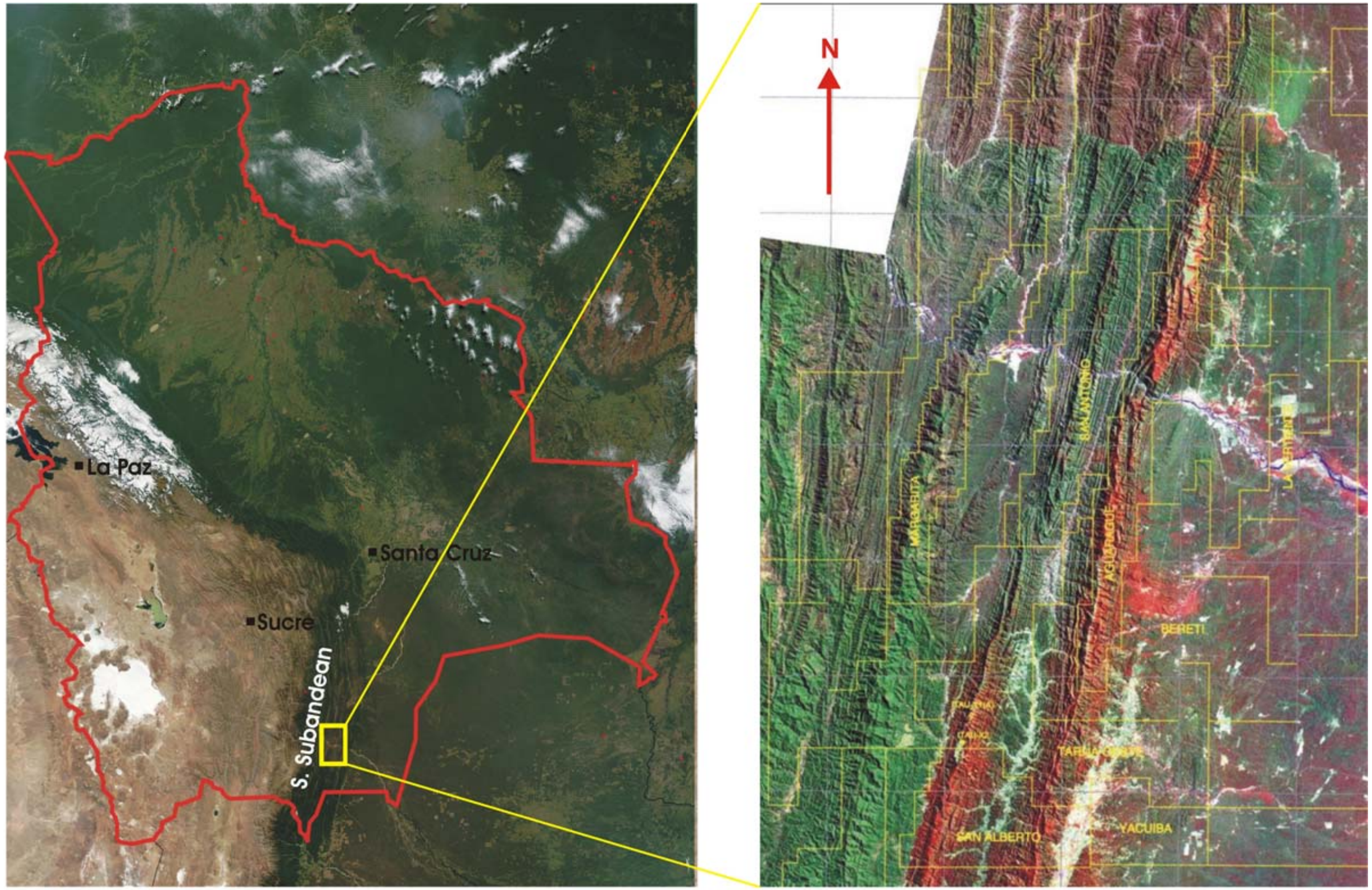


Fig. 1.3. Landsat imagery of Bolivia (left) and with a close-up showing part of the southern Subandean (right) highlighted by the yellow rectangle. Note the NNE-SSW trending ridges on the close-up image. These are thrusted anticlines with Devonian exposures often found in the cores (images courtesy of BG Group).

1.5 Previous stratigraphic investigations

A summary of the earliest work on the Devonian of Bolivia is given in Davila & Rodriguez (1967). Steinman (1929) was the first to divide and name the Devonian stratigraphic units in the Subandean based on his observations made in the late 19th century. Further work by Ahlfeld (1946) and Ahlfeld & Branisa (1960) incorporating new data from private oil companies prospecting in the region further refined these early schemes. Branisa (1965) published a valuable guide to Palaeozoic palaeontology and stratigraphy in Bolivia but little was published on Devonian stratigraphy until Isaacson (1977a, b) who studied several sections to produce a countrywide correlation based on brachiopods.

The importance of palynology in resolving stratigraphic issues in Bolivia was not realised until McGregor (1984) placed the base of the Devonian near the bottom of the Santa Rosa Formation using spores. This refined the earlier work of Branisa (1960) who claimed the Silurian/Devonian boundary was at the base of the overlying Icla Series (=Icla Formation). Although commonly integrated with macrofossil data, the use of palynology for correlation purposes in Bolivia has persisted (Blieck *et al*., 1996; Limachi *et al*., 1996; Racheboeuf *et al*., 1993) with the most recent work integrating palynological data and other disciplines in attempts to apply sequence stratigraphy to the Devonian in Bolivia (Miranda *et al*., 2000, 2003; Albariño *et al*., 2002).

1.6 Biostratigraphy in South America

In Euramerica, marine Devonian sequences are primarily dated using conodonts and a parallel goniatite zonation scheme (**Fig. 1.4**). However, these groups are absent/extremely rare in the Malvinokaffric Realm, with the other potentially useful macrofossil groups such as brachiopods and trilobites being endemic (Boucot & Racheboeuf, 1993) and therefore of little value outside of the realm in terms of chronostratigraphy. However, the use of palynology particularly acritarchs, chitinozoans and spores has proved more rewarding.

There have been attempts at regional zonation schemes in South America for acritarchs (Le Hérissé, 2001; Le Hérissé *et al*., 1996) and chitinozoa (Costa, 1971; Grahn, 2005; Grahn & Paris, 1992a; Lange, 1967a; Ottone & Rossello, 1996; Quadros, 1982; Volkheimer *et al*., 1986). Recent published work on Devonian palynomorphs in South America has focussed mainly on spores from subsurface wells in Brazil (e.g. Melo & Loboziak, 2003, and references therein) where Western European spore zonations (Richardson & McGregor, 1986; Streel *et al*., 1987-**see Fig. 1.5**) are applied. Since the most detailed Devonian palynological studies in the Malvinokaffric Realm have come from Brazil, this country is the main area in which the most worthwhile comparisons can be made with the Bolivian data presented herein.

Due to the general absence of conodonts and goniatites, spores are used to underpin Devonian chronostratigraphy in South America and spore workers date Devonian sections

CHRONO.			CONODONTS		AMMONOID STANDARD ZONES	AMMONOID GENOZONES	ZONE	STUFEN
LATE DEVONIAN (pars.)	FRASNIAN	ADORFIAN	MN-13	*linguiformis*	*Crickites holzapfeli*	*Crickites*	I-L	MANTICOCERAS
				rhenana	*Archoceras varicosum*	*Archoceras*	I-K	
			MN-12		*Neomanticoceras paradoxum*	*Neomanticoceras*	I-J	
			MN-11	*jamieae*	*Playfordites tripartitus*	*Playfordites*	I-I	
			MN-9/10	*hassi*	*Beloceras tenuistriatum*	*Beloceras*	I-H	
			MN-7/8		*Mesobeloceras kayseri*	*Mesobeloceras*	I-G	
			MN-6	*punctata*	*Prochorites alveolatus*	*Prochorites*	I-F	
			MN-5		*Probeloceras lutheri*	*Probeloceras*	I-E	
					Sandbergeroceras syngonum	*Sandbergeroceras*	I-D	
			MN-4	*transitans*	*Timanites keyserlingi*	*Timanites*	I-C	
			MN-2/3	*falsiovalis*	*Koenenites styliophitus*	*Koenenites*	I-B	
			MN-1		*Peltoceras feisti*	*Neopharciceras*	I-A	
MID DEVONIAN	GIVETIAN	MD III		*norrisi*	*Peltoceras errans*	*Peltoceras*	III-E	PHARCICERAS
				disparilis	*Pseudoprobeloceras pernai*	*Pseudoprobeloceras*	III-D	
					Synpharciceras clavilobum	*Synpharciceras*	III-C	
				hermanni	*Stenopharciceras lunulicosta*	*Stenopharciceras*	III-B	
				latifossatus/ semialternans	*Pharciceras lateseptatum*	*Pharciceras*	III-A	
		MD II	*varcus*	*ansatus*	*Afromaenioceras sulcatostriatum*	*Afromaenioceras*	II-D	MAENIOCERAS
					Maenioceras terebratum	*Sellagoniatites*	II-C	
				varcus *timorensis*	*Maenioceras molarium*		II-B	
				hemiansatus	*Maenioceras undulatum*	*Maenioceras*	II-A	
	EIFELIAN	MD I		*ensensis* *kockelianus* *eifelius*	*Agoniatites costatus*	*Agoniatites*	I-F	PINACITES
				australis *pseudofoliatus*	*Cabrieroceras crisp. plebiforme*	*Cabrieroceras*	I-E	
				costatus	*Subanarcestes macrocephalus*		I-D	
					Pinacites jugleri	*Pinacites*	I-C	
				partitus	*Foordites platypleura*	*Foordites*	I-B	
					Anarcestes (-Gyroceratites)		I-A	
EARLY DEVONIAN (pars.)	EMSIAN	LD IV		*patulus*	*Anarcestes lateseptatus*	*Anarcestes*	IV-D	ANARCESTES
		DALEJAN		*serotinus*	*Sellanarcestes wenkenbachii*	*Sellanarcestes*	IV-C	
					Latanarcestes noeggerathi	*Latanarcestes*	IV-B	
				inversus/ laticostatus	*Gyroceratites gracilis*	(*Amoenophyllites*)	IV-A	
		LD III		*nothoperbonus*	*Mimosphinctes tripartitus*	*Mimosphinctes*	III-E	ANETOCERAS
		ZLICHOVIAN		*gronbergi/ excavatus*	*Mimagoniatites fecundus*	*Mimagoniatites*	III-D	
					Teicherticeras teicherti	*Anetoceras*	III-C	
					Ruanites obliqueseptatus		III-B	
				kitabicus/ dehisciens	(?bactritids)		III-A	

Fig. 1.4. Emsian-Frasnian conodont and goniatite stratigraphy. From Becker & House (2000) with modifications from Aboussalam (2003).

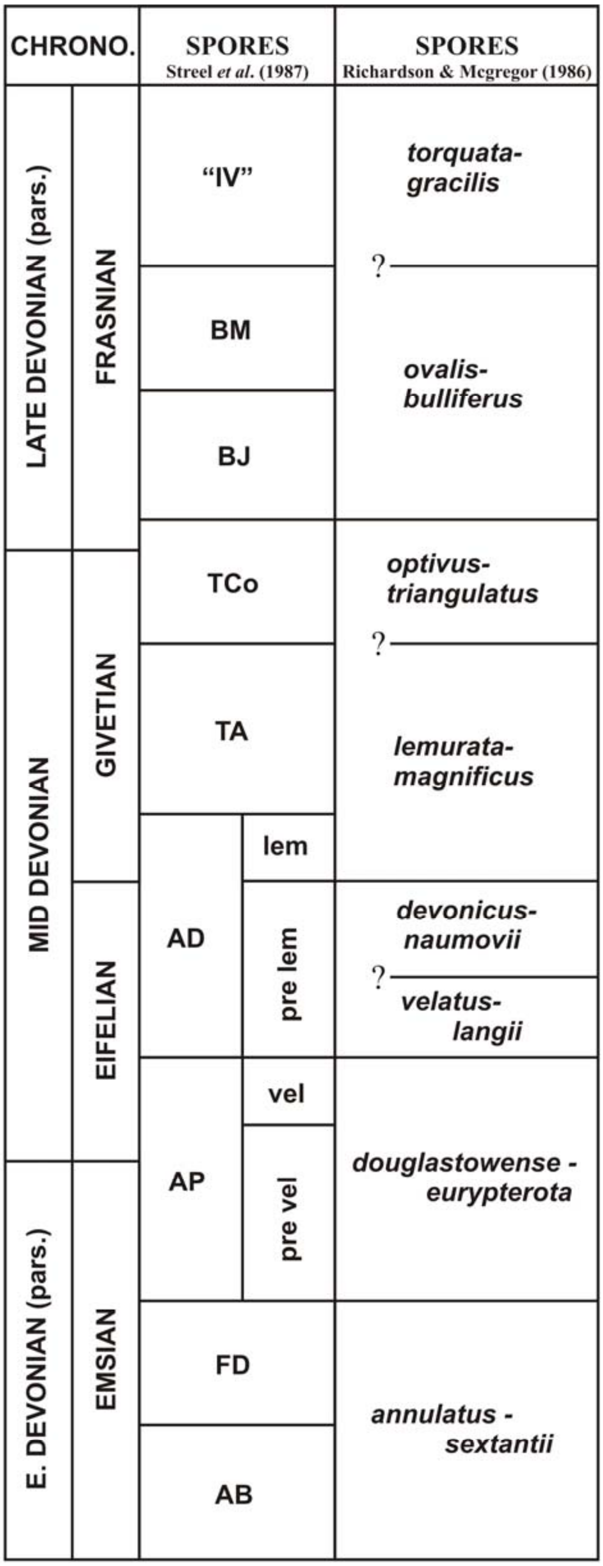


Fig. 1.5. Spore zonation for the investigated Emsian to Frasnian interval (Richardson & McGregor, 1986; Streel *et al.,*1987).

using cosmopolitan spore taxa found in sections with well-constrained biostratigraphy, i.e. conodonts and/or goniatites in Europe (e.g. Streel *et al*., 1987). However, this assumes that these spores have similar stratigraphic ranges in both regions. Studies specifically on Bolivian palynomorphs are rarer (Díaz-Martínez *et al*., 1999; Grahn, 2002; Kimyai, 1983; McGregor, 1984, Ottone & Rossello, 1996; Perez-Leyton, 1990; Racheboeuf *el al*., 1993; Suarez-Riglos *et al*., 1991; Vavrdová & Isaacson, 2000, 1996; Vavrdová *et al*., 1996; Wood, 2004) and in common with most South American Devonian palynological studies, the biostratigraphic data was mainly obtained from well cuttings. Biostratigraphic data derived from cuttings samples is prone to contamination by younger material caved from uphole and consequently the true biostratigraphic ranges (especially bases) of palynomorphs in well sections is often poorly constrained. A detailed palynological investigation at outcrop was therefore undertaken with a view to validating and refining subsurface interpretations/zonations based mainly on ranges derived from cuttings samples.

1.7 Palaeogeography

In the Devonian, Bolivia was located along the western margin of Gondwana (**Fig. 1.6**) around 60^{o}S during the latest Emsian prior to slowly rotating and beginning a northward drift in the Mid-Late Devonian (Isaacson & Díaz-Martínez, 1995). Throughout most of this period, Bolivia occupied a cratonic foreland basin setting, the Bolivia Basin (Isaacson & Sablock, 1990), which ran parallel to the Pacific Margin of South America (**Fig. 1.7**). According to Sempere (1995), the basin deepened along its axis toward the north or northwest with marine transgressions also originating from the northwest. Marine connections existed with other South American countries via shallow epicontinental seaways (**Fig. 1.7**).

There was a high degree of provincialism amongst marine faunas during the Early Devonian (e.g. Boucot & Blodgett, 2001) when Bolivia was part of a distinct Southern Hemisphere realm (Malvinokaffric). Boucot & Racheboeuf (1993) attribute the first recognition of a unique Devonian marine fauna in the Southern Hemisphere to Clarke (1913), however initial use of the term Malvinokaffric was by Richter (1941) to describe his '*Malvinocaffrischen Fauna*'. Subsequently, Richter & Richter (1942) expanded on this with a discussion of the '*Malvinocaffrische Provinz*', which was then assigned realm status by Boucot (1975) to become the Malvinokaffric Realm. The Malvinokaffric Realm comprises Antarctica, the Falkland Islands, the southern two thirds of South America, part of west Africa (Ghana and Guinea) and South Africa. Compared with extra-Malvinokaffric biogeographic units, the marine benthic macrofossils comprise a very restricted fauna with low taxonomic diversity which Boucot & Racheboeuf (1993) claimed was characteristic of ancient and modern cool water faunas at high latitudes. Notable also is the scarcity/absence of several major marine groups including conodonts, goniatites, corals and stromatoporoids.

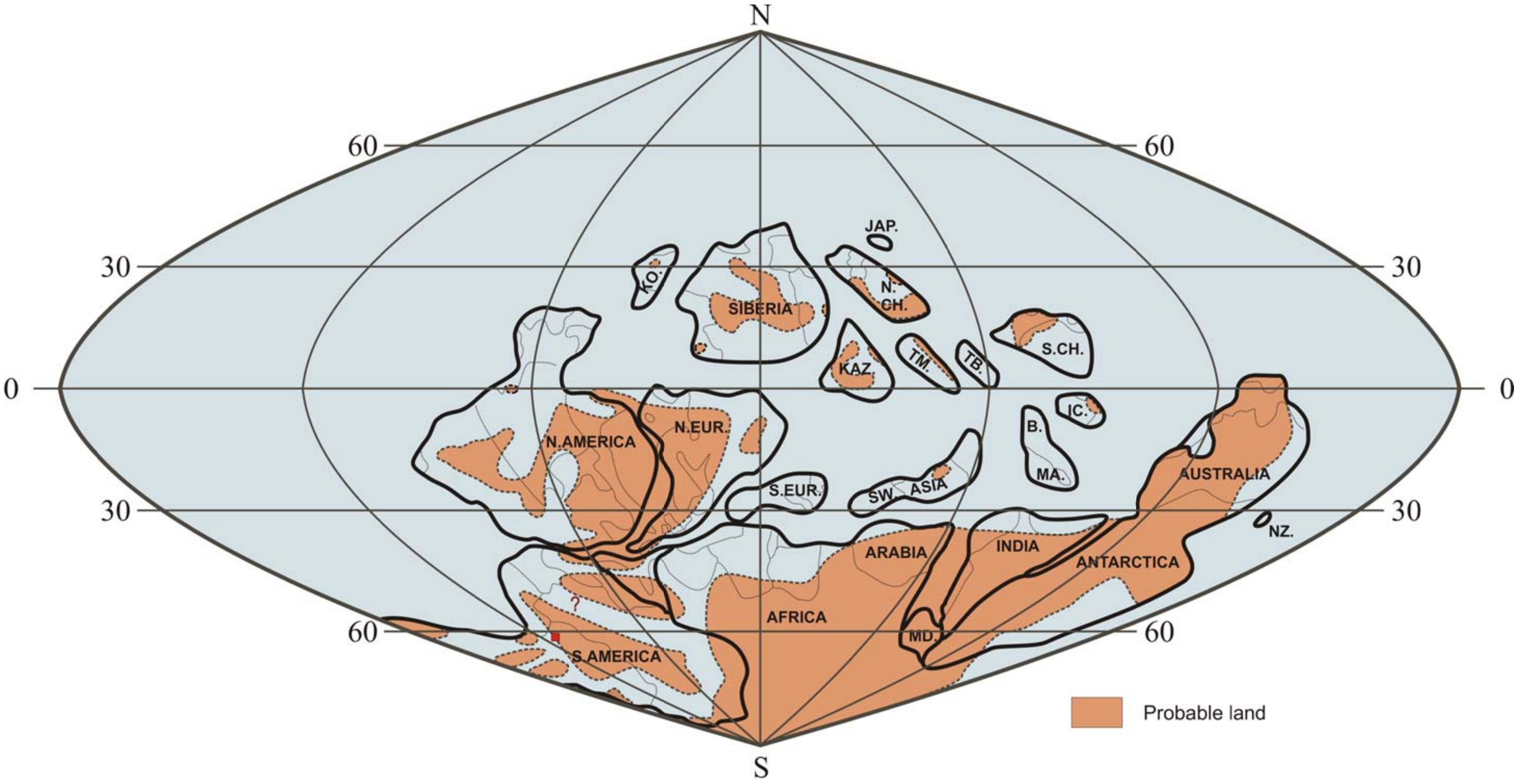


Fig. 1.6. Mid-Devonian palaeogeography of the world (modified from Becker & House, 2000). The red square marks the position of Bolivia.
Key: B=Burma, CH=China, EUR=Europe, IC=Indochina, JAP=Japan, KAZ=Kazakhstan, KO=Kolyma Plate, MA=Malaysia, MD=Madacascar, NZ=New Zealand, TB=Tibet, TM=Tarim Basin.

A presence of a cool water, high latitude Malvinokaffric Realm is further supported by the absence of climatically sensitive sediments suggestive of warmer climates, e.g. coal, limestone and dolomite, reefs, red beds and bauxite.

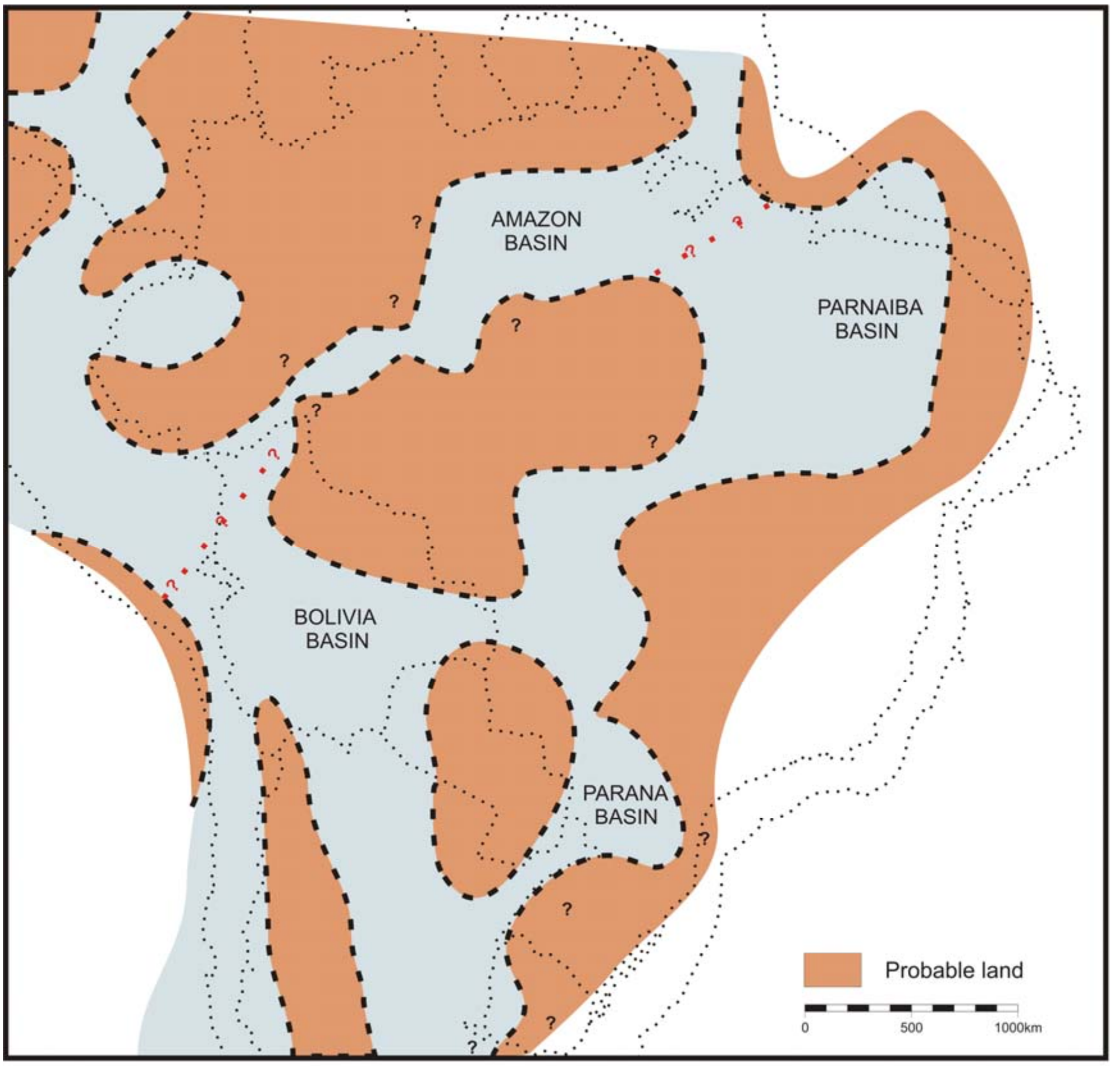


Fig. 1_7. Earliest Mid-Devonian palaeogeography of Bolivia and adjoining regions in South America and western Africa (modified from Melo, 1988). Also shown are the positions of some of the Brazilian basins mentioned in this study. The possible northern and western extents attained by the Malvinokaffric Realm are shown by the red-dotted lines which are based on brachiopod data (Boucot *et al*., 2001; Issacson & Sablock, 1990).

Precisely when the Malvinokaffric Realm broke down is conjectural. It is generally assumed that this occurred sometime in the Mid-Devonian based mainly on the occurrence of the extra-Malvinokaffric brachiopods *Tropidoleptus* and *Rhipidothyris* in Bolivia and South Africa which are both thought to represent warmer water conditions in the realm (Boucot & Theron, 2001; Boucot *et al*., 1983; Issacson, 1993; Isaacson & Díaz-Martínez, 1995; Isaacson & Perry, 1977; Issacson & Sablock, 1990; Melo, 1988; Racheboeuf *et al*., 1993). However, the supposed warm water ‘post-Malvinokaffric’ brachiopod faunas still do not achieve the diversity of coeval faunas in North America and North Africa (Isaacson & Díaz-Martínez, 1995) which may imply the persistence of cold water in ‘South America’.

1.8 Johnson *et* al. (1985) Euramerican sea-level curve

Johnson *et al*. (1985) published a Euramerican sea-level curve (**Fig. 1.8**) using high-resolution conodont biostratigraphy and sedimentology to identify coeval sea-level fluctuations in the Devonian across North America and in Europe. Although, 20 years old, the Johnson *et al*. (1985) curve is still the basis for most literature relating to Devonian sea-level change (e.g. Hüneke, in press; Sandberg *et al*., 2002; Walliser, 1996 and references therein). Johnson *et al*. (1985) assumed that the major sea-level changes on their curve were eustatic, although House *pers.comm*. (2002) noted that unless the sedimentary effects can be recognised synchronously in many areas on all continents they cannot be considered eustatic. This is also true of Devonian 'global' biotic events representing periods of turnover in important marine groups which Walliser (1996) tied to specific sea-level fluctuations on the Johnson *et al*. (1985) curve (**Fig. 1.8**).

Most literature correlating Devonian stratigraphy in South America with the transgressive/regressive TR cycles of Johnson *et al*. (1985) has been from Brazil (e.g. Melo,1988; Loboziak *et al*.,1997), although Albariño *et al*. (2002) noted the main reservoir intervals in Bolivia are related to overall regressive periods on the Euramerican sea-level curve. No attempts at identifying specific 'events', e.g. the Choteč Event have been made due to the general absence of Devonian conodonts and goniatites throughout South America, and the endemicity of the marine macrofauna. Conodonts have been found in the Late Devonian of the Amazon Basin (Hünicken *et al*., 1988) whilst a small number of Mid-Late Devonian goniatites have been recorded from Bolivia and Argentina (Babin *et al*., 1991). An as yet unidentified Early Devonian goniatite was collected by the author from the basal Huamampampa Formation at Campo Redondo in 2004 (**see Chapter 3**). Bioclastic carbonates in the lower Los Monos Formation were processed for conodonts by Daphne Woods (formerly of the National Oceanography Centre, Southampton) but none were recovered.

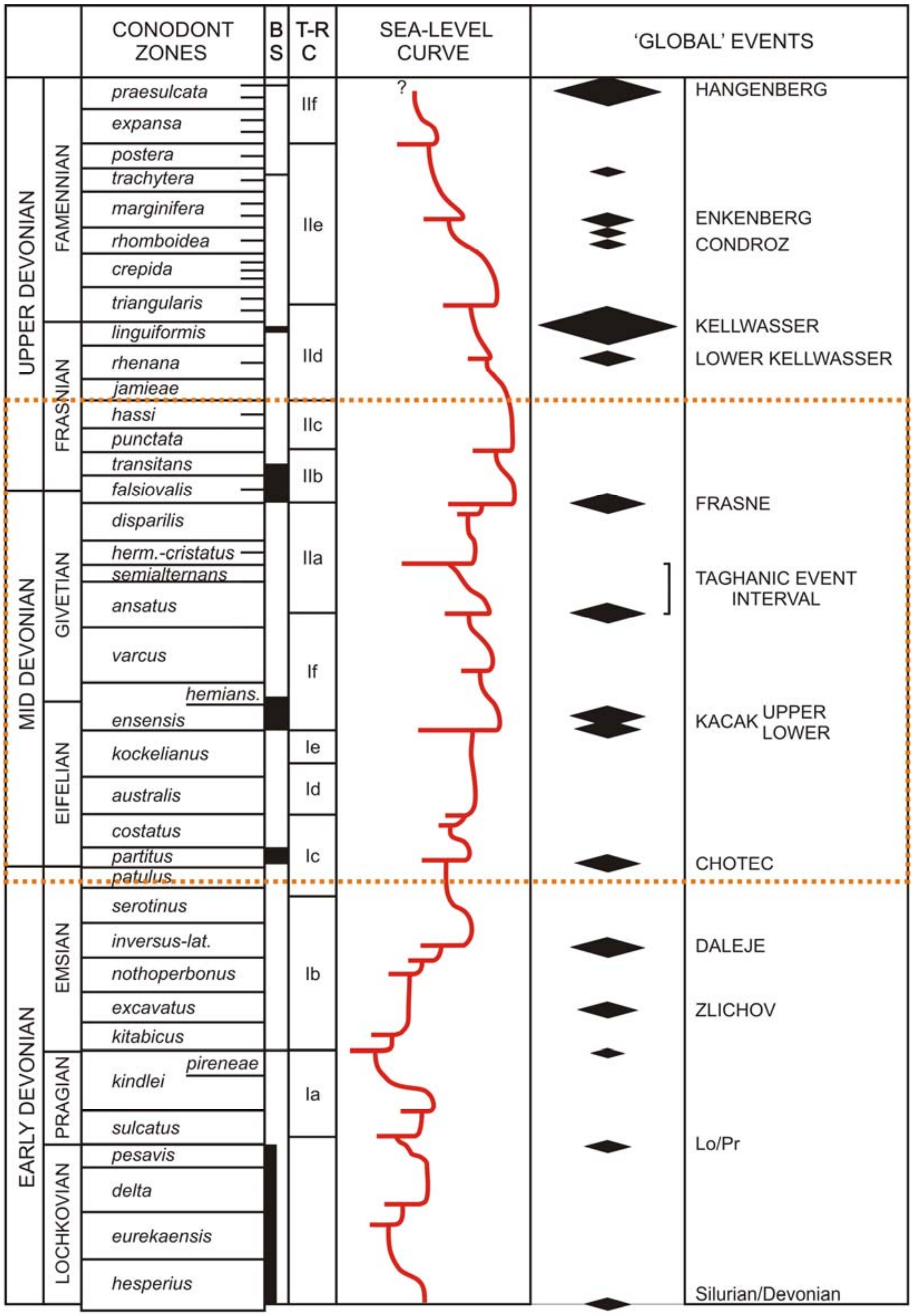


Fig. 1.8. The Devonian Euramerica sea-level curve (Johnson *et al*., 1985) with modifications from Aboussalam (2003) and Sandberg *et al*. (2002). The 'global' Devonian biotic events of Walliser (1996) are also shown with the size of the black rhomb representing the severity of each event. The orange box represents the probable period of time investigated at Bermejo in Bolivia. BS=black shale, TRC=transgressive/regressive cycle.

CHAPTER 2 – METHODOLOGY

2.1 Fieldwork

Initial fieldwork in Bolivia (10/2002) involved locating useful Devonian study sections in the Subandean of central and southern Bolivia. The 1.3km ?latest Early-Late Devonian section (upper Huamampampa-top Iquiri Formation) at Bermejo, Santa Cruz Province was identified as being the most suitable since a near continuous and unthrusted exposure occurs in the Rio Lajas. A total of 145 palynological samples were taken from shales along the 1.3km measured section with the highest density across the Huamampampa/Los Monos boundary corresponding to the assumed stratigraphic position of the *E. sommeri* Epibole **(see Chapter 3)**. All 145 palynology samples from Bermejo were also processed for TOC (% total organic content). The Bermejo section now represents the most continuous and densely sampled surface Devonian palynological record in Bolivia and the data generated has also been fully integrated with the lithostratigraphy. Note that in Chapters 3 and 4 the stratigraphy is inverted to enable comparison with the subsurface.

Due to political unrest, the second field season (9/2003) in Bolivia was abandoned, although a subsequent expedition was completed successfully (7/2004). The final field season involved a palynological investigation of the Devonian sections at Campo Redondo and Cha-Kjeri in Chiquisaca Province **(Chapter 3)** since the only goniatite with a 'well constrained' stratigraphic position (although its Mid-Late Devonian age assignment is doubtful) in Bolivia had been found at Campo Redondo (Hünicken *et al.*, 1980) and Cha-Kjeri is the unofficial type section for the Huamampampa Formation (Chamot, unpublished; Issacson, 1977a). By resolving the age of this goniatite and placing the *E. sommeri* Epibole in stratigraphic context at Cha-Kjeri a revision of Devonian stratigraphy was possible using the Bermejo surface section and pre-existing subsurface data. Selected stratigraphic intervals were re-investigated in more detail in terms of sedimentology and palaeoenvironment at Bermejo during this second field season **(see Chapter 5)**. Furthermore, two organic rich shale packages in the Iquiri Formation were re-sampled at 1m intervals for TOC analysis and RockEval™ pyrolysis.

Using palynology, attempts were also made to correlate more accurately the Devonian stratigraphy in Bolivia with sections in Europe and North Africa which have well-constrained biostratigraphy (conodonts and goniatites). Most samples investigated in these regions came from the Emsian/Eifelian interval since locating a non-South American *E. sommeri* Epibole was the objective. Assuming a similar stratigraphic distribution outside South America for the *E. sommeri* Epibole, locating this event in Europe or North Africa would provide a Euramerican calibrated age assignment for the basal Los Monos Formation. Euramerican calibrated age assignments are lacking in the Devonian of South America (and the Malvinokaffric Realm generally) due to the absence/scarcity of conodonts and goniatites and the endemicity of the marine fauna. Sampled intervals in these regions and the results of this work are discussed in **Chapter 6**.

2.2 Palynological preparation

The samples were processed for palynological examination using HCl and HF preparation techniques. 10g of crushed sample was leached with 100ml. of 28% HCl to remove any carbonate, followed by decant washing to neutral pH, and then by digestion in 60% HF for 24 hours. The residue was decant washed again and spiked with modern *Lycopodium* spores to allow quantitative counts of acritarchs, chitinozoa and spores. The sample was then sieved at 15µm and briefly boiled in concentrated HCl to remove any neoformed fluorides. After the HCl treatment and final sieving, the residues were vialed. Due to the medium-low maturity of the samples, oxidation with concentrated HNO_3 was not necessary and the quality of preservation of the palynomorphs is generally good. After checking for undissolved minerals, the residues were mounted in Elvacite 2044 on glass slides. Palynological investigations were carried out using a conventional transmitted light microscope fitted with a Nikon Coolpix digital camera. All measurements are taken at x40 magnification and are subject to a ± 2.5µm error. Three hundred palynomorphs were counted on each slide and the ratio of marine to non-marine palynomorphs calculated per sample. Due to time constraints, detailed palynofacies work was not undertaken. Although intervals which are visually rich in phytoclasts and AOM were noted.

Samples identified as containing chitinozoa during palynological investigations were sieved at 85µm. From this material, the most pristine chitinozoa were picked and mounted on glass slides. Picking residues for chitinzoa was advantageous since it increased the number of specimens from which descriptions could be generated. However, this method introduced a population bias and subsequently made precise measurements of the abundance of individual taxa difficult (see **Chapter 4**).

2.3 TOC analysis

TOC analysis was undertaken on each of the 145 samples from the first field season at Bermejo and an additional 71 samples from the Givetian (TAG samples) and Frasnian shale (FRA samples, see **Appendix B**) intercalations in the Iquiri Formation collected during the third field season. The samples were crushed individually to a fine homogenous powder and decarbonated (although this was found to be unnecessary since there is negligible carbonate in the Bermejo samples). Two to three milligrams of sample was measured for TOC using a Carlo-Erba EA-1108 elemental analyser operated as per standard conditions.

2.4 RockEval^{TM} pyrolysis

RockEval^{TM} pyrolysis is used to assess the petroleum-generative potential and thermal maturity of rocks (Espitalié *et al.*, 1977; Peters, 1986). Selected powdered and decarbonated samples from Bermejo were sent to the University of Newcastle for analysis by Dr. Martin Jones and the following parameters were measured:

S_1 – the amount of hydrocarbons (HC, in mg) that can be thermally distilled from 1g of rock.
S_2 – the amount of hydrocarbons (in mg) generated by thermal cracking of kerogen in the rock.
T_{max} – the temperature at which the maximum release of S_2 hydrocarbons occurs.

The TOC data for these samples were also supplied enabling the HI (hydrogen index) to be calculated. HI is the S_2 value divided by weight % TOC multiplied by 100 and provides information on the type of kerogen in a rock. Generally, clastic rocks have reasonable source potential if TOC values are >1%, $S_1 > 0.5$, $S_2 > 2.5$ and HI > 100.

CHAPTER 3 - STRATIGRAPHY

3.1 Introduction

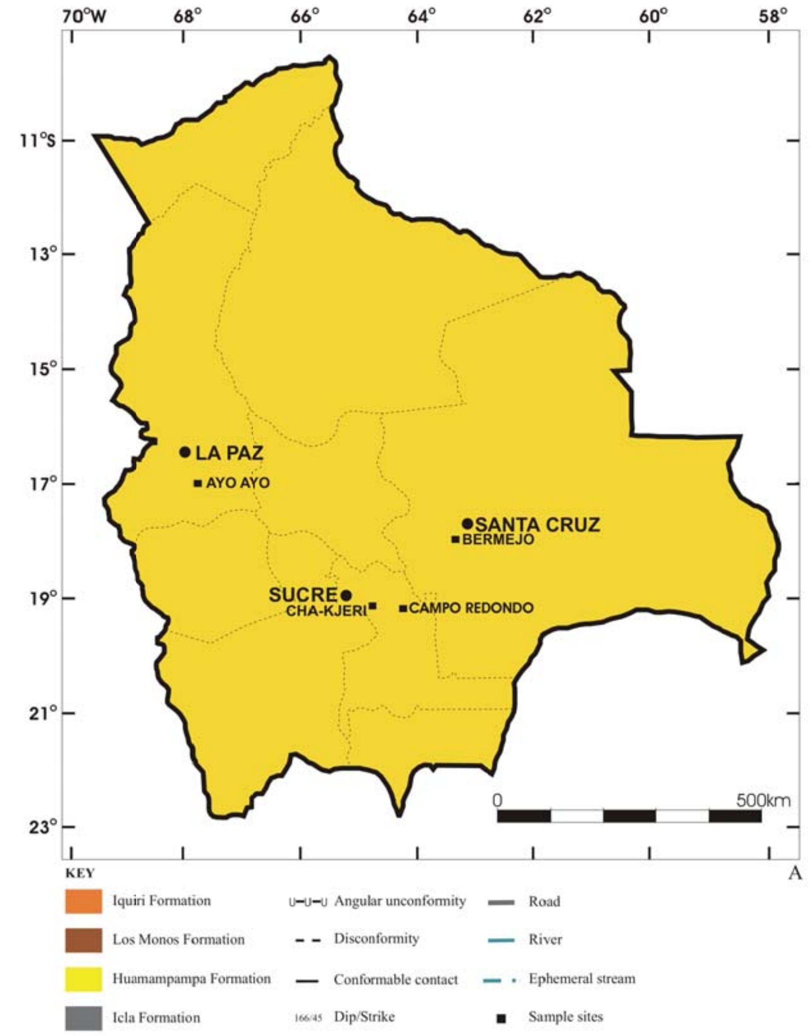
A detailed palynological and sedimentological investigation on the 1.2km Devonian section at Bermejo, Santa Cruz Province was undertaken. At Bermejo a stratigraphic section comprising the uppermost Huamampampa through to the top (truncated) of the Iquiri Formation interval is almost continuously exposed along the banks of the Rio Lajas. Initially, the section was logged and 145 samples were taken for palynology, with over 120 yielding fair to well preserved palynomorphs. Using the palynological data obtained, particular emphasis was placed on validating the subsurface biostratigraphy, especially the validity of the *E. sommeri* Epibole at the base of the Los Monos Formation. This epibole is of particular stratigraphic importance as it marks the approximate top of the Huamampampa Formation (an economically important gas-bearing sandstone reservoir). A review of Devonian stratigraphy in Bolivia was also undertaken, integrating the new data from Bermejo to significantly refine existing stratigraphic interpretations, especially those based on a single goniatite specimen, *Tornoceras bolivianum*.

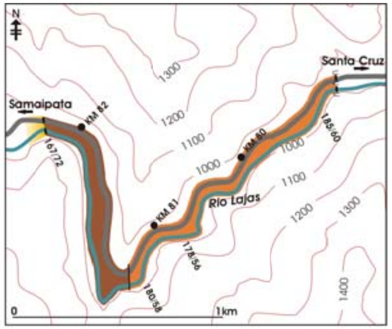
The Devonian subsurface stratigraphy in Bolivia is largely based on palynology and is reasonably reliable since it is underpinned by a large regional dataset. However, the surface stratigraphy in Bolivia is less well known and influenced by poorly applied lithostratigraphy. Correlation based on lithostratigraphy in the Subandean is often problematical, since the region is an active thrust belt, and consequently matching the surface and subsurface stratigraphies on the basis of lithostratigraphy can be difficult. This has led to a debate concerning the age assignments of the various Devonian formations. To resolve this issue, an integrated lithostratigraphic and biostratigraphic framework was developed based on outcrop sections from Bermejo, Santa Cruz Province, which was then applied to other sections at Campo Redondo and Cha-Kjeri in Chiquisaca Province. The lithostratigraphy and detailed biostratigraphy of these sections is discussed below.

3.2 Lithostratigraphy

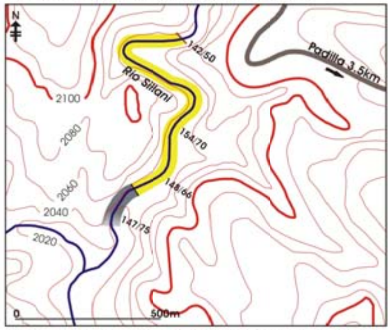
3.21 Bermejo

Bermejo, Santa Cruz Province (**Figs. 3.1-2**) is located approximately 80km SW of Santa Cruz on the Samaipata road (20 K 429876/7994666) and has previously been referred to as Lajas (Issacson, 1977a; Wood, 2004, 1995, 1994). Exposed along the banks of the Rio Lajas immediately south of the road between kilometre posts 80 and 82 is a continuous and undeformed 1.2km ?latest Emsian to mid-Frasnian section comprising the uppermost Huamampampa-Los Monos-Iquiri interval.

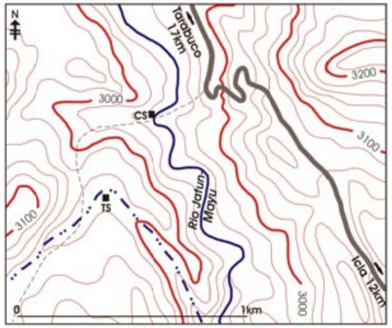




B. Sketch map of the Bermejo section

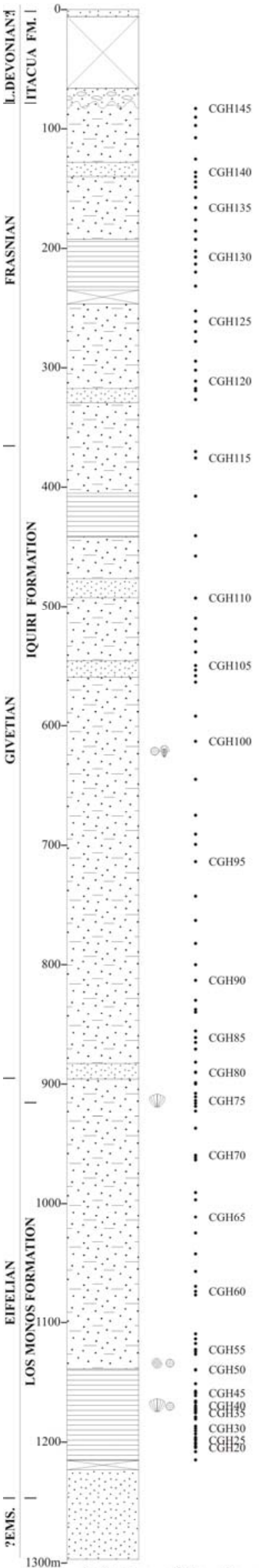


C. Sketch map of the Campo Redondo section



D. Sketch map of the Cha-kjeri section showing sample sites.

Figure 3.1. Location map of studied sections (A) and sketch maps of localities (B-D). CS=Carinatus Shale, TS=Track Shale.



A. Unconformable contact (83m) between the Iquiri and Itacua Formation (diamictite). View towards ~160°.

B. Basal Iquiri Formation at the level of CGH 80 (890m).

C. Huamapampa/Los Monos Formation contact (1240m). Sean is stood at the base of the Los Monos Formation ('Huamampampa Sucio'). View towards ~180°.

Figure 3.2. Log of the Bermejo section, Santa Cruz Province. Pictures of the section are shown in A-C. Sample depths are in **Appendix 1**.

Iquiri Formation ca 840m thick.

The youngest of the studied formations in Bolivia has an unconformable upper contact with ?latest Devonian/Early Carboniferous diamictites of the Itacua Formation (**Fig. 3.2a**) and a gradational lower contact with the underlying Los Monos Formation. Lithologically, the Iquiri Formation consists of grey to black shales, green/grey siltstones and pale sandstones (usually fine to medium grained, rarely coarse grained) that are commonly interbedded on cm/m scales, although discrete sand and shale rich intervals do occur. Common sedimentary structures include channels, cross-bedding, flaser bedding and bioturbation. Fe (siderite)-rich horizons (typically <10cm thick) are common in the basal Iquiri at Bermejo. The informal subsurface interval referred to as the 'TLM' (now the Bermejo beds see **Chapter 5**) was found to be present within the Iquiri Formation at Bermejo. The lowest occurrence of channelised sandstones marks the base of the Iquiri Formation

Los Monos Formation 230m thick

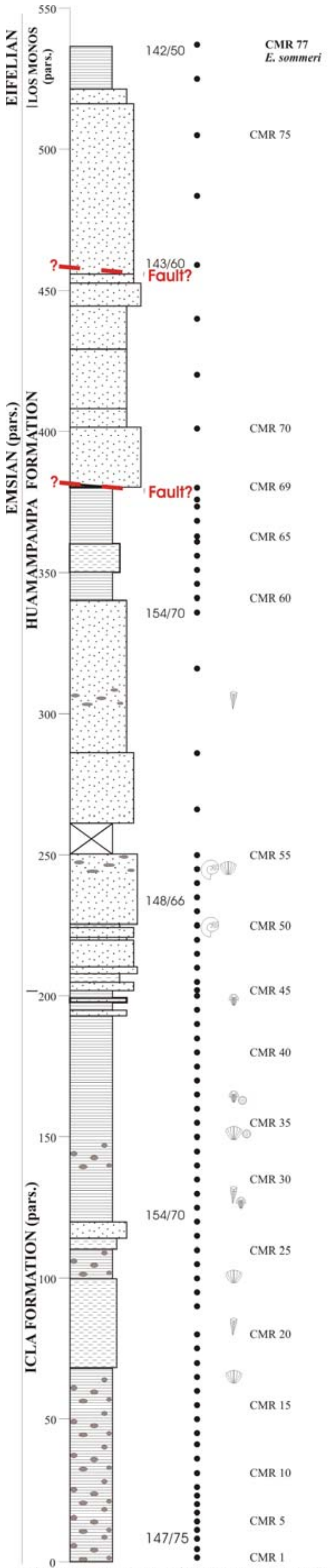
. The top of the Los Monos consists of cm to m scale interbedded fine sandstones, siltstones and mudstones. Eventually, the sand content decreases towards the base of the formation, resulting in a monotonous sequence of grey to dark grey shales containing Fe-rich layers and rare carbonate doggers (up to 2m diameter). The base of the Los Monos Formation is disconformable (**Fig. 3.2b)** with the underlying Huamampampa Formation and consists of green/grey fine sandstone and siltstone (= Huamampampa Sucio, see **Figure 3.2c**).

Huamampampa Formation pars. 75m+ thick

At the top of the Huamampampa Formation, pale channelised, cross-bedded sandstones are developed, the upper surface of which is marked by a disconformity. The remainder of the Formation consists of bioturbated green/grey fine sandstone although the base of the formation is not observed at Bermejo.

3.2.2 Campo Redondo

The section at Campo Redondo (20K 0359902/ 7864249) is located 3km west of Padilla, Chiquisaca Province on the Rio Sillani where the Icla/Huamampampa interval is exposed (**Figs. .3.1, 3.3**). Approximately 560m of section was sampled for palynology. This section was visited since it is the type locality for the goniatite *Tornoceras bolivianum*, a specimen considered to be of great chronostratigraphic importance to the Devonian of the Malvinokaffric Realm (Hünicken *et al.* 1980; see also **Section 3.6.1**). Hence, sampling the section for palynology would validate the lithostratigraphy and therefore age assignment of *T. bolivianum*. There is some faulting on the section within the Huamampampa Formation but



A. Top of the measured section. The shales in the middle of the picture contain *E. sommeri.*

B. Goniatite locality (CMR 54, 245m) in the basal Huamampampa Formation.

C. Icla shales (CMR 17, 65m).

Figure 3.3. Log of the Campo Redondo section near Padilla, Chiquisaca Province. Pictures of the section are shown in A-C.

the displacements are minor. Based on spores and general palynological assemblages, the measured section at Campo Redondo is ?early/mid Emsian to early Eifelian in age.

Huamampampa Formation ca. 350m

The measured section (**Fig. 3.3**) terminates within a 20m thick package of dark shale beneath which is a monotonous sequence of grey/green siltstones and sandstones. The contact between the shale package and underlying lithologies was unexposed. Siltstones and sandstones constitute the majority of the Huamampampa Formation at Campo Redondo but nodular layers do yield conularids and brachiopods associated with rare trilobites and goniatites. The base of the Huamampampa Formation is gradational with the underlying dark shales of the Icla Formation.

Icla Formation (pars) 200m

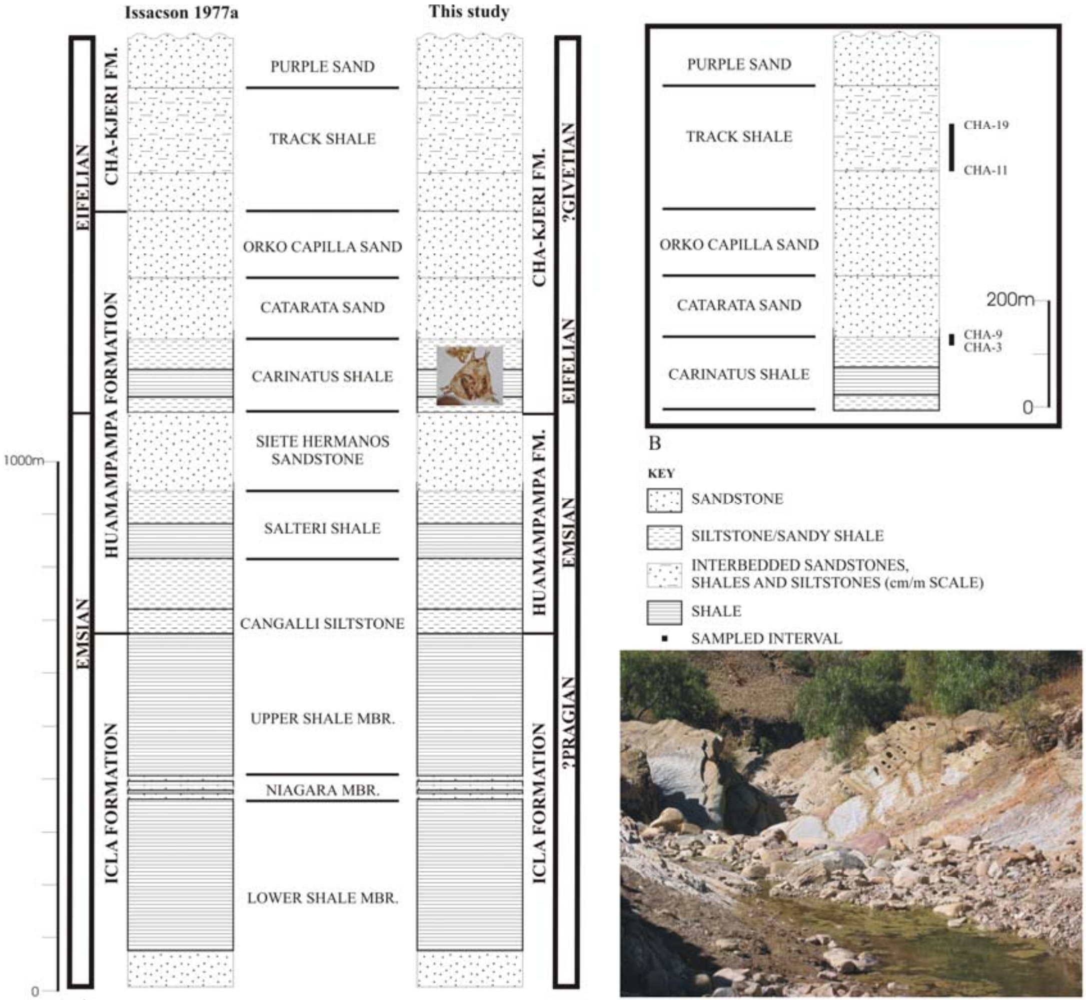
Only 200m of the Icla Formation were measured at Campo Redondo (**Fig. 3.3**) and the base of the formation was not seen. The measured section of the Icla Formation can be subdivided into an upper fossiliferous dark shale package and a lower unit consisting of sandy shales containing siderite beds and nodules. This lower unit is fossiliferous (brachiopods, conularids and trilobites) although not as prolific as the upper shales.

3.2.3 Cha-Kjeri

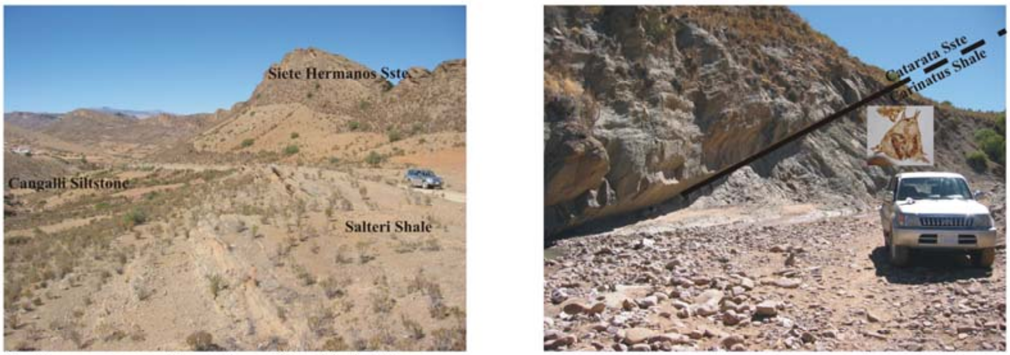
Cha-Kjeri, Chiquisaca Province (**Figs. 3.1, 3.4**) is located on the road from Tarabuco to Icla (20 K 0308461, 7868032) and is the type section for the Huamampampa Formation (770m thick) as defined in an unpublished paper by Chamot (1969) who divided the formation into six members as shown on **Figure 3.4a**. At Cha-Kjeri, spot samples for palynology were taken from each member of the Huamampampa Formation for comparison with Bermejo and the approximate positions of these samples is shown on **Figure 3.4b**. The Track Shale Member of the Cha-Kjeri Formation was also sampled. The section investigated at Cha-Kjeri is Eifelian-Givetian in age.

3.2.4 Stratigraphic comparisons with Bermejo and Campo Redondo/Cha-Kjeri

Integrating the biostratigraphy and lithostratigraphy from Bermejo, it is possible to assess the formation assignments at Campo Redondo and Cha-Kjeri. The essential datum for correlation are the shales in the basal Los Monos Formation containing the acritarch *Evittia sommeri* (**see Sections 3.3.2, 3.8, 3.5.1-3.5.4**) since these are widely used as the subsurface marker for the top of the Huamampampa Formation reservoir. *Evittia sommeri* was found in shale packages at Campo Redondo and Cha-Kjeri (**Figs. 3.3-3.4**) and since *E. sommeri* is unique to the basal Los Monos Formation, these shales have to be the lateral equivalents of the basal Los Monos Formation even if they have not been assigned as such.



C. Track Shale Member



E. Huamampampa Formation at Cha-kjeri. View towards 165°.

D. Contact between the Carinatus Shale (containing *E. Sommeri*) and Catarata Sand. View towards 335°.

Figure 3.4. Log of the Cha-Kjeri section (from Isaacson, 1977a). At this locality the Huamampampa Formation was subdivided into six members by Chamot (1969). Note the revision of Huamampampa/Cha-Kjeri Formation boundary in (A) based on the presence of *E. sommeri* in the Carinatus Shale. Sampled intervals are shown in (B). C-E show images of the Cha-Kjeri and Huamampampa Formations.

The Los Monos Formation has not been previously recognised at Campo Redondo (see Hünicken *et al*., 1980) but its presence is proved by the appearance of *E. sommeri*, which has a restricted occurrence (**Section 3.8**), in the dark shales at the very top of the measured section (**Fig. 3.3A**). At Cha-Kjeri, *E. sommeri* was found in the Carinatus Shale Member of the Huamampampa Formation (**Fig. 3.4D**). The Los Monos Formation is not used in the Cha-Kjeri area therefore to maintain consistency with the subsurface and Bermejo, the top of the Huamampampa is placed at the top of the Siete Hermanos Sandstone and the Carinatus Shale incorporated into the Cha-Kjeri Formation herein. The Track Shale Member of the Cha-Kjeri Formation displays 'Iquiri type' facies and has a palynomorph assemblage characteristic of the Bermejo beds (**see Section 3.3**). Although not sampled for palynology, the Catarata Sandstone and Orko-Capilla Sandstone must be the equivalent of the upper Los Monos/lower Iquiri Formation (mostly sub 'TLM') interval.

3.2.5 Comparison of surface and subsurface lithostratigraphy

The subsurface thickness of the Middle and Upper Devonian (Los Monos and Iquiri Formations) is estimated to be approximately 1km (Marc Bond (BG Group), *pers. comm.*) and at Bermejo a similar value (1070m) is observed. Although the total thickness of this interval is similar, the positioning of the boundary between the Iquiri and Los Monos Formation is different because at Bermejo, the boundary between these formations can be defined lithologically rather than palynologically. Consequently, the Iquiri Formation is much thicker (840m) and the Los Monos Formation thinner (230m) than generally seen in the subsurface. The subsurface palynological boundary between the Iquiri and Los Monos Formations would be defined 650m higher than the lithological boundary at Bermejo after a late Givetian flooding event. An informal palynological division of the Los Monos Formation in the subsurface, the 'TLM' is assigned to the Iquiri Formation due to the correct identification of formation boundaries and is renamed herein the Bermejo beds (see **Chapter 5**).

The 'Huamampampa Sucio' is another informal (but seldom used) subsurface division assigned to an interval of muddy sandstones and siltstones present immediately above the Huamampampa Formation reservoir. Stratigraphically, the 'Huamampampa Sucio' is disconformable with the Huamampampa Formation reservoir at Bermejo and it therefore makes sense to assign these sandstones and siltstones to the Los Monos Formation at Bermejo since lithologically they represent the early part of the basal Los Monos Formation transgression.

3.3 Biostratigraphy

3.3.1 Subsurface Devonian palynology in Bolivia.

There is a wealth of largely unpublished oil industry subsurface palynological data for Bolivia and although cuttings-based, a number of distinct palynological trends/epiboles are consistently identifiable throughout the central and southern Bolivian subsurface (Marshall *et al.,* in prep.). There are differences between surface and subsurface lithological picks and these have been discussed in **Section 3.2.5**. The subsurface formation assignments and their palynological characteristics from youngest to oldest are summarised below (BG, *pers. comm.* 2004):

Iquiri Formation (ca. 500m thick)

The top of the Iquiri Formation is marked by an unconformity overlain by latest Devonian/early Carboniferous age diamictites (Itacua Formation) which can erode down as far as the basal Iquiri Formation as defined in the subsurface, i.e. to the top of the Bermejo beds (Marshall *et al.*, in prep.). Within the Iquiri Formation two discrete levels containing abundant amorphous organic matter (AOM), marine palynomorphs and pulses of prasinophytes are recognised and are interpreted as marine flooding events. These marine transgressions are thought to be Frasnian and latest Givetian in age, with the base of the Givetian flooding being the pick for the base of the Iquiri Formation.

'Terrestrial Los Monos Member' (=Bermejo beds), Los Monos Formation (ca. 300m thick)

The informally assigned TLM, represents the uppermost Los Monos Formation in the subsurface and is characterised by an influx of spores associated with abundant cuticle and large phytoclasts, and a decline in the abundance of marine palynomorphs. The TLM represents a shallowing into a more proximal, possibly nearshore, environment with rare acritarchs and chitinozoa suggesting that the interval is still pervasively marine. Spore assemblages provide a Givetian age for the TLM.

Los Monos Formation (ca. 300m thick)

A decrease in the relative abundance of terrestrial palynomorphs marks the transition from the TLM into the Los Monos Formation proper. The base of the formation is marked by an acritarch and prasinophyte dominated assemblage indicative of a marine flooding and an open shelf environment. Compared to the overlying TLM, the Los Monos interval is relatively impoverished palynologically and as a result it is often difficult to date precisely due to poor quality recovery from the cuttings and the occurrence of caved material from uphole. Furthermore, the base of the formation is dominated by cosmopolitan, long ranging acritarchs and endemic spores. The Los Monos Formation is considered to be of Eifelian age.

Huamampampa Formation (ca. 200m thick)

Apart from caved material, *in situ* palynological yields from the Huamampampa Formation are lean. Based mainly on its stratigraphic position in the subsurface this Formation is considered to be pre-early Eifelian.

Icla Formation (ca. 500m thick)

The Icla Formation is often palynologically barren but does intermittently contain a sparse palynomorph assemblage consisting of simple spores and generally long ranging marine palynomorphs. Rare diagnostic palynomorphs suggest an Emsian-Pragian age for this formation (McGregor, 1984).

Santa Rosa Formation

This formation is rarely encountered in the subsurface and generally highly impoverished with respect to palynomorphs, although Pragian and Lochkovian taxa have been recorded (Marshall, *et al*., in prep.).

3.3.2 Important biostratigraphic markers subsurface in Bolivia

Five distinctive marine palynomorph epiboles comprising short-lived monospecific pulses of acritarchs, chlorophyta and chitinozoa are recognised in the Bolivian subsurface. These comprise (youngest to oldest): the chlorophyte *Petrovina connata*, the acritarchs *Crucidia camirense*, *Bimerga bensonii* and *Evittia sommeri* and the chitinozoan *Ramochitina magnifica*. The *P. connata*, *C. camirense*, *B. bensonii* and *E. sommeri* epiboles are described in **Section 3.8**, and these allow a framework for relative stratigraphical positioning within the Devonian sequence in Bolivia. The acmes (maximum relative abundance) of *P. connata* and *C. camirense* are found in the Iquiri Formation (Frasnian). The *B. bensonii* acme is found in the uppermost Los Monos Formation (Givetian) underneath the ‘TLM’ (=Bermejo beds) and the *E. sommeri* acme is situated in the basal Los Monos Formation (Eifelian). The acme of *R. magnifica* occurs in the basal Icla Formation (Pragian) but is rarely penetrated in the subsurface. Assuming no tectonic repetition, all of the acmes where present subsurface, always occur in the same stratigraphic order (**Fig. 3.5**) although none have been previously identified and precisely dated at outcrop.

The *E. sommeri* acme (or *E. sommeri* Epibole herein) is the most important palynomorph epibole stratigraphically because it occurs immediately above the Huamampampa Formation reservoir in the base of the overlying Los Monos Formation. Consequently, particular emphasis has been placed on understanding the *E. sommeri* Epibole in terms of its precise stratigraphic and geographical extent and its sedimentological context.

3.4 Biostratigraphy and chronostratigraphy of the Bermejo section

3.4.1 General palynological trends at Bermejo

The general palynological trends (**section 3.3**) encountered in the subsurface throughout central and southern Bolivia were all identified at Bermejo. Apart from *R. magnifica* (the Icla Formation in which this taxon occurs is not exposed in the study area), the acmes of the remaining four important palynomorphs were all located stratigraphically with precision (**Fig. 3.6**). Significantly, these epiboles all occur in the same order as previously recorded in the subsurface. The *P. connata* and *C. camirense* acmes are associated with the younger of two marine floodings within the Iquiri Formation. The *B. bensonii* acme occurs during an interval of general marine regression at the base of the Iquiri Formation as defined sedimentologically at Bermejo (**see Chapter 5**) and the *E. sommeri* Epibole is found in black shales marking the marine transgression in the basal Los Monos Formation.

3.4.2 Bermejo chronostratigraphy

At Bermejo seven palynomorph taxa, comprising three chitinozoan and four diagnostic spore species, were identified and used to assign ages to the section. The chitinozoan taxa are also described in **Chapter 4**. The chronostratigraphic implications of these seven taxa to the Bermejo section are discussed below. It is possible to indirectly correlate parts of the Los Monos and Iquiri Formations with Euramerican conodont zones using spores although few conodont zones can be tied to spore zones with certainty. An integrated Euramerica spore and conodont zonation based on Streel *et* al. (2000) is shown on **Figure 3.7**.

Iquiri Formation

The persistence of the spore *Cristatisporites triangulatus* (**Fig. 3.6**) throughout the uppermost Iquiri Formation indicates an age of no younger than mid Frasnian for the top of the Iquiri Formation since this taxon does not range above the early Frasnian (Avkhimovitch *et al.*, 1993). *Urochitina bastosi* (**Fig. 3.6**) found in samples CGH 141-CGH 143 ranges ca. 15m beneath the erosive unconformity at the top of the Iquiri Formation (**Fig. 3.6**). In Grahn & Melo (2002) the *U. bastosi* interval zone in Brazil is found in the upper IV miospore zone (mid to late Frasnian) although the total range of *U. bastosi* extends into the Famennian. A probable mid Frasnian age is therefore assigned to the top of the Iquiri Formation at Bermejo, although a slightly younger Frasnian age cannot currently be ruled out.

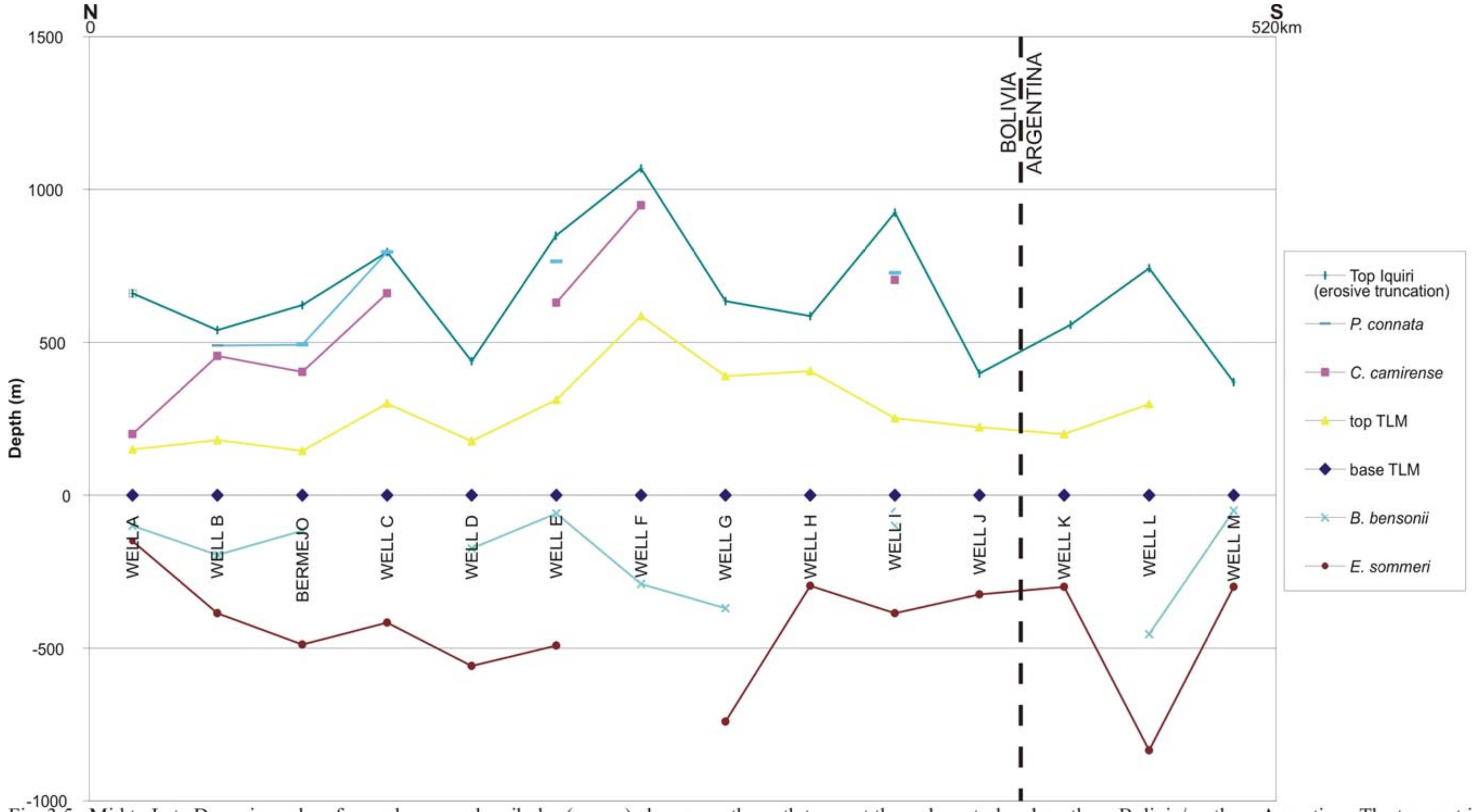


Fig. 3.5. Mid to Late Devonian subsurface palynomorph epiboles (acmes) along a north-south transect through central and southern Bolivia/northern Argentina. The transect is hung on the base of the 'TLM' i.e. base Iquiri Formation (modified from Marshall, 2002 unpublished). Note *E. sommeri, B. bensonii, C. camirense* and *P. connata* occur in the same stratigraphic order in all wells studied and at outcrop (Bermejo).

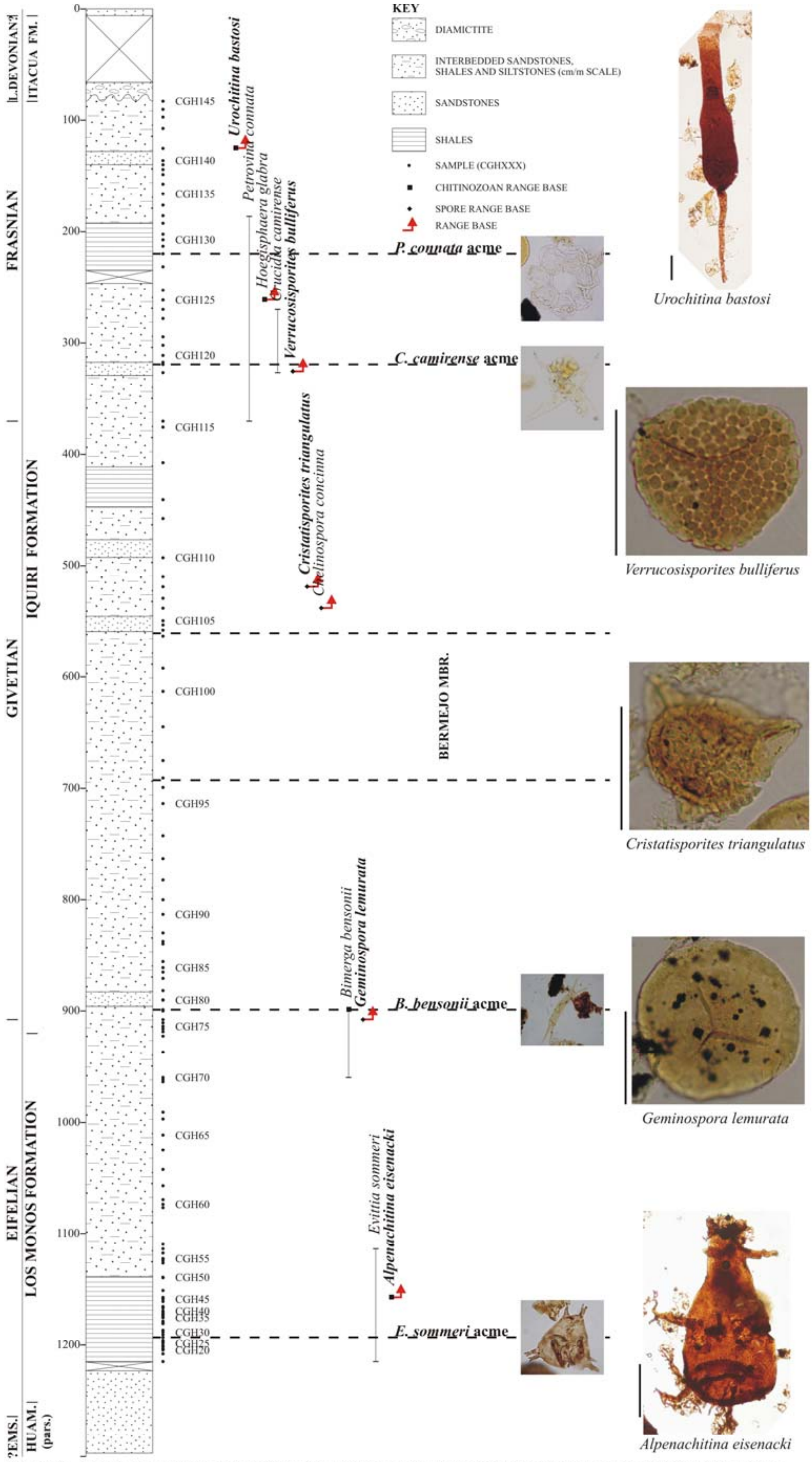


Fig. 3.6. Generalised log of the Bermejo section with the total ranges and range bases of some key taxa shown. Scale bar = 50 µm.

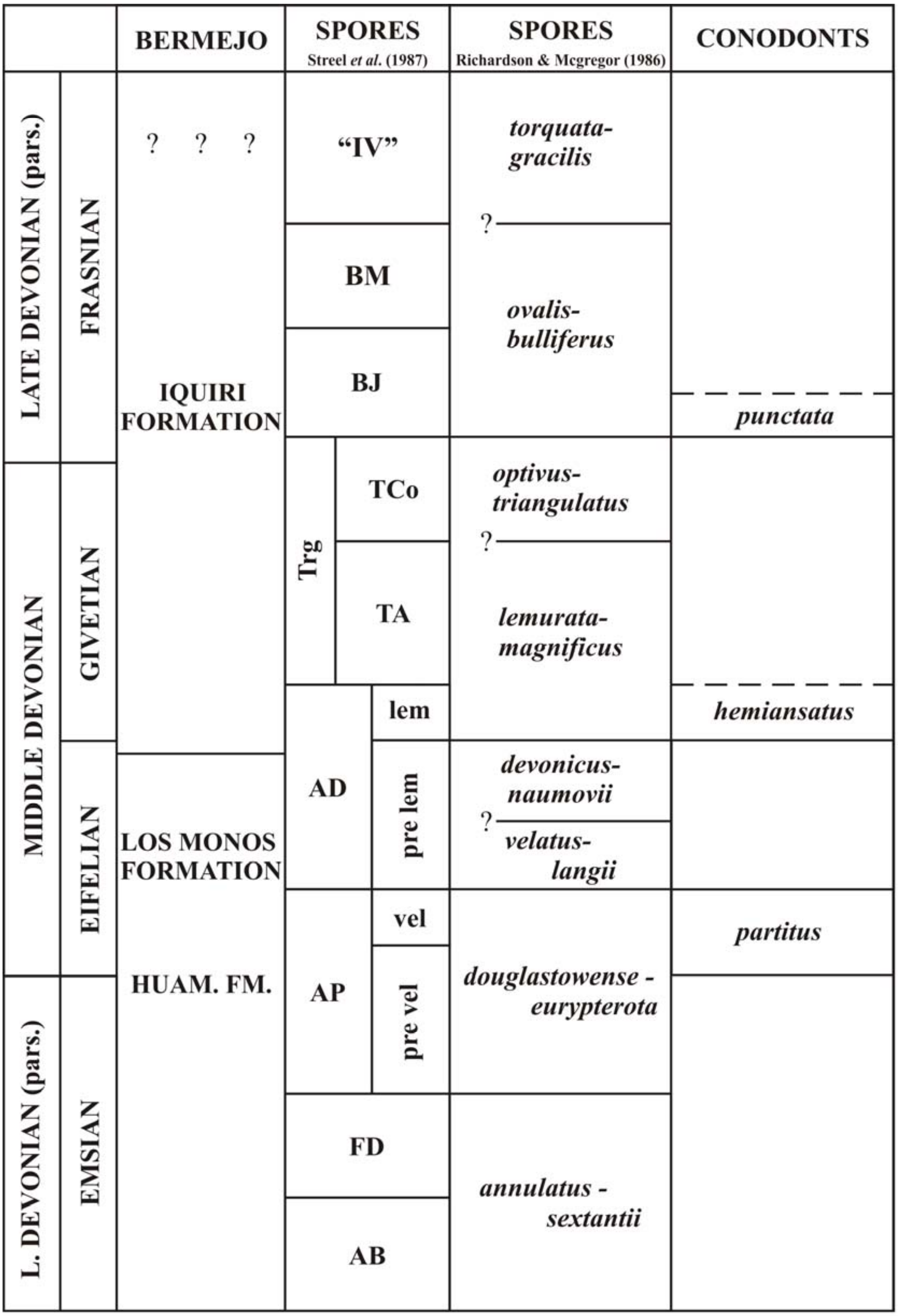


Fig. 3.7. The lithostratigraphy of Bermejo and spore zonation (Melo & Loboziak, 2003; Streel *et al.,*1987; Richardson & McGregor,1986). Also shown is data from Streel *et al.* (2000) who tied the inceptions of zonal spores to the conodont zonation. A similar stratigraphic distribution of zonal spores in South America is assumed. The current spore data from Bermejo only allows indirect correlation with three conodont zones in Euramerica.

The first occurrence of *Verrucosisporites bulliferus* (**Fig. 3.6**) defines the base of the BJ Oppel Zone (Streel *et al.*, 1987) or the *ovalis-bulliferus* Assemblage Zone of Richardson & McGregor (1986) and indicates an early Frasnian age (**Fig. 3.7**). The base of the BJ Oppel Zone does not coincide with the Givetian/Frasnian boundary. Therefore the Givetian/Frasnian boundary is placed around sample CGH 116 corresponding to the first occurrence of *P. connata* (**Fig. 3.6**), an exclusively Frasnian taxon in Brazil (Le Hérissé, 2001) based on spores (Loboziak *et al.*, 1997a,b). *Hoegisphaera glabra* s.s. is a Frasnian chitinozoan (**see Chapter 4**) and occurs in samples CGH 124-CGH 125 and its presence at this level (**Fig. 3.6**) is consistent with the occurrence of *V. bulliferus* in the underlying sample range CGH 117-CGH 121.

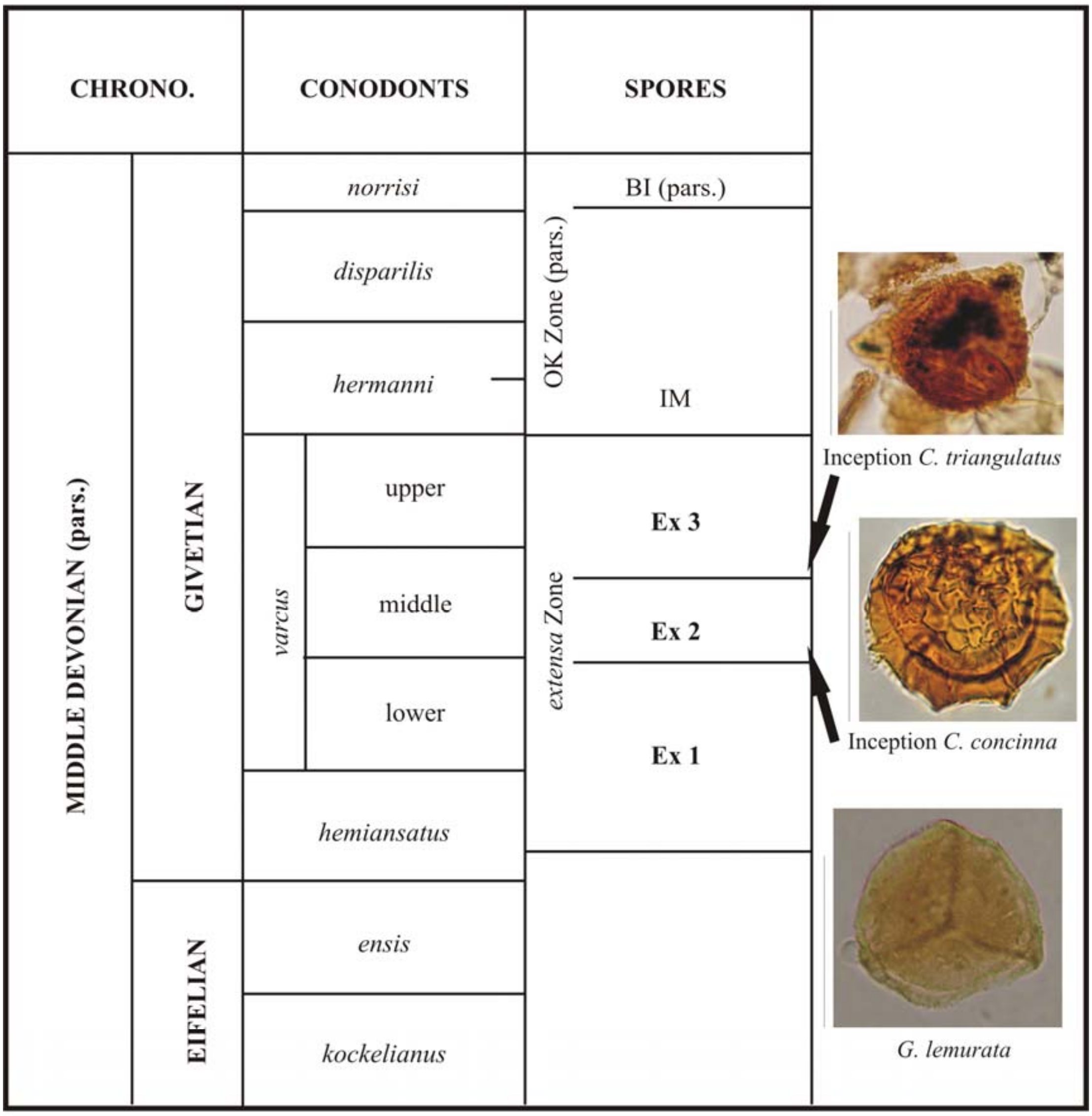


Fig. 3.8. Conodont and spore zonation for the part of the Mid Devonian in Eastern Europe (after Turnau & Racki, 1999). The spores *Cristatisporites triangulatus*, *Chelinospora concinna* and *Geminospora lemurata* that define the Ex 1-3 subzones are illustrated.

Based on work by Turnau & Racki (1999) in Poland, the lower and upper Givetian (in part) can be divided into three spore subzones (oldest – youngest) Ex 1, Ex 2, Ex 3 of the *extensa* Zone (**Fig. 3.8**). These subzones are defined by: the occurrence of *Geminospora lemurata* and other key spore taxa (Ex 1), and the inceptions of *Chelinospora concinna* (base Ex 2) and *Cristatisporites triangulatus* (base Ex 3). This division of the Givetian does create difficulties in fixing the top of Ex 2 and base Ex 3 boundaries since the first occurrence of *C. concinna* appears to be regionally diachronous, e.g. in Belarus (Obukhuskaya, 2000), Russia (Avkhimovitch *et al*., 1993), and Canada (McGregor & Camfield, 1982), the oldest occurrence of *C. triangulatus* is stratigraphically above *C. concinna* whereas in Germany (Loboziak *et al*., 1991) the sequence is reversed. At Bermejo, these spores occur in the same sequence as the non-German records (**Fig. 3.8**). The first occurrence of *C. triangulatus* in CGH 108 marks the base of the TA Oppel Zone (Loboziak *et al*., 1997a; **Fig. 3.7**) although only a single specimen of *C. concinna* was found in sample CGH 106 marking the base of the TCo Oppel Zone. Due to difficulties with the Ex 2/Ex 3 boundary, the Ex 1 – Ex 3 spore division of the Givetian is not adopted at Bermejo. Furthermore, the TA and TCo Oppel Zones are also in reverse order at Bermejo and are not therefore applicable. Melo & Loboziak (2003) resolved this problem in the Amazonas Basin, Brazil by using the Trg Zone which encompasses both Oppel Zones and is defined by the first occurrence of *C. triangulatus*.

The first occurrence of *G. lemurata* which marks the base of the AD lem Oppel Zone (Steel *et al*., 1987) is in sample CGH 77 (907.7m) and is broadly coincident with the boundary between the Los Monos and Iquiri Formations at ca. 920m (**Fig. 3.6**) as defined by sedimentology (**see Chapter 5**). At Bermejo, the Iquiri Formation is assigned an early Givetian to mid-Frasnian age range.

Los Monos Formation

The top of the Los Monos is latest Eifelian based on the presence of the Givetian marker *G. lemurata* in the overlying basal Iquiri Formation, although dating the base of the Los Monos Formation is more problematical. In Euramerica, the Early to Mid Devonian spore assemblages are notable for the few spore forms that become extinct. The spore assemblages are instead characterised by innovation in spore construction with the latest Emsian/early Eifelian interval being marked by an increase in spore size and a proliferation in the abundance of zonate and camerate forms (Richardson & McGregor, 1986). In the subsurface of Bolivia, a similar trend is observed in the basal Los Monos Formation and also at the Campo Redondo outcrop section (**Section 3.6**) where these forms are rare/absent below the uppermost Huamampampa Formation. Although similar trends in spore evolution are identified in Bolivia as in Euramerica (McGregor, 1984), the basal Los Monos spore flora appears to be largely endemic lacking key zonal markers such as *Grandispora* *douglastownense* and *Ancyrospora eurypterota* (Richardson & McGregor, 1986). The acritarch flora at this level is dominated by long ranging forms but a very distinctive chitinozoan, *Alpenachitina eisenacki*, is important as it is a well known cosmopolitan taxon with a conodont-calibrated first occurrence in the early Eifelian (*partitus* Conodont Zone, see **Figure 3.7**) in the USA (Paris *et al.*, 2000; Wright, 1980). The first occurrence of *A. eisenacki* in CGH 46 at Bermejo, and also elsewhere in Bolivia, is associated with abundant large camerate and zonate spores (**Pl. 3, fig. 18**)**,** consistent with an early Eifelian age for the basal Los Monos Formation.

Huamampampa Formation

Palynomorph recovery was poor in the Huamampampa Formation at Bermejo although the formation has to be pre-early Eifelian or older based on stratigraphic relationships. At Campo Redondo the base of the formation was dated as mid Emsian based on palynology (**see Section 3.6.1**).

3.5 The *E. sommeri* Epibole at Bermejo

Although present at the same stratigraphic level in 22 of the 24 wells drilled in Bolivia (basal Los Monos Formation), the precise stratigraphic position and palaeoenvironmental significance of the *E. sommeri* Epibole is only poorly understood. Since the *E. sommeri* Epibole had only been identified in cuttings samples, it was not possible to accurately determine the position of the epibole relative to the top of the Huamampampa Formation, or its stratigraphic thickness. To investigate these parameters, the undeformed Bermejo section was sampled to determine the total stratigraphic range of *E. sommeri* and the precise stratigraphic position and extent of the *E. sommeri* Epibole.

3.5.1 Stratigraphic position and extent of the *E. sommeri* Epibole at Bermejo

E. sommeri is restricted to the Los Monos Formation in samples CGH 18 –CGH 57 a total stratigraphic range of ca. 100m (**Fig. 3.9**). A similar acritarch (see also Loboziak *et al.*, 1997b) is found within the Iquiri Formation in CGH 116 and younger samples but this was identified as *E. geometrica* not *E. sommeri* (**Pl. 1, fig. 14-17**). Analysis of the relative abundance of *E. sommeri* reveals a distinct spike in CGH 27 of 12900 specimens g^{-1} (**Fig. 3.9**). *E. sommeri* dominates the microplankton assemblage at this level with an abundance that is greater than all of the other acritarchs combined (8700 specimens g^{-1}). Only spores have a greater relative abundance in CGH 27, ca. 25000 specimens g^{-1}. CGH 27 represents the *E. sommeri* acme, although the *E. sommeri* Epibole ranges through samples CGH 25-CGH 29 and has an approximate thickness of 10m. The *E. sommeri* acme is clearly visible on **Figure 3.9**.

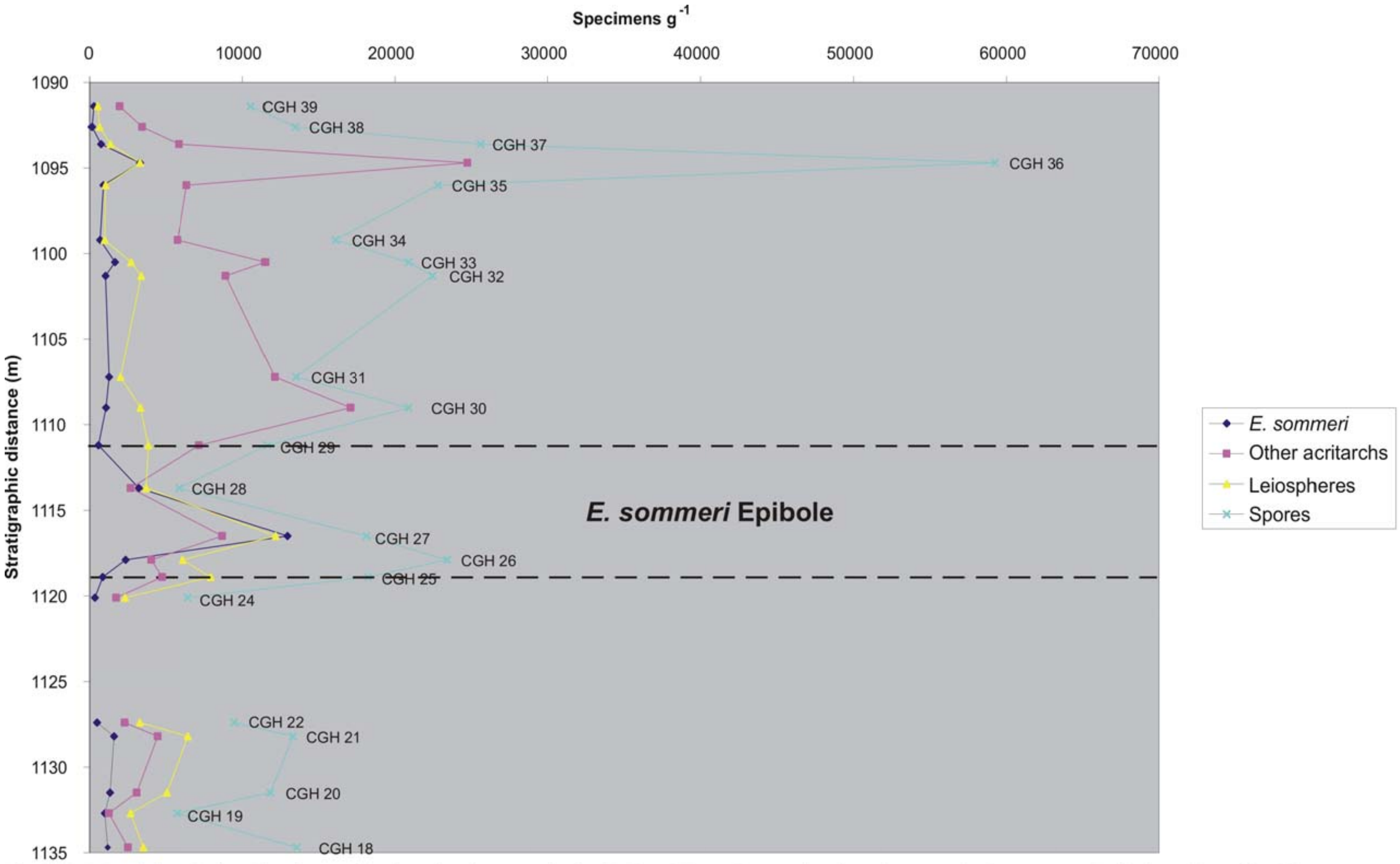


Fig. 3.9. Trends in relative abundance of selected palynomorphs in the Los Monos Formation (pars.) across the *E. sommeri* Epibole at Bermejo. Note coincidence of *E. sommeri* and leiosphere peaks through the *E. sommeri* Epibole. Samples are marked as CGHXX.

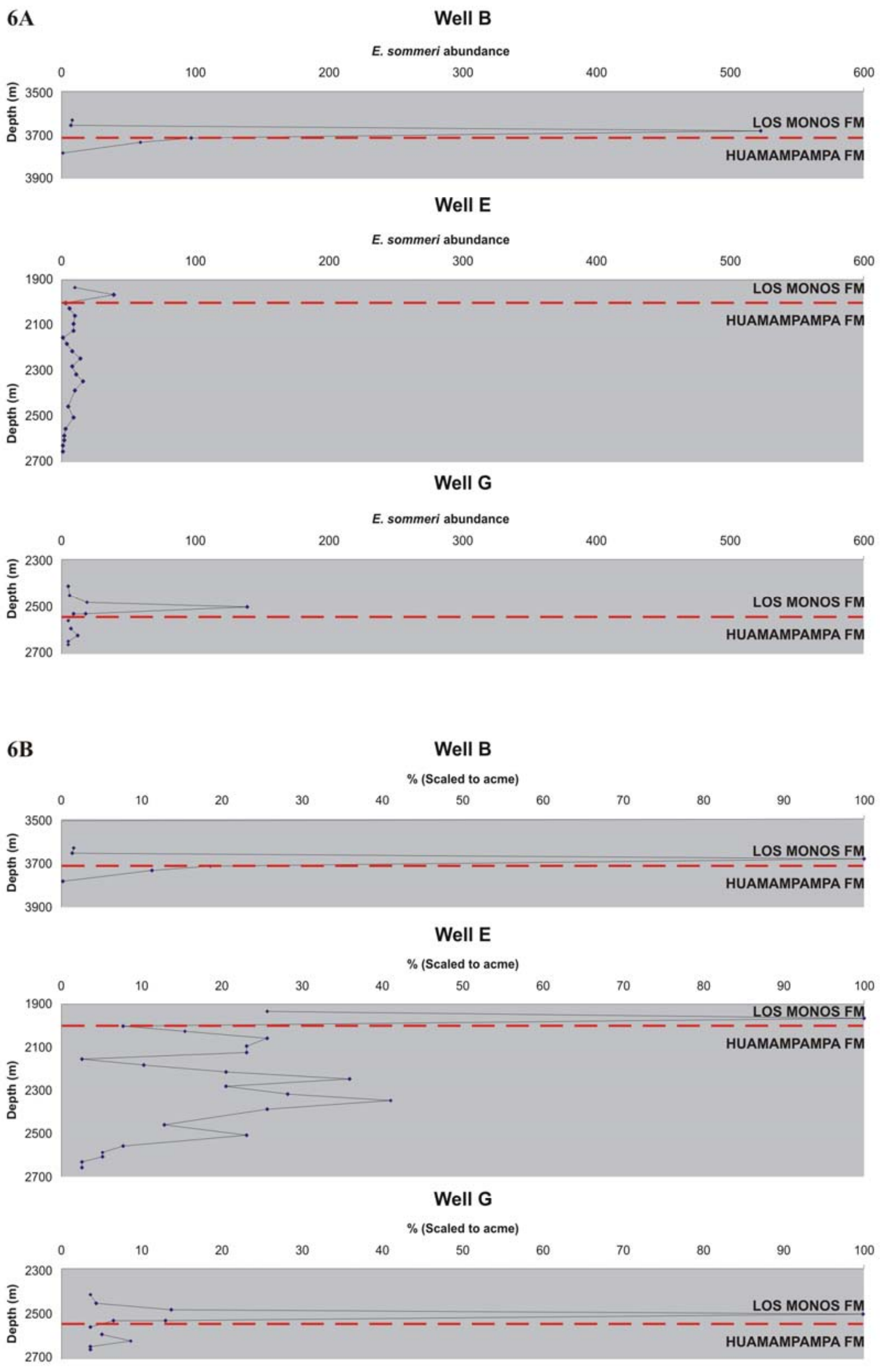


Fig. 3.10. The *E. sommeri* Epibole in three selected wells (6A). Note how the *E. sommeri* Epibole is in a similar stratigraphic position in the three wells. In Well E, the total range of *E. sommeri* is much more extended relative to Bermejo and the other wells. The extension of the range could be attributed to cavings and/or structural repetition. In 6B the number of specimens in each sample is scaled to the acme since the way in which specimens were counted in these wells was not uniform, i.e. in Well B every *E. sommeri* specimen on a slide was counted but this was not the case for the other wells.

3.5.2 Associated palynomorphs

The palynomorph assemblage associated with the *E. sommeri* Epibole (**Plate 3**) comprises long-ranging acritarchs including: *Diexallophasis simplex*, *Estiastra rhytidoa*, *Exochoderma arca*, *Multisplicisphaeridium ramusculosum*, *Navifusa bacillum*, *Triangulina alagarda* and *Veryhachium trispinosum*; the chitinozoa *Ancyrochitina* sp. 1 and *Ramochitina* sp. 1 (described in **Chapter 4**) and common prasinophytes such as *Duvernaysphaera angelae* and leiospheres. These palynomorphs are found in association with common large camerate spores.

3.5.3 Age of the *E. sommeri* Epibole

The *E. sommeri* Epibole occurs 30m below the first occurrence of *Alpenachitina eisenacki*, a cosmopolitan early Eifelian-early Givetian taxon (Burjack & Paris, 1989) and the epibole is therefore assigned an earliest Eifelian age.

3.5.4 Geographical distribution of the *E. sommeri* Epibole

The *E. sommeri* Epibole has been identified in the subsurface throughout central and southern Bolivia and northern Argentina, with representative expressions of this epibole from three widely spaced wells shown in **Figure 3.10**. *E. sommeri* was also recovered from Los Monos Formation-equivalent shaly facies (see **Section 3.8**) at Campo Redondo and Cha-Kjeri, Chiquisaca Province, where it is associated with the same palynomorph assemblage seen at Bermejo. Spot samples collected by Dr. John Marshall (National Oceanography Centre, Southampton) at Ayo Ayo on the Altiplano from the Belén Formation (**Figs. 3.11, 3.13**; Díaz-Martínez *et al.*, 2000) yielded some degraded *E. sommeri* specimens, again associated with a palynomorph assemblage similar to Bermejo. However, the *E. sommeri* Epibole could not be defined precisely due to the low sample density. More detailed sampling at these localities should prove the presence of the *E. sommeri* Epibole.

The type material of *E. sommeri* comes from 1646-1648m depth (Core 48) in Petrobras Well 2-PM-1-MA in the Parnaíba Basin NE Brazil (Brito, 1967; **Chapter 1, Fig. 1.7**). This occurs within a transgressive black shale in the basal Pimenteira Formation which marks an Eifelian marine transgression (Melo, 1988). The Pimenteira Formation at this level can therefore be considered a lateral equivalent of the basal Los Monos Formation and also has a palynomorph assemblage that is very similar to that seen in Bolivia (**Plate 3**). Using spores, Loboziak *et al*. (1992) dated this level in Well 2-PM-1-MA to the Eifelian AD pre lem biozone consistent with the age assigned to *E. sommeri* in Bolivia. The similarity in environment, palynological assemblage and age for both Brazil and Bolivia suggests this event may represent a synchronous marine transgression that took place across South America during early Eifelian time.

3.6 Correlation of Bermejo with other Devonian sections in Bolivia

With an integrated lithostratigraphic and biostratigraphic framework in place at Bermejo it is now possible to more accurately correlate this section with other Devonian sections in Bolivia. Direct correlation using the basal Los Monos Formation (*E. sommeri* Epibole marine transgression) at Bermejo was successful at Campo Redondo and Cha-Kjeri outcrop sections. A revision of the unpublished (but accepted) formation assignments was necessary at Cha-Kjeri to avoid confusion and this has been discussed in **Section 3.2.4.** The samples collected at Ayo Ayo on the Altiplano were used to make a preliminary correlation with the other studied sections (**Fig. 3.11**) and a subsequent revision of the Devonian chronostratigraphy (**Fig. 3.12**).

3.6.1 Implications for Devonian chronostratigraphy in Bolivia

Age assignments for the Devonian formations in Bolivia are shown in **Figure 3.12**. Large differences in opinion regarding age assignments of these formations are due mainly to poorly-defined lithostratigraphy and little or no supporting biostratigraphy. These factors are highlighted when considering the variable ages given to the Huamampampa Formation. The discovery of a single goniatite, *Tornoceras bolivianum*, in the basal Huamampampa Formation at Campo Redondo (Hünicken *et al.*, 1980) was considered a major breakthrough since Devonian goniatites are rare in South America and are important for dating Devonian marine sequences in Euramerica.

T. bolivianum was assigned to the Givetian/Frasnian based on its presumed affinities with the cosmopolitan Mid to Late Devonian genus *Tornoceras*. Despite being a tornoceratid, the generic assignment of this specimen is no longer thought to be valid but its age is still currently accepted (Prof. R.T. Becker *pers. comm.,* 2004). The Huamampampa Formation has therefore been consistently dated as Mid Devonian because of the chronostratigraphic importance placed this single specimen of *T. bolivianum*. To accommodate this Mid Devonian age for the Huamampampa Formation an hiatus was commonly placed within the Lower Devonian (**Fig. 3.12**). Some workers cite the Hünicken *et al.*(1980) specimen as signalling the break up of the cold water Malvinokaffric Realm during the Givetian and Frasnian allowing an influx of warm water goniatites, and this assertion is again based on the presumed Mid Devonian age of *T. bolivianum* (e.g. Boucot, 1988).

The stratigraphic level from which *T. bolivianum* was recovered at Campo Redondo is reasonably well constrained and consequently, the palynology of Campo Redondo was investigated to determine if the lithostratigraphy of this level, and therefore the dating of this specimen, was correct. During sampling at Campo Redondo, another as yet unidentified, goniatite (**Fig. 3.14**) was recovered from a nodular horizon approximately 15m above the presumed level of the Hünicken *et al.* (1980) specimen. However, both this level and the *T.*

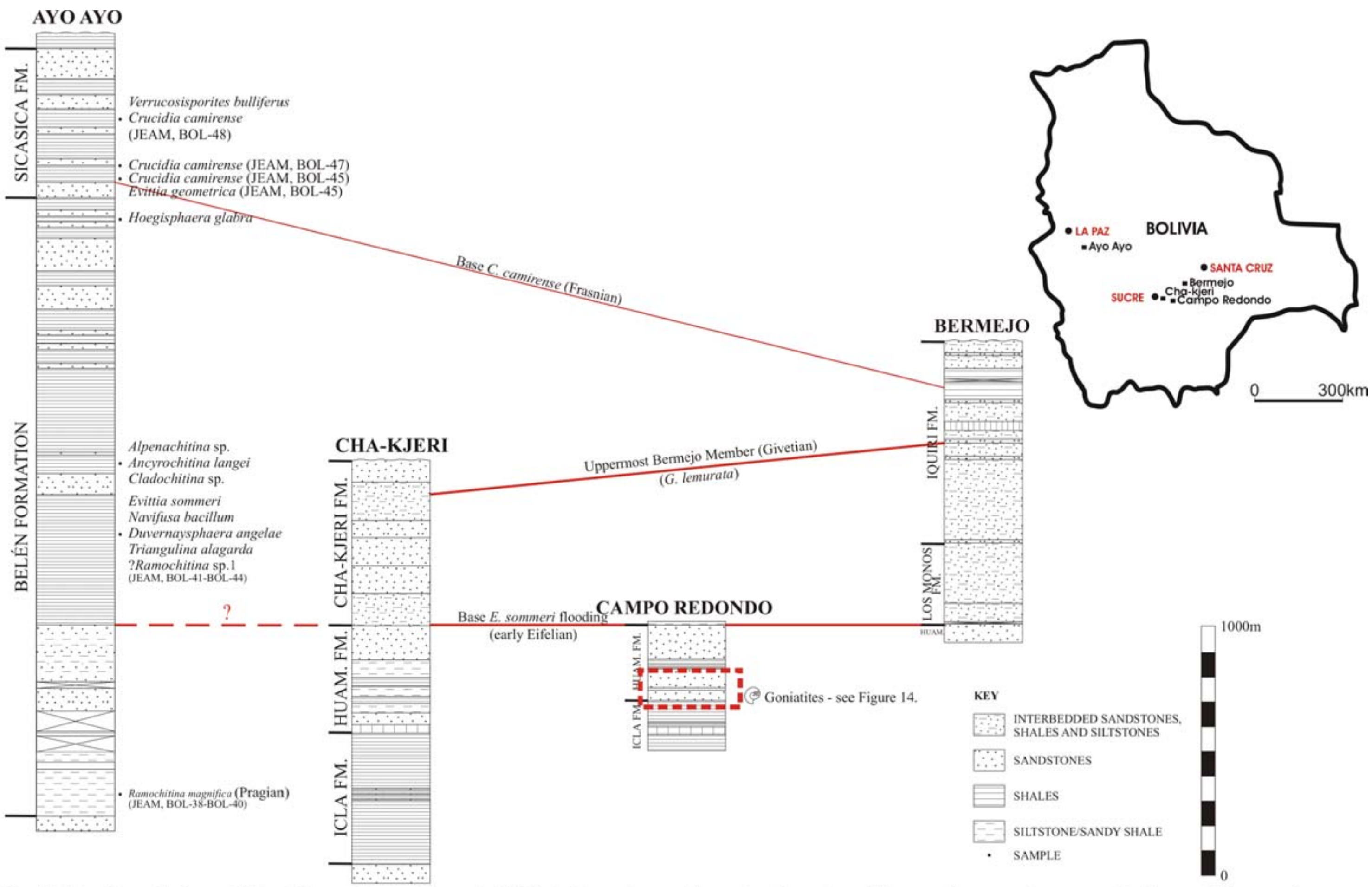


Fig. 3.11. Correlation of four Devonian sections in Bolivia based on palynostratigraphy. The sections are hung on the base of the marine transgression associated with *E. sommeri*. The log for Ayo Ayo has been modified from Isaacson (1977a) and samples not marked JEAM are from Racheboeuf *et al.* (1993). The presence of *H. glabra* stratigraphically below *C. camirense* is the reverse of Bermejo and it is possible that this is not *H. glabra* s.s. (see Systematic Palaeontology). Accordingly, the presence of *C. camirense* is considered a more reliable pick for the base of the Frasnian.

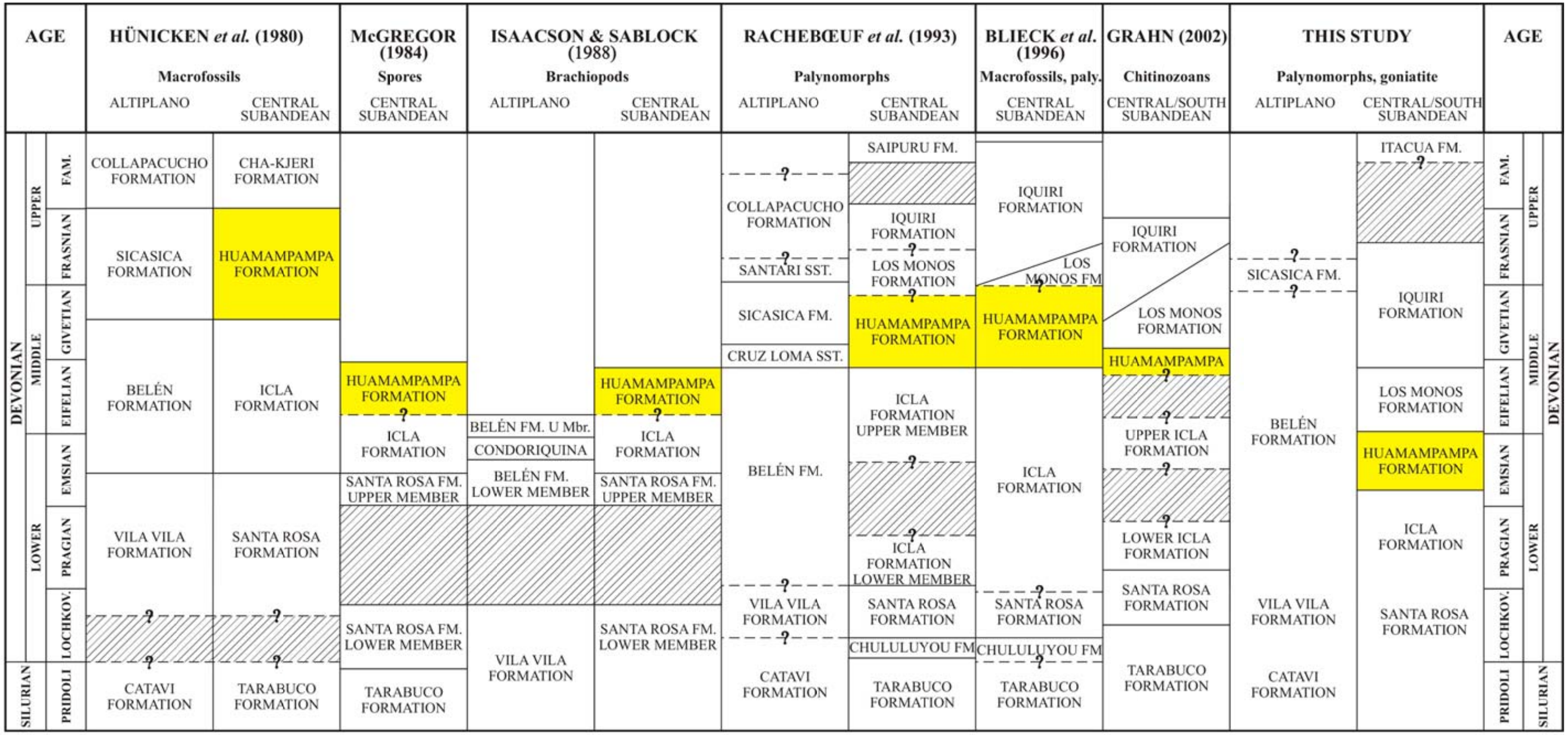


Fig. 3.12. Summary of age assignments for the Devonian formations in the Subandean and Altiplano. Note how the ages placed on the Huamampampa Formation have varied. This variation is largely attributable to an incorrectly dated goniatite in the central Subandean Campo Redondo section (Hünicken *et al.*, 1980) in addtion to poorly integrated lithostratigraphy and biostratigraphy.

bolivianum level were palynologically barren. A sample (CMR 69) taken from the lower Huamampampa Formation approximately 135m above the stratigraphic level that the goniatite in this study was found, yielded *Dictyotriletes emsiensis* and *Camarozonotrilites sextantii* (**Fig. 3.14**), an association no younger than mid Emsian (Richardson & McGregor, 1986). The occurrence of *E. sommeri* and associated palynomorph assemblage 160m stratigraphically higher than CMR 69 further constrains the age of the Huamampampa Formation as mid Emsian to early Eifelian. Therefore, *T. bolivianum* also has to be Emsian and subsequently there is therefore no reason to place a hiatus within the Lower Devonian in Bolivia on account of this goniatite.

According to Grahn (2002), the Huamampampa Formation at Tarabuco, Chiquisaca Province contains a chitinozoan fauna including *Alpenachitina eisenacki* and *Ancyrochitina postdesmea*, a view supported by Racheboeuf *et al.* (1993) who report *A. eisenacki* 25m above the base of the Huamampampa Formation at Presto, Chiquisaca Province. This study demonstrates that *A. eisenacki* is restricted to the Eifelian and *A. postdesmea* is a short lived Givetian taxon (**see Chapter 4**). These taxa are restricted to the Los Monos and Iquiri Formations respectively at Bermejo and therefore the samples in Grahn (2002) and Racheboeuf *et al.* (1993) could not have come from the Huamampampa Formation. Grahn (2002) concluded that the Los Monos/Iquiri Formation boundary was diachronous in order to accommodate a late Eifelian/early Givetian Huamampampa Formation and explain the presence of early Givetian chitinozoans in both the Los Monos and Iquiri Formations. The Los Monos/Iquiri Formation does not need to be diachronous based on the biostratigraphic and lithostratigraphic data from Bermejo, since the Los Monos Formation is Eifelian and the Iquiri Formation is Givetian/Frasnian. Consequently, the age assignments used in Grahn (2002) are questionable on the grounds of suspect lithostratigraphy.

3.7 Summary

In order to validate subsurface biostratigraphy and improve Devonian chronostratigraphy in Bolivia, a detailed palynological study of the Mid to Late Devonian section exposed at Bermejo, Santa Cruz Province was undertaken. The Bermejo section ranges from latest Emsian to mid Frasnian. Biostratigraphic markers identical to those observed in the subsurface were identified and the *E. sommeri* Epibole was shown to represent a single, short-lived but, geographically widespread event that is always found in the basal Los Monos Formation or lateral equivalent. The biostratigraphic data obtained from Bermejo was integrated with lithostratigraphy and correlated with other Devonian sections at Campo Redondo, Cha-Kjeri and Ayo Ayo using the base of the transgressive shale facies associated with the *E. sommeri* Epibole as a datum. Devonian chronostratigraphy and lithostratigraphy in Bolivia were reviewed and problems with formation age assignments demonstrated.

Palynology proved that there was no reason to place an hiatus within the Lower Devonian on account of a single assumed Givetian/Frasnian goniatite since the specimen is in fact Emsian. The need for a diachronous Los Monos/Iquiri Formation has also now been demonstrated to be unnecessary.

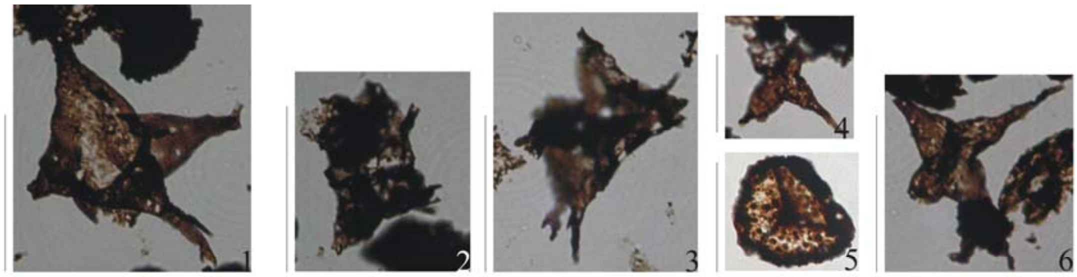


Fig. 3.13. Palynomorphs from Ayo Ayo (see also Figure 11). Scale bar 50µm apart from (4) = 25µm

1) *Evittia geometrica* Playford & Dring, 1981. JEAM BOL-45.
2) *Evittia sommeri* Brito, 1967. JEAM BOL-42.
3) *Evittia sommeri* Brito, 1967. JEAM BOL-43.
4) *Crucidia camirense* Ottone, 1996. JEAM BOL-48.
5) *Verrucosisporites bulliferus* (Taugourdeau-Lantz) Richardson & McGregor, 1986. JEAM BOL-48.
6) *Crucidia camirense* Ottone, 1996. JEAM BOL-47.

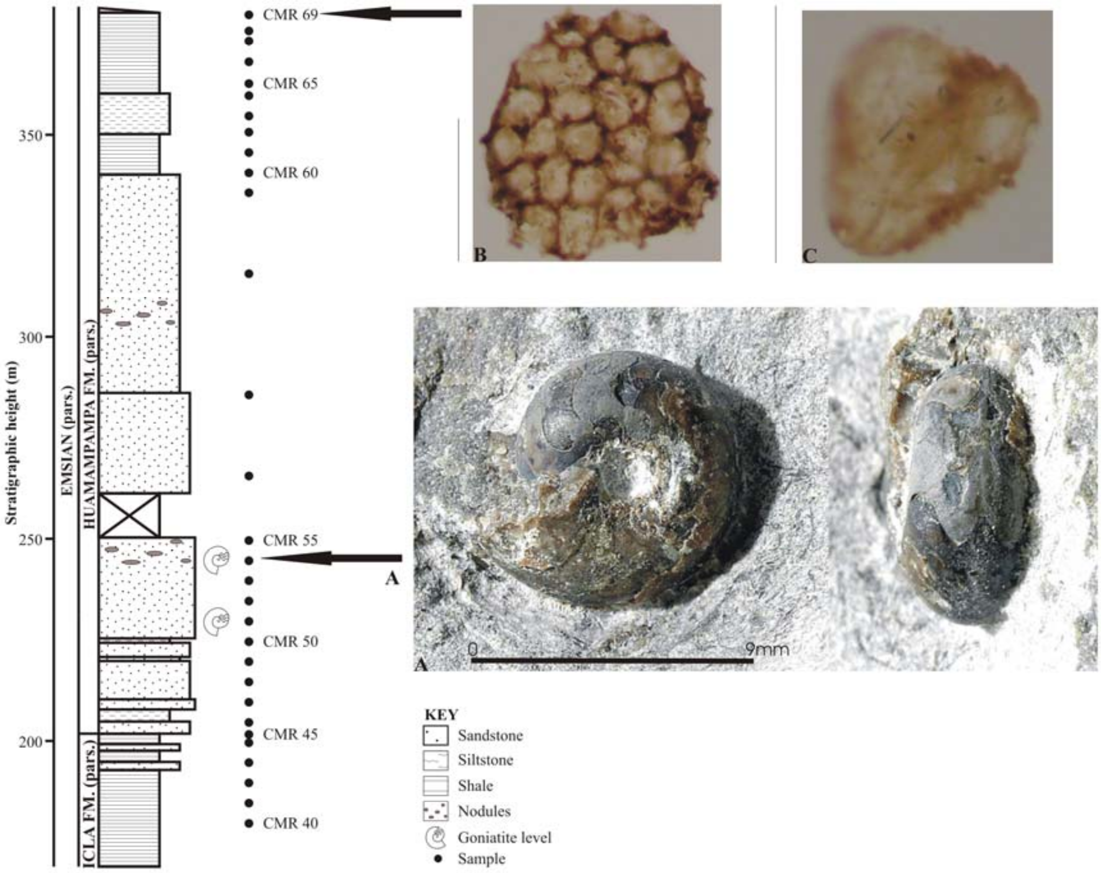


Fig. 3.14. Partial log of Campo Redondo (see Figure 11 for red box marking log position) showing the stratigraphic position of the goniatite recovered in this study (A). The lower goniatite on the log marks the interpreted position of the Hünicken *et al*. (1980) specimen. Figs B and C are *Dictyotriletes emsiensis* and *Camarozonotriletes sextantii* from CMR 69, an association that cannot be younger than mid Emsian (Richardson & McGregor, 1986). Scale bar for spores is 50µm.

3.8 Systematic palaeontology

Group Acritarcha Evitt, 1963

Genus **EVITTIA** Brito emend. Lister, 1970; Sarjeant & Vavrdová, 1997

Type species. *Evittia sommeri* Brito, 1967

Emended diagnosis. (After Sarjeant & Vavrdová, 1997). Vesicle hollow, subpolygonal to polygonal; wall single layered or apparently so. Wall surface laevigate, granulate or echinate. Number of processes low (ca. 4-12), their broad bases modifying but not controlling the vesicle outline. Processes always broad and short, dividing into a low number of rather blunt branches, sometimes secondarily branched but not showing ramification. The processes are hollow, their cavities communicating directly with the vesicle cavity. Excystment by cryptosuture, apical or near equatorial.

Discussion. According to Playford & Dring (1977) *Exochoderma* is the junior synonym of *Evittia* because *E. geometrica* spans the morphological variation proposed by Wicander (1974) to distinguish the two genera, i.e. processes that are easily distinguishable from the vesicle and the method of bifurcation at the distal tip of processes (compare **Pl. 1, fig. 18** with **Pl. 1, fig. 19**). Based on this view and the similarities between *E. sommeri* and *E. geometrica,* the suggestion of *Exochoderma* becoming a junior synonym of *Evittia* is regarded as valid but requires formal publication.

Evittia sommeri Brito, 1967 Pl. 1, figs. 1-8, Pl. 2, figs. 9-13

1966: *Evittia sommeri* Brito, p. 78 *nomen nudum*.
1967: *Evittia sommeri* n. sp. Brito, p. 477, Pl. 1, figs. 9–12.
? 1969: *Baltisphaeridium* sp. – Cramer, Pl. 4, fig.42.
? 1970: *Baltisphaeridium sommeri* comb. nov. Cramer, p. 183–184, fig. 59c.
1973: *Multisplicisphaeridium sommeri* comb. nov. Eisenack, Cramer & Diez p. 799–800.
1982: *Evittia sommeri* Brito – Quadros, p. 47, Pl. 6, fig. 27.
1988: *Evittia sommeri* Brito – Quadros, Pl. 3, fig. 18.
? 1996: *Evittia sommeri* Brito – Vavrdová, Bek, Dufka & Isaacson, Pl. 1, fig. 7.
? 1997: *Evittia sommeri* Brito – Sarjeant & Vavrdová, Pl. 4, fig. 5, text-fig. 3a.
? 1997b *Evittia sommeri* Brito – Loboziak, Melo, Quadros & Streel, Pl. 2, fig. 8.
1999: *Evittia sommeri* Brito – Quadros, Pl. 3, fig. 26.

Holotype. Slide I-7-66, Well 2PM-1-MA, core 48 (1646-1648m), Parnaíba Basin, NE Brazil. D.G.M.; D.N.P.M., Rio de Janeiro.

Diagnosis. (After Brito, 1967). Vesicle triangular, quadrangular or polygonal, with a relatively short process at each corner. Each process has two to six short ramifications. Wall relatively thick and microverrucate. Size of the vesicle about 50-60µm. Thickness of wall about 1 to 1.5µm.

Description. Vesicle originally polyhedral in the form of a trigonal bipyramid or tetragonal bipyramid. Outline triangular, quadrate, rarely pentagonal or hexagonal; sides slightly concave or straight. Vesicle wall granate/echinate or smooth, approximately 0.5µm thick in optical section. Major processes occur at vesicle apices, having a rounded or angular contact with vesicle wall. Processes are subcylindrical hollow extensions of vesicle with simple, bifurcate (up to second order) or rarely digitate morphologies. Bifurcation is typically asymmetrical. Primary bifurcation occurs commonly near the proximal termination of the processes but can take place more distally. Distal terminations are sharp conical to bluntly rounded. Excystment structure, rarely observed, consists of a simple slit in vesicle wall.

Measurements (± 2.5 µm). 72 specimens measured. Maximum diameter 55(102)138µm, diameter of vesicle 47.5(68.8)100µm, length of processes 5(18)27µm, process base width 3(3)7µm.

Discussion. Topotype material from Well 2PM-1-MA was kindly donated by José Henrique Melo (Petrobras, Brazil) for comparison and is figured on **Plate 1, figs. 9-13.** The topotype material is lower in maturity than that from Bermejo (**compare Plate 1, figs. 9-13 with Plate 1, figs. 1-8**) and consequently it is easier to identify features on the vesicle wall. *E. sommeri* is similar to the Late Devonian *Evittia geometrica* Playford & Dring, 1981 (**Pl. 1, figs. 14-18**) but differs in having short, proximally branched processes that lack coarse granulate ornamentation (**Pl. 1, fig. 13**). In addition, *E. geometrica* is restricted to the Frasnian at Bermejo whereas *E. sommeri* as described herein is restricted to the latest Emsian/Eifelian. In Brazil, *E. sommeri* may have been mistaken for *E. geometrica* hence the much longer stratigraphic range reported there (Emsian-Famennian (Strunian), see Quadros, 1982; 1988). This explanation is probable for the specimen reported as *E. sommeri* in Loboziak *et al*. (1997b) in the Caima PH-2 Well, in the Amazonas Basin, although the illustration of this specimen is of insufficient resolution to examine vesicle sculpture.

The specimen referred to as *E. sommeri* in Vavrdová *et al*. (1996) and also refigured in Sarjeant & Vavrdová (1997) presents a problem. This specimen was recovered from core in the Pando X-1 well in northern Bolivia at 1914.4m depth dated on the presence of Early Devonian acritarchs and spores as Lochkovian/Pragian. Explaining the substantial stratigraphic separation between this specimen and those described herein is difficult. Based on evidence from the Bermejo, Campo Redondo and Cha-Kjeri sections (this study) the stratigraphic range of *E. sommeri* is restricted and does not extend below the latest Emsian. In the subsurface of southern and central Bolivia, *E. sommeri* is not observed sub-Huamampampa Formation unless caved (BG, *pers. comm.* 2005). The specimen in Vavrdová *et al*. (1996) thus requires further study. A sample from 1932m in Pando X-1 was obtained from Dr. Milada Vavrdová but this did not yield *E. sommeri* or any of the associated palynomorphs (**Plate 3**).

The location of the slide containing the only recorded specimen of *Baltisphaeridium sommeri* (Brito) Cramer, 1969 is lost and the illustration of this acritarch is poor so it is unclear whether *B. sommeri* is conspecific with *E. sommeri*.

Occurrence at Bermejo. *E. sommeri* is present in samples CGH 18-CGH 57 (102m of section) in the Los Monos Formation and the acme of this species (= *E. sommeri* Epibole) is in CGH 27 where there are ca. 12900 specimens g^{-1} of sample. The oldest occurrence of the cosmopolitan chitinozoan *Alpenachitina eisenacki* Dunn & Miller 1964 is in CGH 46 (**Section 3.4.1, Fig. 3.6**). In the USA, the base of the *A. eisenacki* range is in the *partitus* Conodont Zone (**Section 3.4.1, Fig. 3.7;** Paris *et al.*, 2000; Wright, 1980) in the early Eifelian. The first occurrence of the basal Givetian marker *Geminospora lemurata* (**Section 3.4.1, Figs. 3.6-7**) is 280m above the *E. sommeri* Epibole in CGH 77. Accordingly the total range of *E. sommeri* at Bermejo is early/mid Eifelian.

Global occurrence. *E. sommeri* is also known from Campo Redondo and Cha-Kjeri, Chiquisaca Province, Bolivia. At both localities, *E. sommeri* is associated with the same palynomorphs as at Bermejo and is also of early/mid Eifelian age. Poorly preserved specimens were also noted in the Belén Formation at Ayo Ayo, La Paz Province, during this study (**Figs. 3.11, 3.13**). *E. sommeri* has been found in the subsurface throughout Bolivia and northern Argentina (Marshall *et al.*, in prep.) again associated with a similar assemblage to Bermejo. In Brazil, *E. sommeri* was reported from the Solimões and Parnaíba Basins (Brito, 1967; Quadros 1982, 1988) where its range is questionably Emsian to Famennian (Strunian). Cramer (1969) reported a specimen of *Baltisphaeridium sommeri* (Brito) from an Eifelian road section at San Roque (near San Roman), west of Oviedo in NW Spain. This section and several other time equivalent sections to the basal Los Monos Formation in NW Spain, Morocco and the UK were sampled in detail during this study for *E. sommeri* but no specimens were recovered (**see Chapter 6**).

Genus **BIMERGA** Wood, 1995

Type species. Bimerga bensonii Wood, 1995

Diagnosis. (From Wood, 1995). Vesicle elongate, bilaterally symmetrical; vesicle poles bisected into two broad-based processes. Processes open to the vesicle interior, heteromorphic or homomorphic with simple or branched terminations. Vesicle and process wall unilayered; surface ornamented with grana and/or striations. Excystment structure not observed.

Discussion. *Bimerga* differs from other acritarch genera (see Wood, 1995) in terms of being much more elongate and having a distinctive ‘pitch-fork’ arrangement of processes at both vesicle poles.

Bimerga bensonii Wood, 1995 Pl. 1, figs 20-22

1974: *Leiofusa* sp. 2, Anan-Yorke, p. 128, Pl. 24, fig. 8.
1995: *Bimerga bensonii* n. sp. Wood, p. 227, Pl. 1, figs. 1–3.

Holotype. ‘Los Monos Formation’, Bermejo, Santa Cruz Province, Bolivia. Slide 35226-A-1, Leitz Orthoplan coordinates 6.2/107.7, England Finder coordinates Q5-4; Ohio State University, Orton Museum Type No. 48234.

Diagnosis. (After Wood, 1995). Vesicle elongate, bilaterally symmetrical, vesicle poles bisected into two broad based, equifurcate processes. Processes open to the vesicle interior, heteromorphic or homomorphic with simple, bifurcate, or multifurcate processes. Granulate ornament present, usually more dense at the base of the processes and scattered elsewhere on the vesicle. Faint longitudinal striations are present on the vesicle but absent on the processes. No excystment structure observed.

Measurements (± 2.5 µm). 9 specimens measured. Maximum length 188(198)220µm, maximum vesicle width 21(32)46µm, maximum process length 53(67)77µm, maximum process width 7(9)14µm.

Remarks. The specimens examined in this study conform to the original description of *B. bensonii* in Wood (1995) although striations on the vesicle are difficult to resolve. Granulate ornamentation is common (**Plate 1, fig. 22**).

Occurrence at Bermejo. B. bensonii is found in the uppermost Los Monos and basal Iquiri formations in the sample range CGH 71-CGH 79 (38m thickness) with the maximum abundance of this taxa (approximately 400 specimens g^{-1}) occurring in CGH 79. The oldest occurrence of the basal Givetian marker *Geminospora lemurata* (**Section 3.4.1**, **Fig. 3.6**) is in CGH 77, and since the first occurrence of *B. bensonii* is ca. 30m beneath that of *G. lemurata* the total range of *B. bensonii* is therefore latest Eifelian/earliest Givetian. The type material of *B. bensonii* is also from Bermejo but its precise stratigraphic position is difficult to identify based on the stratigraphic log in Wood (1995). According to Wood (1995) the type material was from a spot sample taken ‘265m below the top of the Los Monos Formation’ but Wood (1995) places the top of this formation much higher stratigraphically than in this study where, it is at the level of CGH 75 (**Section 3.4.1, Fig. 3.6**) based on sedimentology (**see Section 3.2.1**). *B. bensonii* is shown herein to be restricted stratigraphically to a 40m thick interval at Bermejo, so the spot sample in Wood (1995) must lie within the sample range CGH 71-CGH 79.

Global occurrence. *B. bensonii* is also known in the subsurface of both southern Bolivia and Ghana (Anan-Yorke, 1974) where it was assigned to the Eifelian/Givetian D_3, D_4 and $D4_b$ zones of Lange (1967a).

Genus **CRUCIDIA** Ottone, 1996

Type species. *Crucidia camirense* (Lobo Boneta) comb. nov. emend. Ottone, 1996.

Diagnosis. (After Ottone, 1996). Acritarchs cross- or x-shaped, consisting of four subcylindrical, hollow, homomorphic or near homomorphic processes, normally disposed in the same plane. No discrete vesicle discernible. Process interiors open into and communicate freely with the central cavity. Processes terminate in a digitate, occasionally furcate tip. Wall single layered, sculptured by echinae, grana or longitudinal ridges. Excystment by simple rupture of the vesicle wall.

Discussion. The distinctive 'X' shape and absence of a clearly defined vesicle differentiate *Crucidia* from all other acritarch genera (see Ottone, 1996).

Crucidia camirense (Lobo Boneta) comb. nov. emend. Ottone, 1996 Pl. 1, figs. 23-24, Pl. 2, figs. 1-8**.**

1975:	*Veryhachium camirense*, Lobo Boneta, p. 163, Pl. 1, figs. 5–8 *nomen nudum* see Fensome *et al.* (1990).
1996:	*Crucidia camirense* n. sp. Ottone, p. 122, Pl. 5, figs. 1–9.
? 1999:	*Cruzidia camirense* Ottone – Díaz-Martínez, Vavrdová, Bek & Isaacson, Pl. 1, fig. 4.

Holotype. Slide BAFC-P1 857(5), Leitz Orthoplan coordinates 33.2/112.6, Quebrada Galarza well, Tarija Basin, Argentina. Geological Science Department, Buenos Aires University, Argentina.

Diagnosis. (Modified after Ottone, 1996). Acritarchs cross- or 'X'-shaped comprising four homomorphic or near-homomorphic, hollow processes disposed in the same plane. The process bases are circular, 12(18-23)27µm in diameter. Overall, the processes are cricket-bat shaped in outline, cylindrical, parallel-sided up to about half of the distance from base to distal extremity where a shoulder is developed. Distally, the processes taper rapidly and terminate in a digitate or sometimes bifurcate tip. Process extremities normally show two to five simple, solid or party hollow digitations, 1-1.5µm in basal diameter, 2-2.5µm in height. Wall approximately 0.5µm thick and ornamented with sparse or densely distributed echinae/granae up to 1.5µm long. Specimens may also have discontinuous, fine longitudinal ridges that are usually more clearly developed on the distal portion of the processes. Excystment structure rarely observed but consists of a simple rupture in the vesicle wall.

Measurements (± 2.5 µm). 10 specimens measured. Overall diameter 150(165)173µm, length of processes 35(44)57µm, basal process width 17(23)33µm.

Discussion. The specimens from Bermejo are in agreement with the description in Ottone (1996) but generally lack the fine longitudinal ridges on the processes. In most cases the Bermejo specimens have a covering of sparsely distributed grana on the vesicle wall (**Pl. 2, figs. 7-8**). Plate 1, Figure 4 in Díaz-Martínez *et al.* (1999) could be *C. camirense*, but the photograph is poor and the specimen is incomplete.

Occurrence at Bermejo. *C. camirense* is restricted to the Iquiri Formation in the sample range CGH 117-CGH 123 (49m thick interval). The acme of this species (approximately 2350 specimens g^{-1}) is in CGH 121. *Verrucosisporites bulliferus* (**Section 3.4.1, Fig. 3.6**), an early Frasnian marker species in Euramerica, is found in samples CGH 117-CGH 121 and therefore *C. camirense* is also early Frasnian in age.

Global occurrence. *C. camirense* has been recorded from the Iquiri Formation in the Subandean of Bolivia by Lobo Boneta (1975) and also in the Sicasica Formation at Ayo Ayo, La Paz Province (this study; **Figs. 3.11, 3.13**) This species is also common in the subsurface throughout southern and central Bolivia (Marshall *et al*., in prep.). Ottone (1996) recorded *C. camirense* in the subsurface of northern Argentina in the Quebrada Galarza well where he assigned it a Givetian/Frasnian age. The specimens in Ottone (1996) came from cuttings samples that were extensively contaminated by uphole cavings and consequently the total stratigraphic range of *C. camirense* could have been extended in this well.

Phyllum Chlorophyta Pascher, 1914
Order Chlorococcales (Marchand) Pascher, 1915
Family Hydrodictyaceae (Gray) Dumortier, 1829
Genus **PETROVINA** Oliveira & Burjack, 1996

Type species. Petrovina connata Oliveira & Burjack, 1996.

Diagnosis. (Translated and modified from Oliveira & Burjack, 1996). A colonial organism, consisting of a circular colony with a lobed outline and radial symmetry formed of six to seven units joined and disposed in the same plane. The units are joined laterally resulting in a central lumen of variable shape. The distal extremities of the units are unattached but where the units attach proximally, there is a ring shaped thickening of the test. There is no open communication between the elements in the colony. The individual units are identical, hollow spherical or ovoid (sub-circular or elliptical) in shape. The test of the units is thin and can be smooth or ornamented with microgranules. The mechanism of excystment results in the formation of a type of cryptopylome.

Discussion. *Petrovina* forms concentric rings similar to *Pediastrum* (see Pl. 1, fig. 2 in Batten, 1996) but the individual cells forming the rings of *Petrovina* are commonly ovoid rather than triangular. *Pediastrum* also forms colonies usually comprising 4-128 cells but this has not been observed with *Petrovina*, although this could be a result of palynological processing. In terms of morphologically, *Petrovina* is very distinctive with nothing similar being observed throughout the Devonian of South America or elsewhere.

Petrovina connata Oliveira & Burjack, 1996 Pl. 2, figs. 9-12

1996:	*Petrovina connata* n. sp. Oliveira & Burjack, p. 147, Pl. 1, figs. 1–6; Pl. 12, figs. 1–2.
1997b:	*Petrovina connata* Oliveira & Burjack – Loboziak, Melo, Quadros & Streel, Pl. 2, fig. 12.
2000:	*Petrovina connata* Oliveira & Burjack – Le Hérissé, Servais & Wicander, Pl. 1, fig. 1.

Holotype. Slide DGUFG-55, England Finder coordinates N44/1, Departamento de Geografia do Instituto de Química e Geociências da Universidade Federal de Gois, Brazil.

Diagnosis. (Translated and modified from Oliviera & Burjack, 1996). Circular shaped colonial organism with radial symmetry and a lobate outline. The colony is formed of seven, or rarely, six units joined together in the same plane with the join between individual units usually found in the medio-proximal region, leaving the distal extremity of a unit unattached. The spatial distribution of the units results in the formation of a central circular or star shaped lumen. There is a definite ring shaped thickening (14µm in diameter) of the unit wall where two units attach. Individual units are hollow, spherical or ovoid (sub-circular or elliptical) in shape with a relatively thin smooth or microgranulate test. The microgranules are more developed on the distal and proximal edges of the units. On the distal extremity of the various units is a basic circular opening (cryptopylome) suggestive of an excystment structure.

Measurements (± 2.5 µm). 10 specimens measured. Maximum diameter 88(114)153µm, length of units 40(44)57µm, width of units 27(37)43µm.

Discussion. The ring shaped thickening of the test between the units described by Oliveira & Burjack (1996) could not be identified on the Bermejo specimens. In all other respects, the specimens from Bermejo conform to the description of the type material.

Occurrence at Bermejo. *P. connata* is present in the Iquiri Formation in a 45m interval comprising samples CGH 127-CGH 133 (with the acme of this species occurring in CGH 129 at ca. 5100 specimens g^{-1}). A single specimen was recorded in CGH 116 but overall *P. connata* is considered a Frasnian species herein based on its Frasnian acme in CGH 129 (the inception of the early Frasnian marker *V. bulliferus* is in CGH 117, 5m above CGH 116) and its stratigraphic range in Brazil.

Global distribution. *P. connata* is known from the subsurface in the Paraná Basin, southern Brazil (Oliviera & Burjack, 1996) and has been recorded, but not figured, in the subsurface of the Amazonas Basin, northern Brazil (Le Hérissé, 2001; Loboziak, 1997a). In both basins *P. connata* is assigned a Frasnian age.

Plate 1

Black scale bar = 50µm.
Scale bar = 35µm (Figs. 13,18-19)

1. *Evittia sommeri* Brito, 1967. Los Monos Formation, CGH 27/1197.3m, coordinates 17.4/105.
2. *Evittia sommeri* Brito, 1967. Los Monos Formation, CGH 27/1197.3m, coordinates 22.8/104.6.
3. *Evittia sommeri* Brito, 1967. Los Monos Formation, CGH 27/1197.3m, coordinates 28.2/105.
4. *Evittia sommeri* Brito, 1967. Los Monos Formation, CGH 22/1203.4m, coordinates 38.2/103.4.
5. *Evittia sommeri* Brito, 1967. Los Monos Formation, CGH 38/1172m, coordinates 15.8/94.6.
6. *Evittia sommeri* Brito, 1967. Los Monos Formation, CGH 27/1197.3m, coordinates 17.3/97.3.
7. *Evittia sommeri* Brito, 1967. Los Monos Formation, CGH 39/1170.8m, coordinates 7.1/94.9.
8. *Evittia sommeri* Brito, 1967. Los Monos Formation, CGH 27/1197.3m, coordinates 25.1/102.5.
9. *Evittia sommeri* Brito, 1967. Topotype material. Pimenteira Formation, Brazil1/1646.6m Well 2-PM-1-MA, Parnaíba Basin, NE Brazil, coordinates 24.1/112.9.
10. *Evittia sommeri* Brito, 1967. Topotype material. Pimenteira Formation, Brazil2/1646.6m Well 2-PM-1-MA, Parnaíba Basin, NE Brazil, coordinates 20/104.
11. *Evittia sommeri* Brito, 1967. Topotype material. Pimenteira Formation, Brazil2/1646.6m Well 2-PM-1-MA, Parnaíba Basin, NE Brazil. E.F. coordinates 20.9/112.3.
12. *Evittia sommeri* Brito, 1967. Topotype material. Pimenteira Formation, Brazil2/1646.6m Well 2-PM-1-MA, Parnaíba Basin, NE Brazil, coordinates 17.2/98.6.
13. Process detail on *Evittia sommeri* Brito, 1967. Topotype material. Pimenteira Formation, Brazil1/1646.6m Well 2-PM-1-MA, Parnaíba Basin, NE Brazil.
14. *Evittia geometrica* Playford & Dring, 1981. Iquiri Formation, CGH 137/148.7m, coordinates 17.7/106.8. Note small tubercules/granae (arrow).
15. *Evittia geometrica* Playford & Dring, 1981. Iquiri Formation, CGH 141/125.2m, coordinates 24/96.1. Note small tubercules/granae (arrow).
16. *Evittia geometrica* Playford & Dring, 1981. Iquiri Formation, CGH 140/136.2m, coordinates 27.3/95.6. Note small tubercules/granae (arrow).
17. Process detail on *Evittia geometrica* (Pl.1 fig. 14) Playford & Dring, 1981. Iquiri Formation, CGH 137/148.7m, coordinates 17.7/106.8. Note small tubercules/granae (arrow).
18. Process detail on *Exochoderma arca* Wicander, 1974. Los Monos Formation, CGH 27>88µm, coordinates 15.6/102.4.
19. *Bimerga bensonii* Wood, 1995. Iquiri Formation, CGH 78/899.9m, coordinates 34/103.6.
20. *Bimerga bensonii* Wood, 1995. Iquiri Formation, CGH 78/899.9m, coordinates 24.7/99.
21. *Bimerga bensonii* Wood, 1995. Iquiri Formation, CGH 75/913.7m, coordinates 12.8/104.6. Granate ornament is arrowed.
22. *Crucidia camirense* Ottone, 1996. Iquiri Formation, CGH 121/302m, coordinates 29.1/107.8. Note granate texture (arrow).
23. *Crucidia camirense* Ottone, 1996. Iquiri Formation, CGH 122/294.4m, coordinates 32.8/95.5.

Plate 1

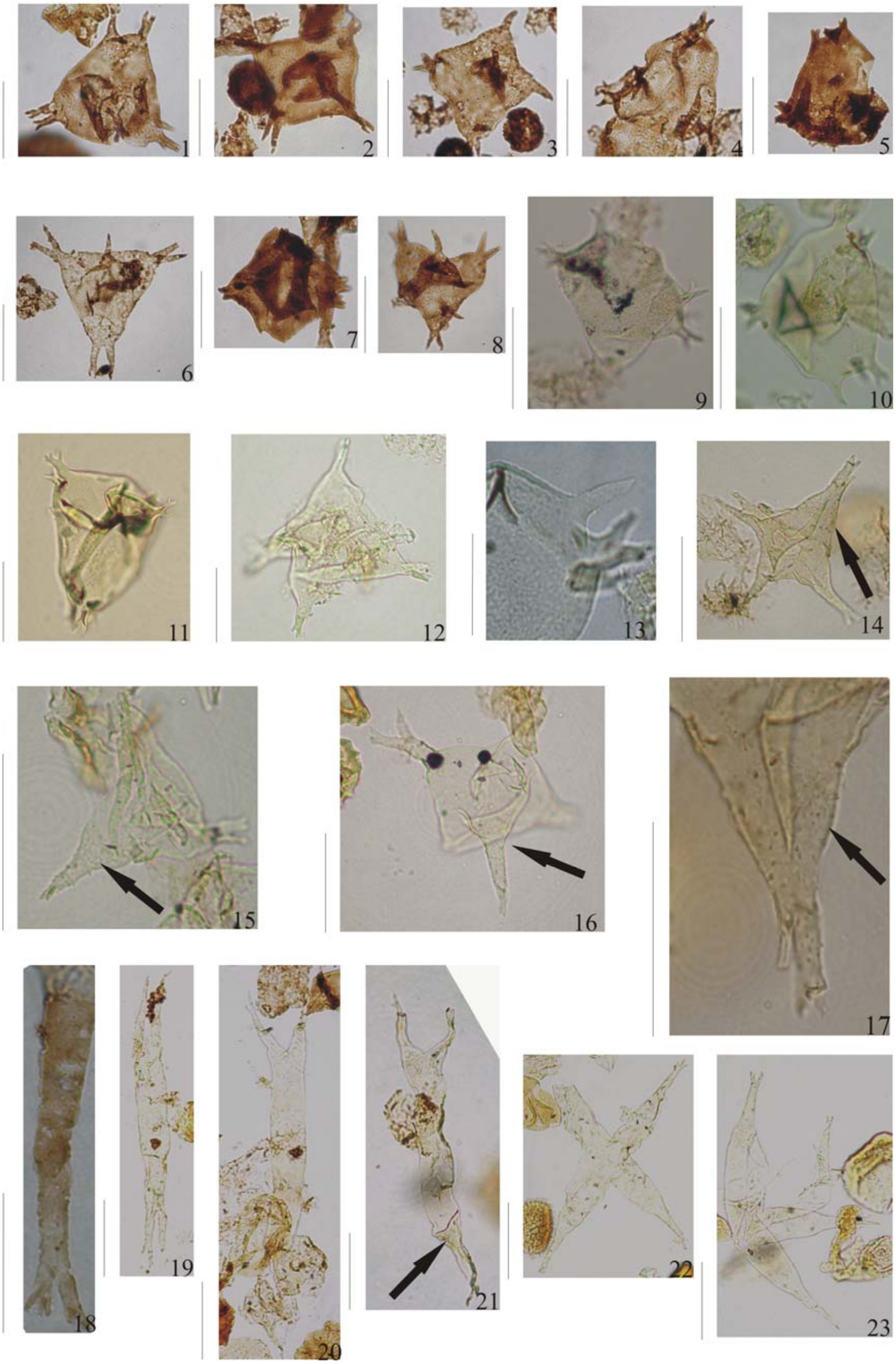


Plate 2

Black scale bar = 50µm (Figs. 1-4, 10-13)
Scale bar = 35µm (Figs. 7-8)

1. *Crucidia camirense* Ottone, 1996. Iquiri Formation, CGH 122/294.4m, coordinates 22.5/101.7.
2. *Crucidia camirense* Ottone, 1996. Iquiri Formation, CGH 121/302m, coordinates 24.6/98.5.
3. *Crucidia camirense* Ottone, 1996. Iquiri Formation, CGH 122/294.4m, coordinates 20.2/101.6.
4. *Crucidia camirense* Ottone, 1996. Iquiri Formation, CGH 121/302m, coordinates 29.1/107.8.
5. *Crucidia camirense* Ottone, 1996. Iquiri Formation, CGH 122/294.4m, coordinates 29/100.2.
6. *Crucidia camirense* Ottone, 1996. Iquiri Formation, CGH 122/294.4m, coordinates 24.5/108.5.
7. Process detail on *Crucidia camirense* Ottone, 1996. Iquiri Formation, CGH120/ 294.4m, coordinates 11.9/95.8. Note small tubercules (arrow).
8. Process detail on *Crucidia camirense* Ottone, 1996. Iquiri Formation, CGH 121/ 302m, E.F. coordinates 29.1/112.1. Note small tubercules/grana (arrow).
9. *Petrovina connata* Oliveira & Burjack, 1997. Iquiri Formation, CGH 132/192.4m, coordinates 38.7/112.1
10. *Petrovina connata* Oliveira & Burjack, 1997. Iquiri Formation, CGH 127/213m, coordinates 10.5/102.3.
11. *Petrovina connata* Oliveira & Burjack, 1997. Iquiri Formation, CGH 127/213m, E.F. coordinates 11.5/107.9.
12. *Petrovina connata* Oliveira & Burjack, 1997. Iquiri Formation, CGH 127/213m, coordinates 20/94.5.

Plate 2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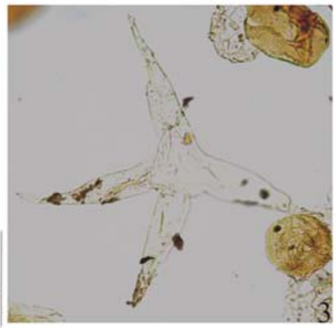
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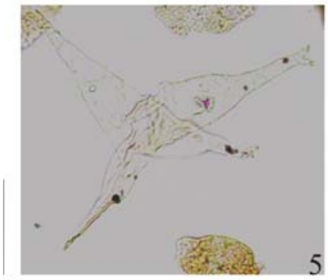
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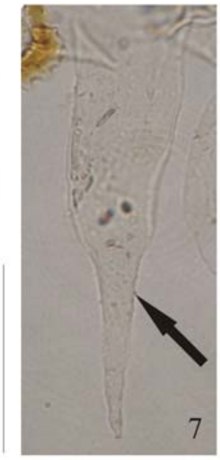
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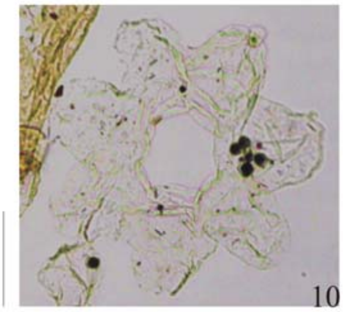
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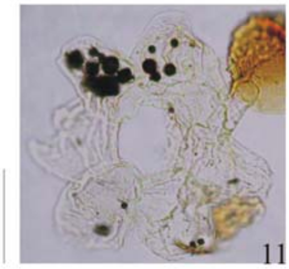
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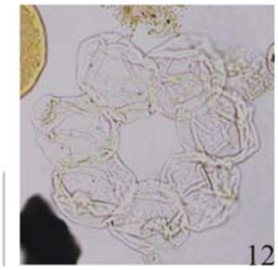
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Plate 3

Black scale bar = 50µm.

1. *Diexallophasis simplex* Wicander & Wood, 1981. Los Monos Formation, CGH 30/1188.4m, coordinates 33.6/102.4.
2. *Diexallophasis simplex* Wicander & Wood, 1981. Pimenteira Formation, Brazil1/1646.6m Well 2-PM-1-MA, Parnaíba Basin, NE Brazil, coordinates 31.8/94.5.
3. *Multisplicisphaeridium ramusculosum* (Deflandre) Lister, 1970. Pimenteira Formation, Brazil1/1646.6m Well 2-PM-1-MA, Parnaíba Basin, NE Brazil, coordinates 33.7/94.4.
4. *Multisplicisphaeridium ramusculosum* (Deflandre) Lister, 1970. Los Monos Formation, CGH 30/1188.4m, coordinates 32.7/103.
5. *Estiastra rhytidoa* Wicander & Wood, 1981. Los Monos Formation, CGH 22>88µm/1203.4m, coordinates 14/110.
6. *Estiastra rhytidoa* Wicander & Wood, 1981. Pimenteira Formation, Brazil1/1646.6m Well 2-PM-1-MA, Parnaíba Basin, NE Brazil, coordinates 31.1/102.5.
7. *Exochoderma arca* Wicander, 1974. Pimenteira Formation, Brazil1/1646.6m Well 2-PM-1-MA, Parnaíba Basin, NE Brazil, coordinates 11.3/107.1.
8. *Exochoderma arca* Wicander, 1974. Los Monos Formation, CGH 27>88µm/1195.9m, coordinates 15.6/102.4.
9. *Navifusa bacillum* (Deunff) Playford, 1977. CGH 28>88µm/1197.3m, coordinates 18.6/101.2.
10. *Navifusa bacillum* (Deunff) Playford, 1977. Pimenteira Formation, Brazil1 /1646.6m Well 2-PM-1-MA, Parnaíba Basin, NE Brazil, coordinates 21.6/98.2.
11. *Triangulina alagada* Cramer, 1964. Pimenteira Formation, Brazil1/1646.6m Well 2-PM-1-MA, Parnaíba Basin, NE Brazil, coordinates 11/111.4.
12. *Triangulina alagada* Cramer, 1964. Los Monos Formation, CGH 27/1197.3m, coordinates 42.4/95.5.
13. *Veryhachium trispinosum* (Eisenack) Deunff, 1954c. Los Monos Formation, CGH 27/1197.3m, coordinates 32.7/103
14. *Duvernaysphaera angelae*, Deunff, 1964. Los Monos Formation, CGH 28>88µm/1193.1m, coordinates 18.6/101.2.
15. *Duvernaysphaera angelae*, Deunff, 1964. Pimenteira Formation, Brazil1/1646.6m Well 2-PM-1-MA, Parnaíba Basin, NE Brazil, coordinates 33.7/94.4.
16. Leiosphere. Pimenteira Formation, Brazil1/1646.6m Well 2-PM-1-MA, Parnaíba Basin, NE Brazil, coordinates 19.6/97.
17. *Grandispora* sp. Los Monos Formation, CGH 28>88µm/1197.3m, coordinates 21/93.9.

Plate 3


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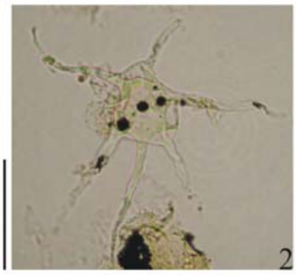
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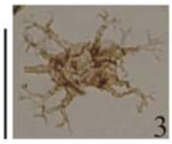
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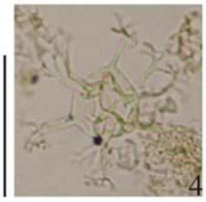
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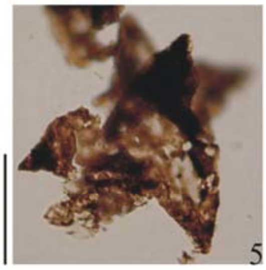
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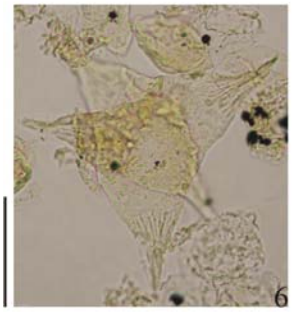
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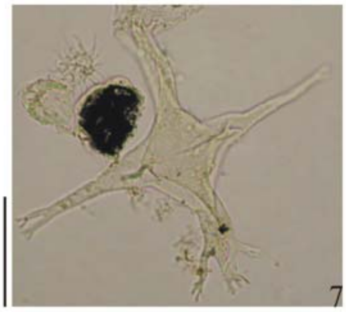
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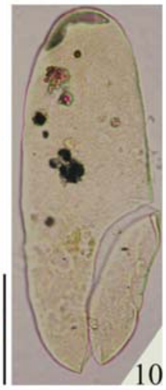
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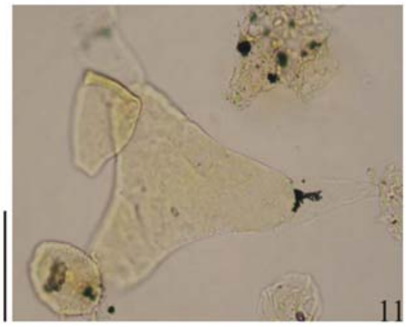
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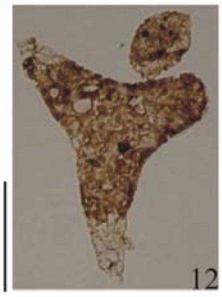
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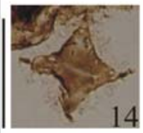
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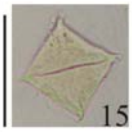
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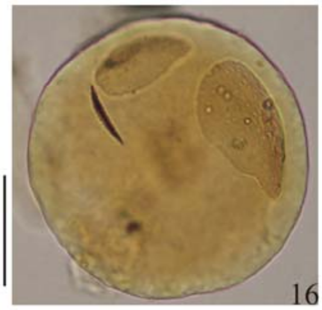
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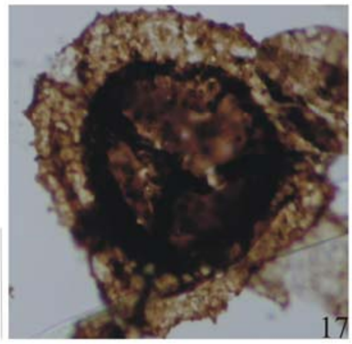
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CHAPTER 4 - CHITINOZOA

4.1 Introduction

This study uses a relatively closely sampled outcrop dataset obtained from the latest Early to Late Devonian section at Bermejo. It is unique in representing the longest and most densely sampled stratigraphic section of this age yet studied in South America. A total of 145 samples were collected from the Los Monos-Iquiri formation interval (ca. 1200m) with the majority of these yielding chitinozoa. Nearly 400 chitinozoan specimens were photographed (see **Appendix 4**), from both standard palynological and hand picked preparations. At least 36 different chitinozoan taxa were identified but only those that were previously known, or relatively common and/or distinctive are described herein. Of these 36 taxa (**Pl. 1-6**), 9 are new species. **Plates 8-11** show distinctive, and for the most part, new taxa. Although not formally described in this study, these chitinozoans are figured for reference and will form the basis of a future publication. Where possible, only complete specimens were measured and recorded.

A general log of the Bermejo section detailing lithostratigraphy, sample positions and stratigraphic ranges is shown in **Figure 4.1**. Sample positions (CGH 1 –CGH 145) are given in **Appendix 1** with the highest sample numbers indicating the youngest samples (i.e. CGH 145). The stratigraphic sample ranges of the chitinozoa described herein are given in the form youngest sample-oldest sample to enable easier correlation with cuttings-based well data.

4.1.1 Chitinozoa

Chitinozoa are organic-walled microfossils found in Early Ordovician to Late Devonian marine deposits. Their cosmopolitan distribution and frequent abundance in Palaeozoic sequences makes them an extremely powerful tool for correlation purposes. Chitinozoa are usually found as single isolated vesicles, although preservation in chains is not uncommon, with single vesicles ranging from 50-2000µm in length but typically averaging 150-250µm (Paris *et al.*, 1999). Based on their presumed chitin-like test and zoological affinities these microfossils were named chitinozoa by Eisenack (1931).

The true biological affinities of the chitinozoans are unclear but several hypotheses have been made (see Sutherland, 1994 for a summary). Kozlowski (1963) suggested that they were eggs of marine metazoan origin and this view has generally been maintained. Since chitinozoans can be found in chains and the production of egg chains is a metazoan characteristic, most workers believe that chitinozoans are the egg cases of an indeterminate, soft bodied marine metazoan (Paris and Nõlvak, 1999).

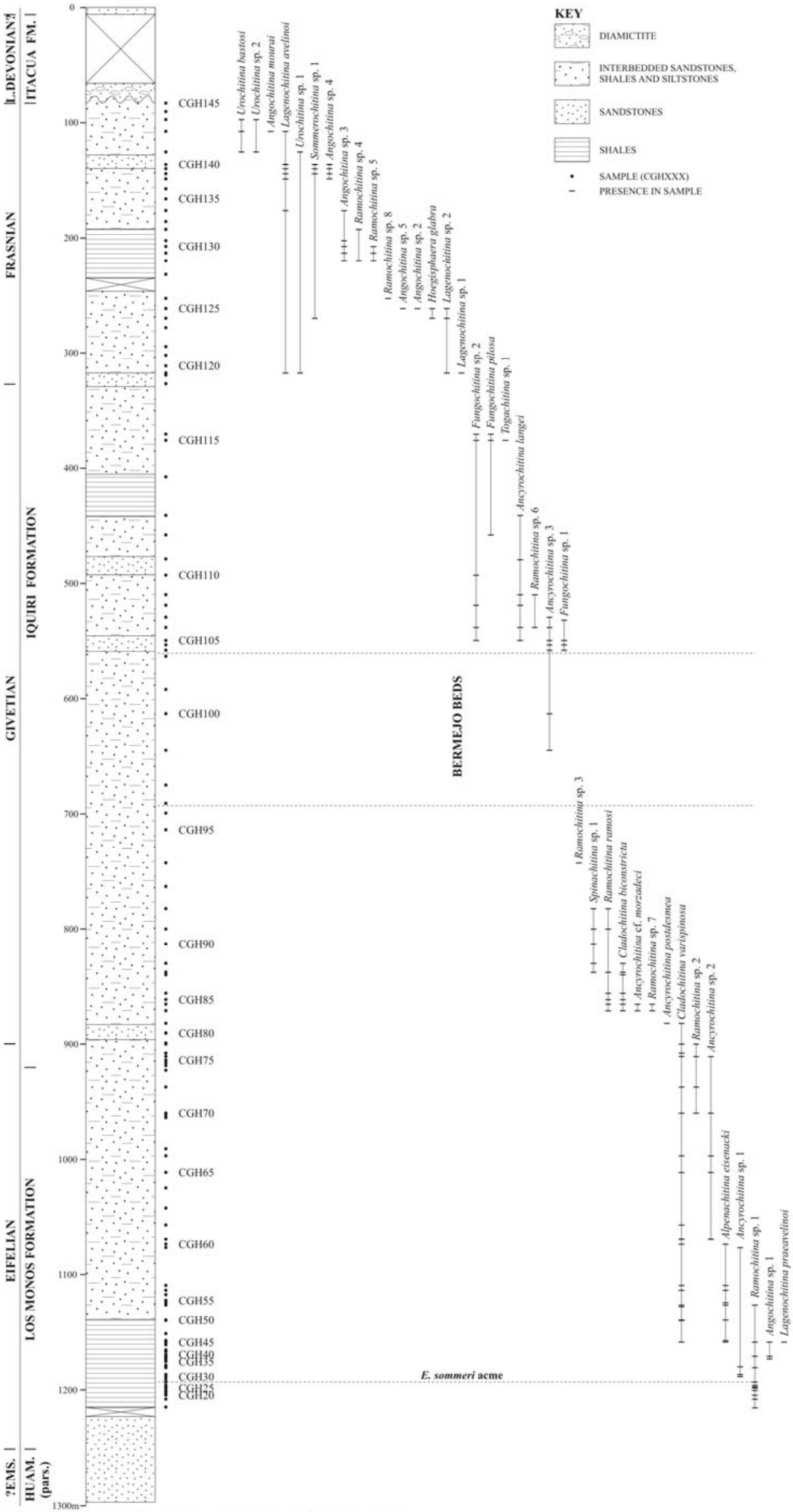


Figure 4.1. Chitinozoan range chart for Bermejo.

4.1.2 Chitinozoan biostratigraphy

Devonian chitinozoa are less well known relative to those in Silurian and Ordovician deposits with an estimated 10% of all described species being of Devonian age (Paris *et al.*, 2000). The first attempt at a global chitinozoan zonation scheme was by Paris *et al.* (2000) although most of the data was from Euramerica and therefore the scheme was regarded as provisional by the authors. The zonation scheme (**Fig. 4.2**) is based on interval range biozones which are defined by the first occurrences of a number of well-defined chitinozoan taxa found on two or more palaeocontinents. The South American data for this scheme is based on the regional work of Lange (1967a), Costa (1971), Quadros (1982), Volkheimer *et al*. (1986) and Grahn & Paris (1992a). Grahn *et al*. (2000; 2002) produced a regional zonation for the Paraná Basin and this data was incorporated into a western Gondwana chitinozoan biozonation scheme (Grahn, 2005). No attempt has been made to construct a regional chitinozoan zonation in Bolivia for reasons outlined in **Section 1.4**.

4.1.3 Chitinozoan palaeoecology

Although not the main focus of this study, chitinozoan palaeoecology still warrants a brief mention. Significant chitinozoan palaeoecological studies are summarised in Paris (1996) in addition to more recent work by Achab *et al.* (1997) and Winchester-Seeto *et al* (2000). The general consensus regarding the chitinozoan mode of life is that they were planktic on the basis of similar faunas being identified at localities separated by thousands of kilometres and taxa whose biogeographic range extended across palaeoclimatic belts (Paris, 1993). Specific examples of palaeoecological or biofacies control on chitinozoans are summarised in Miller (1996).

Generalisations regarding chitinozoan abundance have been made:

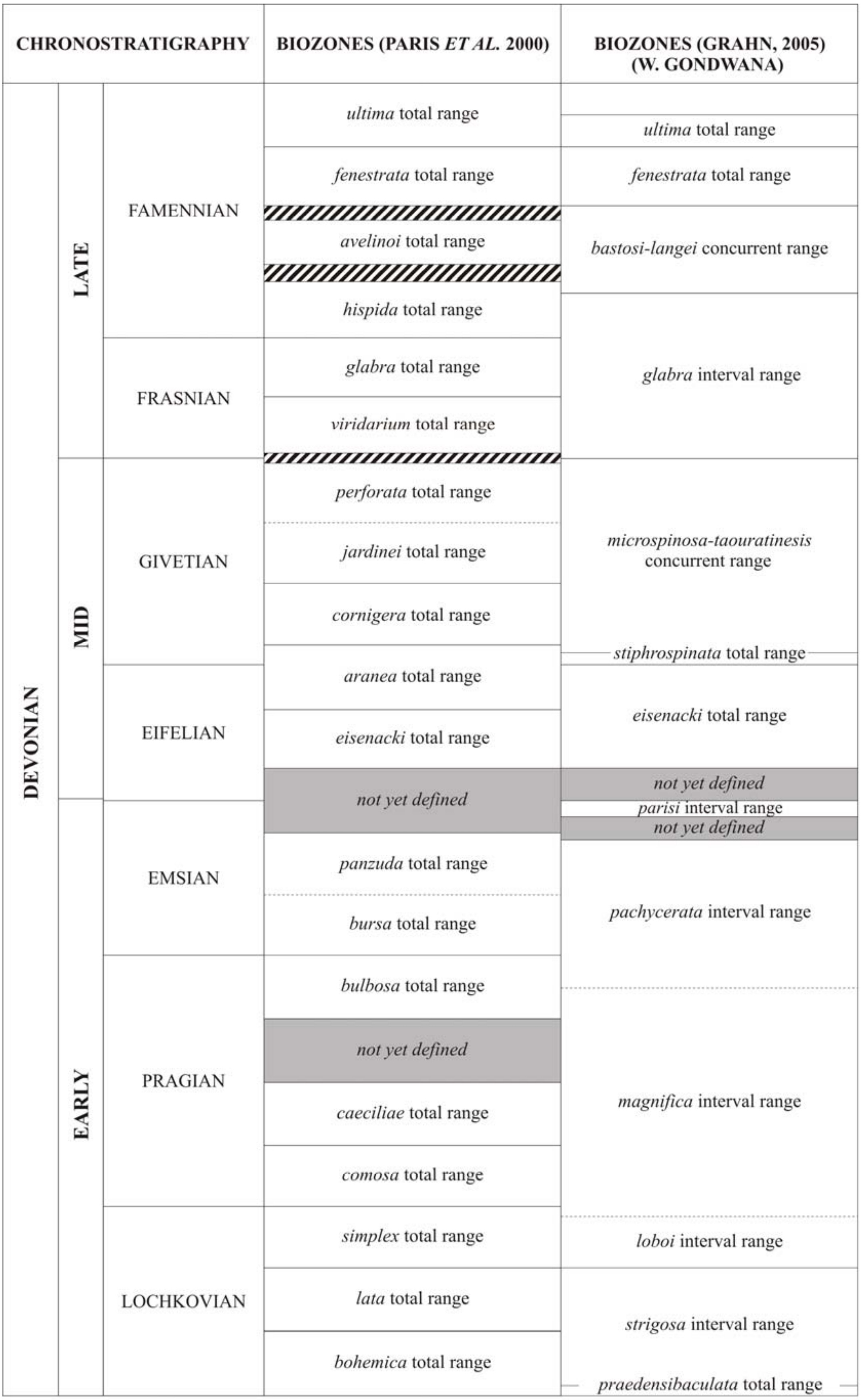
1) The maximum abundance of chitinozoa is favoured in cooler water at high palaeolatitudes (Paris, 1996).

2) There is an inverse relationship between carbonate content in the sediment and chitinozoan numbers (Laufeld, 1974; Achab *et al*., 1997; Winchester-Seeto *et al*., 2000), although this is not applicable to Bermejo since there is little carbonate.

3) Outer shelf and slope facies show maximum abundances of chitinozoa (Nestor, 1994), particularly in shaley facies associated with low energy hydrodynamic conditions.

4) Chitinozoan abundance decreases inshore and where nearshore indicators such as spores and tracheid fragments are common, chitinozoa are rare (Paris, 1996 and references therein).

The apparent maximum abundance of chitinozoa at high palaeolatitudes may be an artefact caused by the low relative abundance of other marine palynomorphs which are more



CHRONOSTRATIGRAPHY			BIOZONES (PARIS *ET AL.* 2000)	BIOZONES (GRAHN, 2005) (W. GONDWANA)
DEVONIAN	LATE	FAMENNIAN	*ultima* total range	*ultima* total range
			fenestrata total range	*fenestrata* total range
			▨	*bastosi-langei* concurrent range
			avelinoi total range	
			▨	
			hispida total range	*glabra* interval range
		FRASNIAN	*glabra* total range	
			viridarium total range	
			▨	
	MID	GIVETIAN	*perforata* total range	*microspinosa-taouratinesis* concurrent range
			jardinei total range	
			cornigera total range	
			aranea total range	*stiphrospinata* total range
		EIFELIAN		*eisenacki* total range
			eisenacki total range	
			not yet defined	*not yet defined* *parisi* interval range *not yet defined*
	EARLY	EMSIAN	*panzuda* total range	*pachycerata* interval range
			bursa total range	
		PRAGIAN	*bulbosa* total range	
			not yet defined	*magnifica* interval range
			caeciliae total range	
			comosa total range	
		LOCHKOVIAN	*simplex* total range	*loboi* interval range
			lata total range	*strigosa* interval range
			bohemica total range	*praedensibaculata* total range

Fig. 4.2. Provisional global chitinozoan biozonation (after Paris *et al*., 2000) and regional chitinozoan biozonation for western Gondwana (after Grahn, 2005). Cross hatching represents zones that do not join.

abundant at lower palaeolatitudes, e.g. acritarchs whilst the decrease in chitinozoan abundance inshore could be the result of dilution due to an increase in phytoclasts abundance.

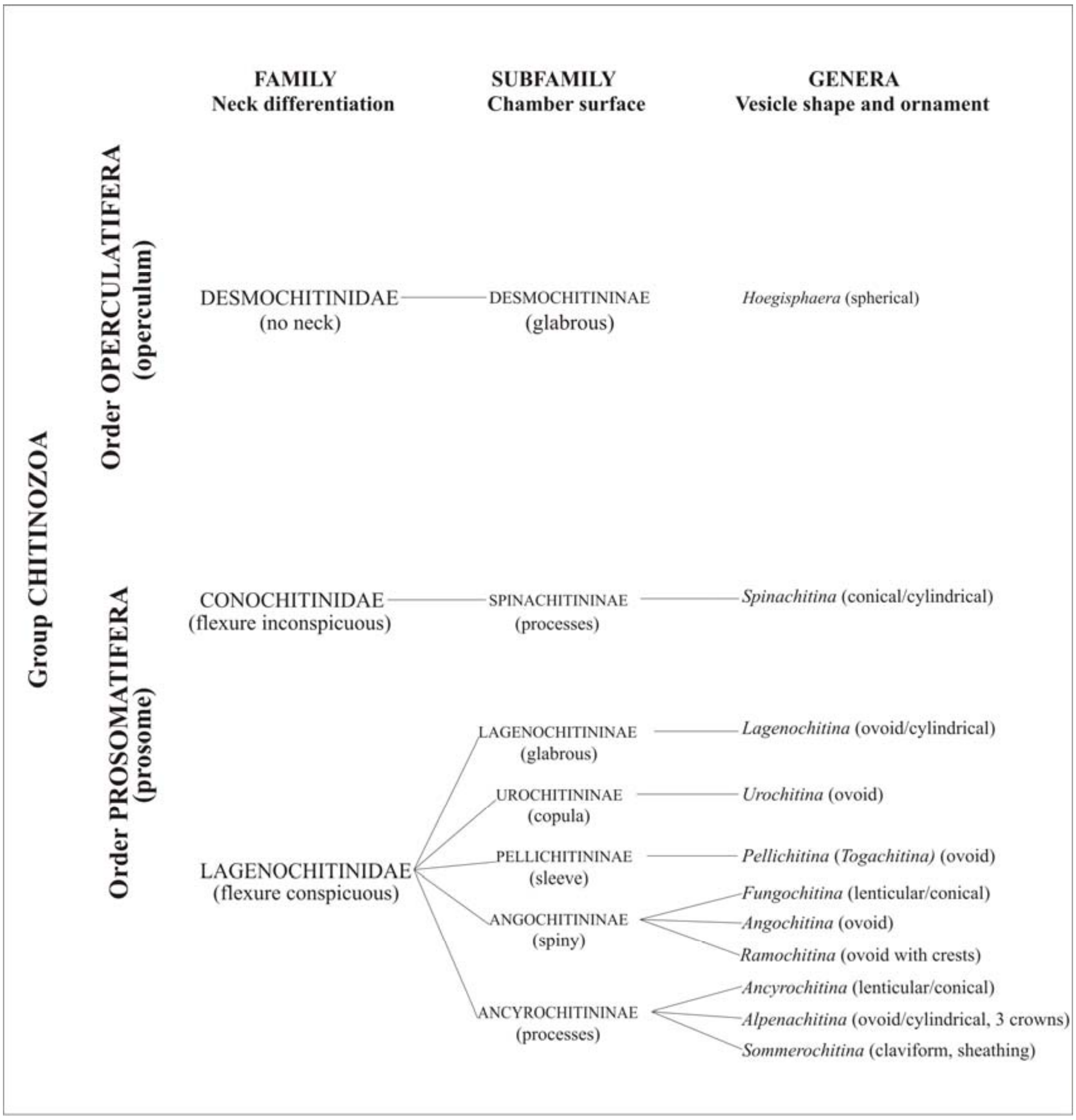


Figure 4.3. Suprageneric and generic classification of the chitinozoans encountered at Bermejo. Based on the chitinozoan classification scheme of Paris *et al*. (1999).

4.1.4 Previous chitinozoan research in Bolivia

Detailed studies on chitinozoa in Bolivia are scarce. Although there are numerous records of Bolivian chitinozoa (see Grahn, 2002) and references therein), very few illustrate and/or adequately describe specimens. These are Grahn (2002), Vavrdova *et al*. (1996) and Wood (1994; 2004) but of these only Grahn (2002) deals with stratigraphic ranges. Fortunately, Devonian chitinozoa in Brazil have been more extensively studied and have assemblages comparable to Bolivia. Brazilian studies that are relevant to this thesis include Grahn (2005), Grahn *et al*. (2000, 2002), Grahn, Loboziak & Melo (2003), Grahn & Melo (2002, 2003, 2004, 2005), Lange (1967, 1967a) and Quadros (1982, 1988). Some of these studies include samples from surface sections, though most are inevitably based on subsurface cuttings from wells and more rarely core. This study therefore concentrates on comparing the downhole inceptions of taxa (i.e. youngest uphole stratigraphic occurrence) since these are more reliable than comparing the total ranges and the last appearances downhole, which can be unreliable due to cavings contamination of cuttings during drilling. Consequently a well-based chitinozoan zonation with clearly defined bases is not possible.

4.1.5 Chitinozoan morphology

In this study, the chitinozoan classification scheme of Paris *et al.*, (1999) was utilised. The Paris *et al.*, (1999) scheme is based on diagnostic features of chitinozoa, e.g. presence of a prosome or operculum, spines, processes etc., with the relative hierarchy of such characteristics being based upon statistical and evolutionary grounds. For the most part, the Paris *et al*. (1999) classification is more than adequate to allow the differentiation of the chitinozoa down to species level. However, a minor issue with the classification scheme is that it can be somewhat rigid at species-level and as such does not allow for species which display a range of morphotypes. Consequently, when the scheme is applied to taxa which display a range of morphological variation, e.g. glabrous and spinose specimens such as the *Lagenochitina* spp. described herein, the end-members of the morphotype range have to be placed in separate genera. The suprageneric and generic classification of the chitinozoan taxa from Bermejo is outlined in **Figure 4.3** and morphological characteristics of the group in **Figures 4.4-4.7**.

A number of 'new taxa' (labelled nov. sp.) are described herein, but are kept in open nomenclature since they require definition in a peer reviewed publication. These taxa are very distinctive and nothing similar has been formally described in published Devonian chitinozoan literature. Other chitinozoa described herein may also be 'new' but are less distinctive and/or require further study to ascertain their taxonomic status. Such taxa are not assigned nov. sp. The number of specimens measured represents the number of complete examples used to generate the description. In many cases, residues were picked for the most complete specimens. Consequently, it is difficult to present unbiased chitinozoan abundance data. However, in relative terms, taxa are termed abundant, common, uncommon or rare. This is far from ideal but the main purpose of this study is to document the stratigraphic ranges of the chitinozoa identified rather than their abundance variations.

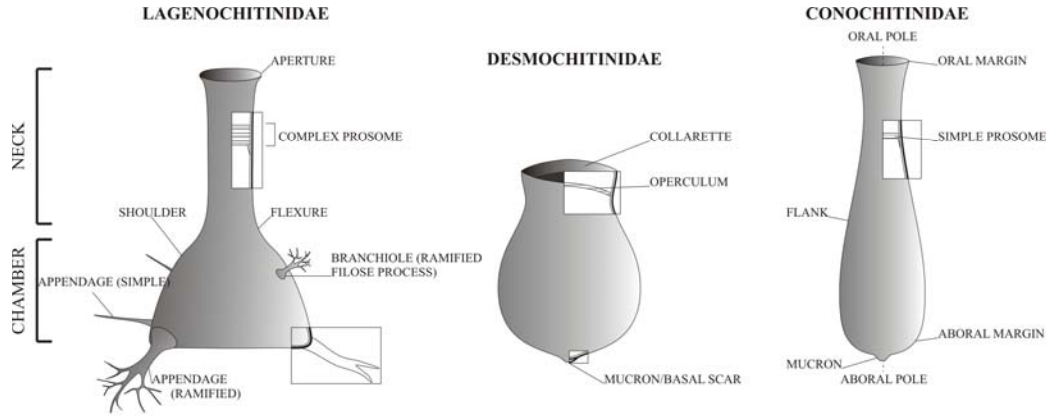


Figure 4.4. The main morphological characteristics of the 3 families of chitinozoans (modified after Sutherland, 1994 and Paris *et al*., 1996).

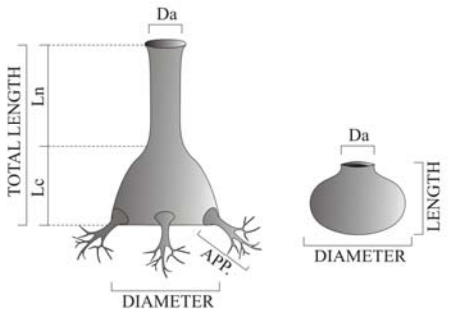


Figure 4.5. Vesicular dimensions; app=length of appendage, Da=diameter of aperture, Lc=length of chamber, Ln=length of neck (modified after Sutherland, 1994).

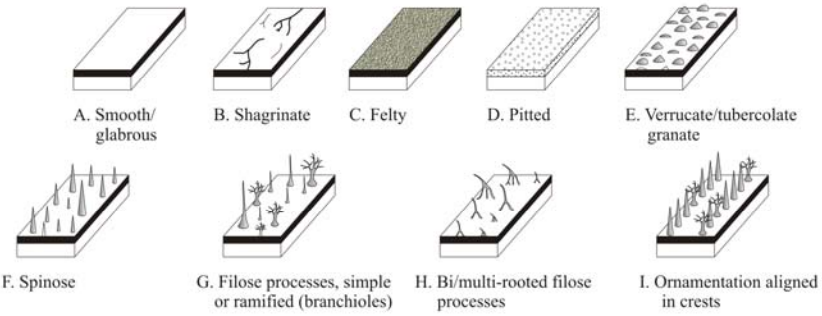

A. Smooth/ glabrous
B. Shagrinate
C. Felty
D. Pitted
E. Verrucate/tubercolate granate
F. Spinose
G. Filose processes, simple or ramified (branchioles)
H. Bi/multi-rooted filose processes
I. Ornamentation aligned in crests

Figure 4.6. Different types of vesicle wall surfaces (modified after Paris *et al*., 1996).

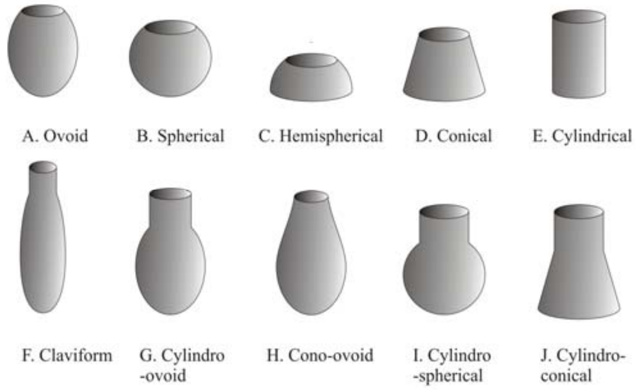

A. Ovoid
B. Spherical
C. Hemispherical
D. Conical
E. Cylindrical
F. Claviform
G. Cylindro -ovoid
H. Cono-ovoid
I. Cylindro -spherical
J. Cylindro-conical

Figure 4.7. Chitinozoan vesicle form (modified after Sutherland, 1994).

4.2.0 Systematic palaeontology

Group Chitinozoa Eisenack, 1931

Order OPERCULATIFERA Eisenack, 1931

Family DESMOCHITININIDAE Eisenack, 1931 emend. Paris, 1981a

Subfamily DESMOCHITININAE

Genus encountered in Bolivia. Hoegisphaera, Staplin, 1961.

Diagnosis. (Modified from Paris, 1981a) Chitinozoa with a spherical or ovoid chamber, lacking a neck but sometimes with a well-developed collarette. The test is thick with an external membrane that can be smooth, shagrinate, felt-like or finely tuberculate. Spinose ornamentation is not observed. The aboral pole sometimes has a short mucron that attaches to the operculum of the previous vesicle. The operculum is simple and discoid, exposed at the oral opening or base of the collarette. Organisation into chains is a common feature with this subfamily.

Genus **HOEGISPHAERA** Staplin, 1961 emend. Paris *et al.*, 1999

Type species. Hoegisphaera glabra Staplin, 1961.

Diagnosis. (From Paris *et al*., 1999). Desmochitinidae with a spherical, glabrous chamber.

Hoegisphaera glabra Staplin, 1961 Pl. 1, figs. 1–2

1961 *Hoegisphaera glabra* n. sp. – Staplin, p. 419-420, Pl. 50, figs. 5-7.
1964 *Hoegisphaera glabra* Staplin – Jansonius, p. 913, pl. 2, fig. 18.
1965 *Hoegisphaera glabra* Staplin – Taugourdeau, p. 66, Pl. 1, figs. 19-22.
1972 *Hoegisphaera glabra* Staplin emend. Urban, p. 23-24, Pl. 4, figs. 4-12.
1973 *Hoegisphaera* cf. *glabra* Staplin – Legault, p. 40-42, Pl. 8, figs. 4-6, 8, 10.
1973a *Hoegisphaera* cf. *glabra* Staplin – Legault, figs. 2-8.
1973 *Hoegisphaera glabra* Staplin – Urban & Newport, p. 241, Pl. 1, figs. 6, 10.
1974 *Hoegisphaera glabra* Staplin emend. Urban 1972 – Wood, p. 135, Pl. 8, figs. 1-2.
1980 *Hoegisphaera glabra* Staplin – Wright, p. 10, pl. 4, figs. 7-8.
1982 *Hoegisphaera glabra* Staplin emend. Urban 1972 – Martin, p. 10-11, Pl. 3, fig.7.
1983 *Hoegisphaera glabra* Staplin – Paris & Feist, Pl. 2, figs. 13-16.
1985 *Hoegisphaera glabra* Staplin – Paris *et al.*, Pl. 28, fig. 11.
1988a *Hoegisphaera glabra* Staplin – Paris, Pl. 19, figs. 5a-b.
1995 *Hoegisphaera glabra* Staplin – Winchester-Seeto & Paris, p. 459, Pl. 2, figs. 7, 9-12.
1996 *Hoegisphaera glabra* Staplin – Paris, Pl. 3, fig. 3.
1997 *Hoegisphaera glabra* Staplin – Wicander & Wood, Pl. VII figs. 1-2.
2000 *Hoegisphaera glabra* Staplin – Paris, Winchester-Seeto, Boumendjel & Grahn, Pl. 2, fig. 10.
2002 *Hoegisphaera glabra* Staplin – Grahn & Melo, p. 3-4, Pl. I, 1.
2002 *Hoegisphaera glabra* Staplin – Grahn, Bergamaschi & Pereira, Pl. 2 fig. G.
2005 *Hoegisphaera glabra* Staplin – Grahn & Melo, Pl. 1, fig. 1.

Holotype. Socony Vegreville no. 1, Duvernay Member, Woodbend Formation, cuttings from 1,067-1097m (3,500-3600 ft), Late Devonian (Frasnian), Alberta, Canada; collections of Imperial Oil Limited, Calgary, Alberta, Canada.

Diagnosis. (After Paris *et al*., 1999) Desmochitininae with a spherical, glabrous chamber.

Description. An *Hoegisphaera* species with a smooth, originally spherical chamber. The oral aperture is usually ornamented with a collar.

Dimensions. 2 specimens measured. Maximum vesicle width 108-118µm, width of aperture 45-50µm.

Discussion. Hoegisphaera glabra has been reported throughout the Devonian but there appears to be a distinctive Frasnian group that is distinguished from the earlier examples by having a well-differentiated collar and a relatively small aperture (Paris, 1988a; Winchester-Seeto & Paris, 1995). According to Winchester-Seeto & Paris (1995), *H. glabra* as described could include a number of different species or be part of an evolutionary sequence but further work is required to resolve this issue. In this study, the specimens from Bermejo are considered *H. glabra* s.s. which defines the Frasnian *H. glabra* Interval Range Biozone following Paris *et al*. (2000) on the basis of morphology i.e. collar, and stratigraphic occurrence.

Occurrence at Bermejo. H. glabra is Frasnian in age but is restricted to samples CGH 125 and CGH 124 in the Iquiri Formation where it is common, although most specimens are fragmentary.

Global distribution. The type specimen of *H. glabra* is from the early Frasnian Duvernay Formation (based on conodonts; see McLean & Klapper, 1998) that was formerly the Duvernay Member of the Woodbend Formation. *H. glabra* is also known from northern France (Taugourdeau, 1965; Paris, 1988a) and southern France (Paris & Feist, 1983; Winchester-Seeto & Paris, 1995; Paris, 1988a, 1996; Paris *et al*., 2000) where this species ranges throughout the Frasnian, but is more abundant in the Lower Frasnian. The first occurrence of *H. glabra* in France is in the *asymmetricus* Conodont Zone at the base of the Frasnian (Paris, 1988a). Late Frasnian specimens have been recorded in Belgium by Martin (1982). In Brazil, *H. glabra* is Frasnian (Grahn *et al*., 2002; Grahn & Melo, 2002, 2005) although according to Grahn (2005), this taxon ranges into the Famennian.

This genus has also been recorded from the Middle Devonian in North America (see Jenkins & Legault, 1979 for geographic distribution) and North Africa (Paris *et al*., 1985). *Hoegisphaera* sp. was seen in the Lower/Mid-Devonian in N. Spain and in the Icla Formation at Campo Redondo during this study.

Order PROSOMATIFERA Eisenack, 1972a

Family CONOCHITINIDAE Eisenack, 1931 emend. Paris (1981a)

Diagnosis. (Modified from Paris, 1981a) The collar and vesicle are poorly differentiated. A simple or complex prosome is present but non-functional in chain formation. The body is conical, ovoid or cylindrical with a vesicle that can be smooth or ornamented with tubercles, processes or hairs. A carina, appendages, mucron or copula may be observed. Chain formation is rare.

Subfamily SPINACHITININAE Paris, 1981a emend. Paris *et al.*, 1999

Genus encountered in Bolivia. Spinachitina, Schallreuter, 1963

Diagnosis. (From *Paris et al*., 1999) Conochitinidae with a conical to cylindrical chamber bearing a crown of processes.

Genus **SPINACHITINA** Schallreuter, 1963

Diagnosis. (Modified from Schallreuter, 1963) Chitinozoa with processes/appendages, a cylindrical neck and a cone-to bell-shaped chamber that forms a sharp edge to the aboral surface.

Type species. Conochitina cervicornis Eisenack, 1931

Discussion. In Paris *et al*. (1999) Conochitinidae species without a distinct flexure are placed into *Spinachitina. Cladochitina biconstricta* should now be referred to *Spinachitina biconstricta* but this combination has never been formally defined and therefore *Cladochitina biconstricta* has to be retained in this thesis.

Cladochitina biconstricta (Lange) Lange, 1967a Pl. 1, figs.3–6

1982: *Cladochitina biconstricta* (Lange) – Quadros, p. 42, Pl. 2, fig. 8.
2002: *Spinachitina biconstricta* (Lange) – Grahn, fig. 7 F.
2002: *Spinachitina biconstricta* (Lange) – Grahn, Bergamaschi & Pereira, figs. 7 B–C.
2005: *Spinachitina* aff. *Spinachitina biconstricta* (Lange) – Grahn & Melo, Pl. 1, figs. 3–4.

Holotype. Ponta Grossa Shales,Vila Ana Rita, Ponto Grossa, Paraná, Brazil. Preparation number P. 213/6, palaeontological collection of the Museu Paranáense, Curitiba.

Diagnosis. (From Lange 1967a) Body chamber cylindrical, elongate. Constriction occurs above the basal rim and a second constriction about mid-length of the vesicle. Neck cylindrical, lip expanded. A series of aborally directed appendages are present on the basal rim (aboral margin) and similarly shaped appendages are randomly distributed across the vesicle with the lowest density between the two constrictions and the highest on the neck. The appendages are short and slender, single or in pairs. A membranous capsule may enclose adjoining appendages.

Description. A *Cladochitina* species with a conical but elongate vesicle, lacking shoulders but having a cylindrical neck and a flared aperture. The neck accounts for ~$^{1}/_{3}$ of the total vesicle length. The flexure is indistinct and most specimens possess a simple prosome. On the aboral margin at least 5 simple appendages are present and sparsely distributed simple filose processes sometimes occur on the neck and chamber. A ring of small simple filose processes may occur just below the aperture. Between these filose processes, the vesicle wall is usually glabrous but can be finely spinose. A constriction of the chamber is often observed on the flanks close to the aboral margin and also, rarely, on the neck. A membranous capsule enclosing the adjoining appendages was not observed.

Dimensions. 12 specimens measured. Total vesicle length 200–325µm, length of neck 0.30–0.51 of total vesicle length, maximum vesicle width 73–105µm, width of aperture 35–58µm, maximum appendage/process length 55µm.

Discussion. Ancyrochitina parisi (**Pl.10, fig. 7**) of Volkheimer *et al*. (1986) is considered very similar to *Cladochitina biconstricta* (Lange, 1949), indeed *Cladochitina* was informally considered a junior synonym of *Ancyrochitina* by these authors. Rare specimens of *A. parisi* were recorded by Volkheimer *et al*. (1986) in association with *Ramochitina magnifica* Lange, 1967a (**Pl. 10, fig. 9-11**) which is a Pragian/Lochkovian species (Gerrienne *et al*., 2001), although the type material of *C. biconstricta* is Emsian. Quadros (1982) noted *C. biconstricta* in the Mid-Devonian of Brazil and the *C. biconstricta* described herein is restricted to the Givetian at Bermejo. Grahn (2002) and Grahn *et al*. (2002) also noted this taxon (referred to as *S. biconstricta*) as Mid-Devonian. Since the type material of *C. biconstricta* and *A. parisi* are Lower Devonian and these taxa do not have a continuous stratigraphic presence through the Emsian-Givetian interval, the *C. biconstricta* described from Bermejo is considered distinct. This is reasonable given the obvious chronostratigraphic and therefore inferred lithostratigraphic separation that exists between these taxa. Consequently, they are retained as distinct species and in future *C. biconstricta* should be used in reference to Early Devonian forms. The Mid Devonian chitinozoans described herein require formal definition as a new species.

Occurrence at Bermejo. *C. biconstricta* is common in the Iquiri Formation in samples CGH89–CGH83 and is Givetian in age.

Global distribution. This species also occurs in Brazil (Quadros, 1982; Grahn, 2002; Grahn *et al*., 2002; Grahn & Melo, 2005), southern central Bolivia (Cousminer, 1964) and Paraguay (Grahn *et al*., 2002).

Spinachitina sp. 1 nov. sp. Pl. 1, figs. 7–8

Description. A *Spinachitina* species with a conical chamber and a very short tapering neck accounting for $^1/_4$–$^1/_3$ of the total vesicle length. A well-developed simple prosome is often seen. The flexure is not conspicuous. There are 3–6 simple appendages on the aboral margin. The vesicle wall is glabrous but can have randomly distributed grana across the vesicle surface.

Dimensions. 5 specimens measured. Total vesicle length 190–223µm, length of neck 0.22–0.34 of total vesicle length, maximum vesicle width 80–105µm, width of aperture 50–65µm, maximum appendage length 90µm.

Discussion. C. biconstricta is generally larger and has constrictions of the vesicle (Pl. 1, fig. 6).

Occurrence at Bermejo. S. sp. 1 is reasonably common in samples CGH 92–CGH 88 at Bermejo in the Iquiri Formation and is Givetian.

Global distribution. Currently known only from Bolivia.

Family LAGENOCHITINIDAE Eisenack, 1931
emend. Paris (1981a)

Diagnosis. (Modified from Paris, 1981a) The neck and body are differentiated. An internal prosome, simple or complex is often observed and it is non-functional in chain formation. The body is ovoid, conical or cylindrical with a glabrous or ornamented surface. A carina or appendages may be present. Chain formation is rare.

Subfamily ANCYROCHITININAE Paris, 1981a

Genera encountered in Bolivia. Alpenachitina Dunn & Miller, 1964; *Ancyrochitina* Eisenack, 1955; *Sommerochitina* Costa Cruz & Quadros, 1985.

Diagnosis. (Modified after Paris, 1981a) Ornamented Lagenochitinidae with a rounded aboral margin supporting simple, branched or anastomosing (joined) appendages. No mucron. Chain formation is rare.

Genus **ALPENACHITINA** Dunn & Miller, 1964

Type species. Alpenachitina eisenacki Dunn & Miller, 1964

Diagnosis. (From Paris *et al.*, 1999) Lagenochitinidae with ovoid to cylindrical chamber and three distinct horizontal crowns of spiny ornamentation.

Alpenachitina eisenacki Dunn & Miller, 1964 Pl. 1, figs. 9–11

1964: *Alpenachitina eisenacki* n. sp. Dunn & Miller, p. 725–726, Pl. 119, figs. 1–12, text–fig. 1.
1966: *Alpenachitina eisenacki* Dunn & Miller – Taugourdeau, p. 29, 49.
1967: Indeterminate chitinozoan – Lange, p. 17, Pl, 1, fig a–b.
1967a: *Alpenachitina eisenacki* Dunn & Miller – Lange, p. 65–67, Pl. 1, figs. 1–3.
non 1968: *Alpenachitina eisenacki* Dunn & Miller – van Boekel, p. 11–12, Pl. 3, fig. 4 (see Almeida Burjack & Paris, 1989).
non 1971: *Alpenachitina eisenacki* Dunn & Miller – Costa, p. 215, fig. 1 (see Burjack & Paris, 1989).
? 1973: *Alpenachitina ontariensis* – Legault, p. 17, Pl. 1, figs. 1–3.
? 1974: *Alpenachitina eisenacki* Dunn & Miller – Anan-Yorke, p. 52, Pl. 5, figs. 12–14.
1976: *Alpenachitina eisenacki* Dunn & Miller – Wright, p. 220, figs. 2/7–2/9.
? 1979: *Alpenachitina crameri* Hutter – Hutter, p. 24–28, Pl. 1, figs. 1–11, Pl. 2, figs. 1–9.
1980: *Alpenachitina eisenacki* Dunn & Miller – Wright, p. 7–8, Pl. 2, figs. 1–6.

1985: *Alpenachitina eisenacki* Dunn & Miller – Paris *et al.*, Pl. 28, figs. 1–2.
1987: *Alpenachitina eisenacki* Dunn & Miller – Boumendjel, p. 99–100, Pl. 22, figs. 3, 5.
1988: *Alpenachitina eisenacki* Dunn & Miller – Quadros, Pl. 4, fig. 20.
1989: *Alpenachitina eisenacki* Dunn & Miller – Burjack & Paris, Pl. 1, figs. 1–4.
2001: *Alpenachitina eisenacki* Dunn & Miller – Grahn & Gutiérrez, fig. 12 A.
2002: *Alpenachitina eisenacki* Dunn & Miller – Grahn, Bergamaschi & Pereira, Pl. 4, figs. F–G.
2003: *Alpenachitina eisenacki* Dunn & Miller – Grahn, Pl. 1, fig. 11.
2003: *Alpenachitina eisenacki* Dunn & Miller – Grahn & Melo, Pl. 1, fig. 1.
2003: *Alpenachitina eisenacki* Dunn & Miller – Grahn, Loboziak & Melo, Pl. 4, figs. 8–9.
2004: *Alpenachitina eisenacki* Dunn & Miller – Grahn & Melo, Pl. 2, figs. 13–14.

Holotype. Dock Street Clay Member, Alpena Limestone, Alpena Michigan, USA. Middle Devonian. USNM collections 144880.

*Diagnosis***.** (From Dunn & Miller, 1964) Nearly straight body chamber walls which break inward to form a shoulder at the upper portion of the body chamber. Single rows of 10 to 12 multibranched processes encircle body chamber at aboral perimeter and at base of shoulder. Row of five or six smaller less complex processes at midlength of cylindrical neck. Oral third of neck fringed with processes.

Description. An *Alpenachitina* species with an ovoid chamber and a short cylindrical neck (~ $^1/_3$ of the total vesicle length) that may have a weakly developed simple prosome. The flexure is conspicuous and the shoulders are broad. On the aboral margin there is a row of about 10 ramified, or rarely, simple appendages and a second row of similar ornamentation at the base of the shoulder. About $^2/_3$ of the way up the neck there is a crown of 5–6 shorter ramified filose processes and the vesicle wall between these is spinose whereas elsewhere on the vesicle the wall is finely verrucate.

Dimensions. 5 specimens measured. Total vesicle length 163–205µm, length of neck 0.29–0.40 of total vesicle length, maximum vesicle width 83–90µm, width of aperture 35–50µm, maximum appendage/shoulder process length 50µm, maximum neck process length 25 µm.

Discussion. Examples of *A. eisenacki* from Bermejo conform with the overall description of the type material.

Occurrence at Bermejo. *A. eisenacki* is fairly common in the Los Monos Formation in samples CGH 60–CGH 46 and is Eifelian in age.

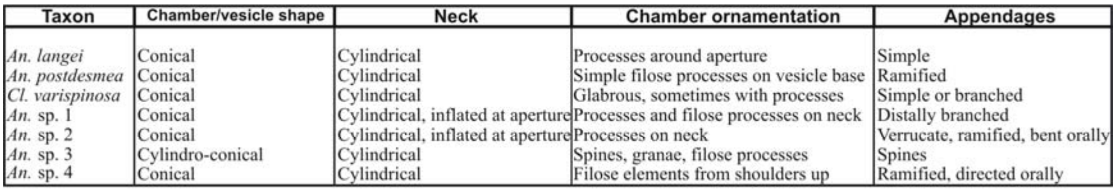
Global distribution. *A. eisenacki* was first described from the Givetian of Michigan (Dunn & Miller, 1964) but is also known elsewhere in the USA (Urban, 1972; Wright, 1976, 1978, 1980). The oldest occurrence of *A. eisenacki* in the USA is in Iowa in the *partitus* Conodont biozone, indicating an early Eifelian age (Paris *et al.,* 2000; Wright, 1980). If the synonymy with *A. ontariensis* Legault, 1973 as proposed in Burjack & Paris (1989) is accepted, then *A. eisenacki* is also present in the early Givetian of Canada. A widely distributed taxon, *A. eisenacki*, has been recorded from the Mid Devonian of Brazil (Grahn, Loboziak & Melo 2003; Grahn & Melo, 2004; Lange, 1967, 1967a; Quadros, 1988), N. Argentina (Grahn, 2003), Algeria (Boumendjel *et al.*, 1988; Taugourdeau, 1966), Libya (Paris *et al*., 1985) and possibly Egypt (the ?*A. crameri* of Hutter, 1979) and Ghana (Anan-Yorke, 1974).

Genus **ANCYROCHITINA** Eisenack, 1955

Type species. *Conochitina ancyrea* Eisenack, 1931

Diagnosis. (From Eisenack 1955) Ancyrochitininae with simple, branched or ramified appendages.

Discussion. A summary of the key features of the *Ancyrochitina* spp. described herein is shown in Table 4.1.



Taxon	Chamber/vesicle shape	Neck	Chamber ornamentation	Appendages
An. langei	Conical	Cylindrical	Processes around aperture	Simple
An. postdesmea	Conical	Cylindrical	Simple filose processes on vesicle base	Ramified
Cl. varispinosa	Conical	Cylindrical	Glabrous, sometimes with processes	Simple or branched
An. sp. 1	Conical	Cylindrical, inflated at aperture	Processes and filose processes on neck	Distally branched
An. sp. 2	Conical	Cylindrical, inflated at aperture	Processes on neck	Verrucate, ramified, bent orally
An. sp. 3	Cylindro-conical	Cylindrical	Spines, granae, filose processes	Spines
An. sp. 4	Conical	Cylindrical	Filose elements from shoulders up	Ramified, directed orally

Table 4.1. A summary of the distinguishing features of the different *Ancyrochitina* species described in this study.

Ancyrochitina langei Sommer & van Boekel, 1964 Pl. 1, figs. 12–13

1964: *Ancyrochitina langei* n. sp. Sommer & van Boekel, p. 427, Pl. 1, fig. 1, text–fig. 4.
1967a: *Ancyrochitina langei* Sommer & van Boekel – Lange, p. 21/22, p. 70, Pl. 1, figs. 8–9.
1968: *Ancyrochitina langei* Sommer & van Boekel – Sommer & van Boekel, p. 10, Pl. III, fig. 6.
1971: *Ancyrochitina langei* Sommer & van Boekel – Costa, p. 219, fig. 7.
1974: *Ancyrochitina langei* Sommer & van Boekel – Anan-Yorke, p.58–59, Pl. V, figs. 1–4.
1982: *Ancyrochitina langei* Sommer & van Boekel – Quadros, p. 40,–41, Pl. 1, fig. 4.
2002: *Ancyrochitina langei* Sommer & van Boekel – Grahn, figs. 5 I, 7 A.
2002: *Ancyrochitina langei* Sommer & van Boekel – Grahn, Bergamaschi & Pereira, Pl. 8 figs. C–E.
2003: *Ancyrochitina langei* Sommer & van Boekel – Grahn, Loboziak & Melo, Pl. 4, fig. 5, Pl. 5, fig. 7.

Holotype. Plate 63–4–1, Ortholux Coordinates 38.9/120.0, D.G.M.; D.N.P.M., Rio de Janeiro.

Diagnosis. (From Sommer & van Boekel, 1968) Cylindrical–conical chamber, cylindrical neck slightly elongated near collar which is short. 2–6 basal appendages, thicker near base and thinning towards the end, slightly curved. Regularly developed spines around the end of the oral tube, variable in number. These spines are smaller and thinner than the basal appendages.

Description. An *Ancyrochitina* species with a conical chamber and a cylindrical neck (~$^{1}/_{2}$ of the total vesicle length). The flexure is distinct but the shoulders are weakly developed. The vesicle surface is glabrous and ornamented with 2 rows of appendages on the aboral margin and processes around the aperture. There are between 3 and 5 simple appendages, which are similar in morphology to, but longer than the processes around the aperture. At least 3 processes are developed around the aperture.

Dimensions. 4 specimens measured. Total vesicle length 155–175µm, length of neck 0.43–0.56 of total vesicle length, maximum vesicle width 95–113µm, width of aperture 43–53µm, maximum appendage length 65µm, maximum aperture process length 45µm (see **Fig. 4.8** for a length *versus* width cross plot).

Discussion. Specimens of *A. langei* from Bermejo conform to the description of the type material but examples in Grahn *et al*. (2002) show much better developed ornamentation (Pl. 8, B–E) than those from Bermejo, particularly in the processes about the aperture.

Occurrence at Bermejo. *A. langei* is fairly common in the sample range CGH 113–CGH 106 and is mid/late Givetian in age.

Global distribution. In southern and central Bolivia, Brazil and Paraguay, *A. langei* is also a Givetian species (Grahn, 2002; Grahn *et al*., 2002; Grahn *et al.*, 2003). Older literature gives a more general latest Early Devonian to Mid Devonian age for *A. langei* (e.g. Anan-Yorke, 1974 (Ghana); Lange, 1967a (Brazil); Quadros, 1982 (Brazil)).

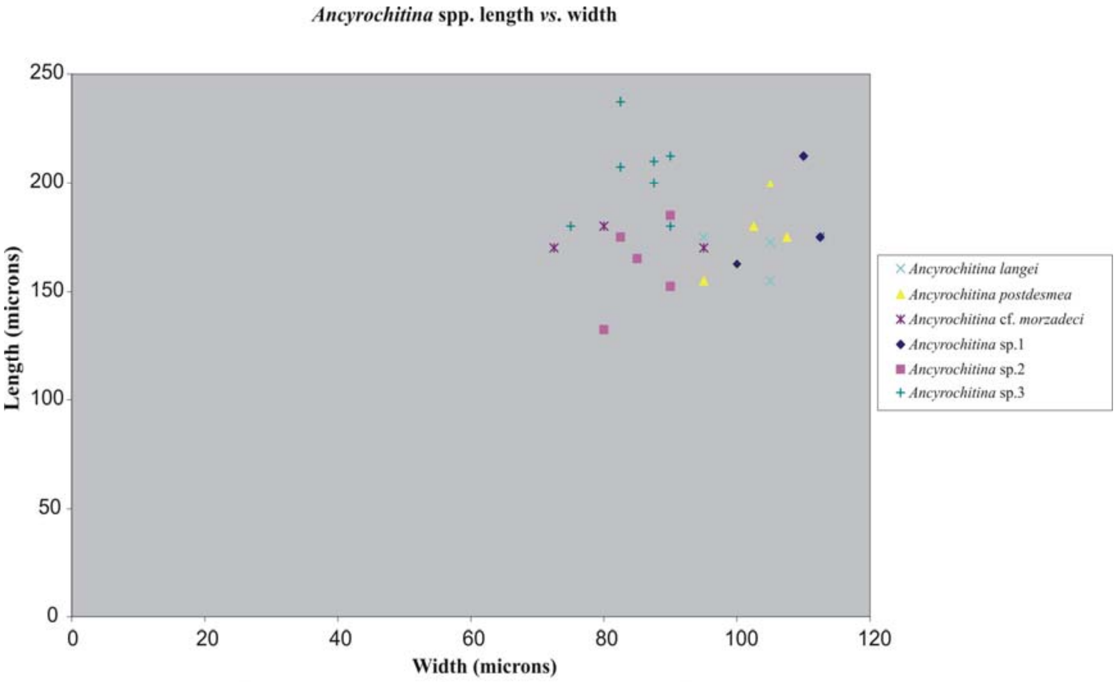


Fig. 4.8. Cross plot of length *vs*. width for *Ancyrochitina* spp. from Bermejo.

Ancyrochitina postdesmea Grahn, 2002 Pl. 1, figs. 14–16, Pl. 2, fig. 1

1967a: *Ancyrochitina* cf. *desmea* – Lange, p. 69–70, Pl. 1, figs. 4–6.
1973: *Ancyrochitina* cf. *desmea* – Legault, p. 18–19, Pl. 2, figs. 1–3.
1974: *Ancyrochitina* cf. *desmea* – Anan-Yorke, p. 61–62, Pl. IV, figs. 14–16.
? 1982: *Ancyrochitina* cf. *desmea* – Quadros, p. 40, Pl. 1, fig. 3.
2002: *Ancyrochitina postdesmea* n. sp. – Grahn, p.323–324, fig. 6 G.
2002: *Ancyrochitina postdesmea* Grahn – Grahn, Bergamaschi & Pereira, Pl. 1, fig. B.
2004: *Ancyrochitina postdesmea* Grahn – Grahn & Melo, Pl. 3, fig. 5.

Holotype. Well RPST–1–MT, core 18. Slide M.N. 4296–1. Museu Nacional, Rio de Janiero.

Diagnosis. (From Grahn, 2002) An *Ancyrochitina* species with a conical body and cylindrical neck of $^{1}/_{3}$–$^{1}/_{2}$ of the total length. Margin provided with 8–10 thick branching appendages, which are often bent orally. Each branch may be further divided into 3–5 smaller branches. Similar processes are present on the neck, usually bent aborally. The vesicle wall between the processes is smooth, and the aperture straight.

Description. An *Ancyrochitina* species with a conical chamber and cylindrical neck that accounts for $^{1}/_{3}$–$^{1}/_{2}$ of the total vesicle length. The flexure is reasonably well defined. Between 3 and 9 thick ramified appendages are present on the aboral margin. The surfaces of the appendages appear pitted and they are often bent apertureward. Small, randomly distributed simple filose processes adorn the vesicle base. A crown of about 6 ramified processes of similar length to the appendages (but more slender), occurs anywhere from approximately $^{3}/_{4}$ of the way up the neck to the aperture. The vesicle wall between these processes and the aperture is spinose whereas on the rest of the vesicle, apart from the vesicle base, the wall is smooth.

Dimensions. 4 specimens measured. Total vesicle length 155–200µm, length of neck 0.31–0.42 of total vesicle length, maximum vesicle width 95–108µm, width of aperture 45–48µm, maximum appendage/process length 68µm (see **Fig. 4.8** for a length *versus* width cross plot).

Discussion. The specimens from Bermejo are largely consistent with the description of the type material in Grahn (2002) but differ in being more inflated and having simple processes on the base of the vesicle. Due to a poor specimen and photograph, it is not entirely clear if Plate 1, Figure 3 in Quadros (1982) is *A. postdesmea*. *A. postdesmea* differs from *An.* sp. 2 (**Pl. 2, figs. 10-12**) described herein by having a longer cylindrical neck without an inflated aperture, a more conical chamber and shorter appendages. In addition, *An.* sp. 2 has an indistinct flexure unlike *A. postdesmea*.

Occurrence at Bermejo. *A. postdesmea* is restricted to the uppermost Los Monos Formation/basal Iquiri Formation (latest Eifelian/earliest Givetian) occurring only in sample CGH 82 where it is reasonably common.

Global distribution. The specimens from south central Bolivia in Grahn (2002) are dated as early to mid Givetian. Representatives of this species are also known from the Mid Devonian of Brazil (Grahn, 2002; Lange, 1967a), Canada (Legault, 1973) and Ghana (Anan-Yorke, 1974).

Cladochitina varispinosa Lange, 1967a Pl. 2, figs. 3–6

Volkheimer *et al*. (1986) claimed that the use of *Cladochitina* as a genus is invalid on the basis that the only difference between *Cladochitina* and *Ancyrochitina* is the length of the neck. This allowed specimens with a neck length greater than half the vesicle length to be placed in either genus. However, in Paris *et al*. (1999) *Cladochitina* species without a distinct flexure were placed into *Spinachitina* but this does not apply to *C. varispinosa* because the type material of this taxon was described as having a conspicuous flexure. *Cladochitina* sp. (**Pl. 11, fig. 8**) is similar to *C. varispinosa* but has different appendage morphology and is restricted to the Emsian. Grahn *et al*. (2002) referred *Cladochitina varispinosa* to *Ancyrochitina varispinosa* but this is invalid since *Ancyrochitina varispinosa* was not defined in the comb. nov. In this thesis, *C. varispinosa* is placed into *Ancyrochitina* following Volkheimer *et al*. (1986) but the taxon is temporarily retained because *Ancyrochitina varispinosa* requires formal definition in a valid publication.

1967a: *Cladochitina varispinosa* n. sp. – Lange, p. 78, Pl. 2, figs. 27–35.
1971: *Cladochitina varispinosa* Lange – Costa, p. 228, fig. 23.
1974: *Cladochitina varispinosa* Lange – Anan-Yorke, p. 87–89, Pl. IX, figs. 1–9.
2002: *Ancyrochitina varispinosa* (Lange) – Grahn Bergamaschi & Pereira, Pl. 5 figs. G–H.

Holotype. AGst–1–MT, core 16. M.N. 4914–1. Museu Nacional, Rio de Janiero.

Diagnosis. (From Lange, 1967a) A species of *Cladochitina* characterized by a high variability in the shape of the aboral and lateral appendages.

Description. A *Cladochitina* species with a conical vesicle chamber and a cylindrical neck. The neck accounts for $^1/_4$–$^1/_2$ of the total vesicle length and becomes inflated towards the aperture. In most specimens the flexure is distinct and a prosome is developed. The vesicle wall is glabrous but some specimens have very small sparsely distributed spines (~5µm) on the chamber wall. Generally, vesicle ornamentation only consists of 3–8 appendages on the aboral margin, the morphology of which is variable. These appendages are often simple but can display low order branching. Large simple processes, comparable in length to the appendages but thinner, are sometimes present on the vesicle neck, close to the aperture.

Dimensions. 9 specimens measured. Total vesicle length 150–253µm, length of neck 0.26–0.56 of total vesicle length, maximum vesicle width 88–105µm, width of aperture 45–55µm, maximum appendage/process length 75µm.

Discussion. *C. varispinosa* is similar to *Cladochitina biconstricta* (Lange, 1967a) but has larger and more slender appendages that may be branched. *Cladochitina biconstricta* (**Pl. 1 fig. 6**) also has constrictions of the vesicle that are absent on *C. varispinosa*.

Occurrence at Bermejo. *C. varispinosa* is a very common and long-ranging species at Bermejo (mid Eifelian–mid Givetian) and is abundant in many samples in the range CGH 82–CGH 46.

Global distribution. C. varispinosa is also known from the Mid Devonian of Brazil (Lange, 1967a; Costa, 1971; Grahn *et al*., 2002) and Ghana (Anan-Yorke, 1974).

Ancyrochitina cf.. **morzadeci** Paris, 1981b Pl. 2, fig. 7

2002: *Ancyrochitina* cf. *morzadeci* Paris – Grahn, fig. 7 D.
? 2002: *Ancyrochitina morzadeci* Paris – Grahn, Bergamaschi & Pereira, Pl. 5 fig. E.
2002: *Ancyrochitina* cf. *morzadeci* Paris – Grahn, Bergamaschi & Pereira, Pl. 6 fig. A.
non 2002: *Ancyrochitina* cf. *morzadeci* Paris – Grahn, Bergamaschi & Pereira, Pl. 6 fig. B.
2003: *Ancyrochitina morzadeci* Paris – Grahn & Melo, Pl. 2, fig. 7.
2004: *Ancyrochitina* cf. *morzadeci* Paris – Grahn & Melo, Pl. 2, fig. 3.
? 2004: *Ancyrochitina* cf. *morzadeci* Paris – Grahn & Melo, Pl. 2, fig. 9.
? 2005: *Ancyrochitina* cf. *morzadeci* Paris – Grahn & Melo, Pl. 7, fig. 4.

Description. An *Ancyrochitina* species with a conical chamber, a cylindrical neck ($^1/_6$-$^1/_3$ of the total vesicle length) and a glabrous surface. A flexure is present and the chamber possesses broad shoulders. There are numerous filose processes between the shoulders and aperture that decrease in size apertureward but are longest at the flexure. The processes are simple, bifurcate or ramified with branching taking place distally from the mid-length onwards. On the aboral margin ramified appendages are present that are bent orally. A prosome is present.

Dimensions. 3 specimens measured. Total vesicle length 170–180µm, length of neck 0.15–0.35 of total vesicle length, maximum vesicle width 73–95µm, width of aperture 40–53µm, maximum appendage length 25µm, maximum process length 25µm (see **Fig. 4.8** for a length *versus* width cross plot).

Discussion. *A.* cf. *morzadeci* differs from *Ancyrochitina morzadeci* Paris, 1981b in that *A. morzadeci* has a conical vesicle chamber without shoulders and the appendages of *A.* cf. *A. morzadeci* are shorter, bent orally and therefore do not extend perpendicularly from the aboral margin as in *A. morzadeci*. In addition, *A.* cf. *A. morzadeci* also has visibly fewer appendices than *A. morzadeci*. Plate 6 B in Grahn *et al*. (2002) is not *A.* cf. *A. morzadeci* since the vesicle more slender and elongate than the material described herein and also the adjacent illustration (Pl. 6 A) of Grahn *et al*. (2002).

Occurrence at Bermejo. *A.* cf. *A. morzadeci* is a Givetian species and is found in CGH 84–CGH 83 but is uncommon.

Global distribution. *A.* cf. *A. morzadeci* is known from the Givetian of Brazil (Grahn, 2002; Grahn et al., 2002; Grahn & Melo, 2004).

Ancyrochitina sp. 1 nov. sp. Pl. 2, figs. 8–9

Description. An *Ancyrochitina* species with a conical, glabrous vesicle. Shoulders are not developed on the chamber but the flexure is distinct. The neck is relatively long (~$^1/_2$ of the total vesicle length) becoming inflated towards the aperture. There are 3–7 distally branched appendages on the aboral margin that extend apertureward and about 5 thinner simple filose processes $^2/_3$–$^3/_4$ distance up the neck which extend aborally. The vesicle wall between the neck processes and the aperture may be ornamented with very low density, minute simple filose elements which are randomly distributed.

Dimensions. 3 specimens measured. Total vesicle length 163–213µm, length of neck 0.40–0.48 of total vesicle length, maximum vesicle width 100–113µm, width of aperture 45–48µm, maximum appendage length 81µm, maximum process length 50µm (see **Fig. 4.8** for a length *versus* width cross plot).

Discussion. *Ancyrochitina langei* Sommer & van Boekel 1964 (**Pl. 1, figs. 12-13**) resembles *A*. sp. 1 in terms of vesicle shape and spine distribution but only has simple processes. In addition, *A. langei* occurs 600m stratigraphically higher than *A*. sp. 1. On this basis, *A*. sp. 1 is considered a separate species. *A*. sp. 2 (**Pl. 2, figs. 10-12**) has a more elongate conical vesicle shape and ramified appendages.

Occurrence at Bermejo. *A*. sp. 1 is restricted to the Eifelian in the sample range CGH 59–CGH 30 where it is relatively uncommon.

Global distribution. Fragments of *A*. sp. 1 were found at Campo Redondo (this study) and also in Well 2-PM-1-MA (this study) in the Parnaíba Basin, NE Brazil (**see Pl. 10, fig. 4**).

Ancyrochitina sp. 2 Pl. 2, figs. 10–12

Description. An *Ancyrochitina* species possessing an elongate conical chamber with a short tapering neck (~$^1/_4$ of total vesicle length) and an inflated oral margin. A prosome is usually present. The flexure is distinct and the aboral margin rounded. The vesicle wall is glabrous but ornamented with a row of appendages and a crown of processes around the aperture. About the aperture there are 4–5 simple processes that are spinose on the upper surface and finely verrucate all over. The appendages are also verrucate but somewhat thicker than the apertural processes and ramified often bending apertureward. Up to 5 appendages are observed on most specimens.

Dimensions. 5 specimens measured. Total vesicle length 133–258µm, length of neck 0.19–0.30 of total vesicle length, maximum vesicle width 80–125µm, width of aperture 40–63µm, maximum appendage/process length 83µm (see **Fig. 4.8** for a length *versus* width cross plot).

Discussion. The specimens of the Mid Devonian *Ancyrochitina*. cf. *A. tumida* Taugourdeau & de Jekhowsky, 1960 in Legault (1973) resemble *A*. sp. 2 especially Plate 3, Figure 7 but specimens of *A*. sp. 2 have a more elongate vesicle chamber and longer aperture margin processes. The appendages on *A*. cf. *tumida* do not generally bend apertureward nor do the apertural processes bend aborally unlike *A*. sp. 2. In addition, the figured specimens of *An*. cf. *tumida* in Legault (1973) are all smaller (<130 µm) than *A*. sp. 2. *A. postdesmea* (**Pl. 1, figs. 14-16, Pl. 2, fig. 1**) has a less elongate vesicle chamber with shorter appendages and a cylindrical neck.

Occurrence at Bermejo. An. sp. 2 is reasonably common in the Los Monos and Iquiri Formations in samples CGH 76–CGH 61 corresponding to an Eifelian–earliest Givetian age range.

Global distribution. Currently known only from Bolivia.

Ancyrochitina sp.3 Pl. 2, figs. 13–14

? 2005: *Ancyrochitina morzadeci* Paris – Grahn & Melo, Pl. 7, fig. 5.

Description. An *Ancyrochitina* species with a cylindro-conical vesicle, a cylindrical neck (~$^1/_3$ of the total vesicle length) and an inflated aperture. The flexure is weakly defined. The vesicle surface is spinose/granate sometimes with a scattering of simple filose processes that may be bi-rooted. Spines are present on the aboral margin but are commonly broken on most specimens.

Dimensions. 9 specimens measured. Total vesicle length 180–238µm, length of neck 0.29–0.41 of total vesicle length, maximum vesicle width 75–100µm, width of aperture 50–80µm, maximum appendage length 16µm, maximum process length 10 µm (see **Fig. 4.8** for a length *versus* width cross plot).

Discussion. A. sp. 3 is similar to Plate 7, figure 5 (*A.* cf. *A. morzadeci*) in Grahn & Melo (2005) but has significantly more ornamentation (e.g. **Pl. 2, fig. 13**) on the neck and upper chamber.

Occurrence at Bermejo. A. sp. 3 is a Givetian species and is common in the Iquiri Formation in samples CGH 107–CGH 99.

Global distribution. Currently known only from Bolivia.

Genus **SOMMEROCHITINA** Costa Cruz & Quadros, 1985

Type species. Sommerochitina langei Costa Cruz & Quadros, 1985.

Diagnosis. (From Paris *et al*., 1999, p. 564) Lagenochitininae with a claviform chamber with sheathing processes.

Sommerochitina sp. 1 Pl. 2, fig. 15, Pl. 3, figs.1-5

1982: *Lagenochitina* sp. – Quadros, Pl. 2, fig. 12.
2002: Unnamed chitinozoans – Grahn figs. 8 C–D.
2005: *Sommerochitina* aff. *S. langei* Cruz & Quadros – Grahn & Melo, Pl. 7, figs. 8–9.

Description. A *Sommerochitina* species with a long neck, glabrous claviform vesicle chamber and an ornamented aboral margin. The flexure is indistinct and the shoulders are poorly developed or absent. The chamber base can be flat or rounded with the basal margin possessing simple short appendages. Most specimens possess one or two appendages but up to 6 have been observed. A prosome may be developed.

Dimensions. 11 specimens measured. Total vesicle length 365–580µm, length of neck 0.55–0.68 of total vesicle length, maximum vesicle width 50–80µm, width of aperture 38–65µm, maximum process length 10µm (see **Fig. 4.9** for a *length* versus width cross plot).

Discussion. *S*. sp. 1 is indistinguishable from *L*. *avelinoi* (**Pl. 5, figs. 15-17, Pl. 6. fig. 1**) and *L*. sp. 1 (**Pl. 6, figs. 2-3**) apart from possessing ornamentation on the basal margin. All three taxa may be conspecific given that they occur in the same samples and they may represent a population that has a wide range of morphotypes. However, due to convention (Paris *et al*., 1999) *S*. sp. 1 cannot be placed into *Lagenochitina* due to the presence of the ornamented basal margin. Grahn (2002) records specimens of *L*. *avelinoi* from Bermejo displaying simple spines on their basal margin and suggests that they are evolutionary predecessors of *Sommerochitina langei* but this assertion cannot be tested because *S. langei* has not been found in the Bermejo section, possibly because the sequence does not extend beyond the mid–Frasnian and this taxon is only known from the latest Frasnian/Famennian of Brazil (Costa Cruz & Quadros, 1985). *S*. sp. 1 differs from *S*. *langei* by having simple spines located close to or on the basal margin, rather than the ring of processes situated more centrally on the chamber base.

Occurrence at Bermejo. S. sp. 1 is abundant in the sample range CGH 142–CGH 119 and is Frasnian in age.

Global distribution. Known from Bolivia and possibly the Upper Devonian of the Parnaíba Basin, NE Brazil (see Quadros, 1982).

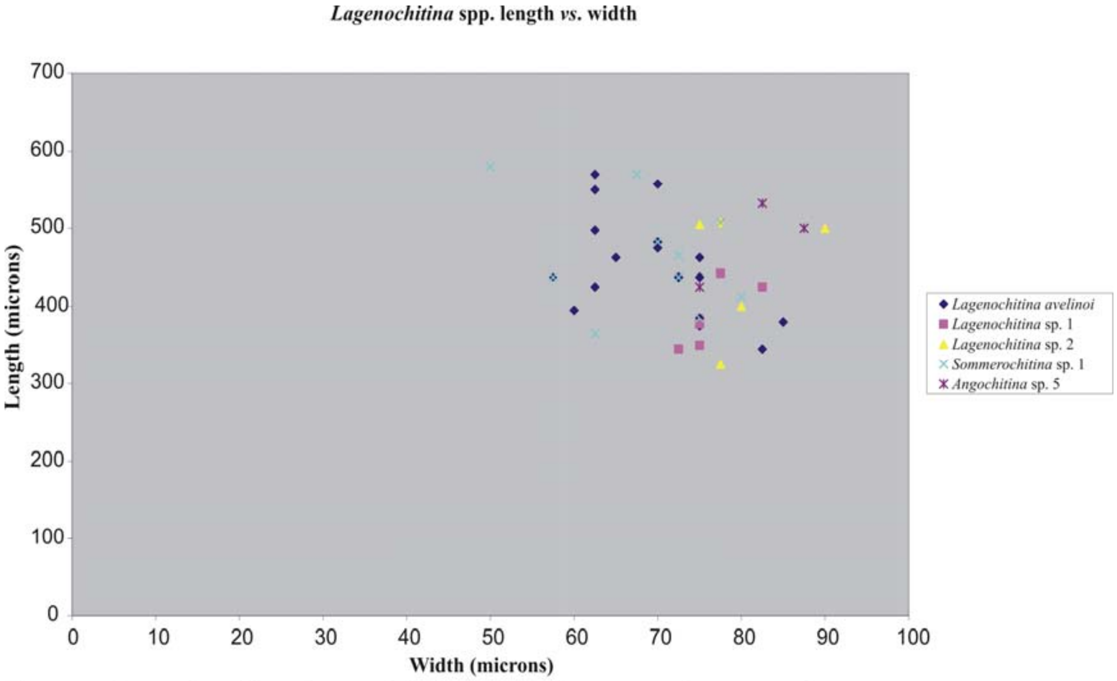


Fig. 4.9. Cross plot of length *vs*. width for *Lagenochitina* spp. from Bermejo.

Subfamily ANGOCHITININAE Paris, 1981a

Genera encountered in Bolivia. *Angochitina* Eisenack, 1931; *Fungochitina* Taugourdeau, 1966; *Ramochitina* Sommer & van Boekel, 1964.

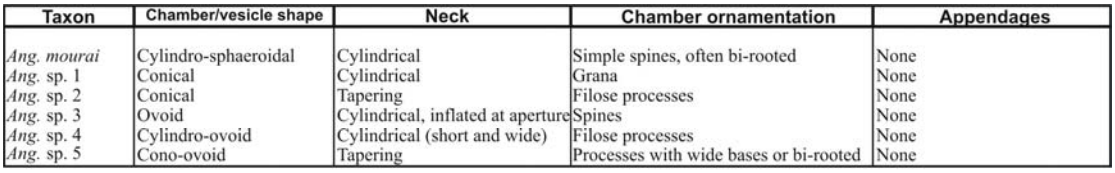
Diagnosis. (Modified from Paris, 1981a) Ornamented Lagenochitinidae with a distinct flexure and shoulder. The body is ovoid, conical or cylindrical with a glabrous or ornamented surface. A carina or appendages may be present. Chain formation is rare.

Genus **ANGOCHITINA** Eisenack, 1931

Type species. *Angochitina echinata* Eisenack, 1931.

Diagnosis. (Modified from Paris, 1981a) Angochitininae with an ovoid or spheroid body. The neck is sub–cylindrical and the vesicle covered by randomly distributed processes and filose processes.

Discussion. A summary of the key features of the *Angochitina* spp. described herein is shown in Table 4.2.



Taxon	Chamber/vesicle shape	Neck	Chamber ornamentation	Appendages
Ang. mourai	Cylindro-sphaeroidal	Cylindrical	Simple spines, often bi-rooted	None
Ang. sp. 1	Conical	Cylindrical	Grana	None
Ang. sp. 2	Conical	Tapering	Filose processes	None
Ang. sp. 3	Ovoid	Cylindrical, inflated at aperture	Spines	None
Ang. sp. 4	Cylindro-ovoid	Cylindrical (short and wide)	Filose processes	None
Ang. sp. 5	Cono-ovoid	Tapering	Processes with wide bases or bi-rooted	None

Table 4.2. A summary of the distinguishing features of the different *Angochitina* species described in this study.

Angochitina mourai Lange, 1952 Pl. 3, figs. 6–7

1952: *Angochitina mourai* n. sp. – Lange, p. 377–379, Pl. 18, figs. 7–9, Pl. 19, figs. 10–12.
non 1958: *Angochitina mourai* Lange – Collinson & Scott, p. 16–17, Pl. 1, fig. 16, Pl. 3, fig. 11.
non 1959: *Angochitina mourai* Lange – Dunn, p. 1012, Pl. 125, figs. 9, 11.
1959: *Angochitina mourai* Lange – Eisenack, Tafel 1, fig. 16.
? 1964: *Angochitina mourai* Lange – Grigani & Mantovani, p. 245, fig. 20.
1967: Tipo 26 – Lange, Pl. 3, figs. 26a–b.
1967a: *Angochitina mourai* Lange – Lange, p. 74–76, Pl. 2, figs. 17–20.
1967a: *Angochitina mourai* Lange – van Boekel, p. 98–99, Pl. I, fig. 6.
1971: *Angochitina mourai* Lange – Costa, p. 227, fig. 21.
? 1974: *Angochitina mourai* Lange – Anan-Yorke, p. 77–78, Pl. XVII, fig. 6.
1982: *Angochitina mourai* Lange – Quadros, Pl. 2, fig. 7.
1988: *Angochitina mourai* Lange – Quadros, Pl. 4, fig. 21.
non 2002: *Angochitina mourai* Lange – Grahn & Melo, Pl. 2, fig. 1.
non 2002: *Angochitina mourai* Lange – Grahn, Bergamaschi & Pereira, Pl. 3 fig. B.
2003: *Angochitina mourai* Lange – Grahn, Loboziak & Melo, Pl. 3, fig. 6.
non 2005: *Angochitina mourai* Lange – Grahn & Melo, p. 22, Pl. 1, figs. 10–11, Pl. 3, figs. 3–4.

Holotype. Barreirinha Formation, Paredão de Tajaquara, Rio Tapajós, Pará, Brazil. Slide DGM 4258, DGM, D.N.P.M, Rio de Janiero.

*Diagnosis***.** (From Lange, 1952) A species belonging to *Angochitina*, characterised by its large size, by its rather broad and well developed body chamber with a proportionally short and wide neck ($^{1}/_{3}$–$^{1}/_{2}$ of the total vesicle length), and by its rather short spines.

Description. An *Angochitina* species having a spherical vesicle chamber and a short neck ($^{1}/_{3}$–$^{1}/_{2}$ of the total vesicle length) with a translucent collar. The flexure is conspicuous and the shoulders are poorly developed. Ornamentation consists of numerous short simple processes, often bi–rooted, that are distributed evenly across the vesicle.

Dimensions. 8 specimens measured. Total vesicle length 145–188µm, length of neck 0.24–0.48 of total vesicle length, maximum vesicle width 98–120µm, width of aperture 43–70µm, maximum process length 10–24µm (see **Fig. 4.10** for a length *versus* width cross plot).

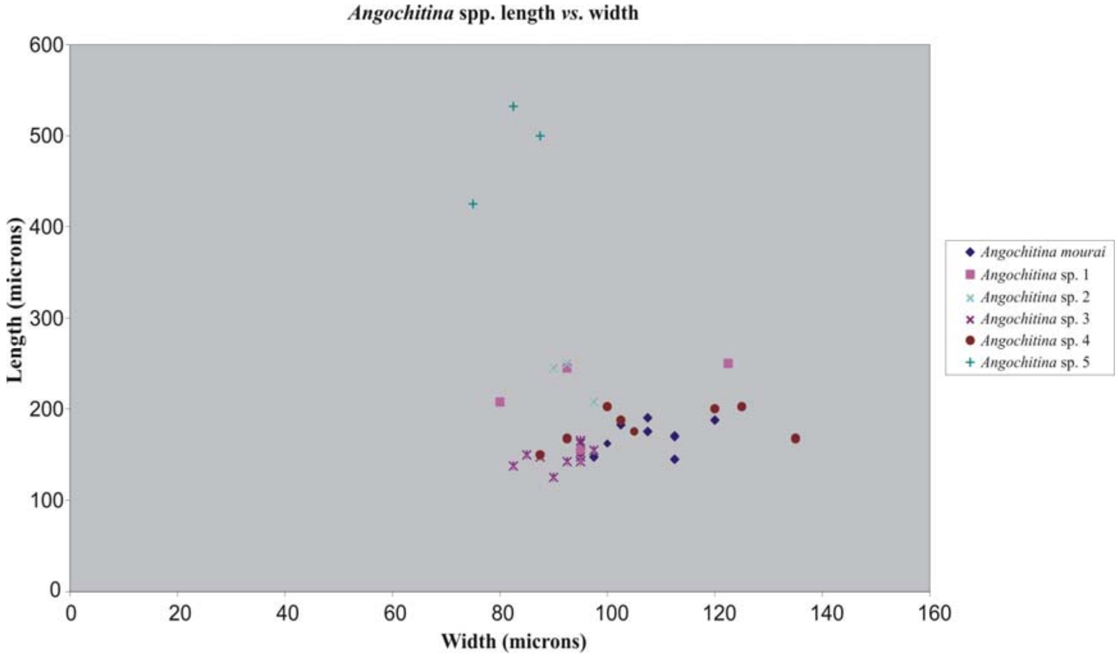


Fig. 4.10. Cross plot of length *vs*. width for *Angochitina* spp. from Bermejo.

Discussion. The specimens from Bermejo fit the overall description of the type material but the population does not have specimens that are as long as some of the type material which is up to 268µm in length. Although not mentioned in the original description, coalescent ornamentation was subsequently considered to be a key characteristic of this taxon (Lange 1967a). Consequently, the specimens in Collinson & Scott (1958), Dunn (1959) and Figure 1 in Grahn & Melo (2002) should no longer be assigned to *A. mourai* because they lack this characteristic sculpture. In addition, the specimens in Collinson & Scott (1958) and Dunn (1959) also have tapering necks and/or an inflated aperture. Figure 20 in Grigani & Mantovani (1964) has the correct vesicle shape to be *A. mourai* but lacks any intact ornamentation. Plate 1, Figure 10 in Grahn & Melo (2005) is referred to *Ramochitina* sp. 5 described herein and Plate 1, Figure 11 in the same paper is similar to CH 290 (Plate 8, fig. 16). Plate 3, Figures 3-4 in Grahn & Melo (2005) have a pronounced lip around the aperture which absent both on the type material and the specimens figured here (**Pl. 3, figs. 6-7**).

Occurrence at Bermejo. Angochitina mourai is restricted to the uppermost Iquiri Formation at Bermejo where it is common in sample CGH 142 (mid Frasnian).

Global distribution. In Brazil, *A. mourai* is generally considered an Upper Devonian species (Lange, 1967a; Quadros, 1988; Grahn *et al*., 2002; 2003) although Quadros (1982) does extend its range into the Mid Devonian . According to Grahn & Melo (2002), *Ang. mourai* is most common in the Frasnian but has scattered occurrences throughout the Famennian of Brazil. *A. mourai* has been recorded in the subsurface in the Upper Devonian in southern Morocco (Grigani & Mantovani, 1964).

Angochitina sp. 1 Pl. 3, fig. 8

Description. The vesicle chamber is conical in appearance with a cylindrical neck about $^1/_4$ of the total vesicle length without a prosome. The flexure is conspicuous and the shoulders are weakly defined. On the vesicle wall there are randomly distributed grana whose size and density are greatest on the vesicle chamber.

Dimensions. 3 specimens measured. Total vesicle length 207–250µm, length of neck 0.17–0.27 of total vesicle length, maximum vesicle width 80–123µm, width of aperture 43–55µm (see **Fig. 4.10** for a length *versus* width cross plot).

Discussion. *Angochitina* sp. 1 is very similar to *Ramochitina* sp. 1 (**Pl.4, figs. 11-17, Pl. 5, fig. 1**) in terms of vesicle shape and dimensions but lacks spinose ornamentation and a prosome.

Occurrence at Bermejo. *A.* sp. 1 is found in the basal Los Monos Formation in the sample range CGH 46-CGH 39 but is rare. *A.* sp. 1 is Eifelian in age.

Global distribution. Currently known only from Bolivia.

Angochitina sp. 2 nov. sp. Pl. 3, fig. 9

Description. An *Angochitina* species with an elongated ovoid chamber and a long initially cylindrical neck (~$^1/_3$ and $^1/_2$ total vesicle length) that becomes inflated towards the aperture. The flexure is distinct and a complex prosome is developed. The vesicle surface has a sparse covering of randomly distributed spines.

Dimensions. 3 specimens measured. Total vesicle length 275–300µm, length of neck 0.44–0.48 of total vesicle length, maximum vesicle width 90–98µm, width of aperture 55–60µm, maximum process length 13µm (see **Fig. 4.10** for a length *versus* width cross plot).

Discussion. *Angochitina* sp. 2 is distinguishable from the other species of *Angochitina* described herein, apart from *Angochitina* sp. 1 and *Angochitina* sp. 5, in terms of length (**Fig. 4.10**). *A*. sp. 2 has a different vesicle shape to *A*. sp. 1 (**Pl. 3, fig. 8**) and a longer neck whereas *A*. sp. 5 (**Pl. 4, figs. 1-2**) is probably an ornamented end member of the *Lagenochitina* population.

Occurrence at Bermejo. *A.* sp. 2 is rare and is restricted to sample CGH 125 in the Iquiri Formation. This taxon is Frasnian in age.

Global distribution. Currently known only from Bolivia.

Angochitina sp. 3 Pl. 3, fig. 10-11

? 2002: *Angochitina mourai* Lange – Grahn & Melo, Pl. 2, fig. 1.

Description. An *Angochitina* species with a cylindro-spherical vesicle and a broad flexure. The neck is cylindrical but is short and wide, rarely becoming inflated towards the aperture. There is a covering of randomly distributed simple filose processes across the vesicle surface but these are commonly broken off leaving only the bases. Prosoma were not observed.

Dimensions. 11 specimens measured. Total vesicle length 125–170µm, length of neck 0.27–0.35 of total vesicle length, maximum vesicle width 90–98µm, width of aperture 40–60µm, maximum process length 5µm (see **Fig. 4.10** for a length *versus* width cross plot).

Discussion. Angochitina pilosa (Collinson & Scott, 1958) is essentially a waste-basket taxon for similar looking Mid-Late Devonian chitinozoans with short, spinose ornamentation and therefore *Angochitina* sp. 3 has been placed in *A. pilosa* by previous workers. *A. pilosa* (**Pl. 4, figs. 3-5**) described herein has a different vesicle chamber shape being more conical in appearance. In addition, there is a 150m stratigraphic separation between the ranges of *A. pilosa* and *Ang*. sp. 3.

Occurrence at Bermejo. *A*. sp. 3 is common in the sample range CGH 134–CGH 128 within the Iquiri Formation and is Frasnian in age.

Global distribution. Currently known only from Bolivia.

Angochitina sp. 4 nov. sp. Pl. 3, figs. 12–13

Description. An *Angochitina* species with a cono-ovoid vesicle chamber. The neck is ~$^1/_{10}$ and $^1/_3$ total vesicle length and often tapers towards the aperture. The flexure is somewhat indistinct. There are numerous short, simple processes across the vesicle surface but the highest density is found on the uppermost region of the chamber and on the neck. Larger branching processes can be seen on the flanks of the lower half of the chamber on some specimens, the bases of which are relatively wide or bi-rooted compared to the other processes.

Dimensions. 9 specimens measured. Total vesicle length 150–203µm, length of neck 0.12–0.30 of total vesicle length, maximum vesicle width 95–188µm, width of aperture 45–60µm, maximum process length 20µm (see **Fig. 4.10** for a length *versus* width cross plot).

Discussion. Angochitina sp. 4 is a distinctive chitinozoan and is unique amongst the other species of *Angochitina* described here from Bermejo on account of its branching spines being restricted to the lower flanks of the chamber (**Pl. 3, fig. 12**).

Occurrence at Bermejo. *A*. sp. 4 is common in the uppermost Iquiri Formation at Bermejo in the sample range CGH 140–CGH 137 and is mid-Frasnian in age.

Global distribution. Currently known only from Bolivia.

Angochitina sp. 5 Pl. 4, figs. 1-2

Description. An *Angochitina* species with an ovoid vesicle and a very long cylindrical neck (~$^2/_3$ of the total vesicle length). Towards the oral aperture the neck becomes inflated and the uppermost $^2/_3$ of the neck is transparent. The lower $^1/_3$ of the neck is occupied by a complex prosome. The flexure is reasonably distinct. There is a scattering of simple filose processes or grana across the vesicle surface.

Dimensions. 3 specimens measured. Total vesicle length 425–533µm, length of neck 0.56–0.59 of total vesicle length, maximum vesicle width 48–75µm, width of aperture 48–75µm, maximum process length 5µm (see **Fig. 4.10** for a length *versus* width cross plot).

Discussion. Apart from having ornamentation, *Angochitina* sp. 5 is identical to *Lagenochitina* sp. 2 (**Pl. 6, figs. 2-3**) described herein and may represent an ornamented end member of the *Lagenochitina* sp. 2 population since it occurs in the same samples. However, the presence of ornamentation on *A*. sp. 5 precludes its assignment to *Lagenochitina*.

Occurrence at Bermejo. *A*. sp. 5 is rare and is restricted to sample CGH 125. This taxon is Frasnian in age.

Global distribution. Currently known only from Bolivia.

Genus **FUNGOCHITINA** Taugourdeau, 1966

Type species. *Conochitina fungiformis* Eisenack, 1931.

Diagnosis. (From *Paris et al*., 1999) Lagenochitinidae with a conical to lenticular chamber and randomly distributed spines.

Angochitina pilosa (Collinson & Scott) Paris, 1980 Pl. 4, figs. 3–5

Sphaerochitina pilosa Collinson & Scott, 1958 was transferred to *Angochitina* by Paris (1980), however its use does not appear to have been widespread and subsequently *Fungochitina pilosa* appeared in Paris *et al*. (1985). *F. pilosa* was never defined as a comb. nov., nevertheless its use has persisted. *Angochitina pilosa* is valid but inappropriate for this species based on the classification scheme of Paris *et al.* (1999) on the grounds of vesicle shape. Returning the species to *Sphaerochitina* would also be invalid for the same reason. *Fungochitina* is a suitable genus for this species but formal assignment to *Fungochitina* is required.

1958: *Sphaerochitina pilosa* n. sp. – Collinson & Scott, p. 21.
1958: *Sphaerochitina schwalbi* n. sp. – Collinson & Scott, p. 23, Pl. 3, figs. 6-10.
1959: *Sphaerochitina schwalbi* Collinson & Scott – Dunn, Pl. 127, figs. 5-8.
1973: *Sphaerochitina pilosa* (Collinson & Scott) – Urban & Newport, Pl. 2, figs 13-16.
1985: *Fungochitina pilosa* (Collinson & Scott) – Paris *et al.*, Pl. 28, figs. 3, 5, 10a-b.

2002: *Fungochitina pilosa* (Collinson & Scott) – Grahn, Bergamaschi & Pereira, Pl. 8 fig. H.
2004: *Fungochitina pilosa* (Collinson & Scott) – Grahn & Melo, Pl. 1, fig. 6.
non 2005: *Fungochitina pilosa* (Collinson & Scott) – Grahn & Melo, Pl. 2, fig. 6.

Diagnosis. (Modified from Collinson & Scott, 1958). Test shaped like a short-necked conical flask with a body chamber that is widest near the broad, slightly convex base. The short cylindrical neck is terminated orally by a short, transparent collar. With the exception of the collar, the entire surface of the test is covered by numerous very short simple spines.

Description. A *Fungochitina* species with a rounded conical, almost hemispherical, vesicle chamber and a short neck (~$^1/_3$ and $^1/_2$ total vesicle length) that tapers slightly towards the base on some specimens. The flexure is distinct and the shoulders are broad. There are numerous randomly distributed simple filose processes/grana on the vesicle surface. A prosome is usually developed.

Dimensions. 11 specimens measured. Total vesicle length 120–158µm, length of neck 0.29–0.47 of total vesicle length, maximum vesicle width 88–103µm, width of aperture 48–67µm, maximum process length 5µm.

*Discussion****.*** According to Collinson & Scott (1958) *Sphaerochitina pilosa* and *Sphaerochitina schwalbi* had similar vesicle chamber characteristics but the two taxa were distinct species on the basis that *S. schwalbi* had a much shorter neck than *S. pilosa.* Later work by Urban & Newport (1973) demonstrated that the neck length of these species showed continuous variation resulting in *S. schwalbi* becoming the junior synonym of *S. pilosa*. At Bermejo, only the short neck end member of the *A. pilosa* range has been recognised and chitinozoa similar to these are listed on the synonomy.

Belonechitina holfelzii Ottone, 1996 from the Mid Devonian of northern Argentina is similar to *A. pilosa* in terms of appearance with the only difference being a more inconspicuous flexure. However, given the stratigraphic overlap of these two taxa, this may not be sufficient to distinguish between them. Plate 2, Figure 6 in Grahn & Melo (2005) has the wrong chamber shape to be assigned to *Fungochitina*. A thorough revision of *A. pilosa* is needed since it has become a wastebasket taxon for any similar looking Mid to Late Devonian chitinozoa.

Occurrence at Bermejo. *F. pilosa* is common in the Iquiri Formation in samples CGH 116–CGH 112 and is latest Givetian in age.

Global distribution. Similar forms to those described herein have been noted in the early Givetian-early Frasnian of Brazil (Grahn *et al.*, 2002; Grahn & Melo, 2004), the mid-late Givetian of Iowa, USA (Collinson & Schwalb, 1955; Urban & Newport, 1973) and the Mid Devonian of NE Libya (Paris *et al.*, 1985).

Fungochitina sp. 1 Pl. 4, figs. 6–7

? 2002: *Ancyrochitina* sp. A – Grahn, Bergamaschi & Pereira, Pl. 7 A.

Description. A *Fungochitina* species with a broad conical chamber and long cylindrical neck (~$^1/_2$ and $^3/_4$ of the total vesicle length). The flexure is poorly defined but a simple prosome is present. The vesicle surface is glabrous with a sparse covering of spines.

Dimensions. 10 specimens measured. Total vesicle length 128–155µm, length of neck 0.56–0.72 of total vesicle length, maximum vesicle width 75–103µm, width of aperture 23–45µm, maximum process length 8µm.

Discussion. F. sp. 1 has similarities with *Ancyrochitina* sp. A from the Mid Devonian of the Paraná Basin, Brazil in Grahn *et al*. (2002) but this specimen is only illustrated and not described.

Occurrence at Bermejo. *F*. sp. 1 is common in the Iquiri Formation in the sample range CGH 106–CGH 103 and is therefore Givetian in age.

Global distribution. Known from Bolivia and possibly the Mid Devonian of Brazil.

Fungochitina sp. 2 Pl. 4, fig. 8

Description. An *Angochitina* species with a conical chamber and a tapering neck (~$^1/_5$ and $^2/_5$ total vesicle length) that becomes transparent towards the aperture. The flexure is distinct. There are numerous simple filose processes across the vesicle surface but they are longest on the vesicle chamber. The aboral margin is rounded. A prosome is usually present.

Dimensions. 7 specimens measured. Total vesicle length 125–175µm, length of neck 0.20–0.41 of total vesicle length, maximum vesicle width 78–103µm, width of aperture 40–60µm, maximum process length 12.5µm.

Discussion. F. sp. 2 differs from *F*. sp. 1 (**Pl. 4, figs. 6–7**) by having a tapering neck and a much denser cover of filose processes.

Occurrence at Bermejo. *F*. sp. 2 is not uncommon in the Iquiri Formation at Bermejo in the sample range CGH 116–CGH 105 and is Givetian in age.

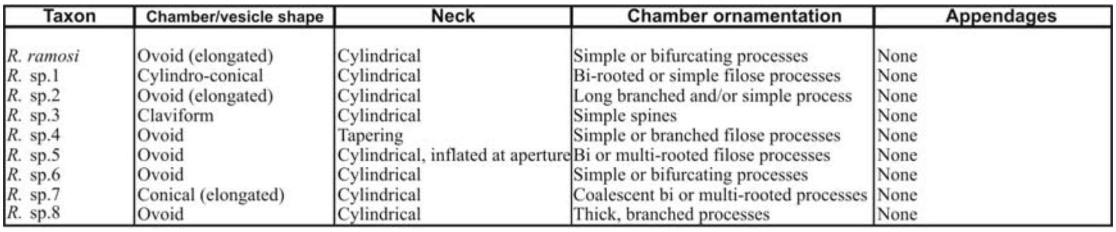
Global distribution. Currently known only from Bolivia.

Genus **RAMOCHITINA** Sommer & van Boekel, 1964,
emend. Paris *et al*., 1999

Type species. Ramochitina ramosi Sommer & van Boekel, 1964

Diagnosis. (From Paris *et al*., 1999) Lagenochitinidae with an ovoid chamber and distinct crests (vertical rows of processes or membranes).

Discussion. Laufeld (1974) erected *Gotlandochitina* as a genus but this has the same morphological characters, (i.e. vertical crests) as *R. ramosi*, the type species of *Ramochitina*. Therefore *Gotlandochitina* is now considered the junior synonym of *Ramochitina* (Paris *et al*., 1999). A summary of the key features of the *Ramochitina* spp. described herein is shown in Table 4.3.



Taxon	Chamber/vesicle shape	Neck	Chamber ornamentation	Appendages
R. ramosi	Ovoid (elongated)	Cylindrical	Simple or bifurcating processes	None
R. sp.1	Cylindro-conical	Cylindrical	Bi-rooted or simple filose processes	None
R. sp.2	Ovoid (elongated)	Cylindrical	Long branched and/or simple process	None
R. sp.3	Claviform	Cylindrical	Simple spines	None
R. sp.4	Ovoid	Tapering	Simple or branched filose processes	None
R. sp.5	Ovoid	Cylindrical, inflated at aperture	Bi or multi-rooted filose processes	None
R. sp.6	Ovoid	Cylindrical	Simple or bifurcating processes	None
R. sp.7	Conical (elongated)	Cylindrical	Coalescent bi or multi-rooted processes	None
R. sp.8	Ovoid	Cylindrical	Thick, branched processes	None

Table 4.3. A summary of the distinguishing features of the different *Ramochitina* species described in this study.

Ramochitina ramosi Sommer & van Boekel, 1964 Pl. 4, figs. 9–10

1964: *Ramochitina ramosi* n. sp. – Sommer & van Boekel, p. 426, Pl. 1 figs. 3–4. text–fig. 3.
1967a: *Ramochitina ramosi* Sommer & van Boekel – Lange p. 81, Pl. 4, figs. 37–38.
1971: *Ramochitina ramosi* Sommer & van Boekel – Costa p. 255, fig. 74.
1974: *Angochitina ramosi* Sommer & van Boekel – Anan-Yorke, p. 78–79, Pl. II, figs. 1,2, Pl. XII, figs. 1– 2, 6–17.
1982: *Ramochitina ramosi* Sommer & van Boekel – Quadros, p. 43–44, Pl. 4. fig. 13.
2000: *Ramochitina ramosi* Sommer & van Boekel – Grahn, Pereira & Bergamaschi Pl. 5, fig. 7.
2002: *Ramochitina ramosi* Sommer & van Boekel – Grahn, fig. 7 G.
2002: *Ramochitina ramosi* Sommer & van Boekel – Grahn, Bergamaschi & Pereira, Pl. 4 fig. A.
non 2002: *Ramochitina ramosi* Sommer & van Boekel – Grahn, Bergamaschi & Pereira, Pl. 4, fig. C.
2003: *Ramochitina ramosi* Sommer & van Boekel – Grahn & Melo, Pl. 1, fig. 10.
2005: *Ramochitina ramosi* Sommer & van Boekel – Grahn & Melo, Pl. 5, fig. 3.
non 2005: *Ramochitina ramosi* Sommer & van Boekel – Grahn & Melo, Pl. 5, fig. 4.

Holotype. Mid-Devonian, Tocantiná, Paraná Basin, Goías, Brazil. Plate 63–4–4; Ortholux Coordinates 37.8/119.7; D.G.M., D.N.P.M., Rio de Janeiro.

Diagnosis. (From Sommer & van Boekel, 1964) Specimens cylindro–ovoid and elongated. Body chamber occupies $^3/_4$ of overall length, being ellipsoid in shape with a convex base. Flexure inconspicuous. Neck conoid, collar short. Prosome distinct. Many thin and repeatedly branched processes, situated all over the body.

Description. A *Ramochitina* species that has an ovoid vesicle chamber and a cylindrical neck with a short transparent collar. The neck occupies between $^1/_6$–$^1/_3$ of the total vesicle length and the flexure is indistinct. Vesicle ornamentation consists of several vertical crests of simple or bifurcating processes that can branch at their base or more distally. All the specimens observed have a distinctive prosome.

Dimensions. 10 specimens measured. Total vesicle length 155–233µm, length of neck 0.18–0.31 of total vesicle length, maximum vesicle width 80–95µm, width of aperture 38–70µm, maximum process length 30µm (see **Fig. 4.11** for a length *versus* width cross plot).

Discussion. The specimens from Bermejo are in general agreement with the original diagnosis in Sommer & van Boekel (1964) but the processes are normally aligned in crests (not mentioned in the description of the type material). *R. ramosi* is similar to *R.* sp. 1 (**Pl.4, fig. 13**) but has bifurcating and not bi-rooted, processes. Plate 4, Figure C in Grahn *et al.* (2002) is referred to *R.* sp. 1 herein rather than *R. ramosi* (see below). Plate 5, Figure 4 in

Grahn & Melo (2005) has no ornamentation on the bottom half of the vesicle and cannot therefore be assigned to *R. ramosi*.

Occurrence at Bermejo. R. ramosi is restricted to the Iquiri Formation and is fairly common in the range CGH 92–CGH 84 corresponding to a Givetian age.

Global distribution. Grahn (2002) records this species from 'early-mid Givetian of the Huamampampa and Los Monos Formations in central and south Bolivia'. In reality, these formations are probably the Iquiri Formation as defined herein **(Chapter 3)**. *R. ramosi* is known from both the outcrop and subsurface throughout Brazil (Costa, 1971; Grahn, 2000; Grahn & Melo, 2005; Grahn *et al*., 2002; Lange, 1967a; Quadros, 1982; Sommer & van Boekel, 1964). There is also a record from Ghana (Anan-Yorke, 1974). In both countries *R. ramosi* is Mid Devonian in age.

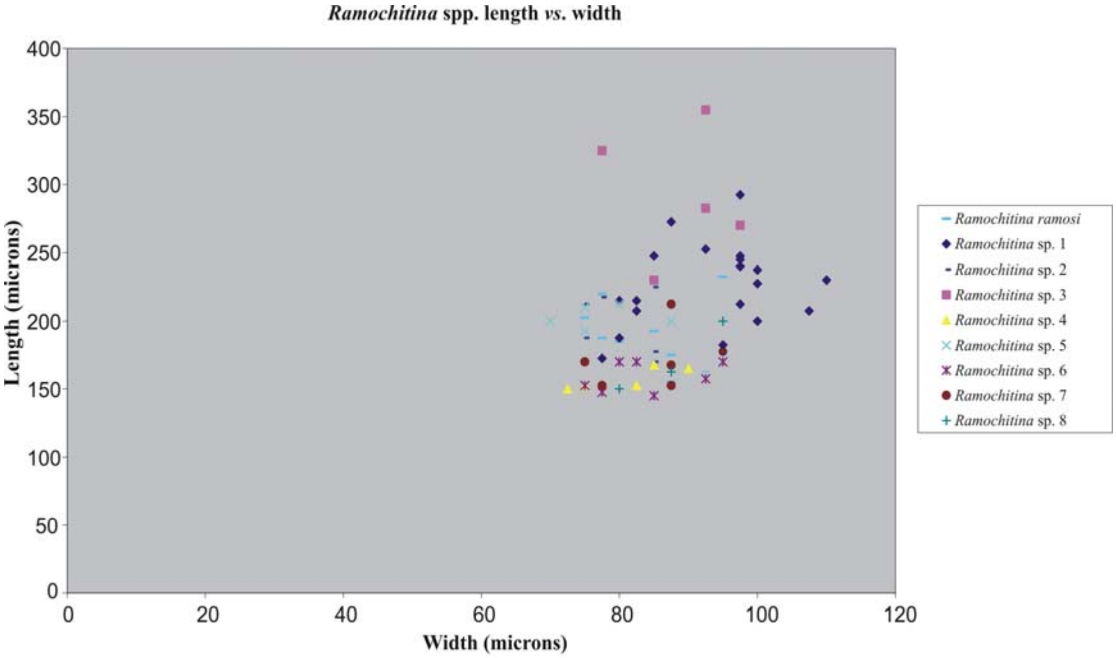


Fig. 4.11. Cross plot of length *vs.* width for *Ramochitina* spp. from Bermejo.

Ramochitina sp. 1 nov. sp. Pl. 4, figs. 11–17, Pl. 5, fig. 1

? 1974: *Angochitina* (*Ramochitina*) *ramosi* comb. nov. – Anan-Yorke, Pl. XII, figs. 11, 16.
? 2002: *Ramochitina ramosi* Sommer & van Boekel – Grahn, Bergamaschi & Pereira, Pl. 4, fig. C.

Description. The vesicle is cylindro–conical with a rounded aboral margin and a slightly convex base lacking ornamentation. The flexure is usually distinct and the shoulders range from poorly to well–developed. The neck is cylindrical and constitutes between $^1/_6$–$^1/_2$ of the total vesicle length. A flared aperture may be observed and all specimens have a distinctive simple prosome. Bi–rooted or simple unbranched filose processes are present on the vesicle walls aligned vertically and/or horizontally. Typically the processes are most strongly aligned in a vertical plane but the degree of alignment is variable. Apart from the base, which lacks ornamentation, the density of processes is even across the vesicle. The vesicle wall between the processes is glabrous.

Dimensions. 19 specimens measured. Total vesicle length 172–292µm, length of neck 0.15–0.45 of total vesicle length, maximum vesicle width 80–110µm, width of aperture 30–60µm, maximum process length 17µm (see **Fig. 4.11** for a length *versus* width cross plot).

Discussion. *R*. sp. 1 resembles *R. ramosi* (**Pl. 4, figs. 9–10**) but differs in being less bulbous in shape and always having unbranched simple processes that are commonly bi–rooted (**Pl. 4, figs. 14, 17)**. *R. ramosi* lacks bi–rooted process bases and has both simple and branched processes. Furthermore, *R. ramosi* is a Givetian taxon with a restricted stratigraphic range, that begins ca. 260m higher than the youngest *R.* sp. 1 and with no intermediate forms identified these two taxa are sufficiently distinct to be considered separate species. *R.* sp. 1 appears to be conspecific with Figures 11 and 16, Plate XII of Anan-Yorke (1974) since these chitinozoans have similar vesicle characteristics and possess bi–rooted, unbranched simple processes. Plate 4, Figure C in Grahn *et al*. (2002), placed here in *R*. sp. 1, had been assigned to *R. ramosi,* however the figured specimen has simple processes that in some cases appear bi–rooted. The neck of the specimen in Grahn *et al*. (2002) is also too long to be *R. ramosi* and it is most likely this specimen is a long necked variant of *R*. sp. 1 (**Pl. 1, figs. 11–12**).

Occurrence at Bermejo. *R.* sp. 1 is restricted to the Los Monos Formation (Eifelian) at Bermejo in samples CGH 55–CGH 18 where it is very common.

Global distribution. *R*. sp. 1 has also been found in subsurface cuttings samples from the Los Monos Formation in southern Bolivia but here it is, perhaps, commonly placed in *R. ramosi.* Poorly preserved specimens were noted to be associated with *E. sommeri* at Campo Redondo (this study). The two apparently conspecific specimens in Anan-Yorke (1974) are from the Atiavi–1 well (1298–1300m) in Ghana and are assigned to the Mid Devonian. *R.* sp. 1 also occurs in the lower Pimenteira Formation (Mid Devonian) in well 2–PM–1–MA (1646.6m) in the Parnaíba Basin, NE Brazil (**Pl.10, fig. 5**) and possibly in the early Givetian of the Paraná Basin, SE Brazil (Grahn *et al*., 2002).

Ramochitina sp. 2 Pl. 5, figs. 2–3

Description. A species of *Ramochitina* with an ovoid and elongated chamber. The neck is short and cylindrical ($^1/_6$ - $^1/_3$ of the total vesicle length) and the flexure is weak. Some specimens have well developed prosomes. The vesicle wall is smooth between several crests of sparsely distributed branched and rarely simple processes. These usually branch towards the distal tip, typically showing 1–2 orders of branching. Towards the aperture, the processes decrease in size.

Dimensions. 7 specimens measured. Total vesicle length 170–225µm, length of neck 0.15–0.35 of total vesicle length, maximum vesicle width 75–85µm, width of aperture 37.5–50µm, maximum process length 40µm (see **Fig. 4.11** for a length *versus* width cross plot).

Discussion. *Ramochitina* sp. 2 is similar in terms of shape, dimensions and sparsely distributed processes to *Ramochitina boliviensis* Grahn, 2002 but lacks the massive tapering simple processes and variable process base thickness characteristic of *R. boliviensis*. *R.* sp. 2 can be distinguished from *R. ramosi* (**Pl. 4, figs. 9-10**) by having rather distinct much longer sparsely distributed processes and a more elongated ovoid vesicle chamber. *R.* sp. 3 (Pl. 5, figs. 4-5) has different process morphology and is larger overall (**Fig. 4.11**).

Occurrence in Bermejo. *R.* sp. 2 is reasonably common in the uppermost Los Monos Formation and the basal Iquiri Formation in samples CGH 78–CGH 70 giving this taxon a latest Eifelian–Givetian range.

Global distribution. Currently known only from Bolivia.

Ramochitina sp. 3 nov. sp. Pl. 5, figs. 4–5

Description. A *Ramochitina* species with a claviform vesicle and a short cylindrical neck occupying $^{1}/_{5}$–$^{1}/_{3}$ of the total vesicle length. Both the shoulder and flexure are very weakly developed. Specimens have several crests of simple spines and the vesicle wall between the crests is smooth. The spines decrease in size towards the aboral margin and the spine density also decreases slightly towards the aperture. A simple prosome may be present.

Dimensions. 5 specimens measured. Total vesicle length 230–355µm, length of neck 0.17–0.32 of total vesicle length, maximum vesicle width 78–98µm, width of aperture 53–60µm, maximum process length 15µm (see **Fig. 4.11** for a length *versus* width cross plot).

Discussion. *R.* sp. 3 has a distinctive appearance (long body) but resembles *R. jutaiense* Grahn, Loboziak & Melo 2003 although lacking multi-rooted processes. *R*. aff. *ramosi* Sommer & van Boekel 1964 in Le Hérissé *et al*. (1996) is similar but has some multibranched processes. That specimen has now been placed in *R. jutaiense* by Grahn *et al*. (2003).

Occurrence at Bermejo. *R.* sp. 3 is rare and is found only in sample CGH 94 (742.4m) in the Iquiri Formation that corresponds to a Givetian occurrence. *R. jutaiense* is markedly older being Lochkovian in age.

Global distribution. Currently known only from Bolivia.

Ramochitina sp. 4 Pl. 5, fig. 6

Description. A *Ramochitina* species with an ovoid chamber, tapering neck ($^{1}/_{4}$–$^{1}/_{3}$ of the total vesicle length) and an inflated aperture. The flexure is distinct, but rounded and the chamber shoulders are broad. Ornamentation consists of several vertical crests of simple and more rarely branched filose processes. A prosome is usually developed.

Dimensions. 5 specimens measured. Total vesicle length 150–165µm, length of neck 0.25–0.37 of total vesicle length, maximum vesicle width 103–115µm, width of aperture 43–58µm, maximum process length 38µm (see **Fig. 4.11** for a length *versus* width cross plot).

Discussion. *R*. sp. 4 can be distinguished from *R*. sp. 5 (**Pl. 5, fig. 7**) by having a neck that tapers towards its base and branched filose processes that are not multi-rooted.

Occurrence at Bermejo. *R*. sp. 4 is moderately common in two samples; CGH 132 and CGH 128 in the Iquiri Formation corresponding to a Frasnian age.

Global distribution. Currently known only from Bolivia.

Ramochitina sp. 5 nov. sp. Pl. 5, fig. 7

2005: *Angochitina mourai* Lange – Grahn & Melo, p. 22, Pl. 1, fig. 10

Description. A *Ramochitina* species with an ovoid chamber, cylindrical neck (~$^1/_3$–$^1/_2$ of the total vesicle length) and a slightly inflated aperture. The flexure is reasonably indistinct. There are several vertical crests of bi- or multirooted filose processes across the vesicle surface.

Dimensions. 5 specimens measured. Total vesicle length 193–213µm, length of neck 0.26–0.43 of total vesicle length, maximum vesicle width 75–88µm, width of aperture 45–53µm, maximum process length 28µm (see **Fig. 4.11** for a length *versus* width cross plot).

Discussion. *R*. sp. 5 has multi-rooted processes that are absent in the other species of *Ramochitina* described herein. Plate 1, Figure 10 in Grahn & Melo (2005) assigned to *Angochitina mourai* Lange, 1952 is identical to *R*. sp. 5 which has a different chamber shape and ornamentation to *A. mourai* (compare **Pl. 5, fig. 7** with **Pl. 3, figs. 6–7**). *A. mourai* has a spherical chamber and bi-rooted processes.

Occurrence at Bermejo. *R*. sp. 5 is moderately uncommon in the sample range CGH 130–CGH 128 and is Frasnian in age.

Global distribution. Currently known only from Bolivia.

Ramochitina sp. 6 Pl. 5, figs. 8–9

? 1967a: *Angochitina devonica* Eisenack – Lange, p. 72–74, Pl. 2, Fig. 15.
non 1967a: *Angochitina devonica* Eisenack – Lange, p. 72–74, Pl. 2, Fig. 14, 16
non 1972: *Angochitina devonica* Eisenack – Urban, p. 14–15, Pl. 2, figs. 1–7.
non 1973: *Angochitina devonica* Eisenack – Urban & Newport p. 240-241, Pl. 1, fig. 16.
? 1985: *Gotlandochitina* sp. B – Paris *et al.*, Pl.28, figs 7, 9.
? 2002: *Ramochitina* sp. B – Grahn, Bergamaschi & Pereira, Pl. 7, figs. G, H.
2005: *Ramochitina stiphrospinata* – Grahn & Melo, Pl. 5, fig. 7.

Description. A *Ramochitina* species with an ovoid chamber and a cylindrical neck (~$^1/_4$–$^2/_5$ of the total vesicle length). The flexure is rounded but slightly indistinct on some specimens. The ornamentation consists of vertical crests of simple or bifurcating processes. A simple prosome is present.

Dimensions. 7 specimens measured. Total vesicle length 145–170µm, length of neck 0.31–0.46 of total vesicle length, maximum vesicle width 45–75µm, width of aperture 45–53µm, maximum process length 28µm (see **Fig. 4.11** for a length *versus* width cross plot).

Discussion. The holotype of *R. stiphrospinata* (Pl. 5, fig. 7 in Grahn & Melo, 2005) is identical to Plate 5, Figure 9 herein, albeit less well preserved since it is missing many processes. *R*. sp. 6 is similar in appearance to *Ramochitina* sp. B of Grahn *et al*., 2002 (Pl. 7 figs. G–H). According to Grahn *et al*. (2002) *R*. sp. B is identical to *Gotlandochitina* sp. B of Paris *et al*. (1985) but no explanation is offered because *R*. sp. B is not described. Curiously, Grahn & Melo (2005) do not include Plate 7, Figures G–H of Grahn *et al.* (2002) in the synonomy of *R. stiphrospinata* despite these specimens having more similarity with *R. stiphrospinata* than the records in their synonomy.

The synonomy of *R. stiphrospinata* in Grahn & Melo (2005) is doubtful since supposed records of this taxon in South America are attributable to other taxa. Plate 1, Figure 5 B in Grahn *et al*. (2002) has the wrong vesicle shape and a non-cylindrical neck, and Figure 1 H (referred to as *R*. sp. B) in Grahn *et al*. (2002) has a crown of processes around the aperture which is not described or seen on the type material of *R. stiphrospinata*. Plate 1, Figure 16 in Urban & Newport (1973) only has simple spines which have thicker bases than seen on *R. stiphrospinata.* Plate 5, Figures 1-7 referred to as *Angochitina devonica* in Urban (1972) are distinct from *R. stiphrospinata* on the basis of vesicle shape and having a lower density of processes. Furthermore, some of the Urban (1972) specimens also have multi-branched and/or wider processes (e.g. Pl. 5, fig. 4, 6–7), unlike the holotype of *R. stiphrospinata* which only bifurcate and are thinner. Lange's (1967a) specimens of *A. devonica* have different ornamentation to *R. stiphrospinata*. Clearly, there are some problems in the proper recognition of *R. stiphrospinata* and whilst this taxon may be valid, more specimens need to be studied and figured. For this reason, the use of this taxon as a zonal index species (Grahn, 2005) is perhaps questionable and consequently *R.* sp. 6 is kept in open nomenclature pending further study.

Occurrence at Bermejo. *R*. sp. 6 is common in the sample range CGH 109–CGH 106 and is Givetian in age.

Global distribution. Currently known only from Bolivia and the Givetian of Brazil (Grahn & Melo, 2005).

Ramochitina sp. 7 nov. sp. Pl. 5, fig. 10

? 2002: *Ramochitina* sp. C – Grahn, Bergamaschi & Pereira, Pl. 7, fig. J.

Description. A *Ramochitina* species with an elongate conical chamber and a short cylindrical neck (~$^1/_4$ of the total vesicle length). The flexure is indistinct. The vesicle surface is granulate but there are also sparsely distributed bi- or multi-rooted processes that coalesce to form crests. Most specimens have a simple prosome.

Dimensions. 6 specimens measured. Total vesicle length 153–213µm, length of neck 0.11–0.21 of total vesicle length, maximum vesicle width 75–95µm, width of aperture 35–50µm, maximum crest height 9µm (see **Fig. 4.11** for a length *versus* width cross plot).

Discussion. *R*. sp. 7 is similar to *Ramochitina* sp. C (Plate 7, J) in Grahn *et al*. (2002) in that *R*. sp. C has simple spines that coalesce to form crests. However, this specimen in Grahn *et al*. (2002) is of poor quality and is not described. There is a second illustrated specimen of *R*. sp. C (Plate 8, A) in Grahn *et al*. (2002) but this has a different vesicle shape and style of ornamentation and therefore should be considered a separate species.

Occurrence at Bermejo. R. sp. 7 is common in the sample range CGH 84–CGH 83 and is Givetian in age.

Global distribution. Currently known only from Bolivia.

Ramochitina sp. 8 nov. sp. Pl. 5 figs. 11–13

Description. A *Ramochitina* species with an ovoid chamber and a short cylindrical neck (~$^1/_3$ of the total vesicle length). The flexure is broad. Ornamentation consists of crests of distinctive thick-branched processes that may coalesce with adjacent processes. The processes have a distinctive pitted surface.

Dimensions. 3 specimens measured. Total vesicle length 150–200µm, length of neck 0.25–0.31 of total vesicle length, maximum vesicle width 80–95µm, width of aperture 43–50µm, maximum process length 25µm (see **Fig. 4.11** for a length *versus* width cross plot).

Discussion. Although rare, *R*. sp. 8 is easily distinguished from the other species of *Ramochitina* described herein on account of its distinctive thick branching and coalescent ornamentation.

Occurrence at Bermejo. R. sp. 8 is restricted to CGH 126 in the Iquiri Formation and is Frasnian in age.

Global distribution. Currently known only from Bolivia.

Subfamily LAGENOCHITININAE Paris, 1981a

Genera encountered in Bolivia. Lagenochitina Eisenack, 1931.

Diagnosis. (Modified from Paris, 1981a). Lagenochitinidae with a smooth, foveolate, felt like or granulate vesicle surface. The vesicle is lenticular-spheroidal, ovoid or sub cylindrical and the flexure and shoulders are distinct. The aboral margin is rounded and a mucron may be present. Forms fragile chains.

Genus **LAGENOCHITINA** Eisenack, 1931

Type species. *Lagenochitina baltica* Eisenack, 1931.

Diagnosis. (From Paris *et al*., 1999). Lagenochitinidae with an ovoid to cylindrical glabrous chamber.

Discussion. Ornamented Frasnian *Lagenochitina* forms are observed at Bermejo and through convention these have to be referred to separate genera (see *Angochitina* sp. 5 and *Sommerochitina* sp. 1). However, this practice can create difficulties, e.g. specimen CH384 (**Pl. 10, fig. 6**) which has both spines and appendages, and therefore cannot be assigned to *Angochitina*, *Lagenochitina* or *Sommerochitina*. Apart from being ornamented or non-ornamented, otherwise identical *Lagenochitina* forms occur together in the same samples at Bermejo, consequently it not unreasonable to assume that the Frasnian *Lagenochitina* populations exhibit a wider range of morphotypes compared to other species. Referring separate morphotypes to different genera masks this relationship as does speciating them. Further work is needed on the Frasnian *Lagenochitina* populations and for this reason *L.* sp. 1 and *L.* sp. 2 are kept in open nomenclature.

Lagenochitina praeavelinoi Grahn & Melo, 2004 Pl. 5, fig. 14

2004: *Lagenochitina praeavelinoi* n. sp. – Grahn & Melo, p. 75, Pl. 1, figs. 4–5.

Holotype. Ch. 66, Well 1–MS–5–AM, core 26 (1542.2–1546.0m). Swedish Museum of Natural History.

Diagnosis. (From Grahn & Melo, 2004) Elongated ovoid body and a cylindrical neck with a straight aperture. The vesicle is glabrous.

Description. A *Lagenochitina* species with a claviform, glabrous vesicle and a long cylindrical neck.

Dimensions. 1 specimen measured. Vesicle length 235µm, maximum vesicle width 53µm, width of aperture 30µm.

Discussion. The single specimen of *L. praeavelinoi* is broken. Although probably having a similar vesicle shape and texture to *L. avelinoi* (claviform and glabrous) based on its stratigraphic position within the Los Monos Formation this form cannot be *L. avelinoi* (**Pl. 5, figs. 15-17, Pl. 6, fig. 1**) which is restricted to the upper Iquiri Formation 800m higher stratigraphically.

Occurrence at Bermejo. L. praeavelinoi is restricted to the Los Monos Formation in sample CGH 46 and is Eifelian in age.

Global distribution. L. praeavelinoi is present in the latest early Eifelian to early Givetian of the Amazonas Basin, Brazil (Grahn & Melo, 2004).

Lagenochitina avelinoi Lange, 1952 Pl. 5, figs. 15–17, Pl. 6, fig. 1

1952: *Lagenochitina avelinoi* n. sp. – Lange, p.376–377, Pl. 19, figs. 1–6.
1955: *Lagenochitina avelinoi* – Eisenack, Tafel 1, fig. 17.
1967a: *Lagenochitina avelinoi* Lange – Lange, p. 80–81, Pl. 4, fig. 36.

1971: *Lagenochitina avelinoi* Lange – Costa, p. 243–244, fig. 46:52.
2002: *Lagenochitina avelinoi* Lange – Grahn & Melo, p. 5, Pl. I figs. 2–3.
2002: *Lagenochitina avelinoi* Lange – Grahn, Bergamaschi & Pereira, Pl. 2 fig. H.
2002: *Lagenochitina avelinoi* Lange – Grahn, figs. 8 B, 8 E.

Holotype. Barreirinha Formation, Paredão de Tajaquara, Rio Tapajós, Pará, Brazil. Slide DGM 4255, DGM, D.N.P.M, Rio de Janeiro.

Diagnosis. (From Lange, 1952) A species of *Lagenochitina* distinguished by its combination of large dimensions and by its club–shaped elongate body. The anterior region of the body (base) is rounded.

Description. A *Lagenochitina* species with a glabrous, claviform vesicle chamber and a characteristic long cylindrical neck (~$^1/_2$–$^2/_3$ of the total vesicle length). The aperture has a flared collar and most specimens possess a distinctive complex prosome that occupies the majority of the neck. The flexure is not prominent and the vesicle base is rounded.

Dimensions. 18 specimens measured. Total vesicle length 345–570µm, length of neck 0.51–0.64 of total vesicle length, maximum vesicle width 60–85µm, width of aperture 30–65µm (see **Fig. 4.9** for a length *versus* width cross plot).

Discussion. L. avelinoi is identical to *Sommerochitina* sp. 1 (**Pl. 2, figs. 15, Pl. 3, figs. 1-5**) but lacks ornamentation on the aboral margin. *L*. sp. 1 (**Pl. 6, figs. 2-3**) has a flat vesicle base. Paris *et al.* (2000) assigned the species *avelinoi* to *Angochitina* on account of minute hairs on the vesicle but the specimen of *Angochitina avelinoi* figured in Paris *et al.* (2000) from the Late Devonian of Algeria has a very short neck and its dimensions are too small to be *L. avelinoi,* consequently the *avelinoi* species should be retained in *Lagenochitina.*

Occurrence at Bermejo. *L. avelinoi* is observed in CGH 119 in the basal Iquiri Formation but is more common in samples CGH 142–CGH 139 near the top of the Iquiri Formation. *L. avelinoi* is therefore a Frasnian species.

Global distribution. L. avelinoi has a Late Devonian stratigraphic range in Brazil (Lange, 1967a; Grahn & Melo, 2002; Grahn, 2002; Grahn *et al*., 2002).

Lagenochitina sp. 1 Pl. 6, figs. 2–3

Description. A *Lagenochitina* species with a smooth claviform vesicle but a flat base. The neck is long (~$^1/_2$–$^2/_3$ of the total vesicle length) and cylindrical becoming inflated at the aperture and a complex prosome may be present. The flexure is indistinct and shoulders are poorly developed on the chamber.

Dimensions. 5 specimens measured. Total vesicle length 345–443µm, length of neck 0.53–0.63 of total vesicle length, maximum vesicle width 73–83µm, width of aperture 55–60µm (see **Fig. 4.9** for a length *versus* width cross plot).

Discussion. *L*. sp. 1 is similar to *L. avelinoi* (**Pl. 5, figs. 15–17, Pl. 6, fig. 1**) but has a less elongate vesicle chamber with a flat base.

Occurrence at Bermejo. *L*. sp. 1 is only found in sample CGH 119 from the basal Iquiri Formation where it is fairly common and is Frasnian in age.

Global distribution. Currently known only from Bolivia.

Lagenochitina sp. 2 Pl. 6, figs. 4–5

Description. A *Lagenochitina* species with an ovoid vesicle chamber and a long neck (~$^1/_2$–$^2/_3$ of the total vesicle length) that becomes more inflated towards the oral margin and terminates in a short expanded collar. The uppermost $^1/_3$ of the neck is more transparent relative to the rest of the vesicle. A complex prosome may be present. The flexure is usually indistinct and shoulders are not developed on the vesicle chamber.

Dimensions. 5 specimens measured. Total vesicle length 425–533µm, length of neck 0.55–0.63 of total vesicle length, maximum vesicle width 75–90µm, width of aperture 48–75µm (see **Fig. 4.9** for a length *versus* width cross plot).

Discussion. *L*. sp. 2 differs from *L. avelinoi* (**Pl. 5, figs. 15–17, Pl. 6, fig. 1**) and *L*. sp. 2 (**Pl. 6, figs. 4–5**) in terms of vesicle chamber shape which is ovoid and having a section of transparent neck. *L*. sp. 3 attains larger dimensions than *L*. sp. 1 (**Fig. 4.9**) and often has a gradually flaring aperture unlike *L*. sp. 1 and *L. avelinoi*. *Angochitina* sp. 5 is considered herein to be an ornamented form of *L*. sp. 2.

Occurrence at Bermejo.. *L*. sp. 3 is reasonably common in the sample range CGH 125–CGH 119 within the Iquiri Formation and is Frasnian in age.

Global distribution. Currently known only from Bolivia.

Subfamily TOGACHITININAE Wood, 1994

Genera encountered in Bolivia. *Togachitina* Wood, 1994.

Diagnosis. Bilayered Lagenochitinidae possessing a flask (ancyrochitinid) shaped vesicle. (From Wood, 1994)

Genus **TOGACHITINA**

Type species. Togachitina eamesi Wood, 1994

Diagnosis. (From Wood, 1994) Bilayered, flask-shaped vesicle characterized by a hyaline outer wall layer separated from an inner vesicle. Outer wall forms a sheath enclosing an internal vesicle and extends into a long neck. Inner chamber possesses a prosome.

Discussion. *Togachitina* was rejected as a genus by Paris *et al*. (1999) and considered a junior synonym of *Pellichitina* Achab, Asselin & Soufiane, 1993, an Ordovician genus. Grahn (2002) continued to use *Togachitina* and since *Pellichitina eamesi* has not been formally defined, *Togachitina* is retained herein.

Togachitina sp. 1 Pl. 6, figs. 6–7

? 1994: ?*Togachitina* sp. – Wood, Pl. 2, figs. 5–6.

Description. A *Togachitina* species with a glabrous membrane enclosing a cylidro-conical vesicle. The neck of the vesicle is short, tapering slightly towards the aperture but is further extended by the outer membrane ($^1/_2$ – $^2/_3$ total vesicle length). The flexure is well-defined and a prosome is absent. Most specimens are damaged often resulting in the membrane outline being obscured.

Dimensions. 3 specimens measured. Total vesicle length 158–175µm, length of neck 0.48–0.64 of total vesicle length, maximum vesicle width 95–108µm, width of aperture 30–45µm.

Discussion. *Togachitina* sp. 1 differs from *T. eamesi* Wood, 1994 by having a much shorter neck and lacking a prosome. *T*. sp. 1 is similar to ?*Togachitina* sp. Wood, 1994 but has a tapering rather than a cylindrical neck. In addition, small spinae around the aperture on this specimen were not seen on *T*. sp. 1. *Togachitina* is a distinctive genus that is not seen elsewhere in the Devonian of Bolivia and it is highly likely that *T*. sp. 1 and those species described in Wood (1994) are related, since they are also of similar age and from Bermejo. Further work is required to determine the exact relationship, if any, between the specimens in Wood (1994) and this study.

Occurrence at Bermejo. *T*. sp. 1 is rare and was found only in sample CGH 115. This taxon is latest Givetian-Frasnian in age.

Global distribution. Currently known only from Bolivia.

Subfamily UROCHITININAE Paris, 1981a

Genera encountered in Bolivia. Urochitina Taugourdeau & de Jekhowsky, 1960.

Diagnosis. (Modified after Paris, 1981a) Lagenochitinidae with a smooth ovoid chamber and often a collar possessing simple or anastomosing ornamentation. There is a copula at the base of the chamber in the form of a long elongated peduncle. Chain formation may occur but the chains are rather fragile.

Genus **UROCHITINA**

Type species. *Urochitina simplex* Taugourdeau & de Jekhowsky, 1960.

Diagnosis. (From Paris *et al*., 1999) Lagenochitinidae with an ovoid chamber bearing a long solid peduncle.

Urochitina bastosi van Boekel, 1967 Pl. 6, fig. 8

1967: Tipo 125 – Lange, Pl. 9, figs. 125a,b.
1967: *Urochitina bastosi* n. sp. – van Boekel, p. 274–275, Pl. 1, figs. 1–7, text–figs. 1a-b.
1968: *Urochitina bastosi* van Boekel – van Boekel, Pl. 1, figs. 1–3.

1971: *Urochitina bastosi* van Boekel – Costa, p. 265–266, fig. 34:92
1988: *Urochitina bastosi* van Boekel – Quadros, Pl. 5, fig. 26.
2002: *Urochitina bastosi* van Boekel – Grahn & Melo, Pl. 1, fig. 4.
2005: *Urochitina bastosi* van Boekel – Grahn & Melo, Pl. 1, fig. 7, Pl. 2, fig. 9, Pl. 3, fig.1.

Holotype. Indeterminate horizon, Rio Tapajós, Pará, Brazil. Slide 65/12/23 Zeiss coordinates 101,9/41,2. D.G.M.; D.N.P.M., Rio de Janeiro.

Diagnosis. (Modified from van Boekel, 1968) Chitinozoans with an elliptical chamber and long cylindrical neck. The vesicle surface is glabrous.

Description. An *Urochitina* species with a claviform glabrous vesicle chamber. The neck accounts for ~$^1/_2$ of the total vesicle length and has a flared, unornamented aperture. A complex prosome may be present. The flexure is not always well defined and the shoulders are broad. Most specimens show evidence of a slender peduncle but often this has become detached from the vesicle. On complete specimens, the peduncle is glabrous and is between $^1/_3$ – $^1/_2$ of the total vesicle length. The peduncle thins towards the distal tip.

Dimensions. 4 specimens measured. Total vesicle length (excluding peduncle) 235–375µm, length of neck 0.45–0.52 of total vesicle length, maximum vesicle width 78–98µm, width of aperture 53–60µm, maximum peduncle length 185µm (see **Fig. 4.12** for a length versus width cross plot).

Discussion. The genus *Urochitina* is rarely encountered in the Devonian of South America. Apart from *U. bastosi*, there is currently only one other species formally described, *U. loboi* Volkheimer, Melendi & Salas, 1986 from Argentina where this taxon is restricted to the Early Devonian. *U. loboi* has a much shorter neck than *U. bastosi* and an ornamented aperture. The peduncle on *U. loboi* is spinose and is attached to the vesicle via a membraneous funnel that does not connect internally with the vesicle chamber. These features are absent in *U. bastosi*. *U. bastosi* has a flared aperture and is generally longer (**Fig. 4.12**) and more slender than *U*. sp. 1 (**Pl. 6, figs. 9-10**) and *U*. sp. 2 (**Pl. 6, figs. 11-13**) described herein.

Occurrence at Bermejo. U. bastosi is moderately common and is only found near the very top of the (eroded) Iquiri Formation in samples CGH 143–CGH 141 that are mid–Frasnian in age.

Global distribution. U. bastosi was first described from Brazil (van Boekel, 1967) and was originally considered to be Mid Devonian. More recent studies that show that in Brazil *U. bastosi* is restricted to the Late Devonian (Quadros, 1988; Grahn & Melo, 2005; 2002). Grahn (2005) gives *U. bastosi* a late Frasnian-late Famennian (approaching 10My) range which is unusual considering the general trend at Bermejo suggests that most taxa have much shorter ranges (Fig. 1).

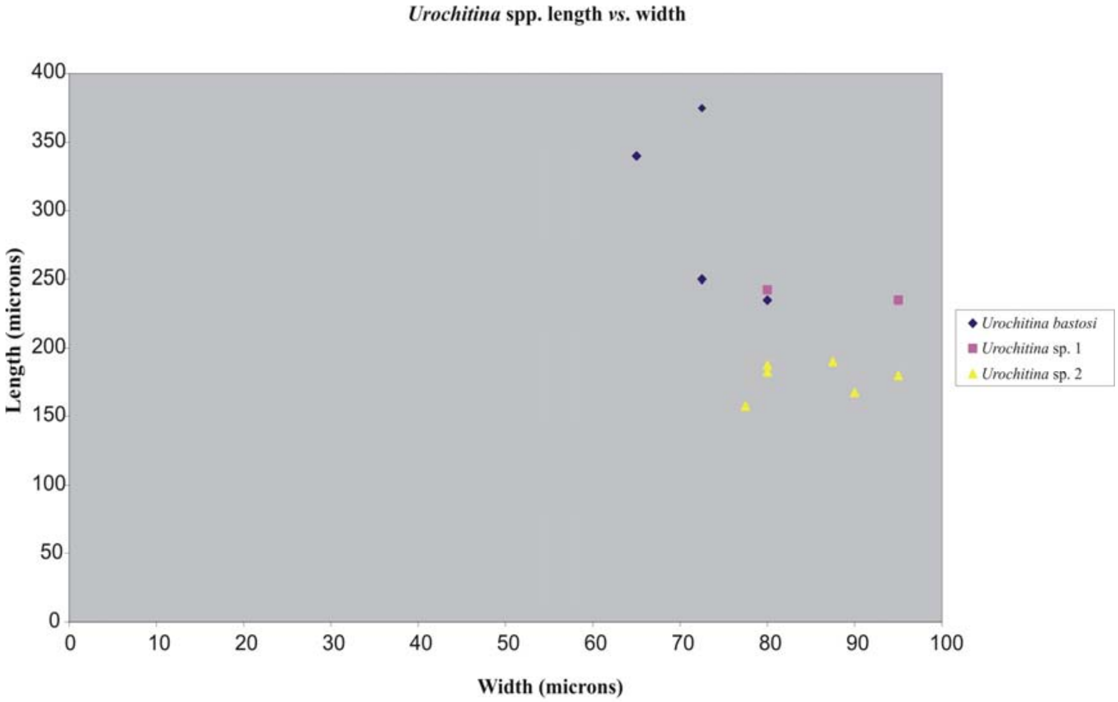


Fig. 4.12. Cross plot of length *vs*. width for *Urochitina* spp. from Bermejo.

Urochitina sp. 1 Pl. 6, figs. 9–10

Description. An *Urochitina* species with an opaque ovoid vesicle chamber and a cylindrical or slightly tapering neck (~$^1/_2$ of the total vesicle length) that becomes transparent from approximately its midpoint to the aperture. The flexure is fairly well defined but the shoulders less so. On complete specimens there is a peduncle that is thickest at its base becoming thinner towards the distal tip.

Dimensions. 2 specimens measured. Total vesicle length (excluding peduncle) 235–243µm, length of neck 0.52–0.55 of total vesicle length, maximum vesicle width 80–95µm, width of aperture 53µm, maximum peduncle length 175µm (see **Fig. 4.12** for a length *versus* width cross plot).

Discussion. *U*. sp. 1, although very rare, is reasonably long ranging at Bermejo. This species differs from *U. bastosi* in having a more ellipsoid vesicle chamber whilst lacking a flared aperture. *U*. sp. 1 differs from *U*. sp. 2 (**Pl. 6, figs. 11-13**) by being a different shape, being longer (**Fig. 4.12**) and having a longer peduncle.

Occurrence at Bermejo. *U*. sp. 1 was found in samples CGH 141 and CGH 119 in the Iquiri Formation and is Frasnian in age.

Global distribution. Currently known only from Bolivia.

Urochitina sp. 2 Pl. 6, figs. 11-13

Description. An *Urochitina* species having an ovoid vesicle chamber and a short cylindrical neck constituting ~$^1/_3$ of the total vesicle length. The flexure is weak and the shoulders are poorly developed. Ornamentation consists of a crown of nodes/spine bases? around the aperture margin and a peduncle.

Dimensions. 6 specimens measured. Total vesicle length (excluding peduncle) 158–190µm, length of neck 0.28–0.38 of total vesicle length, maximum vesicle width 78–95µm, width of aperture 40–53µm, maximum peduncle length 50µm (see **Fig. 4.12** for a length versus width cross plot).

Discussion. *U*. sp. 2 is the smallest of the *Urochitina* species encountered at Bermejo. The neck to body ratio is smaller than that of the other species and *U*. sp. 2 possesses ornamentation around the oral margin not seen on either *U. bastosi* (**Pl. 6, fig. 8**) or *U*. sp. 1 (**Pl. 6, figs. 9–10**).

Occurrence at Bermejo. *U*. sp. 2 is restricted to samples CGH 143 and CGH 141 but is reasonably common. This species is mid Frasnian in age.

Global distribution. Currently known only from Bolivia.

Plate 1

Black scale bar = 100µm.

1. *Hoegisphaera glabra* Staplin, 1961. Iquiri Formation, CH378, CGH 124/ 269.7m, coordinates 13.5/110.8.
2. *Hoegisphaera glabra* Staplin, 1961. Iquiri Formation, CH377, CGH 124/ 269.7m, coordinates 18.5/110.2.
3. *Cladochitina biconstricta* (Lange, 1949) Lange, 1967b. Iquiri Formation, CH157, CGH 87/839.7m, coordinates 22/100.5.
4. *Cladochitina biconstricta* (Lange, 1949) Lange, 1967b. Iquiri Formation, CH152, CGH 85/861.2m, coordinates 8.5/94.4.
5. *Cladochitina biconstricta* (Lange, 1949) Lange, 1967b. Iquiri Formation, CH159, CGH 87/839.7m, coordinates 32.2/103.2.
6. *Cladochitina biconstricta* (Lange, 1949) Lange, 1967b. Iquiri Formation, CH379, CGH 84/865.2m, coordinates 13.1/104.9. A constriction of the vesicle is arrowed.
7. *Spinachitina* sp. 1 nov. sp. Iquiri Formation, CH351, CGH 90/813.1m, coordinates 18.5/107.1.
8. *Spinachitina* sp. 1 nov. sp Iquiri Formation, CH352, CGH 90/813.1m, coordinates 18.5/107.1.
9. *Alpenachitina eisenacki* Dunn & Miller, 1964. Los Monos Formation, CH42, CGH 46(Chits)/1158.5m, coordinates 22.3/109.2.
10. *Alpenachitina eisenacki* Dunn & Miller, 1964. Los Monos Formation, CH47, CGH 47A(Chits)/1157.2m, coordinates 22.3/106.8.
11. *Alpenachitina eisenacki* Dunn & Miller, 1964. Los Monos Formation, CH51, CGH 47B(Chits)/1157.2m, coordinates 14/105.8.
12. *Ancyrochitina langei* Sommer & van Boekel, 1964. Iquiri Formation, CH211, CGH 108/518.8m, coordinates 14.1/104.8.
13. *Ancyrochitina langei* Sommer & van Boekel, 1964. Iquiri Formation, CH212, CGH 108/518.8m, coordinates 13/111.6.
14. *Ancyrochitina postdesmea* Grahn, 2002. Iquiri Formation, CH136, CGH 82A(Chits)/ 881.7m, coordinates 8.5/103.6.
15. *Ancyrochitina postdesmea* Grahn, 2002. Iquiri Formation, CH137, CGH 82A(Chits)/ 881.7m, coordinates 9.5/101.5.
16. *Ancyrochitina postdesmea* Grahn, 2002. Iquiri Formation, CH138, CGH82B(Chits)/ 881.7m, coordinates 9.5/95.4.

Plate 1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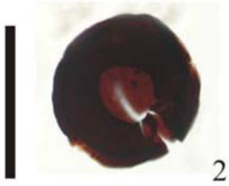
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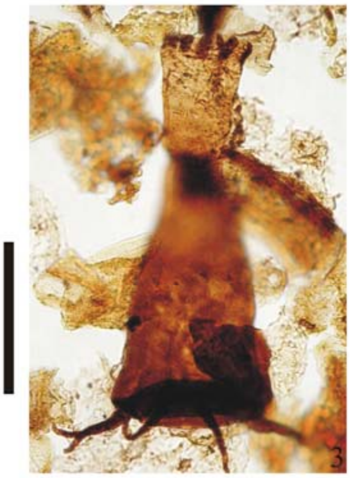
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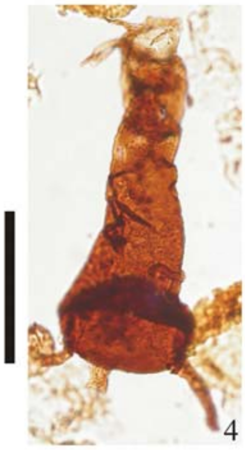
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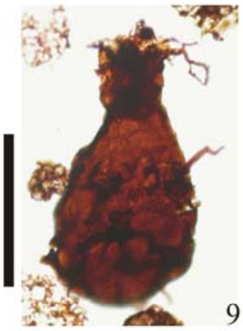
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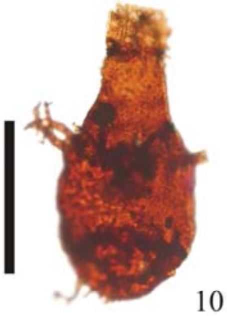
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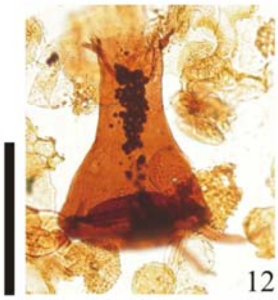
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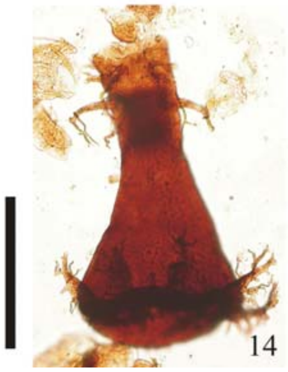
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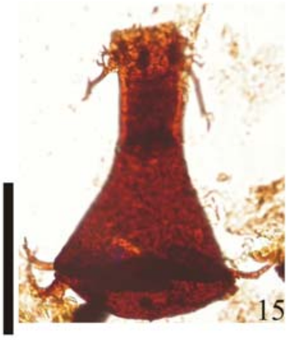
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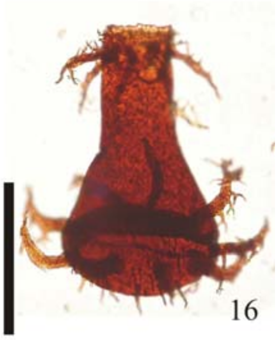
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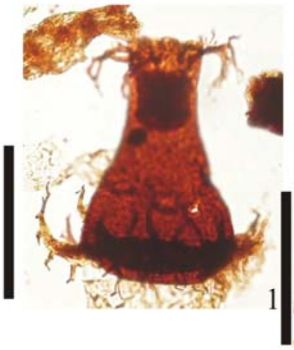
Plate 2

Black scale bar = 100μm.

1. *Ancyrochitina postdesmea* Grahn, 2002. Iquiri Formation, CH146, CGH 82/881.7m, coordinates 21/97.8.
2. *Cladochitina varispinosa* Lange, 1967b. Los Monos Formation, CH99, CGH 71/937m, coordinates 13.2/107.8.
3. *Cladochitina varispinosa* Lange, 1967b. Iquiri Formation, CH102, CGH 76A(Chits)/937m, coordinates 21/108.7.
4. *Cladochitina varispinosa* Lange, 1967b. Iquiri Formation, CH119, CGH 76/910.6m, coordinates 15/96.3.
5. *Cladochitina varispinosa* Lange, 1967b. Iquiri Formation, CH101, CGH 76A (Chits)/910.6m, coordinates 13.4/109.6.
6. *Cladochitina varispinosa* Lange, 1967b. Los Monos Formation, CH88, CGH 65B(Chits)/1011.2m, coordinates 17.8/96.9.
7. *Ancyrochitina* cf. *morzadeci* Grahn, 2002. Iquiri Formation, CH366, CGH 83/870.8m, coordinates 19.6/100.5.
8. *Ancyrochitina* sp. 1 nov. sp. Los Monos Formation, CH78, CGH 53/1124.4m, coordinates 7.5/112.6.
9. *Ancyrochitina* sp. 1 nov. sp. Los Monos Formation, CH24, CGH 39A(Chits)/ 1170.8m, coordinates 17/109.
10. *Ancyrochitina* sp. 2. Los Monos Formation, CH100, CGH76A(Chits)/910.6m, coordinates 8.2/104.1.
11. *Ancyrochitina* sp. 2. Iquiri Formation, CH121, CGH 76/910.6m, coordinates 28.7/108.2.
12. *Ancyrochitina* sp. 2. Los Monos Formation, CH337, CGH 70/959.6m, coordinates 27.7/96.8.
13. *Ancyrochitina* sp. 3. Iquiri Formation, CH172, CGH 104A(Chits)/553.2m, coordinates 20.1/96.8.
14. *Ancyrochitina* sp. 3. Iquiri Formation, CH173, CGH 104B(Chits)/553.2m, coordinates 26.5/95.1.
15. *Sommerochitina* sp. 1. Iquiri Formation, CH230, CGH 119/317.3m, coordinates 9.1/96.6.

Plate 2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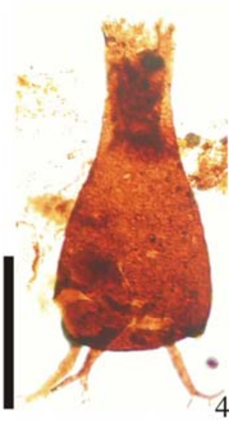
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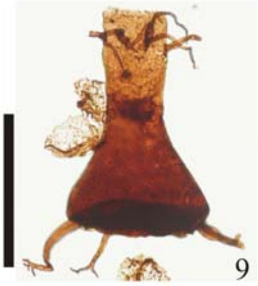
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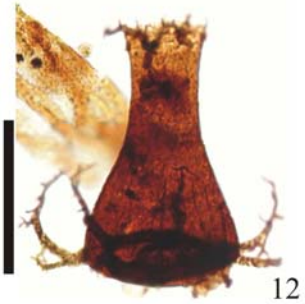
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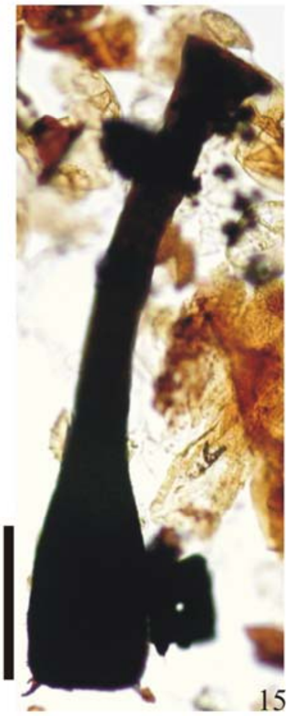
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Plate 3

Black scale bar = 100µm.

1. *Sommerochitina* sp. 1. Iquiri Formation, CH252, CGH 138D(Chits)/144.2m, coordinates 12/101.7.
2. *Sommerochitina* sp. 1. Iquiri Formation, CH325, CGH 140/136.2m, coordinates 23/104.6.
3. *Sommerochitina* sp. 1. Iquiri Formation, Lag-13, CGH 119B(Chits)/317.3m, coordinates 16.2/102.3.
4. *Sommerochitina* sp. 1. Iquiri Formation, CH256, CGH 139B(Chits)/144.2m, coordinates 16.5/103.8.
5. *Sommerochitina* sp. 1. Iquiri Formation, Lag-8, CGH 119A(Chits)/317.3m, coordinates 11.8/107.7.
6. *Angochitina mourai* Lange, 1952. Iquiri Formation, CH331, CGH 142/ 107.4m, coordinates 28.9/97.7.
7. *Angochitina mourai* Lange, 1952. Iquiri Formation, CH369, CGH 142/ 107.4m, coordinates 23.6/101.4.
8. *Angochitina* sp. 1. Los Monos Formation, CH30, CGH 37/1173m, coordinates 15.4/106.
9. *Angochitina* sp. 2 nov. sp. Iquiri Formation, CH268, CGH 125/261.2m, coordinates 15.9/102.5.
10. *Angochitina* sp. 3. Iquiri Formation, CH280, CGH 128/219.7m, coordinates 9.3/101.6.
11. *Angochitina* sp. 3. Iquiri Formation, CH299, CGH 134/176.1m, coordinates 16.5/93.7.
12. *Angochitina* sp. 4 nov. sp. Iquiri Formation, CH309, CGH 137/148.7m, coordinates 13.4/96.7.
13. *Angochitina* sp. 4 nov. sp. Iquiri Formation, CH317, CGH 139/139.9m, coordinates 20.5/111.6.

Plate 3


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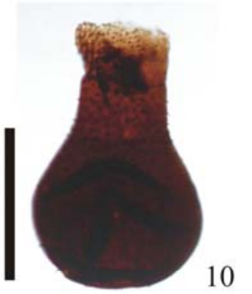
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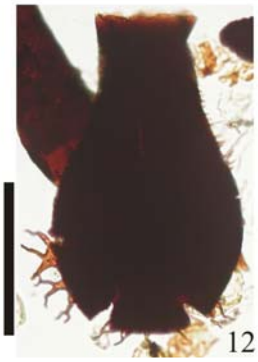
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Plate 4

Black scale bar = 100µm.

1. *Angochitina* sp. 5. Iquiri Formation, CH238, CGH 125B(Chits)/261.2m, coordinates 15.5/107.9. Spines arrowed.
2. *Angochitina* sp. 5. Iquiri Formation, CH266, CGH 125/261.2m, coordinates 23.6/96.3. Small spines arrowed.
3. *Angochitina pilosa* (Collinson & Scott, 1958). Iquiri Formation, CH191, CGH 116A(Chits)/370.2m, coordinates 13.7/104.
4. *Angochitina pilosa* (Collinson & Scott, 1958). Iquiri Formation, CH223, CGH 115/375.6m, coordinates 26.3/99.3.
5. *Angochitina pilosa* (Collinson & Scott, 1958). Iquiri Formation, CH215, CGH 112/457.6m, coordinates 3.7/96.5.
6. *Fungochitina* sp. 1. Iquiri Formation, CH129, CGH 106B(Chits)/538.1m, coordinates 11.5/110.
7. *Fungochitina* sp. 1. Iquiri Formation, CH208, CGH 106/538.1m, coordinates 10.2/105.5.
8. *Fungochitina* sp. 2. Iquiri Formation, CH203, CGH 105/549.4m, coordinates 21.5/109.5
9. *Ramochitina ramosi* Sommer & van Boekel, 1964. Iquiri Formation, CH382, CGH 84C(Chits)/865.2m, coordinates 17.5/96.
10. *Ramochitina ramosi* Sommer & van Boekel, 1964. Iquiri Formation, CH383, CGH 84/865.2m, coordinates 19.9/101.8.
11. *Ramochitina* sp. 1 nov. sp. Los Monos Formation, CH2, CGH 21(Chits)/1203.8m, coordinates 29.5/95.
12. *Ramochitina* sp. 1 nov. sp. Los Monos Formation, CH10, CGH 28(Chits)/1193.1m, coordinates 19.6/106.6.
13. *Ramochitina* sp. 1 nov. sp. Los Monos Formation, CH25, CGH 39A(Chits)/1170.8m, coordinates 12.7/100.4.
14. *Ramochitina* sp. 1 nov. sp. Los Monos Formation, CH27, CGH 39A(Chits)/1170.8m, coordinates 18.5/101.9. Bi-rooted spine arrowed.
15. *Ramochitina* sp. 1 nov. sp. Los Monos Formation, CH3, CGH 24(Chits)/1200.4m, coordinates 22.3/99.5.
16. *Ramochitina* sp. 1 nov. sp. Los Monos Formation, CH77, CGH 52/1126.4m, coordinates 21/100.3.
17. *Ramochitina* sp. 1 nov. sp. Los Monos Formation, CH69, CGH 55C(Chits)/1122.4m, coordinates 18.9/99.6. Bi-rooted spine arrowed.

Plate 4


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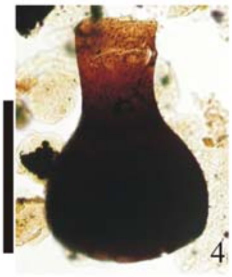
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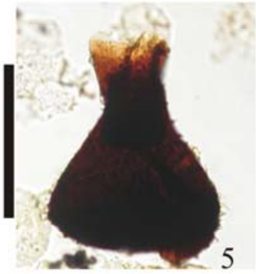
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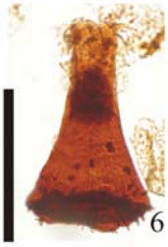
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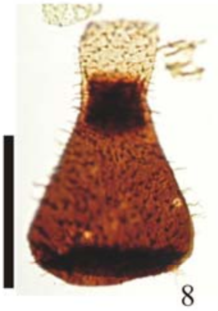
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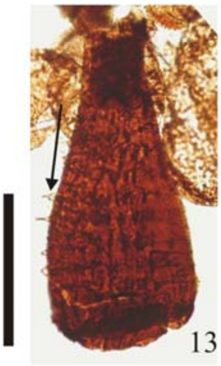
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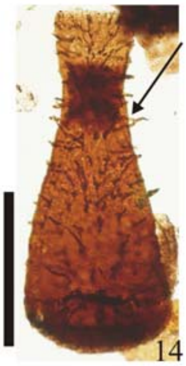
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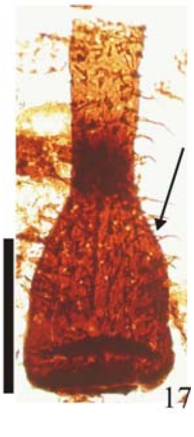
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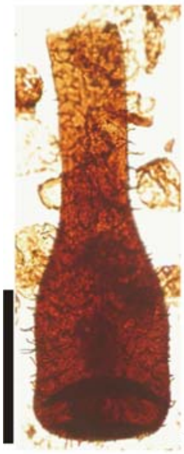
Plate 5

Black scale bar = 100µm.

1. *Ramochitina* sp. 1 nov. sp. Los Monos Formation, CH70, CGH 55C(Chits)/1122.4m, coordinates 12.1/98.5.
2. *Ramochitina* sp. 2. Los Monos Formation, CH346, CGH 70/959.6m, coordinates 20/99.8.
3. *Ramochitina* sp. 2. Los Monos Formation, CH98, CGH 71(Chits)/937m, coordinates 20.9/103.1.
4. *Ramochitina* sp. 3 nov. sp. Los Monos Formation, CH346, CGH 70/959.6m, coordinates 20/99.8.
5. *Ramochitina* sp. 3 nov. sp. Los Monos Formation, CH98, CGH 71(Chits)/937m, coordinates 20.9/103.1.
6. *Ramochitina* sp. 4. Iquiri Formation, CH246, CGH 133(Chits)/185.6m, coordinates 9.8/97.4.
7. *Ramochitina* sp. 5. Iquiri Formation, CH289, CGH 130/207.2m, coordinates 26.7/102.1. Multi-rooted spine arrowed.
8. *Ramochitina* sp. 6. Iquiri Formation, CH174, CGH 106A(Chits)/538.1m, coordinates 17.2/102.3.
9. *Ramochitina* sp. 6. Iquiri Formation, CH175, CGH 106A(Chits)/538.1m, coordinates 15/102.8.
10. *Ramochitina* sp. 7. Iquiri Formation, CH149, CGH 84/865.2m, coordinates 24.7/97.5.
11. *Ramochitina* sp. 8. Iquiri Formation, CH270, CGH 126/252.4m, coordinates 24.3/94.6.
12. *Ramochitina* sp. 8. Iquiri Formation, CH271, CGH 126/252.4m, coordinates 29.8/110.2.
13. *Ramochitina* sp. 8. Iquiri Formation, CH272, CGH 126/252.4m, coordinates 10.1/110.2.
14. *Lagenochitina praeavelinoi* Grahn & Melo, 2004. Los Monos Formation, CH46, CGH 46(Chits)/1158.5m, coordinates 17.3/97.3.
15. *Lagenochitina avelinoi* Lange, 1952, CH254, CGH 139A(Chits)/139.9m, coordinates 8.8/98.8.
16. *Lagenochitina avelinoi* Lange, 1952, Lag-11, CGH 119B(Chits)/317.3m, coordinates 8.2/110.5.
17. *Lagenochitina avelinoi* Lange, 1952, Lag-3, CGH 119/317.3m, coordinates 9.5/102.2.

Plate 5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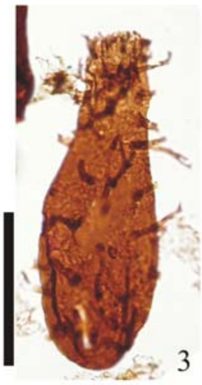
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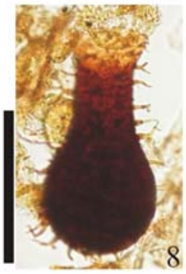
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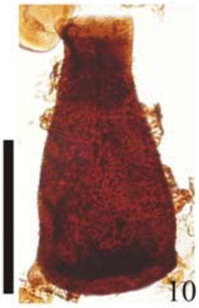
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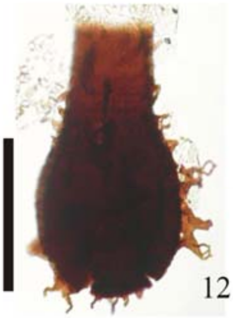
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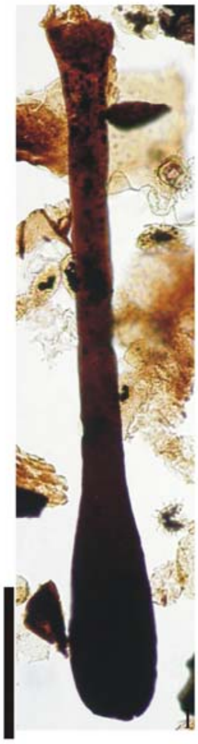
Plate 6

Black scale bar = 100µm.

1. *Lagenochitina avelinoi* Lange, 1952, Lag-4, CGH 119/317.3m, coordinates 14.9/102.9.
2. *Lagenochitina* sp. 1. Iquiri Formation, CH193, CGH 119A(Chits)/317.3m, coordinates 13.9/101.4.
3. *Lagenochitina* sp. 1. Iquiri Formation, CH194, CGH 119B(Chits)/317.3m, coordinates 20/95.9.
4. *Lagenochitina* sp. 2. Iquiri Formation, Lag-15, CGH 124(Chits)/261.2m, coordinates 28.2/104.4.
5. *Lagenochitina* sp. 2. Iquiri Formation, Lag-16, CGH 125A(Chits)/261.2m, coordinates 14.1/95.8.
6. *Togachitina* sp. 1. Iquiri Formation, CH342, CGH 115/375.6m, coordinates 8.6/105.9.
7. *Togachitina* sp. 1. Iquiri Formation, CH344, CGH 115B(Chits)/375.6m, coordinates 13.1/109.8.
8. *Urochitina bastosi* van Boekel, 1967. Iquiri Formation, CH263(Chits), CGH 143/97.2m, coordinates 13.7/108.5.
9. *Urochitina* sp. 1, Iquiri Formation, CH329, CGH 141/125.2m, coordinates 19.6/101.2.
10. *Urochitina* sp. 1, Iquiri Formation, CH233, CGH 119/317.3m, coordinates 33.4/108.8.
11. *Urochitina* sp. 2, Iquiri Formation, CH249, CGH 138(Chits)/144.2m, coordinates 20.6/96.9.
12. *Urochitina* sp. 2, Iquiri Formation, CH314, CGH 138/144.2m, coordinates 13.3/95.9.
13. *Urochitina* sp. 2, Iquiri Formation, CH315, CGH 138/144.2m, coordinates 15/99.

Plate 6

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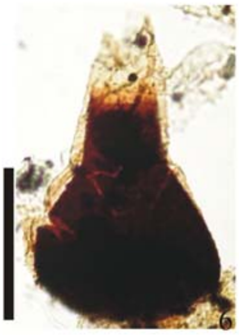
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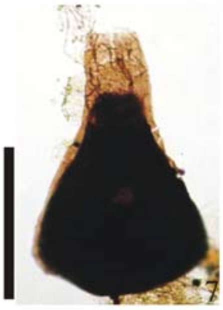
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Plate 7

Black scale bar = 100μm.

1. CH130. *Lagenochitina* sp. Iquiri Formation, CGH 80/890.3m, coordinates 24.9/101.
2. CH349. *Ramochitina* sp. Iquiri Formation, CGH 88/837.5m, coordinates 23.1/111.
3. CH363. *Ramochitina* sp. Iquiri Formation, CGH 97/690.7m, coordinates 13.7/98.4.
4. CH365. ?*Ramochitina* sp. Iquiri Formation, CGH 97/690.7m, coordinates 23.5/106.2.
5. CH373. ?*Angochitina* sp. Iquiri Formation, CGH 113/440.7m, coordinates 17/100.7.
6. CH362. *Ancyrochitina* sp. Iquiri Formation, CGH 98/674.9m, coordinates 29.9/102.
7. CH364. *Ancyrochitina* sp. Iquiri Formation, CGH 97/690.7m, coordinates 15.2/104.
8. CH339. *Ramochitina* sp. Iquiri Formation, CGH 84/865.2m, coordinates 21.2/97.8.
9. CH169. *Ancyrochitina* sp. Iquiri Formation, CGH 101(Chits)/592m, coordinates 12.7/101.8.
10. CH195. ?*Ancyrochitina* sp. Iquiri Formation, CGH 103/557.9m, coordinates 20.2/106.8.
11. CH359. ?Indet. Iquiri Formation, CGH 105/549.4m, coordinates 12.8/96.8.
12. CH224. *Angochitina* sp. Iquiri Formation, CGH 116/370.2m, coordinates 21.1/99.5.
13. CH182. *Fungochitina* sp. Iquiri Formation, CGH 106C(Chits)/538.1m, coordinates 23.1/106.2.
14. CH210. ?*Ramochitina* sp. Iquiri Formation, CGH 108/518.8m, coordinates 27.2/103.
15. CH168. *Ramochitina* sp. Iquiri Formation, CGH 101/592m, coordinates 22.3/102.6.
16. CH214. *Angochitina* sp. Iquiri Formation, CGH 112/457.6m, coordinates 12/96.9.
17. CH374. *Angochitina* sp. Iquiri Formation, CGH 125/261.2m, coordinates 33.1/101.

Plate 7


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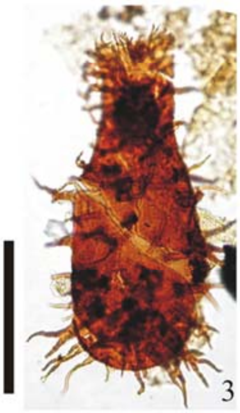
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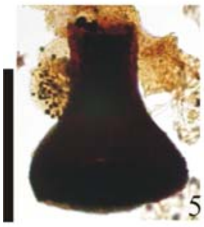
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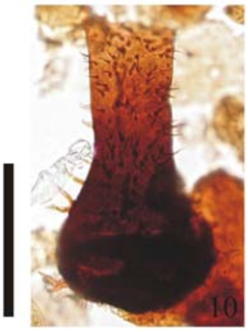
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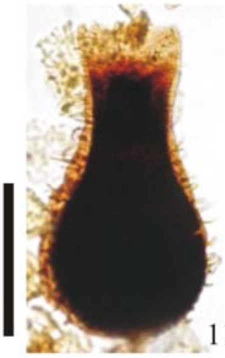
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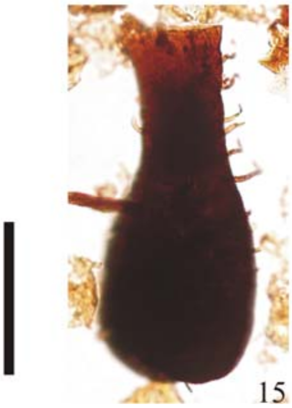
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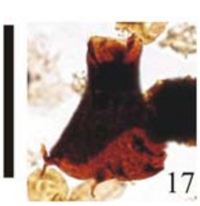
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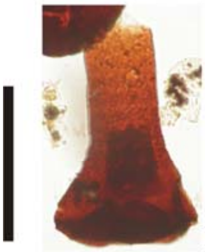
Plate 8

Black scale bar = 100µm.

1. CH218. ?*Fungochitina* sp. Iquiri Formation, CGH 115/375.6m, coordinates 7.4/107.6.
2. CH360. ?*Angochitina* sp. Iquiri Formation, CGH 116/370.2m, coordinates 7.3/100.3.
3. CH357. *Ramochitina* sp. Iquiri Formation, CGH 117/326.6m, coordinates 24/109.6.
4. CH239. *Angochitina* sp. Iquiri Formation, CGH 125B(Chits)/261.2m, coordinates 10.9/107.
5. CH361. *Angochitina* sp. Iquiri Formation, CGH 119/317.3m, coordinates 27.9/104.6.
6. CH232. *Angochitina* sp. Iquiri Formation, CGH 119/317.3m, coordinates 20.5/101.9.
7. CH269. ?*Angochitina* sp. Iquiri Formation, CGH 125/261.2m, coordinates 18.2/100.7.
8. CH278. *Ramochitina* sp. Iquiri Formation, CGH 128/219.7m, coordinates 16.9/96.2.
9. CH376. *Angochitina* sp. Iquiri Formation, CGH 126/252.4m, coordinates 25.8/93.8.
10. CH274. *Lagenochitina* sp. Iquiri Formation, CGH 127/231.4m, coordinates 15.7/97.8.
11. CH275. *Ancyrochitina* sp. Iquiri Formation, CGH127/231.4m, coordinates 25.4/101.7.
12. CH356. *Ramochitina* sp. Iquiri Formation, CGH 129/213m, coordinates 9.5/96.9.
13. CH375. *Angochitina* sp. Iquiri Formation, CGH 128/219.7m, coordinates 23.5/100.6.
14. CH279. ?*Angochitina* sp. Iquiri Formation, CGH 128/219.7m, coordinates 11.7/98.3.
15. CH241. *Angochitina* sp. Iquiri Formation, CGH 128A(Chits)/219.7m, coordinates 14.5/101.9.
16. CH290. *Ramochitina* sp. Iquiri Formation, CGH 130/207.2m, coordinates 23.8/105.5.

Plate 8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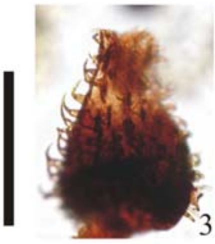
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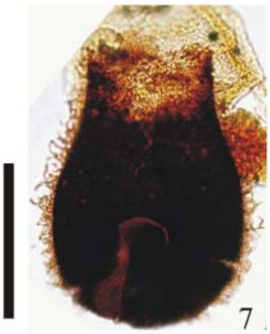
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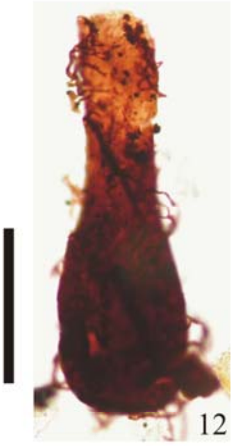
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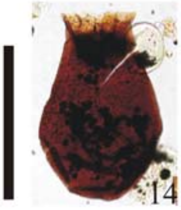
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Plate 9

Black scale bar = 100µm.

1. CH291. *Angochitina* sp. Iquiri Formation, CGH 130/207.2m, coordinates 32.4/105.3.
2. CH295. *Lagenochitina* sp. Iquiri Formation, CGH 133/185.6m, coordinates 15.2/98.2.
3. CH247. *Angochitina* sp. Iquiri Formation, CGH 133(Chits)/185.6m, coordinates 10.3/105.3.
4. CH326. ?*Ramochitina* sp. Iquiri Formation, CGH 141/125.2m, coordinates 32.5/103.9.
5. CH248. ?*Ramochitina* sp. Iquiri Formation, CGH 138A(Chits)/144.2m, coordinates 19.7/108.1.
6. CH308. *Angochitina* sp. Iquiri Formation, CGH 137/148.7m, coordinates 31.1/97.8.
7. CH312. *Ramochitina* sp. Iquiri Formation, CGH 138/144.2m, coordinates 9/112.8.
8. CH265. ?*Ramochitina* sp. Iquiri Formation, CGH 139A(Chits)/139.9m, coordinates 10.6/106.
9. CH300. *Angochitina* sp. Iquiri Formation, CGH 134/176.1m, coordinates 20.8/100.
10. CH302. *Angochitina* sp. Iquiri Formation, CGH 135/166m, coordinates 26.9/105.7.
11. CH257. ?*Angochitina* sp. Iquiri Formation, CGH 140A(Chits), coordinates 13.9/98.
12. CH304. *Angochitina* sp. Iquiri Formation, CGH 137/148.7m, coordinates 31.1/97.8.
13. CH255. ?*Plectochitina* sp. Iquiri Formation, CGH 139B(Chits)/139.9m, coordinates 12.6/109.6.
14. CH319. *Angochitina* sp. Iquiri Formation, CGH 139/139.9m, coordinates 24.7/109.2.
15. CH322. *Ramochitina* sp. Iquiri Formation, CGH 140/136.2m, coordinates 16.2/98.7.
16. CH260. *Angochitina* sp. Iquiri Formation, CGH 140D(Chits)/136.2m, coordinates 22.1/101.2.

Plate 9


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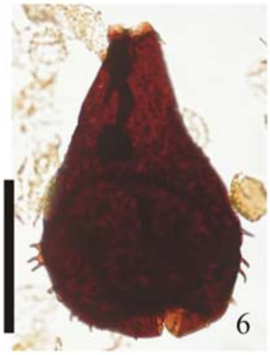
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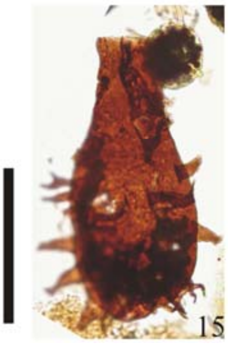
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Plate 10

Black scale bar = 100µm.

1. CH385. ?*Angochitina* sp. Iquiri Formation, CGH 139/139.9m, coordinates 8.5/97.4.
2. CH372. *Angochitina* sp. Iquiri Formation, CGH 141/125.2m, coordinates 30/109.
3. CH327. *Angochitina* sp. Iquiri Formation, CGH 141/125.2m, coordinates 30.5/93.7.
4. CH386. ?*Plectochitina* sp. Iquiri Formation, CGH 139/139.9m, coordinates 6.9/109.2.
5. CH264. *Angochitina* sp. Iquiri Formation, CGH 143/97.2m, coordinates 12.8/102.8.
6. CH384. *Lagenochitina* morphotype. Iquiri Formation, CGH 140/136.2m, coordinates 26/92.8.
7. *Ancyrochitina parisi* Volkheimer, Melendi & Salas 1986. Slide 3100-3110m (approximate level of sample C271 in Volkheimer *et al.*, 1986), coordinates 32.3/103.4. San Pedrito X-1, Salta, N Argentina.
8. *Cladochitina* sp. Slide 2950-2960m, coordinates 21.9/102.8. San Pedrito X-1, Salta, N Argentina.
9. *Ramochitina magnifica* Lange 1967a. Slide 3500-3520m (approximate level of sample C275 in Volkheimer *et al.*, 1986), coordinates 34.2/97.5. San Pedrito X-1, Salta, N Argentina. Note the widespread geographical distribution of this taxon (Figs. 10-11).
10. *Ramochitina magnifica* Lange 1967a. Belén Formation, Ayo Ayo. BOL-38, coordinates 38.7/105.5.
11. *Ramochitina magnifica* Lange 1967a. Fox Bay Formation, Roy Cove, Falkland Islands. PN-33, (~380m see Figure 3 in Marshall, 1994), coordinates 34.2/97.5.
12. *Ancyrochitina* sp. 1 nov. sp. Braz 1, coordinates 17.9/98. Pimentiera Formation, Well 2-PM-1-MA, Core 48, 1646-1646.6m. Parnaíba Basin, NE Brazil.
13. *Ramochitina* sp. 1 nov. sp. Braz 2, coordinates 14.4/110.8. Pimentiera Formation, Well 2-PM-1-MA, Core 48, 1646-1646.6m. Parnaíba Basin, NE Brazil.
14. CH388. ?*Ramochitina* sp. Basal Track Shale Member, Cha-Kjeri Formation, spot sample CHA-12, coordinates 7.5/107.3.

Plate 10


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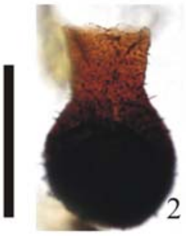
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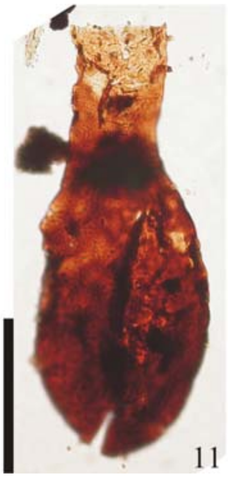
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4.3 Discussion

4.3.1 Comparison of chitinozoan ranges with Brazil

The majority of data on the stratigraphic distribution of Devonian chitinozoans in South America has come from the study of subsurface sections (wells) from Brazil. Unfortunately, the stratigraphic distribution of the published material is from widely spaced samples often with large sample gaps and is consequently of limited use for detailed correlation with the Bolivian Bermejo section. The only published biostratigraphic data that can be used are from Well RSP-1-MT in the Paraná Basin, SE Brazil (Grahn *et al*., 2002). This well penetrates ~360m of the Mid to Late Devonian São Domingos Formation which is broadly equivalent to the Los Monos/Iquiri Formation interval at Bermejo.

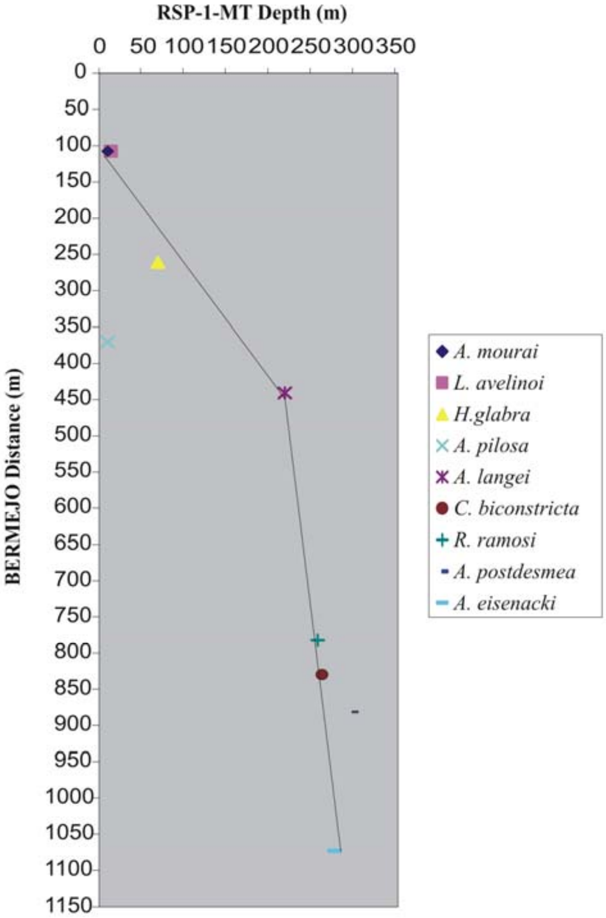


Fig. 4.13. Shaw Plot of inceptions (first downhole occurrences) for selected chitinozoan taxa from Bermejo, Bolivia and Well RSP-1-MT, Parana Basin, Brazil. Note the condensed nature of RSP-1-MT relative to Bermejo, particularly below 220m.

In RSP-1-MT, the stratigraphic tops of 9 distinctive and well-known taxa (*Urochitina bastosi, Angochitina mourai*, *Lagenochitina avelinoi*, *Hoegisphaera glabra*, *Angochitina pilosa*, *Ancyrochitina langei*, *Cladochitina biconstricta*, *Ramochitina ramosi*, *Ancyrochitina postdesmea* and *Alpenachitina eisenacki*) are recorded from cuttings samples and correlated with Bermejo using a Shaw Plot (**Fig. 4.13**) based on the Graphic Correlation Method (see Shaw,1964; Dowsett, 1989). This method can be used to correlate sequences without making prior assumptions as to whether fossil events such as inceptions are synchronous. A comparison with the sequence of inceptions at Bermejo shows that the well data is reliable (**Fig. 4.13**), since apart from *Ang. pilosa*, the inceptions occur in the same order and therefore the two sections correlate. The *Ang. pilosa* inception could be 'out of sequence' due to misidentification since identication of this taxon is not straightforward (**see Section 2.0**) and the specimens from RSP-1-MT are not illustrated. The inception of *An. postdesmea* is out of sequence in RSP-1-MT and this could also be due to misidentification since this chitinozoan has a very restricted range and should occur above *A. eisenacki* (ca. 200m stratigraphic separation at Bermejo).

4.3.2 Comments on the Paris *et al*. (2000) and Grahn (2005) zonation schemes

The zonation scheme of Paris *et al*. (2000) can only be applied in part to Bolivia because of the general absence of all but three taxa that define the Emsian and Frasnian interval range biozones (**Fig. 4.2**). At present, the interval range biozones of potential use in Bolivia are *eisenacki* (Eifelian) and *glabra* (Frasnian). The *avelinoi* Interval Range Biozone, defined by *Angochitina avelinoi* (Lange), is problematical since it has been assigned to the Famennian by Paris *et al.* (2000) although this taxon is most common in the Frasnian in Bolivia (this study) and Brazil (Grahn *et al.* (2002) where the *avelinoi* interval range acme is mid-late Frasnian). For further discussion on *A. avelinoi* see *Lagenochitina avelinoi*. The poor applicability of this zonation scheme to Bolivia illustrates the endemic nature of the Malvinokaffric Realm (**see Section 3.3**).

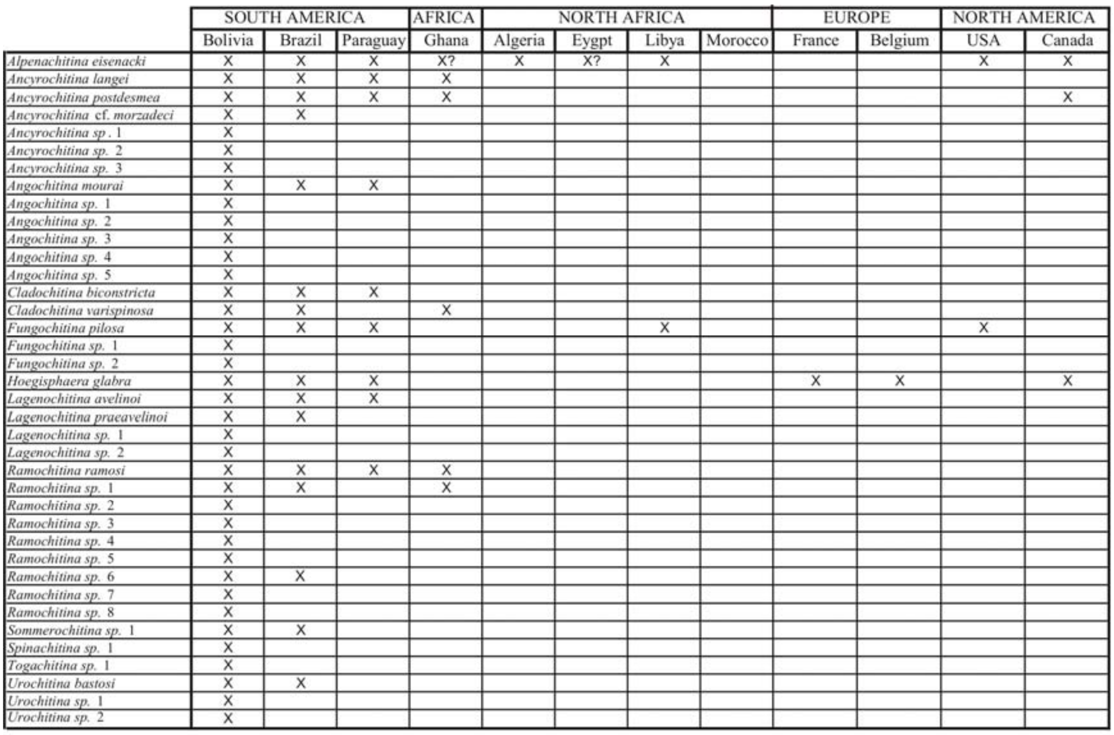
Examination of the chitinozoan ranges in Paris *et al*. (2000) reveals that some of the listed taxa (not necessarily index species) have much longer ranges than observed in Bolivia e.g. *Ancyrochitina langei* (**Plate 1, figs 12-13**), *Cladochitina biconstricta* (**Plate 1, figs. 3-6**), *Hoegisphaera glabra* (**Plate 1, figs. 1-2**) and *Ramochitina magnifica* (**Plate 10, fig. 7-9**). At Bermejo and throughout Bolivia, most chitinozoan species appear to be short-lived and consequently have relatively short stratigraphic ranges e.g. *H. glabra*. The most likely reasons for the presumed longer ranges and misdating of these taxa in South America are generally due to poorly constrained lithostratigraphy and species misidentification**.** These issues will be resolved as more integrated biostratigraphic and lithostratigraphic data become available to better constrain the chronostratigraphy, particularly in South America.

Most of the data for the western Gondwanan biozonation scheme of Grahn (2005) have come from the subsurface in Brazil and there are difficulties in applying this scheme to Bolivia since some of the Bolivian data quoted in Grahn (2005) have come from sections with uncertain lithostratigraphy. This is apparent when considering the stratigraphic positions of the *A. eisenacki* Interval Range Zone and *R. stiphrospinata* Total Range Zone which are assigned to a Mid-Devonian Huamampampa Formation. In this study, the Huamampampa

Formation is shown to be pre-early Eifelian (**Chapter 2**) on the basis of surface and subsurface data. Furthermore, there are issues with identifying *R. stiphrospinata* (see description for *R*. sp. 6) which may not be a suitable zonal species. *Fungochitina microspinata* and *Ancyrochitina taouratinensis*, zonal taxa for the *F. microspinata*-*A. taouratinensis* Concurrent Range Zone have not yet been identified at Bermejo although specimen CH361 (Pl. 8, fig. 5) could be *F. microspinata*. Further study is required before the Grahn (2005) zonation can be properly applied to Bolivia although comparing downhole inceptions/stratigraphic tops may prove more rewarding.

4.3.3 Global distribution of the described Bermejo chitinozoans

A summary of the global distributions of the described chitinozoan taxa from Bermejo is shown in Table 4.4. The majority of species are endemic to Bolivia and Brazil. With more detailed studies on sections of similar age outside of Bolivia and Brazil, most of the taxa from Bermejo will probably be shown to be present elsewhere in South America and central/South Africa since these regions were also part of the same highly endemic Malvinokaffric Realm.



	SOUTH AMERICA			AFRICA	NORTH AFRICA				EUROPE		NORTH AMERICA	
	Bolivia	Brazil	Paraguay	Ghana	Algeria	Eygpt	Libya	Morocco	France	Belgium	USA	Canada
Alpenachitina eisenacki	X	X	X	X?	X	X?	X				X	X
Ancyrochitina langei	X	X	X	X								
Ancyrochitina postdesmea	X	X	X	X								X
Ancyrochitina cf. *morzadeci*	X	X										
Ancyrochitina sp . 1	X											
Ancyrochitina sp. 2	X											
Ancyrochitina sp. 3	X											
Angochitina mourai	X	X	X									
Angochitina sp. 1	X											
Angochitina sp. 2	X											
Angochitina sp. 3	X											
Angochitina sp. 4	X											
Angochitina sp. 5	X											
Cladochitina biconstricta	X	X	X									
Cladochitina varispinosa	X	X		X								
Fungochitina pilosa	X	X	X				X				X	
Fungochitina sp. 1	X											
Fungochitina sp. 2	X											
Hoegisphaera glabra	X	X	X						X	X		X
Lagenochitina avelinoi	X	X	X									
Lagenochitina praeavelinoi	X	X										
Lagenochitina sp. 1	X											
Lagenochitina sp. 2	X											
Ramochitina ramosi	X	X	X	X								
Ramochitina sp. 1	X	X		X								
Ramochitina sp. 2	X											
Ramochitina sp. 3	X											
Ramochitina sp. 4	X											
Ramochitina sp. 5	X											
Ramochitina sp. 6	X	X										
Ramochitina sp. 7	X											
Ramochitina sp. 8	X											
Sommerochitina sp. 1	X	X										
Spinachitina sp. 1	X											
Togachitina sp. 1	X											
Urochitina bastosi	X	X										
Urochitina sp. 1	X											
Urochitina sp. 2	X											

Table 4.4. Geographic distributions of the described taxa from Bermejo. Note the high degree of endemism within the Bolivian fauna and strong similarity with Brazil.

4.3.4 Comments on chitinozoan palaeoecology at Bermejo

Chitinozoans are common throughout most of the Bermejo section and this may reflect the high palaeolatitude position of Bolivia during the Devonian. Chitinozoans are rare throughout the Bermejo beds which are interpreted as representing the most proximal part of the section due to the high abundances of spores and large phytoclasts associated with a decrease in the relative abundance of marine palynomorphs (**see Chapter 2**). Above the Bermejo beds, the diversity and visible abundance (the sampling bias resulting from increasing chitinozoan yields by picking residues makes precise analysis of chitinozoan abundances throughout the Bermejo section difficult) of the chitinozoan fauna is highest (**Fig. 4.1** and see also many of the undescribed forms on **Pl. 8-11** that are post Bermejo beds). This may suggest the persistence of cold water in the region throughout the Givetian and Frasnian since many of these chitinozoans are probably endemic to the Malvinokaffric Realm. In contrast, Grahn (2005) claims the highest chitinozoan abundance and diversity in western Gondwana (including Bolivia) occurs in the early Givetian with a decrease during the late Givetian/early Frasnian interval. According to Grahn (2005) the supposed abundant and diverse chitinozoan fauna during the early Givetian is linked to a latest Eifelian marine transgression. However, there are currently no documented marine transgressions of this age in South America and this time interval is represented by general regression in Bolivia.

4.4 Summary

Thirty-six chitinozoan taxa from the Mid to Late Devonian section at Bermejo, Bolivia are described and illustrated of which 9 are considered to be new species, with an additional 14 taxa possibly being previously unknown but requiring further study. These are kept in open nomenclature and not designated nov. sp. Thirty-three (92%) of these taxa are currently endemic to Bolivia and probably also endemic to the Malvinokaffric Realm as a whole. Only 3 (8%) of the recorded taxa are cosmopolitan.

CHAPTER 5 – PALAEOENVIRONMENTS

5.1 Introduction

Palaeogeographic reconstructions (e.g. Issacson & Díaz-Martínez, 1995) show that central Bolivia was submerged beneath an epicontinental seaway during the Devonian (**Fig. 5.1**). Detailed attempts to characterise the Subandean Devonian formations in terms of palaeoenvironment have mainly been undertaken by oil companies and most of this data is therefore confidential/unpublished. Miranda *et al*. (2003, and references therein) provide details of depositional environments although supporting evidence such as sedimentary logs, photographs, etc., is generally lacking.

The data generated during this study permits definition of the palaeoenvironments during the Mid to Late Devonian at Bermejo. Where possible, the percentage of marine palynomorphs in samples CGH 18-CGH 145 (samples CGH 1-17 were palynologically lean) was calculated and used as a guide to infer the degree of marine influence/terrestrial input. Selected stratigraphic intervals (**Fig. 5.2 and Appendix 1**) were investigated sedimentologically. A total organic carbon (TOC) profile for the Los Monos-Iquiri Formation interval was produced (**Figs. 5.2-5.3**). More detailed TOC measurements (1m spacing) were taken through the important Givetian and Frasnian shales (TAG and FRA samples) within the Iquiri Formation since these have higher overall TOCs than the basal Los Monos Formation shales, possibly related to depositional environment (**Figs. 5.3-5.6**). Selected samples were analysed using RockEval^{TM} pyrolysis in order to assess hydrocarbon generative potential and this data is presented in **Appendix 2.**

5.1.1 Comments on palaeogeography

The palaeogeographic reconstruction for Bolivia (**Fig. 5.1**) also shows Mid-Late Devonian stratigraphic thicknesses in selected wells. Stratigraphic thickness between palynomorph acmes is used rather than subsurface lithostratigraphy since these are more reliable. The data on **Figure 5.1** shows an increase in Devonian thicknesses south of Bermejo which can be interpreted as representing a proximal-distal trend with Bermejo and the immediately adjacent wells being distal. This would suggest sediment input from the south. However, according to Sempere (1995), palaeocurrents came from an easterly direction during the Mid Devonian and part of the Late Devonian which would make the Brazilian shield or the land mass to the east of Bermejo a more likely sediment source. In this scenario, the data can be interpreted in terms of accommodation space whereby more basinal localities can accumulate a greater thickness of sediment and therefore the proximal to distal trend becomes reversed. Alternatively, since the area was a shallow seaway surrounded by landmasses, there actually may not be any discernable proximal-distal trend. Furthermore, most of the wells are in the Subandean thrust belt and consequently the increased thicknesses may be a tectonic artefact. Further study is required.

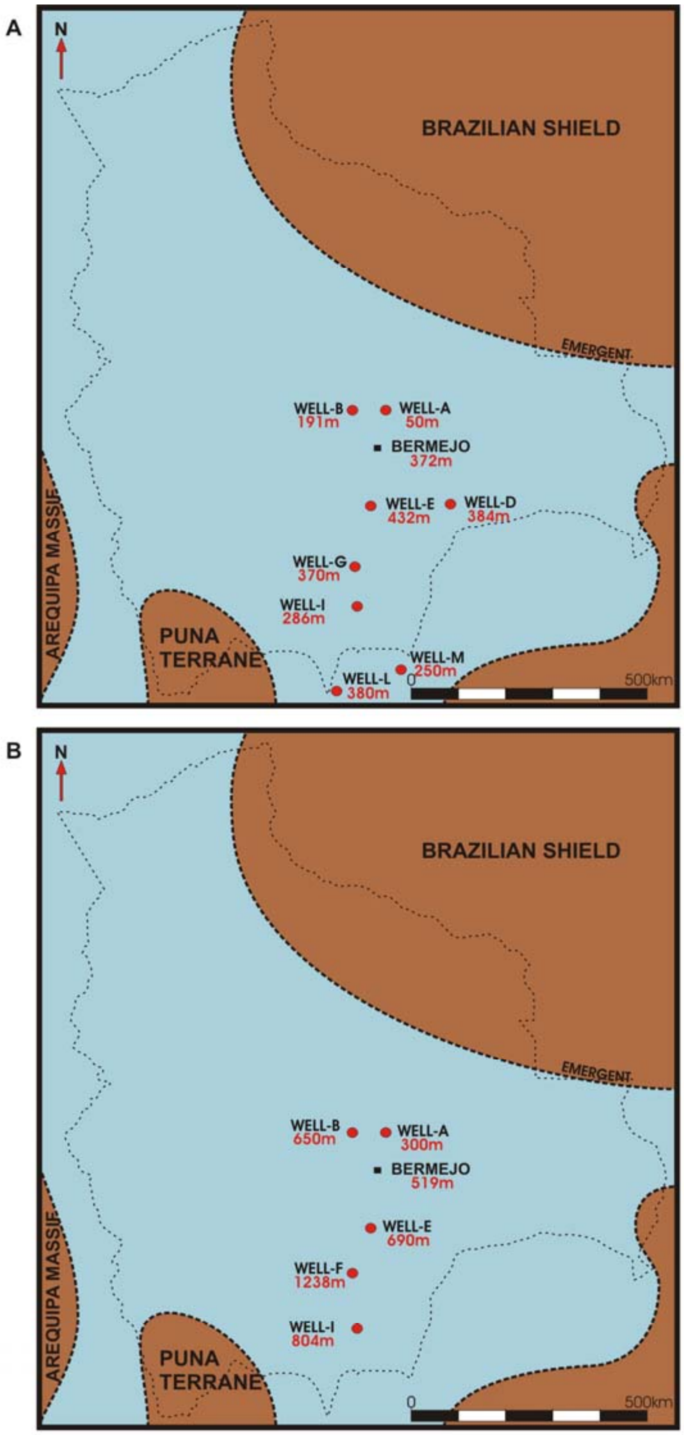


Fig. 5.1. Stratigraphic thickness between the *E. sommeri* and *B. bensonii* (1A) and *B. bensonii* and *C. camirense* (1B) acmes. The acmes are used rather than formation thicknesses since they are more reliable than subsurface lithostratigraphy. Palaeogeography based on Issacson & Díaz Martínez (1995), Wiens (1995) and Melo (1988).

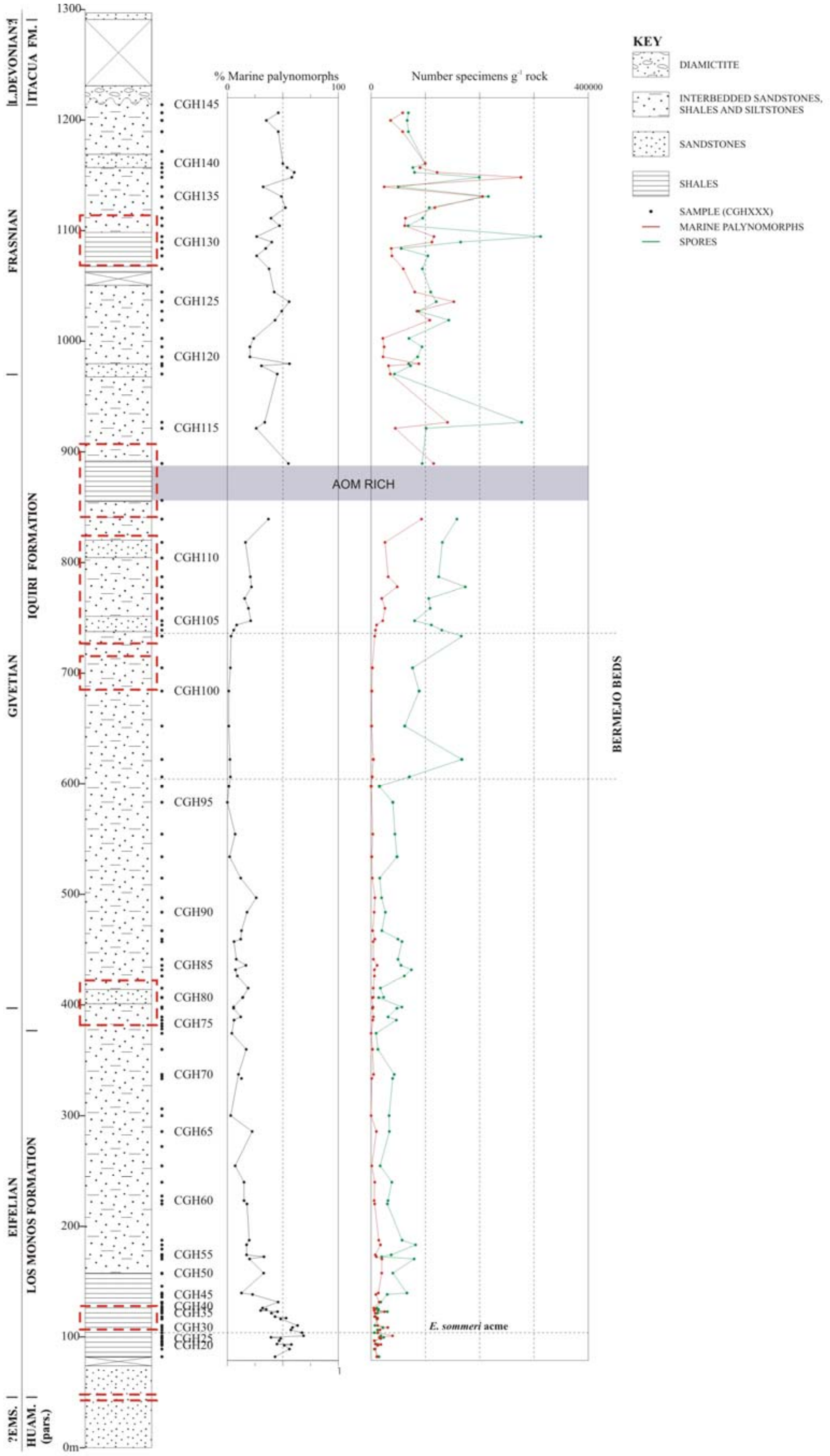


Fig. 5.2. Plots of the percentage of marine palynomorphs (acritarchs, chitinozoa and prasinophytes) in each sample and the number of marine palynomorphs/spores per gram of sample. Note while the Bermejo beds have a terrestrially dominated signal it is still pervasively marine based on the presence of rare chitinozoa and acritarchs.

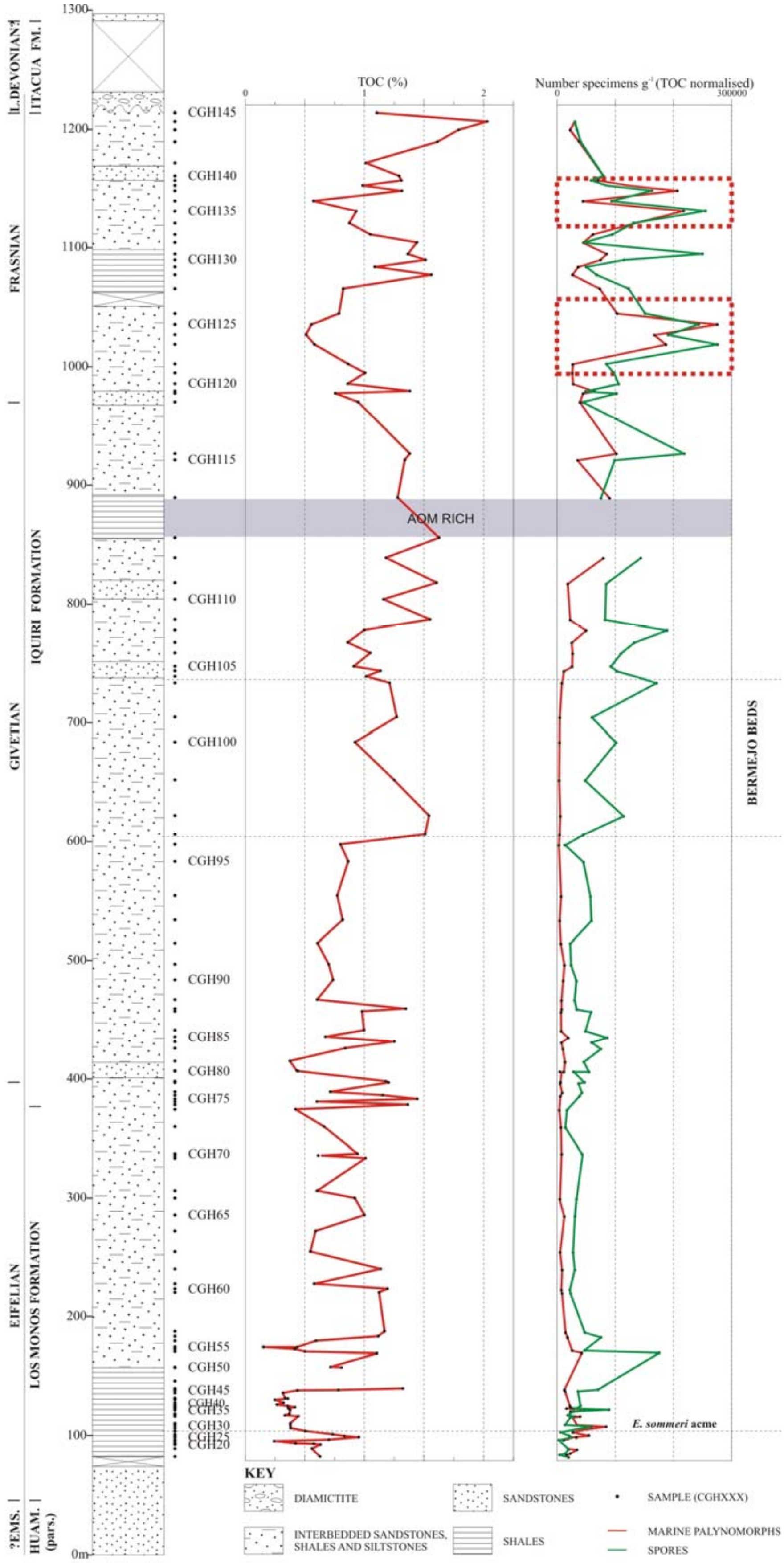
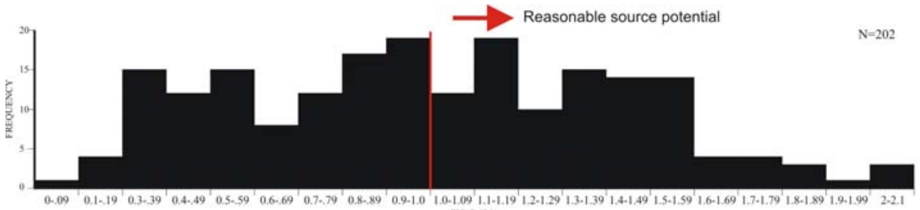
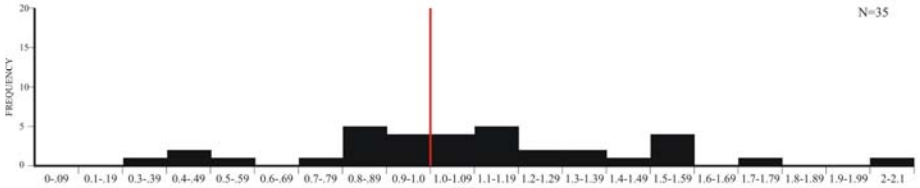


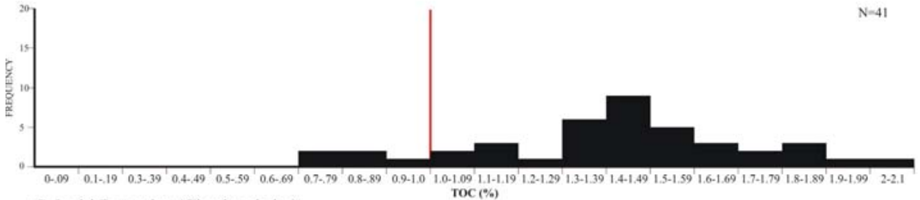
Fig. 5.3. TOC profile and TOC normalised numbers of palynomorphs g^{-1} sample. Note that pulses in marine palynomorph abundance do not always coincide with marine transgressions (red boxes) and may be related to organic matter preservation.



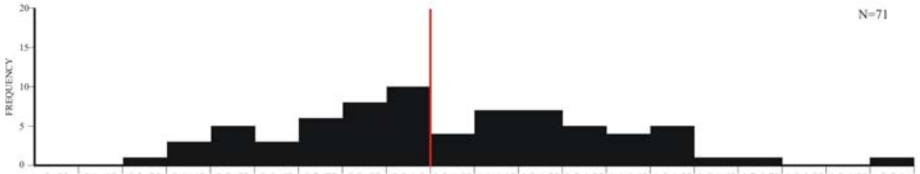
E. Los Monos and Iquiri Formations (including Givetian and Frasnian shales)



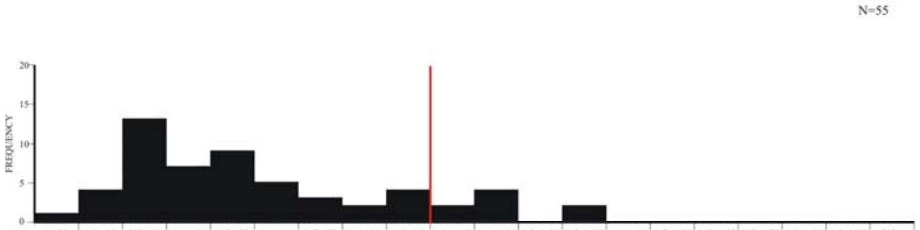
D. Iquiri Formation (Frasnian shales).



C. Iquiri Formation (Givetian shales).



B. Iquiri Formation (excluding Givetian and Frasnian shales)



A. Los Monos Formation

Fig. 5.4. TOC histograms of the Los Monos and Iquiri Formation samples at Bermejo. TOC values >1% are reasonable source rocks (red line). Note the higher frequency of TOC values over 1% in the Iquiri Formation, especially the Givetian shales.

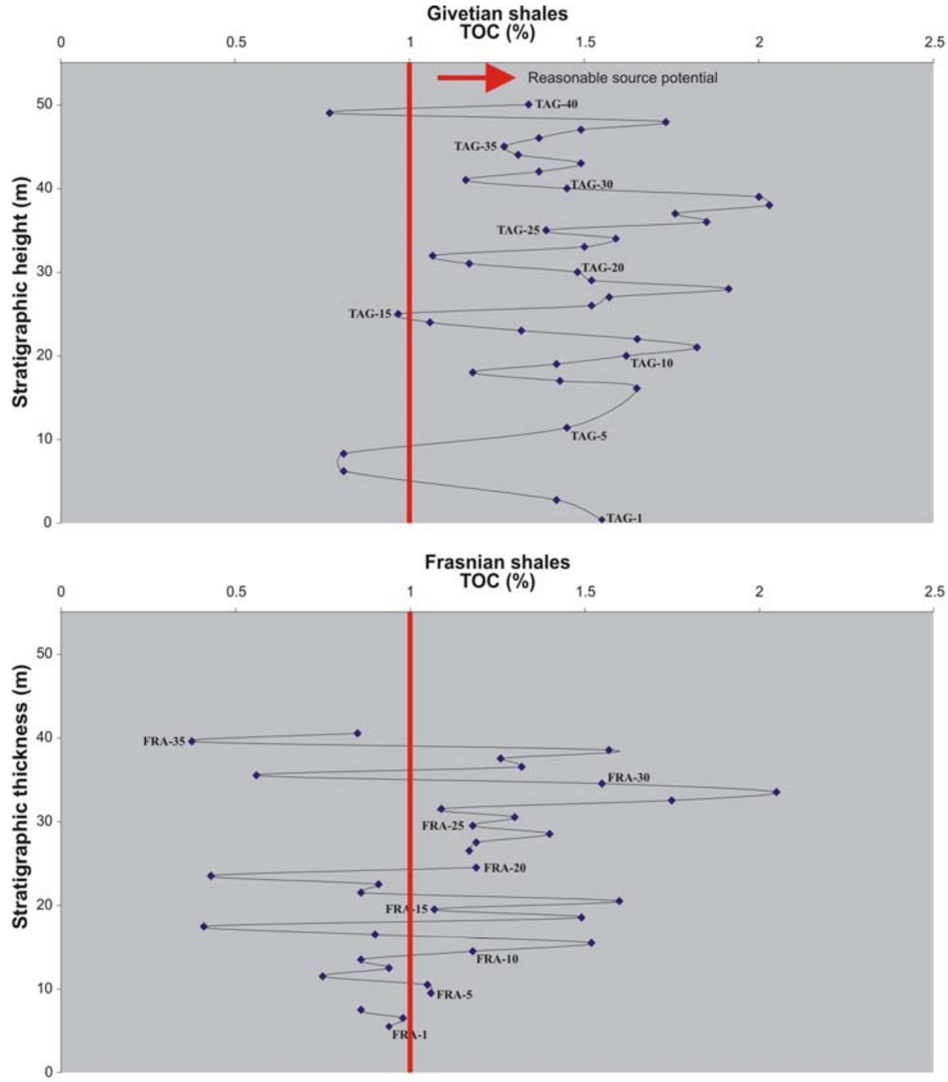


Fig.5.5. TOC profiles for the Givetian and Frasnian shale intercalations in the Iquiri Formation. Note the cyclicity and also the number of TOC values <1% in the Frasnian shales relative to the Givetian shales.

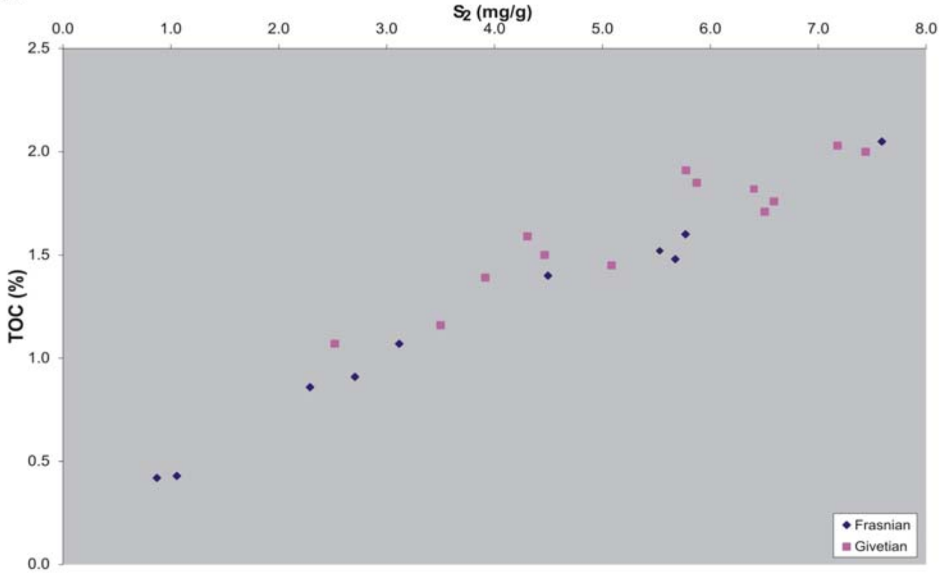


Fig.5.6. TOC (%) vs. S_2 for Givetian and Frasnian shale samples selected for RockEval™ pyrolysis. The Givetian shales represent better source rocks overall on account of their higher TOC and S_2 values. The hydrogen index (HI) values of these samples are similar (200-380).

5.2 Palaeoenvironmental interpretation

5.2.1 Huamampampa Formation (Fig. 5.2, 0-46m)

Localities: Bermejo, Cha-Kjeri and Campo Redondo.

Distribution: The full thickness of the Huamampampa Formation is not seen at Bermejo. At Campo Redondo the thickness is 330m although there is some faulting of this section. Tectonic repetition of strata does not appear to be an issue. Isaacson (1977a) reported a thickness of 770m at Cha-Kjeri but following revisions of the formational boundaries at this locality based on biostratigraphy (**this study see Chapter 3**) the thickness of the Huamampampa Formation is now considered to be 110m. All localities display similar facies consisting predominately of siltstones and fine/medium-grained sandstones.

Description: Bioturbated green/grey silty quartz sandstones were observed at the base of the measured section, overlain by white, well-cemented, medium-grained subarkosic sandstones. These are channelised and cross-bedded. An erosive surface (disconformity) at the top of this unit marks the Huamampampa/Los Monos Formation boundary (**Fig. 5.7**). There is also an abrupt lithological change from white subarkosic sandstones to grey, silty sandstones across the disconformity.

Palynology samples from the uppermost part of the formation at Bermejo were very lean and macrofossils were absent (the lower part is not exposed). At Campo Redondo, the formation was more productive in terms of palynomorphs (acritarchs, poorly preserved chitinozoa and spores in rare shale units) and macrofossils including common brachiopods, conulariids, trilobites and rare goniatites were also recorded in nodular horizons from this locality. Acritarchs, chitinozoa and spores were also found at Cha-Kjeri and there are records of brachiopods from the Siete Hermanos Sandstone Member in Isaacson (1977a) at this locality.

Age: The Huamampampa Formation is pre-early Eifelian and the base of the formation cannot be older than Emsian due to the presence of goniatites (see **Chapter 3**).

Environmental interpretation: Shallow-angle trough cross-bedding, channelisation and medium/coarse grain size in the uppermost Huamampampa Formation at Bermejo suggest deposition in a reasonably high energy environment. The quartz-rich sandstones also contain some feldspar, micas and chlorite suggesting that they are slightly mineralogically immature. The underlying finer-grained sandstones contain more silt/mud, are bioturbated and were deposited in a quieter, perhaps slightly deeper water marine environment based on the occurrence of marine palynomorphs (very rare acritarchs and chitinozoan fragments). Deposition of the Huamampampa Formation, therefore probably occurred in a nearshore environment with the quartz-rich sandstones deposited in a more proximal setting and the siltier sandstones in a deeper, possibly more offshore environment.

Fig. 5.7. Huamampampa Formation/basal Los Monos Formation boundary with the disconformity at the top of Huamampampa Formation highlighted (inset). The transition from the Huamampampa Formation into the Los Monos Formation is interpreted as a marine flooding event based on palynology and sedimentology.

Fig.5.8. Dark grey shales in the basal Los Monos Formation. These shales contain *Evittia sommeri* and are also rich in prasinophytes. Based on palynology and sedimentological context, the shales represent the period of maximum flooding. Green arrow indicates way up.

5.2.2 Los Monos Formation (Fig. 5.2, 46-377m)

Localities: Bermejo, Campo Redondo and Cha-Kjeri (equivalent facies).

Distribution: The unthrusted Los Monos Formation is 331m thick in the Rio Lajas at Bermejo and consists of black/ dark grey shales which grade into siltier and sandier facies towards the Iquiri Formation boundary. At Campo Redondo only part of the Los Monos Formation is exposed and at Cha-Kjeri the lithostratigraphic nomenclature is somewhat different (**see Chapter 3**). However, at both localities, dark black/grey shales containing *Evittia sommeri* (**see Chapter 3**) mark the base of this formation or its equivalent (Carinatus Shale at Cha-Kjeri). Unlike Bermejo, thick sandstones are developed immediately above these *E. sommeri* bearing shale units (**e.g. Chapter 3, Figs. 5.3-5.4**) at Campo Redondo and Cha-Kjeri. Since these were not sampled for palynology, and nothing similar is developed in the Los Monos Formation at Bermejo, placing the Los Monos/Iquiri Formation boundary at these localities is difficult. Moreover, this level may not be present at Campo Redondo due to truncation. The Los Monos Formation at Campo Redondo is at least 20m thick and its 'equivalent', the Carinatus Shale has a published thickness of 135m (Isaacson, 1977a).

Description: The base of the Los Monos Formation is disconformable with the underlying Huamampampa Formation at Bermejo. Above the disconformity, grey/green, fine-grained silty sandstones overlie medium/coarse-grained quartz-rich sandstones of the upper Huamampampa Formation. These silty sandstones are bioturbated (vertical burrows only since bedding planes are rarely exposed throughout the Bermejo section) with rare centimetre scale cross-bedding and they eventually fine upwards into dark grey shales that are occasionally banded on a centimetre scale with Fe-rich horizons (**Fig. 5.8**). Rare carbonate concretions (up to 2m diameter) are present within the shale and these often display undulose lamination or cross-bedding and contain abundant bioclasts including brachiopods, crinoid ossicles, gastropods, ostracods and tentaculitids (**Fig. 5.9-5.10**). Sand content increases towards the top of these shales indicated by the appearance of millimetre scale sand laminae (**Fig. 5.11**) and sandy ripples (**Fig. 5.12**).

The sand content increases up-section and centimetre scale interbedded sands/silts and cm scale wavy muds become the dominant lithofacies (**Figs. 5.13-5.16**) The relative amounts of these lithologies varies, i.e. some interbedded units (usually over a few metres stratigraphic thickness) are more mud- or sand-rich than others (**compare Figs. 5.14-5.16**). Bioturbation is common at certain levels within the interbedded facies and rare/absent in others (**see Figs. 5.14-5.15),** although only vertical burrows were observed, since exposures consisted of cross-sections perpendicular to bedding. The appearance of sandstone channels and siderite marks the base of the overlying Iquiri Formation.

The silty sands at the base of the Los Monos Formation are palynologically lean. The overlying dark shales contain abundant marine palynomorphs including *Evittia sommeri* and leiospheres, and terrestrial palynomorphs in the form of large camerate spores. Following the *E. sommeri* Epibole, the proportion of terrestrial palynomorphs in the samples increases (**Fig. 2**). A TOC profile and histogram of these shales are shown in **Figures 5.3-5.6**. Compared to the Givetian and Frasnian shales (Iquiri Formation), TOCs are lower (typically <0.5% versus >1%) and there is no AOM.

Some of the carbonate concretions towards the base of the Los Monos Formation are fossiliferous and contain abundant brachiopods, benthic tentaculitids, crinoid ossicles, gastropods and ostracods. Macrofossils from these concretions are generally calcitic or pyritic and three dimensional (**Fig. 5.10**), unlike those in the shales which are crushed and decalcified.

Age. Based on palynomorphs (chitinozoa and spores, **see Chapter 2**), the Los Monos Formation is Eifelian in age.

Environmental interpretation: The decrease in grain size, increase in silt content and transition into dark shales containing abundant acritarchs and prasinophytes above the disconformity at the base of the Los Monos Formation is interpreted as a marine flooding event. However, the environment of deposition for the dark shales could not have been too distal due to the presence of common large camerate spores and phytoclasts in the palynomorph assemblage. The overall lower TOCs in the Los Monos Formation compared to the Iquiri Formation explains the lower abundances of palynomorphs in Los Monos samples with the *E. sommeri* Epibole interval being most recognisable (apart from down a microscope) only when the number of specimens g^{-1} of sample is normalised to TOC (**Figs. 5.2-5.3). ** Lower levels of organic matter in the Los Monos Formation suggest either there was less organic material present in the water column and/or environmental conditions in the Iquiri Formation were generally more favourable for preservation.

The presence of carbonate channels (**Figs. 9-10**) containing intact delicate fossils such as benthic tentaculitids also suggests that these could not have been transported over great distances. Once emplaced, these channels must have undergone rapid diagenesis in order to preserve the calcitic fossils since the fossils in the enclosing shales are all decalcified. The increase in sand content and development of ripples within the shales towards the Iquiri Formation boundary shows that the water depth had decreased to a level above storm wave base. This view is supported by the presence of wavy bedding (**Fig. 5.14**) in the uppermost Los Monos Formation, which although often characteristic of tidal flat environments, can also form as a result of storms (Reineck & Singh, 1980), particularly in an inner shelf environment where an alternating supply of sediment (sand/mud) is present.

The Los Monos Formation therefore records a shift in deposition from a proximal shallow marine environment to a more open water marine shelf environment, below storm wave base for a time, with a subsequent regression to an inner shelf, storm-influenced environment.

Fig. 5.9. A large carbonate concretion in the lower Los Monos Formation. The author is pointing to a dark, bioclastic rich layer that may represent a channel fill. Green arrow indicates younging direction.

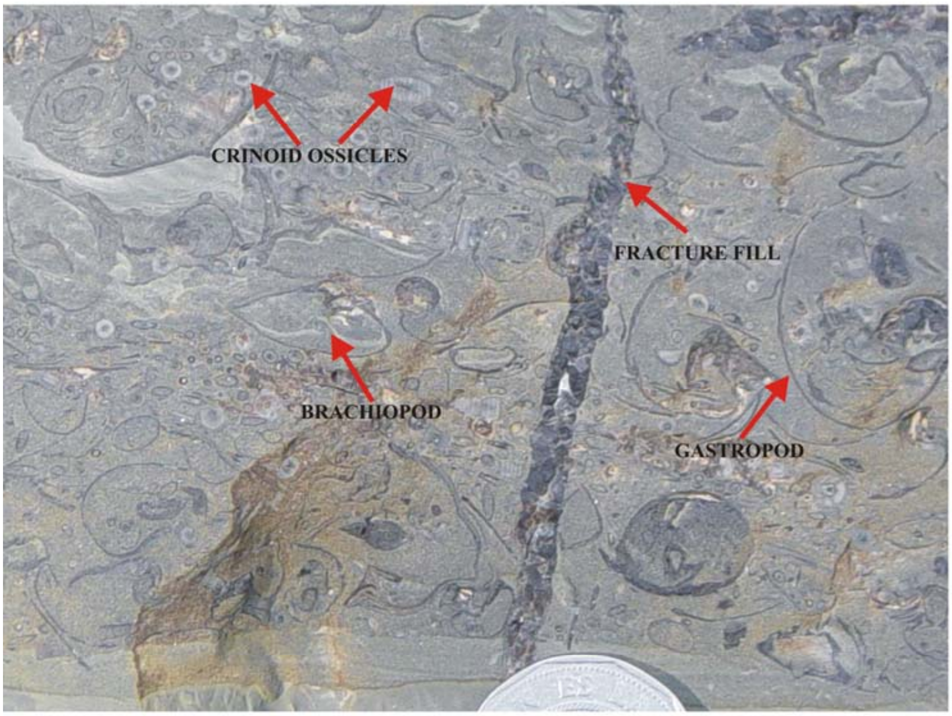


Fig. 5.10. Close up of the bioclastic layer in Fig. 9. This layer yielded brachiopods, crinoid ossicles, gastropods and although not visible above, benthic tentaculitids and ostracods. 20kg of this rock was processed for conodonts but none were recovered.

Fig. 5.11. Sub-millimetre/millimetre scale sand laminae in the lower Los Monos Formation. Way up indicated by arrow.

Fig. 5.12. Increasing sand content in the Los Monos Formation beneath CGH 40. Note development of thicker sandy horizons compared to Fig. 11. Green arrow shows way up.

Fig. 5.13. More persistent sandstone horizons (right bottom) beneath CGH 56. Weathered brown carbonate concretions can be seen in the foreground to the left (arrowed). Green arrow shows way up.

Fig. 5.14. Wavy/lenticular bedding in the upper Los Monos Formation. Arrow shows way up.

Fig. 5.15. Sandier intervals (lighter grey) in the upper Los Monos Formation. Note bioturbation (arrowed). Green arrow indicates younging direction.

Fig. 5.16. Mud-dominated interval in the upper Los Monos Formation. Millimetre scale sand horizons (lighter coloured) are present but decrease in abundance towards the top of the picture. Green arrow indicates way up.

5.2.3 Iquiri Formation (Fig. 5.2, 377-1214m)

Localities: Bermejo and Cha-Kjeri (equivalent facies).

Distribution: The Iquiri Formation is 837m thick at Bermejo and consists of interbedded shales, siltstones and sandstones with variable siderite development throughout this formation. Similar facies are also seen in the Track Shale Member (227m thick) at Cha-Kjeri (**Chapter 2**). The Track Shale Member is Givetian, contains abundant phytoclasts and is therefore probably the facies equivalent of the Bermejo beds (see below). Due to the development of sandstones beneath the Track Shale Member (Orko-Capilla and Catarata Sandstones) at Cha-Kjeri, locating the level equivalent to the Los Monos/Iquiri Formation boundary at Bermejo is difficult.

Description: The Iquiri Formation displays similar facies to the uppermost Los Monos Formation, e.g. wavy/lenticular beds (**Figs. 5.14-5.16**) throughout at Bermejo. However, the Iquiri Formation also contains channels (**Figs. 5.17-5.19**), sandstone-dominanted units (up to 15m thick**, Fig. 5.21**) and siderite (**Figs. 5.18-5.24**) with the appearance of these features marking the boundary between the two formations. Channel fills occur singly or as part of multiple channel complexes where the channels are vertically stacked. Most are saucer-shaped in cross section (<3m in width and <1m depth) and comprise fine/medium grained quartz-rich sandstones with mm to cm scale planar lamination and, often show low angle trough cross-stratification (**Figs. 5.18, 5.21-5.24**). Wave ripples are common on the tops of channels (**Fig. 5.19**). Siderite is commonly associated with the channels in the form of rip-up clasts (**Figs. 5.18-5.19, 5.20-5.22**), although laterally persistent layers usually less than 20cm thick do occur (**Fig. 5.23**).

Towards the middle of the Iquiri Formation (605m) the Bermejo beds (=‘TLM’ in the subsurface) are found. The Bermejo beds are approximately 130m thick and consist predominantly of centimetre scale lenticular bedded, interbedded muds, silts and sandstones (**Fig. 5.25**). Persistent bands of centimetre thick siderite horizons are also present, in addition to rare continuous beds (<10cm thick) of fine-grained muddy sandstone (**Fig. 5.26**). Some of these sandstones are rather coarse and moderately/poorly-sorted comprising mm size angular clasts of quartz, feldspar and rounded carbonate clasts within a sideritic matrix. The sandstone horizons can have a rippled appearance in cross section (**Fig. 5.27**). There are no sandstones comparable to these in terms of grain size elsewhere in the section. However, while there are some distinctive sedimentological features in the Bermejo beds, they are probably insufficient to enable recognition of this unit on other sections by sedimentology alone. Like the ‘TLM’ in the subsurface, the Bermejo beds are best recognised in terms of palynology (see below).

A 15m thick sandstone dominated body with metre scale, laterally continuous, medium-grained quartz-rich sandstone horizons interbedded with occasional centimetre thick mudstone horizons occurs at 805m (**Figs. 5.28-5.30**). The majority of the sandstone horizons show planar and low angle cross lamination (**Fig. 5.29-5.30**) with some horizons also possessing wave ripple lamination (**Fig. 5.30**). Water escape structures, some of which are truncated, also occur (**Fig. 5.30**), as does a 20cm thick horizon of sandstone rip-up clasts within the sandstone package (**Fig. 5.31**).

There is a return to typical 'Iquiri facies' (channels, wavy bedding, etc.) above the sandstone body before the occurrence of the Givetian shales at 850m (**Fig. 5.32**) consisting mainly of dark coloured relatively organic-rich shales (**Figs. 5.4-5.6**). These shales have higher TOCs (typically 1-1.5%) than seen in the lower Los Monos Formation (**Fig. 5.4**). This shale package is 32m thick and shows increasing sand content (ripples, etc.) up-section before the onset of the more usual channels, wavy bedding etc. (**Fig. 5.33**). Another significant dark shale unit (Frasnian shales) occurs at 1065m (**Figs. 5.34-5.35**). The Frasnian shales are 36m thick and also relatively organic rich with most TOC values >1% (**Figs. 5.3-5.5**). Like the other shale packages described, the sand content increases towards the top of the unit culminating in the reappearance of more typical 'Iquiri facies' (**Fig. 5.36**) that are subsequently truncated by an angular unconformity and overlain by diamictites of the Itacua Formation as shown in **Figure 5.37**.

The Iquiri Formation is richer in palynomorphs relative to the Los Monos Formation. From the base of the formation upwards into the Bermejo beds there is a steady increase in the abundance of large spores and phytoclasts, both of which dominate the Bermejo beds (**Fig. 5.2**) although small numbers of acritarchs and chitinozoa are also present. Above the Bermejo beds, the palynomorph assemblage becomes increasingly marine influenced (**Fig. 5.2**) with acritarchs and chitinozoans becoming more abundant and diverse. Spores although still common comprise smaller forms. Amorphous organic matter (AOM) and prasinophytes are also abundant in the Givetian and Frasnian shale intervals. Due to the presence of abundant AOM in CGH 113 and the TAG samples from the Givetian shales (**Fig. 5.5**) it was not possible to count the numbers of palynomorphs without using an ultrasonic probe to break-up the AOM which may have biased the palynomorph assemblage.

Macrofossils are rare in the Iquiri Formation. In the basal Iquiri Formation a sideritic channel fill containing disarticulated brachiopods was seen (**Fig. 5.24**) and within the Bermejo beds there are levels containing crinoids, starfish and trilobites (**Figs. 5.38-5.40**). No other macrofossils were observed.

Age: The Iquiri Formation is latest Eifelian to mid-Frasnian in age based on acritarchs, chitinozoans and spores (**Chapter 3**).

Environmental interpretation: The siderite in the Iquiri Formation is early diagenetic since rip-up clasts are often seen within sandstone channels suggesting active siderite precipitation elsewhere **(Figs. 5.18, 5.20-5.21)**. Furthermore, *in-situ* laterally continuous siderite cemented horizons are also observed in close proximity to horizons containing rip-up clasts (**Figs. 5.20, 5.23, 5.27**). Siderite formation is restricted to reducing environments (Berner, 1971,1981; Mozley & Wersin, 1992), such as the sub-oxic and methanogenic zones (Froelich *et al.*, 1979), with low concentrations of dissolved sulphide, high concentrations of dissolved carbonate, a high Fe^{2+}/Ca^{2+} ratio, low Eh and near neutral pH. In reducing environments, high concentrations of sulphide favour pyrite precipitation whereas if the Fe^{2+}/Ca^{2+} ratio and sulphide concentrations are low, calcite formation will take place.

Wilkinson *et al.* (2000) in their geochemical analysis of siderite from shallow marine sandstones of the Jurassic Brent Field in the North Sea observed that siderite cements form preferentially within ripple cross-laminated sands. In this environment, wave reworking oxygenates the sediment inhibiting the process of sulphate reduction and pyrite formation during shallow burial. This results in the development of a strong sub-oxic zone favouring the precipitation of siderite. Rippled sandstones also host siderite at Bermejo (**Figs. 5.23-5.27**) and the method of formation of this siderite could therefore be analogous to that invoked for the Brent Field by Wilkinson *et al.* (2000). As stated previously, high concentrations of Fe^{2+} are also required to form siderite. Fe^{2+} can be supplied into the marine environment via run off from continental weathering. The palynology of the lower Iquiri Formation/Bermejo beds shows increasing terrestrial input (**Fig. 5.2**) supporting the view of continentally derived Fe^{2+}.

The Bermejo beds are interpreted as representing the most proximal portion of the Iquiri Formation at Bermejo and also in the subsurface (Marshall *et al.*, in prep.) based on a spore and phytoclast dominated palynological assemblage that could be related to the close proximity of fluvio-deltaic input (Tyson, 1995). The thin rippled sandstone bands within the Bermejo beds (**Fig. 5.27**) are the coarsest observed in the measured section. Although moderately sorted in terms of grain size, the angularity of the clasts and mineralogical immaturity of the sandstones suggests they have not been transported far or undergone much reworking. Integrating the palynological and sedimentological data, the Bermejo beds may have been deposited in a more proximal nearshore setting relative to the rest of the Iquiri Formation and/or during a period of increased continental run-off. The presence of articulated echinoderms (**Figs. 5.38-5.40**) that do not preserve easily (e.g. starfish) would support fairly rapid sedimentation and therefore perhaps increased terrestrial input. Echinoderms are stenohaline and their presence combined with the occurrence of marine palynomorphs suggests the Bermejo beds were mainly deposited in a normal salinity marine environment.

The sandstone package at 805m displays structures indicative of rapid deposition and/or a high energy environment (**Figs. 5.28-5.31**). Some of these structures are considered by Reading (1996 and references therein) to be characteristic of modern storm layers but a key feature of storm deposits, hummocky cross stratification (HCS), was not observed. It is clear that this sandstone package is an amalgam of 'events' based on the erosive bases of some sandstone units, shaley intervals and truncated water escape structures (**Fig. 5.30**). Without HCS, it is difficult to decide whether these sandstones are tempestites or turbidites but the presence of wave ripple lamination identified in **Figure 5.30** does suggest storm related deposition since turbidites lack this structure (Johnson & Baldwin (1996) and references therein). Furthermore the channels seen throughout the Iquiri Formation are common in storm influenced environments (Einsele & Seilacher, 1991). The lack of bioturbation within the sandstones suggests rapid and/or proximal deposition since a marked increase in bioturbation occurs in tempestites deposited distally (Aigner & Reineck, 1982).

The Givetian and Frasnian shale packages (at 850 and 1065m respectively) are considered marine transgressions based on the palynology and sedimentology. The sedimentology of these shales, like the flooding event in the basal Los Monos Formation, suggests deposition below storm wave base during maximum flooding although there was a subsequent shallowing based on increased sand content. In contrast to the basal Los Monos Formation flood, the marine palynomorph assemblage in the Givetian/Frasnian shales is much more diverse, with larger spores generally absent and locally abundant AOM. In modern marine deposits, an abundance of AOM is considered diagnostic of dysoxic to anoxic environments (Tyson, 1995, and references therein). The relative percentage of AOM in ancient deposits is higher in more offshore, darker-coloured and more organic rich sediments than in inner shelf facies (Bujak *et al*., 1977a; Dow & Person, 1975). Based on these observations, the Givetian and Frasnian shale intercalations within the Iquiri Formation were deposited under oxygen deficient conditions in a more distal shelf environment than the shales in the basal Los Monos Formation hence allowing AOM preservation. Conditions for organic matter preservation were more optimal during the deposition of the Givetian shales and this is supported by the TOC and RockEval^{TM} data. These data show that the Givetian shales have higher average TOC and S_2 values than the Frasnian shales (1.6% vs. 1.1% and 5.4% vs. 3.9%, see also **Figs. 5.3-5.6**). Consequently, the Givetian shales have relatively more source rock potential.

Preservation of organic matter may explain why the largest peaks in marine palynomorph abundance in the Iquiri Formation occur outside of the transgressive Frasnian shales (the Givetian shales have not been investigated since they are AOM-rich) and also the associated increase in abundance of non-palynomorphs. Two such intervals are highlighted on **Figure 5.3**. To assume that marine floods are often associated with a pulse in abundance of marine palynomorphs and a corresponding decrease in the numbers of non-marine palynomorphs is an oversimplification since preservational controls (i.e., depositional environment) must also exert some influence. If conditions for organic matter preservation become more optimal there will be an associated increase in the numbers of non-marine and marine palynomorphs preserved which would explain both the overall higher palynomorph abundances and TOC values in the Iquiri Formation.

The overall persistence of facies similar to those in the uppermost Los Monos Formation (**Figs. 5.13-5.16**) suggests that most of the Iquiri Formation was also deposited above storm wave base in an inner shelf environment. However, the occurrence of channels, tempestites and siderite throughout the formation would support deposition more proximally than the upper Los Monos Formation. Based mainly on palynology, the lower Iquiri and Bermejo beds interval experienced greatest terrestrial input. Consequently, the Givetian and Frasnian flooding events represent temporary shifts toward a quieter, low-oxygen distal shelf environment. A summary of the depositional environments encountered at Bermejo is shown in **Figure 5.41**. The interpretation of the depositional environments at Bermejo is consistent with the broad palaeogeographic setting of Bolivia during the Devonian, i.e., an epicontinental seaway (**Fig. 5.1**). Since littoral or continental facies were not observed at Bermejo, it is not possible to precisely characterise the most proximal/nearshore portion of **Figure 5.41** in terms of environment. According to Sempere (1995), Mid-Devonian palaeocurrents originated in the east, and if correct, the likely source of sediment for Bermejo was the Brazilian Shield and/or the landmass to the south-east (**Fig. 5.1**), but further study is required.

Fig. 5.17. Sandstone channels at the base of the Iquiri Formation oreintated approximately E-W. Green arrow indicates younging direction.

Fig. 5.18. Siderite clasts (brown) at the base of a channel in the basal Iquiri Formation. The first appearance of sandstone channels and siderite mark the boundary between the Los Monos and Iquiri Formations. Note low angle cross bedding. Younging direction shown by green arrow.

Fig. 5.19. Rippled upper surfaces on sandstone horizons in the basal Iquiri Formation.

Fig. 5.20. Sandstone package at the base of the Iquiri Formation (400m, Fig. 2). Note low angle cross-bedding and siderite clasts following laminae (arrowed). Within this sandstone package, siderite occurs as rip-up clasts (Figs. 5.21-22) and laterally continuous layers (Fig. 5.23). Green arrow indicates younging direction.

Fig. 5.21. Close up of siderite rip-up clasts within the sandstone package shown in Fig. 5.20. Siderite occurs both as rip-up clasts and laterally continuous horizons at Bermejo (see Fig. 5.23). The presence of rip-up clasts suggests active siderite precipitation in their source area, consequently the siderite is considered early diagenetic in origin. Note the elongate mud clast to the right of the pencil. Way up shown by green arrow.

Fig. 5.22. Planar laminated sandstone with siderite rip-up clasts and flow rolls near the top of the sandstone package in Figure 20. Green arrow indicates younging direction.

Fig. 5.23. A laterally continuous siderite horizon associated with wave rippled sandstone in the sandstone package shown in Figure 5.20. Green arrow indicates younging direction.

Fig.5.24. Brachiopods (mostly leached molds) within a sideritic channel fill in the basal Iquiri Formation. Macrofossils are rare within the Iquiri Formation at Bermejo.

Fig. 5.25. Lenticular/wavy bedding in the Bermejo beds. Arrow shows way up.

Fig. 5.26. Dirty sandstone and siderite within the Bermejo beds. The dirty brown sandstones (left) are unique to the Bermejo beds. Green arrow indicates younging direction.

Fig.5.27. A coarse sideritic sandstone horizon in the Bermejo beds. These sandstones in the Bermejo beds were the coarsest observed throughout the Huamampampa-Iquiri Formation interval at Bermejo and therefore may have been deposited in a more proximal environment compared to the rest of the Iquiri Formation. Arrow shows way up

Fig. 5.28. The sandstone package at 805m (Fig. 5.2). Figures 5.29-31 illustrate features observed in this unit. Note thin mud layers (arrowed) between sandstone horizons. Green arrow shows younging direction.

Fig. 5.29. Top of the sandstone package shown in Fig. 5.28. Note planar lamination, shallow angle cross bedding and sharp erosive basal contact of the horizon below the author. Arrow shows way up.

Fig. 5.30. Truncated water escape structure (arrowed), paralled lamination (bottom) and wave ripple lamination (top). Green arrow indicates younging direction.

Fig. 5.31. Rip-up clasts in muddy matrix overlain by parallel laminated sandstone. Arrow shows younging direction.

Fig. 5.32. Dark organic-rich shale package at 850m in Figure 2 (Givetian shales), overlying the sandstone package shown in Fig. 5.28. Green arrow shows way up.

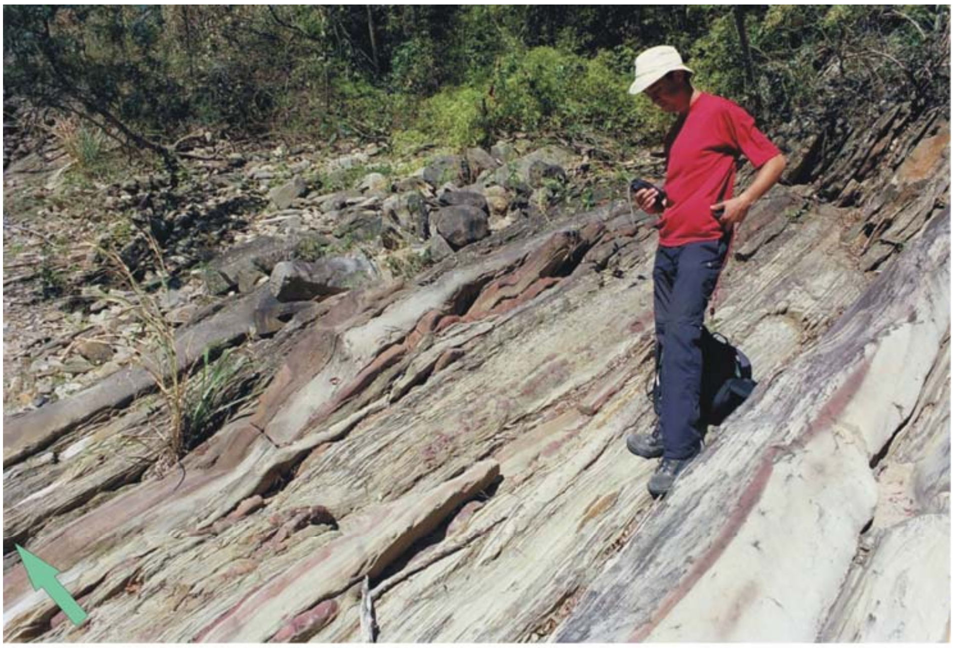


Fig. 5.33. Typical Iquiri facies following deposition of the Givetian shales in Fig. 5.32. Way up indicated by green arrow.

Fig. 5.34. The dark organic-rich shales at 1065m on Figure 5.2 (Frasnian shales). Green arrow shows way up.

Fig. 5.35. Close up of the Frasnian shales in Fig. 5.34. Note red/brown Fe-rich layers and concretions. Green arrow indicates younging direction.

Fig. 5.36. The uppermost Iquiri Formation at Bermejo. Green arrow shows way up.

Fig. 5.37. Contact between the Iquiri and Itacua Formation at Bermejo. The author is stood on the angular unconformity between the two formations, with the Iquiri Formation to the right. Arrow shows younging direction.

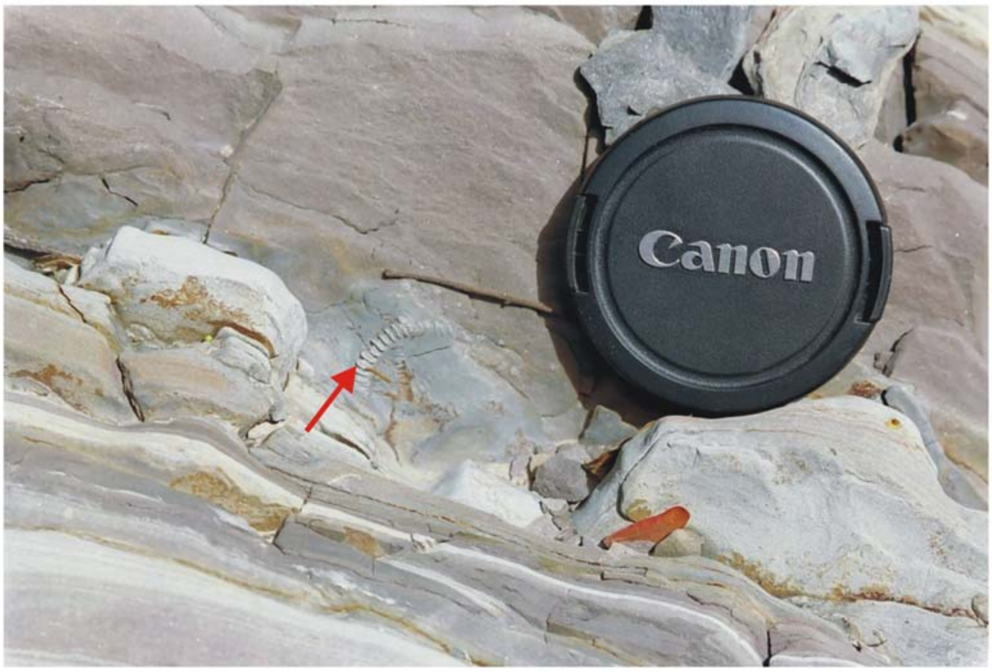
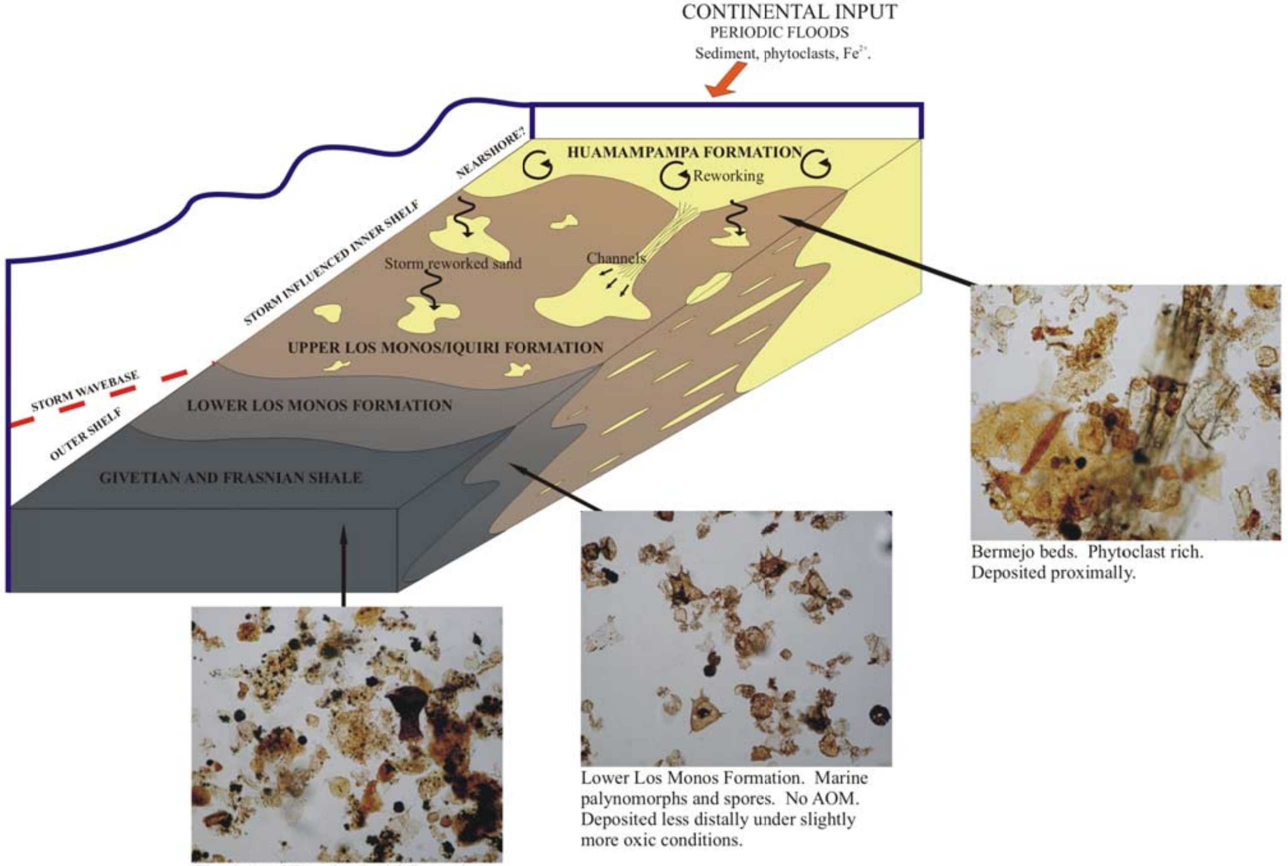


Fig. 5.38. Articulated crinoid arms near the top of the Bermejo beds.

Fig. 5.39. Starfish remains in the uppermost Bermejo beds. The presence of echinoderms (see also Fig. 5.38) suggests deposition under normal salinities.

Fig. 5.40. Trilobite remains (arrowed) in the Bermejo beds.



Bermejo beds. Phytoclast rich. Deposited proximally.

Lower Los Monos Formation. Marine palynomorphs and spores. No AOM. Deposited less distally under slightly more oxic conditions.

Givetian and Frasnian Iquiri Formation shale packages. AOM and marine palynomorph rich. Deposited under anoxic conditions.

Fig. 5.41. Summary of the inferred depositional environments at Bermejo. Palaeogeographic reconstructions show the closest emergent land to Bermejo during the Mid-Devonian was the Brazilian Shield to the north and another landmass to the south-east (see Fig. 5.1). It is assumed that these areas were the source of terrestrial input. However, a detailed palaeocurrent study of Bermejo and other nearby localities is needed to prove this.

5.3 Sequence stratigraphy and sea-level change

A basic sea-level curve for Bermejo based on integrated palynology and sedimentology is proposed in **Figure 5.42**. Three flooding events are identifiable and in terms of sequence stratigraphy and these are classified as 3rd order events (Schwarzacher, 2000; Vail *et al*., 1991) since they probably lasted less than 1my based on the known chronostratigraphy. Third order sequences have a duration of 0.5 to 3my (Schwarzacher, 2000; Vail *et al*., 1991) and although 3rd order events are recognised in the Devonian of Bolivia, they are thought to have lasted at least 5my (e.g. Miranda *et al*., 2000; 2003). The transgression at the base of the Los Monos Formation was recently assigned to the Givetian (Sempere, 1995; Miranda *et al*. 2000) and according to Miranda *et al*. (2003) the maximum flooding surface of this event is in the mid Givetian. However, the basal Los Monos Formation is earliest Eifelian based on palynomorphs (**Chapter 3**) and while there is a mid to late Givetian flooding event (**Figure 5.42**), it is unrelated. Poorly applied lithostratigraphy is responsible for the Givetian assignment of the basal Los Monos Formation flooding event and this could also explain the apparent longer duration of the recognised 3rd order events. Little published work has appeared on the sequence stratigraphy of the Iquiri Formation and consequently, there is no mention of the Frasnian flooding event in the literature.

The sea-level curve in **Figure 5.42** is also applicable to the subsurface in southern and central Bolivia since the three transgressive events and the Bermejo beds have been recognised in many wells with biostratigraphic precision (Marshall *et al*., in prep.). In addition, the early Eifelian transgression is identifiable at Campo Redondo and Cha-Kjeri, above which sandstone units (metres thick) are developed at both localities. In the palaeogeographic reconstructions of Albariño *et al*. (2002), it is assumed there is emergent land immediately west of these localities and their more proximal position relative to Bermejo may explain the development of thick sandstones at this level, although this requires further investigation.

While the depth curve in **Figure 5.42** is adequate for this study, it should be noted that there is an alternative way of interpreting the palynological and sedimentological data from Bermejo. If the data are viewed in terms of TOC and organic matter preservation then a different scenario for the upper Los Monos-Bermejo beds interval is possible. This new scenario hinges on a potential mechanism that would explain the formation of the basal Los Monos, Givetian and Frasnian shale packages based on the work of Wells *et al*. (2005) who proposed a numerical model to explain the formation of anoxic shales in epicontinental seaways with restricted tidal mixing in the Late Carboniferous of NW Europe. The palaeogeography of NW Europe during the Late Carboniferous was not dissimilar to South America for much of the Devonian other than the palaeolatitude, and Wells *et al*. (2005) suggest than in such an environment, with weak tidal mixing, during a sea-level highstand stratification will be promoted and therefore so will the deposition of organic-rich sediments. Assuming the Bolivia Basin had weak tides (no tidally influenced Devonian deposits currently have been documented in Bolivia and none were seen at Bermejo), then this model explains the formation of the Givetian and Frasnian shales, although the lower organic content of the basal Los Monos Formation could be attributed to a highstand of a lower magnitude than these events which enabled some mixing to take place.

TOC values in the Iquiri Formation are generally higher than the underlying Los Monos Formation with many samples being >1%. Taking into consideration the Wells *et al.* (2005) model and the ‘global’ sea-level which was thought to be increasing during the Eifelian-Frasnian interval (Johnson *et al.*, 1985), the increase in organic matter preservation could be a result of higher eustatic sea-level promoting low oxygen conditions due to weak tidal mixing. This situation is contrary to the shallowing inferred on **Figure 5.42** following the basal Los Monos Formation transgression and consequently, the increase in phytoclast abundance would not represent a pronounced shift toward a more proximal depositional environment i.e. decrease in water depth. Instead, the terrestrially-dominated signal could be purely climatic suggesting a period of increased continental run-off and since the Bermejo beds/’TLM’ has been identified throughout central and southern Bolivia then this is not unreasonable.

However, this assertion is complex, difficult to prove and would require global palynological/sedimentological investigations of coeval strata. Since there are chronostratigraphic issues when correlating with extra-Malvinokaffric regions, identifying the latter with precision may prove problematic. Therefore **Figure 5.42** remains valid.

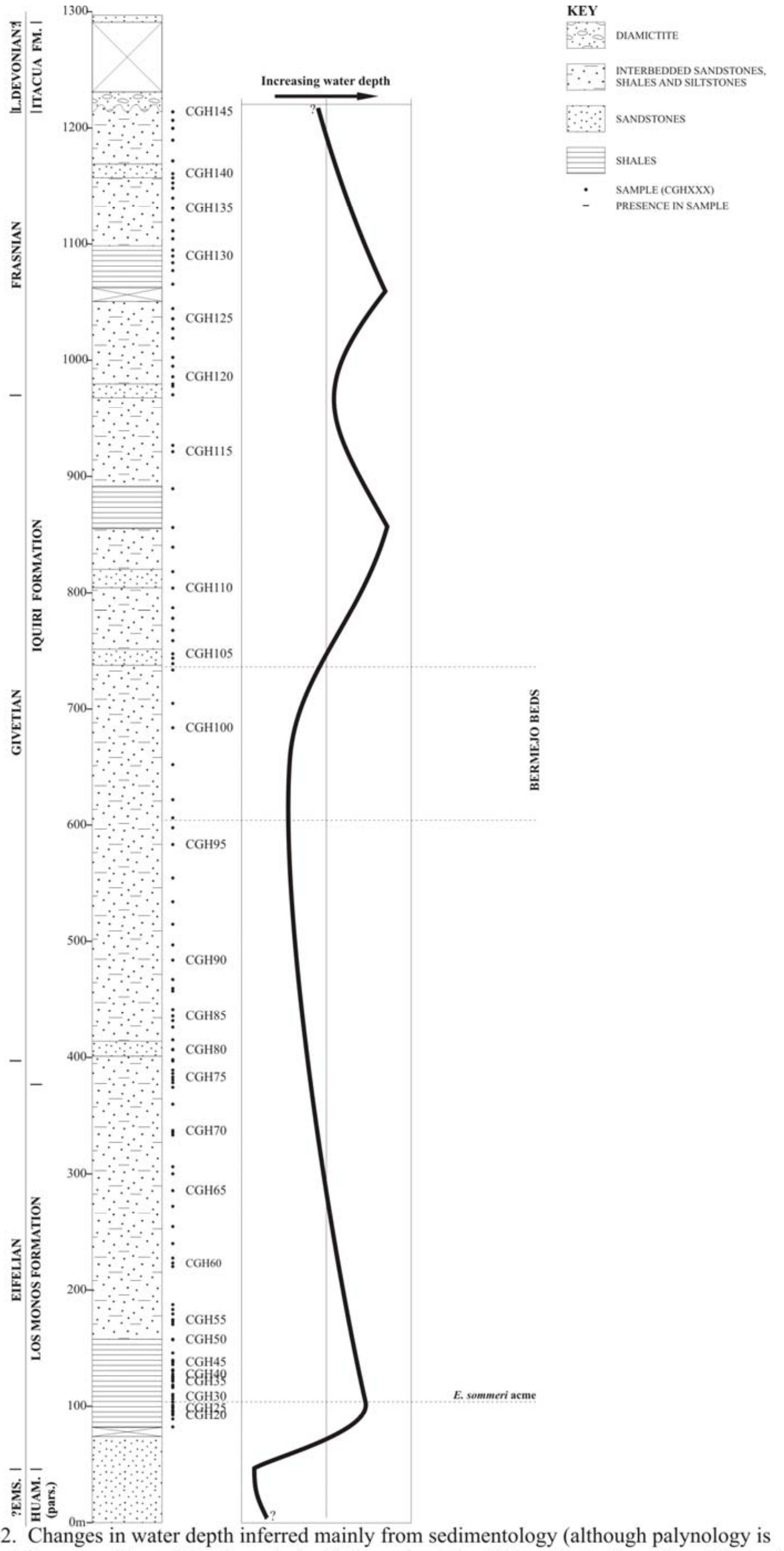


Fig. 5.42. Changes in water depth inferred mainly from sedimentology (although palynology is important for recognition of the Bermejo beds) throughout the Mid and Late Devonian at Bermejo.

CHAPTER 6 – THE SEARCH FOR *E. SOMMERI*

6.1 Introduction

The *E. sommeri* Epibole and the associated marine transgression in the basal Los Monos Formation are early Eifelian **(see Chapter 3)**. There is one major transgressive event during this interval in Euramerica and it occurs within the *partitus* Conodont Zone (Johnson *et al.*, 1985). It is associated with a turnover in marine fauna (goniatites and trilobites) and is known as the Choteč Event (**Chapter 1**, **Fig. 1.8**). The Choteč Event is identifiable throughout Euramerica and is characterised by the onset of deposition of dark, organic-rich sediments. This event may be represented by the early Eifelian transgression at the base of the Los Monos Formation. However, conodonts and goniatites have not been recorded from the basal Los Monos Formation or its equivalents in Bolivia and a Choteč Event assignment for this level cannot be defined with confidence. The test of this correlation would be to find the *E. sommeri* Event at a Choteč Event level in Euramerica which would indicate that the basal Los Monos Formation transgression is coeval, and this would confirm the broad applicability of the Euramerican sea-level curve at high palaeolatitudes for the early Eifelian.

E. sommeri has a potentially widespread geographical distribution with reported occurrences outside South America in the Mid-Devonian of North America and Europe (Eisenack *et al.*, 1973; Cramer,1969). Consequently, identifying the *E. sommeri* Event in Euramerica is feasible assuming *E. sommeri* has a similar stratigraphic distribution to that seen in Bolivia. Attempts have been made to locate *E. sommeri* and its associated assemblage in the Emsian-Givetian sections of Spain (2003-4), UK (2003), Morocco (2004), Siberia (2005) and the Czech Republic (2005) in order to further validate the age assigned to the basal Los Monos Formation in this study. Sampling localities are shown on **Figure 6.1** with the lithostratigraphy of these sections in **Figure 6.2.** Locality details, sample levels and selected logs are given in **Appendix 1**. A total of 149 samples from these localities were collected and processed.

6.2 Spain

E. sommeri was reported from Eifelian shales in the Cantabrian Mountains, north Spain by Cramer (1969). Although this record is somewhat dubious (**see Chapter 3, 3.3**), the Lower to Middle Devonian formations in the Cantabrians (**Fig. 6.2**) are well known to the author (as he mapped here as an undergraduate in 2000), and are generally well-exposed in road and railway cuttings. On this basis, two visits were made to Cramer's (1969) locality near San Roman (San Roque) and the Choteč Event intervals at Ciñera, Huergas, Moniello and Arbejal (**Fig. 6.3-6.8).** These localities are described in García-Alcalde *et al.* (1979) and Henn (1985). In terms of palaeoenvironment, Ciñera, Huergas, La Vid, Moniello and San Roman are in the nearshore Asturo Leonese Domain with Arbejal representing a more distal,

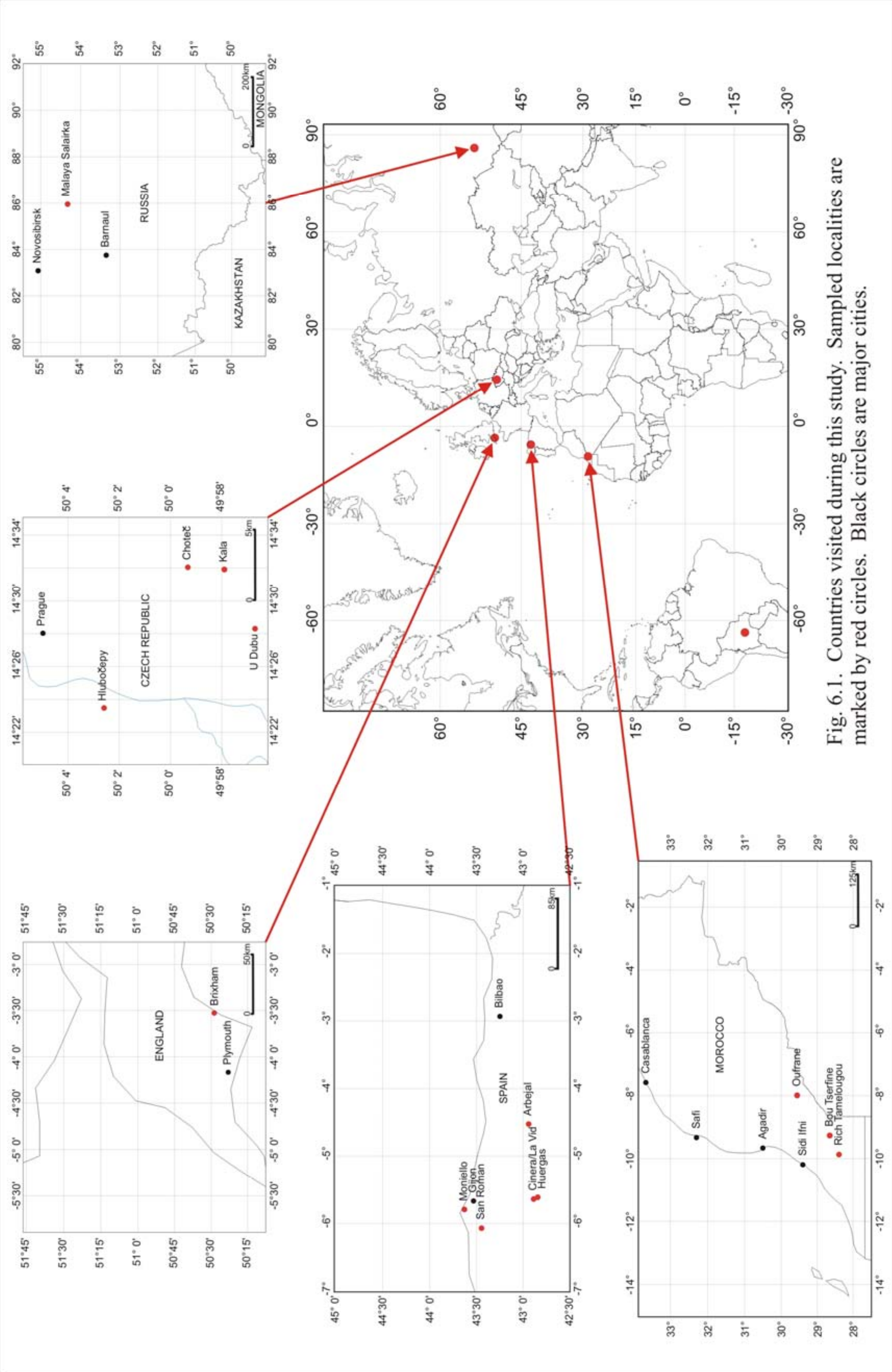


Fig. 6.1. Countries visited during this study. Sampled localities are marked by red circles. Black circles are major cities.

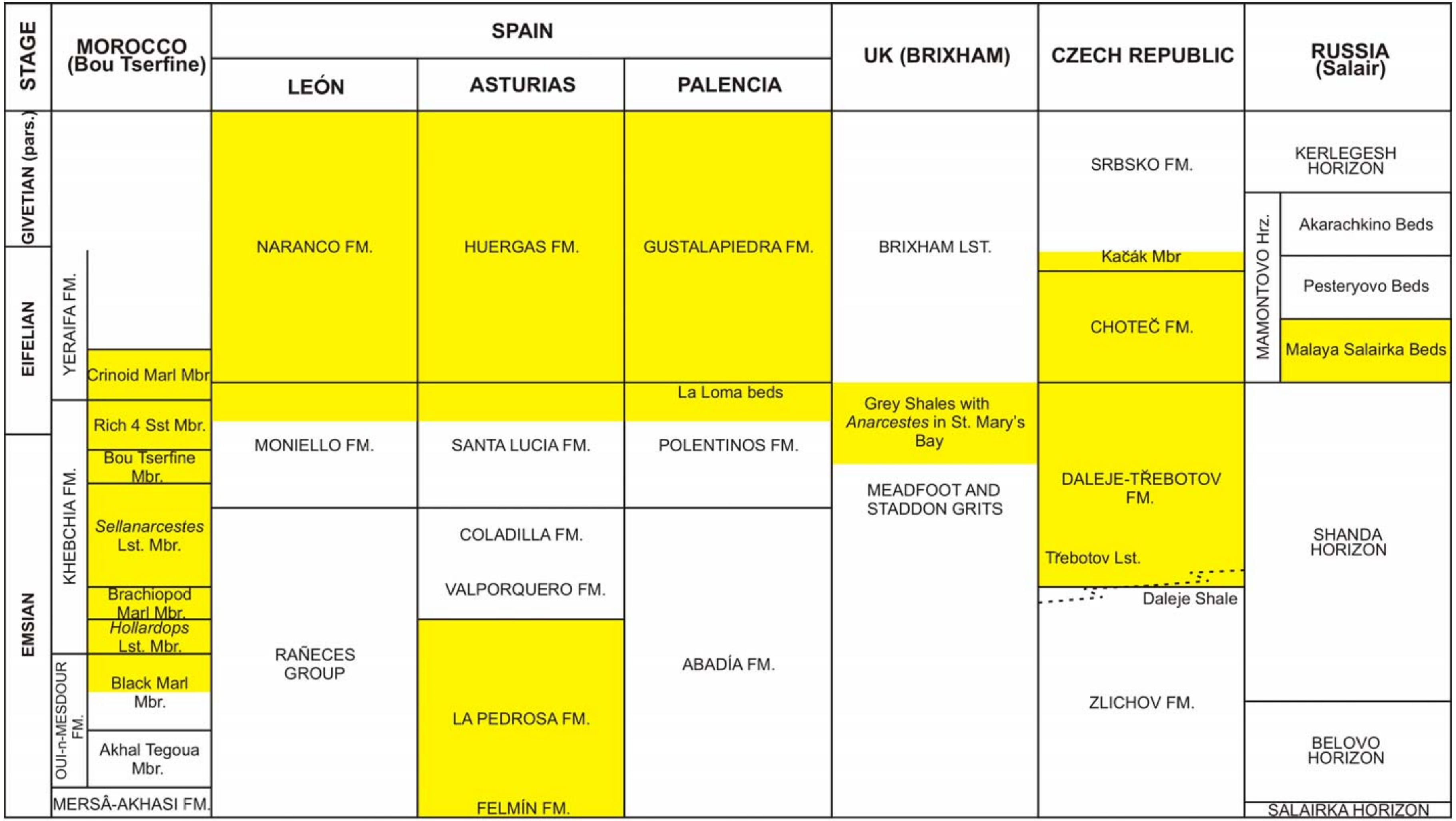


Fig. 6.2. Lithostratigraphy in the sampled regions (based on data from Becker *et al.*, 2004 (Morocco), Chlupáč, 1998 (Czech Republic), Garcia-López, 2002 (Spain), House *et al.*, 1977 (UK), Yolkin *et al.*, 2005 (Russia)).

hemipelagic setting in the Palentine Domain (see Garcia-López, 2002 for discussion).

In northern Spain, the Choteč Event is recognised lithologically as a change from light coloured limestones (upper Moniello, Santa Lucia and Polentinos Formations) to dark to black shales, with interbedded marls, siltstones or sandstones (Naranco and Huergas Formations) or dark to black micritic limestones ('La Loma beds' in the upper Polentinos Formation). The Devonian lithostratigraphy of N. Spain is shown in **Figure 6.2.**

A total of 69 samples were processed with all localities yielding palynomorphs although yields were variable, possibly due to weathering. The most abundant well-preserved palynomorphs were found in the basal Huergas Formation at Ciñera. None of the samples from Ciñera or the other localities (including Cramer's (1969) locality near San Roman) yielded *E. sommeri*. Some of the more common palynomorphs are illustrated on **Plates 1-2.** Whilst the Eifelian acritarch assemblage (**Pl. 2, figs. 1-8**) contains elements in common with Bolivia, e.g. *Multisplicisphaeridium ramusculosum*, *Navifusa bacillum* and *Triangulina alagarda* (**Pl. 2, figs. 3, 6-7; Chapter 2, Pl. 3**), the spore assemblage consists of similar genera (e.g. *Grandispora*) but different species (**e.g. Pl.2, figs. 10-11**) and the chitinozoa are completely different (**Pl. 1, figs. 4, 6-7 and 9-10**). The same is true of the Emsian chitinozoa from La Vid (**Pl. 1, Figs. 3, 11 and 13**; Cramer ,1964) although *Hoegisphaera* was identified in samples LP-20 to LP-22 and this genus is also present in the Icla Formation at Campo Redondo. Specimens of *Hoegisphaera* sp. are also present in the mid/late Eifelian at Arbejal (**samples GER-19 and 20**, **see Appendix D**).

The localities sampled in Spain represent a proximal (San Roman) to distal (Arbejal) basinal transect. Since *E. sommeri* was not found in any of these settings, its absence cannot be attributed to palaeoenvironment (i.e. water depth). The chitinozoa are distinct from coeval forms in Bolivia, emphasising the endemism of this group in Bolivia. Although there are currently no records of the cosmopolitan taxon *Alpenachitina eisenacki* in Spain, the inception of this species (if found) could be used to correlate with Bolivia. The behaviour of *Hoegisphaera* is intriguing since it is present in the Emsian (La Vid) and Eifelian (Arbejal) but only for short stratigraphic intervals (<10m). A similar pattern is observed at Bermejo in the Frasnian (**Chapter 4, Fig. 4.1**) and there may be an environmental significance to its occurrence. Further study is required.

6.3 UK (St. Mary's Bay, near Brixham)

Mid-Devonian shales are exposed in St. Mary's Bay, 1 mile south of Brixham in SW England (**Fig. 6.1**). These shales are heavily deformed and locating precise stratigraphic positions is difficult. The Choteč Event has not been identified in the UK. However, there is a band of goniatites in the middle of St. Mary's Bay (**Fig. 6.9**) which suggest a latest Early Devonian/earliest Mid Devonian age for this part of the sequence based on the occurrence of

Fig. 6.3. La Vid/Vegacervera road section, 1km NE of Ciñera (looking west). Exposed are marine carbonates and shales. The Santa Lucia/Huergas Formation locality at Ciñera (Fig. 4) is out of view in the extreme centre left. The younging direction is to the south (green arrow). Samples LP-15 and LP-25 are marked. Photo courtesy of Clive Boulter.

Fig. 6.4. The boundary between the Santa Lucia and Huergas Formations in the railway cutting at Ciñera looking west. Samples HGSL-1 (out of sight) and HGSL-4 to 6 were most palynologically productive. Note the section is inverted (younging to the left).

Fig. 6.5. Base of the measured section at Huergas (view towards NE). The same lithologies (limestones and shales) are exposed as at Ciñera. The green arrow shows younging direction.

Fig. 6.6. The Naranco Formation (sandstones with interbedded silts and shales) at San Roman looking east. This is the Cramer (1969) locality (San Roque). The samples were phytoclast-and spore-rich and *E. sommeri* was not found. The section becomes younger to the west (green arrow).

Fig. 6.7. Moniello Inlet (looking ESE). Samples were taken from shale interbeds in the foreground (Moniello Formation) and out of sight round the first cut off point (Naranco Formation). The position of the Naranco Formation samples is marked by the red arrow.

Fig. 6.8. Arbejal, 1km NNE of Arbejal village (view towards west). The base of the measured section is in the Polentinos Formation in the bottom right with the strata becoming younger downslope (green arrow).

Anarcestes (House, 1963; Becker & House, 2000). These goniatite-bearing levels were sampled for palynology and although probably pre-Choteč in age (there are no records of the Choteč level goniatite *Pinacites jugleri* from these beds), this interval represented the best opportunity of finding *E. sommeri* in the UK.

Fifteen samples from St. Mary's Bay were processed and yielded very few palynomorphs. The palynomorphs recovered were un-identifiable and black indicating a very high level of organic matter maturity.

These results were as expected. Even if *E. sommeri* or the *E. sommeri* Event had been found, placing either in stratigraphic context within an area which is structurally complex would be difficult.

6.4 Morocco

In March 2004, the Subcommission on Devonian Stratigraphy (SDS) ran a fieldtrip associated with the SDS meeting in Rabat (see Hassani, 2004). The fieldtrip was in the Dra Valley area (western Anti Atlas Mountains) with the aim being to examine the biostratigraphy and lithostratigraphy of the region and also the principle Devonian biotic events. Numerous localities were visited, but the Choteč interval was only seen and sampled at Bou Tserfine, Oufrane and Rich Tamelougou (**Fig. 6.1**) where it is represented by shaly facies. The lithostratigraphy and biostratigraphy of these sections is discussed in El Hassani (2004) and references therein. General lithostratigraphy of the western Dra Valley region is shown in **Fig. 6.2**.

Sixty-nine samples were processed from Morocco, although none of the Choteč intervals sampled contained well-preserved palynomorphs (probably due to deep weathering) and *E. sommeri* was not found. Apart from Bou Tserfine, which yielded some acritarchs (e.g. *Multisplicisphaeridium*, *Navifusa* and *Veryhachium*) and locally abundant chitinozoa (*Ancyrochitina* and *Angochitina*) in the Emsian *Hollardops* Limestone and Black Marl Members (**Fig. 6.10, Pl. 1, figs. 1 and 8**), palynomorph recovery from the other localities was poor to non-existent. Palynological comparision with Bermejo was not possible since the equivalent levels are not exposed, although possible similarities with Campo Redondo could be investigated in the future. Overall, the collection of macrofossils was most rewarding in Morocco (**Pl. 2, fig. 14; Pl. 3, figs. 1A-C**).

Weathering was a problem at the Moroccan localities, although there is clear potential for palynological study in the Dra Valley. The productive samples from Bou Tserfine are important since they represent the first record of palynomorphs from this part of the Dra Valley. Further field work is required in the western Dra Valley to identify less weathered localities which may be more suitable for palynology.

6.5 Siberia

Following Morocco, the next SDS meeting was in Novosibirsk, Russia during August 2005. The fieldtrip attached to this meeting involved investigation of Devonian sequences south of Novosibirsk in the Salair, Rudny and Gorny Altai. Further details of this excursion are in Yolkin *et al*. (2005). This part of Siberia is essentially a frontier region in terms of Devonian research with much work still in progress. However, a probable early Eifelian marine transgression is recorded in the Malaya Salairka Beds at Malaya Salairka Quarry (**Fig. 6.11-6.12**). The transgression is manifested by dark calcareous shales and limestone lenses containing abundant goniatites confirmed in the field as early Eifelian by Prof. R.T. Becker.

Unfortunately, the Malaya Salairka Beds had been quarried out prior to the SDS visit with only piles of rubble left on the quarry floor. Three random spot samples (shale) were taken but these yielded only non-descript palynodebris.

Malaya Salairka was in the northern hemisphere (~30^{o}N, Kazakh terrane) during the Devonian unlike much of Euramerica and South America (**Chapter 1, Fig. 1.6**) and like today was further away from Bolivia than the Czech Republic, Morocco, Spain and the UK- none of which yielded *E. sommeri*. Coupled with Devonian chronostratigraphic issues, success was not anticipated in Siberia. Nevertheless, the opportunity to try could not be missed.

6.6 Czech Republic

In the Prague area (**Fig. 6.1**), the Choteč Event is recognised lithologically in the basal Choteč Formation (**Fig. 6.2**) being marked by the onset of dark coloured biomicritic and biosparitic layers within lighter micritic limestones (Chlupáč & Kukal, 1988). There have been some Devonian palynological studies in the region, e.g. Lele (1972), McGregor (1979), Vavrdová (1989). With the kind assistance of Dr. J. Fryda and S. Berkyova from the Czech Geological Survey, the author visited the stratotype section of the Choteč Event in Škrábek Quarry near Choteč village (**Fig. 6.1**) during October 2005. Exposures of the Daleje Shale and Kačák Member (**Fig. 6.2**) were sampled at Kala (=Pekárkův mlýn in Chlupáč, *et al*., 1979; **Fig. 6.1**) and U Dubu (=Seven Brothers' Oak in Budil, 1995; **Fig. 6.1**) to see if they would yield palynomorphs (**Figs. 6.13-6.15**). Samples were also collected from conspicuous, cyclic black shale horizons in the Třebotov Limestone (**Figs. 6.2, 6.16)** at Hlubočepy shown on **Figure 1** (=Praha-Hlubočepy in Chlupáč, *et al*., 1979).

Fig. 6.9. Goniatite yielding interval in the middle of St. Mary's Bay near Brixham. This photograph does not do justice to the diabolical British weather at the time.

Fig. 6.10. *Hollardops* (trilobite) Limestone Mbr. (Khebchia Formation) at Bou Tserfine (view towards north). Samples BT-16 to BT-22 (out of view) from this Member yielded palynomorphs. BT-12 -15 from the underlying covered Black Marl Member (Oui-n-Mesdoûr Formation) and BT-26 in the overlying Bou Tserfine Mbr. (out of view) were also productive. Arrow shows younging direction.

Fig. 6.11. Malaya Salairka Quarry in the Mamonotov Horizon limestones looking NE. Arrowed are the rubble piles containing the Malaya Salairka Beds (see Fig. 12).

Fig. 6.12. Rubble containing the Malaya Salairka Beds (dark rocks). This locality yielded Eifelian goniatites.

Fig. 6.13. The Daleje Shales at Kala. The hammer marks the base of the measured section. Samples DJE 1-3 shown in picture, DJE 4 and 5 are out of view. Arrow shows younging direction.

Fig. 6.14. The Choteč Event represented by a black foetid limestone band in the Choteč limestone at Škrábek Quarry, Choteč. Compare the thickness of this unit with the basal Los Monos transgression (tens m). Arrow shows younging direction.

Fig. 6.15. The boundary between the Choteč Formation (limestone) and the Kačák Member (black/grey calcareous shales) at U Dubu. KAC-6 is just out of view. Younging direction to the right (green arrow).

Only one of the samples from the Choteč level in Škrábek Quarry (CHO-2) was productive for palynology (**Fig. 6.14**). CHO-2 contained degraded prasinophytes and a large unusual chitinozoan (**Pl. 1, fig. 5**). *E. sommeri* was not observed. At Kala, sample DJE-3 (**Fig. 6.13**) contained abundant chitinozoa particularly *Ramochitina* sp. A (**Pl. 1, fig. 13**) associated with rare specimens of *Ancyrochitina* sp. A (**Pl. 1, fig. 2**). Numerous large prasinophytes were found in DJE-2 (**Fig. 6.13; Pl. 2, fig. 12).** Samples through the Kačák Member at U Dubu were AOM- and prasinophyte-rich (**Fig. 6.15, Pl. 2, fig. 13**). The cyclic black shales in the Třebotov Limestone at Hlubočepy all yielded prasinophyte rich assemblages (previously noted by Chlupáč, *et al*., 1979) with *Navifusa* also common thoughout (**Fig. 6.16, Pl. 2, fig 9**).

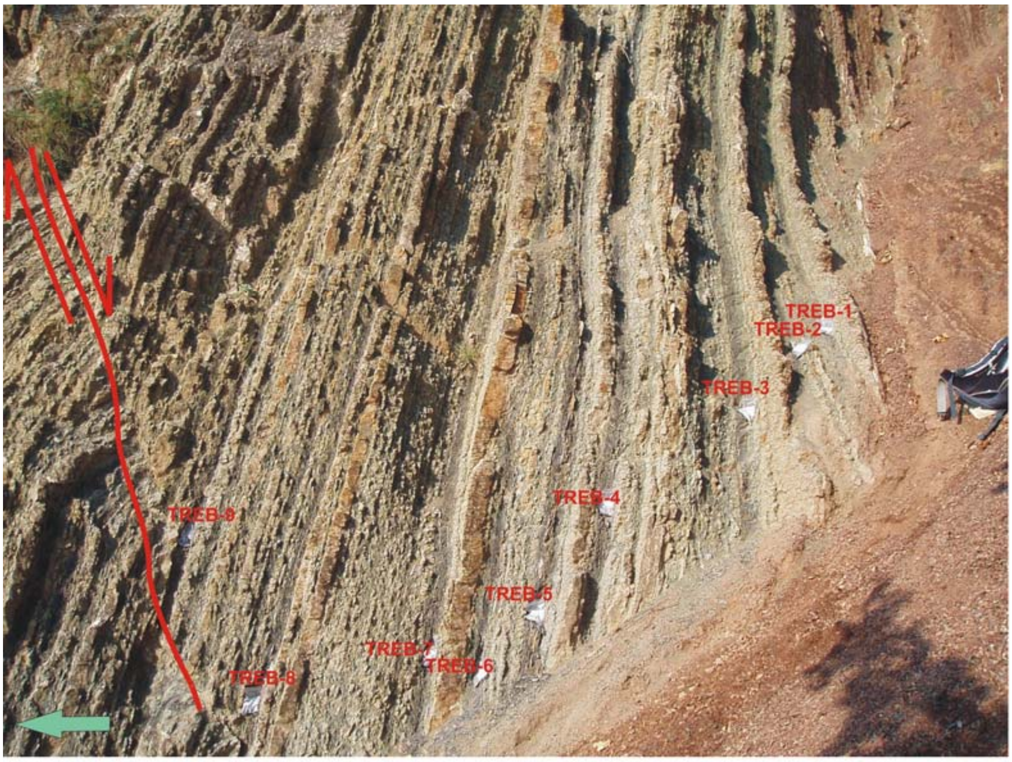


Fig. 16. The Třebotov Limestone at Hlubočepy. Note the cyclic black shales and fault to the left of the picture. Arrow shows younging direction.

The palynomorph assemblages (apart from sample DJE-3) are prasinophyte dominated and AOM is common (particularly in the Kačák Member) with such features being consistent with deepening events at these levels. The cyclic black shales in the Třebotov Limestone at Hlubočepy could also represent deepening events, albeit on shorter timescales. Samples from the Daleje Shale should also be broadly coeval with the upper La Pedrosa Formation, Spain, and *Hollardops* Limestone Member, Morocco (García-Alcalde, 1998; Becker *et* al., 2004), since these intervals also encompass the Daleje Event. With further sampling at Kala and more detailed investigation of the samples from Morocco and Spain, it may be possible to identify key palynomorph markers (especially chitinozoans) for this event.

6.7 Conclusion

Attempts to find *E. sommeri* in the Emsian-Givetian interval around Euramerica and Siberia were not successful. However, there are notable differences between the Emsian/Eifelian chitinozoan fauna in Euramerica and Bolivia, although the acritarch flora did contain some common elements. Consequently, it is not possible to definitively assign the Choteč Event transgression to the basal Los Monos Formation flooding event.

Based on the data currently available, *E. sommeri* is probably restricted to South America since the North American records (Eisenack, Cramer & Diez, 1973) cannot be verified. Given the clear endemicity of the Bolivian chitinozoan fauna during the Emsian/Eifelian, this assertion is reasonable. Using *Alpenachitina eisenacki*, it may yet be possible to tie the basal Los Monos Formation transgression to the Choteč Event, and North America would be an ideal location to attempt this since the inception of this taxon is in the *partitus* conodont zone in Iowa (Wright, 1980), and recent palaeogeographic reconstructions place southern North America at ~45^{o}S during the Mid Devonian (Torsvik & Cocks, 2004; **Fig. 6.17**). An alternative to North America would be to persist with sampling in Morocco since *A. eisenacki* has also been recorded in North Africa (e.g. Boumendjel *et al*. 1988).

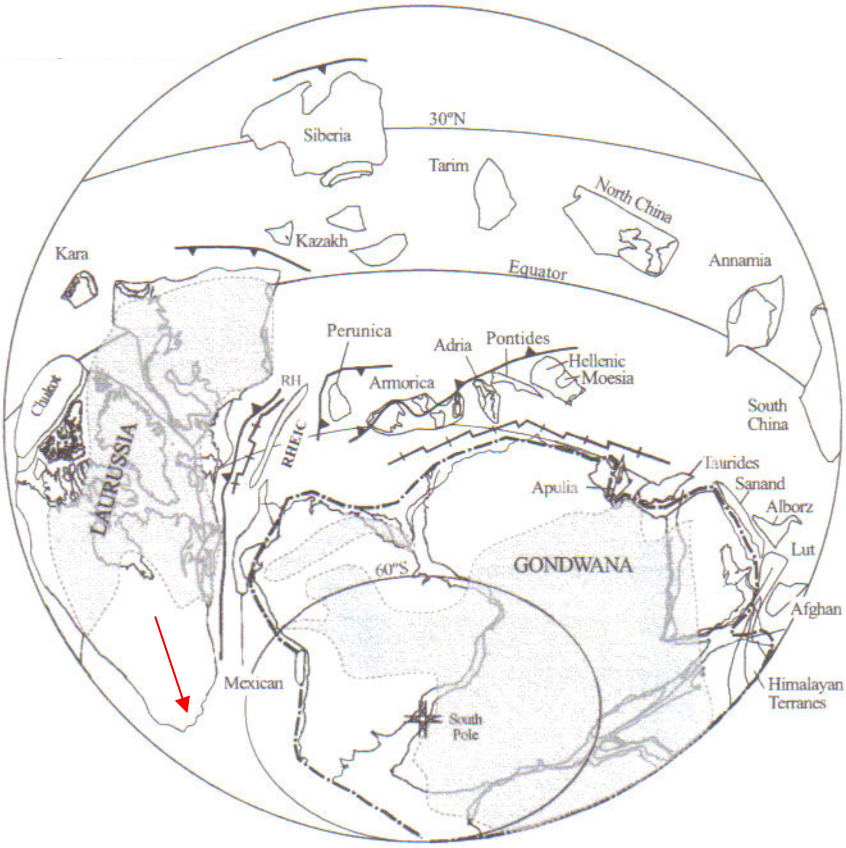


Fig 6.17. Early Devonian palaeogeography (from Torsvik & Cocks, 2004). Note the position of southern North America (arrowed) at high palaeolatitutes in the southern hemisphere (cf. Chapter 1, Fig. 1.6).

Plate 1

Black scale bar = 100µm.

1. *Ancyrochitina* sp. A. Black Marl Member, Oui-n-Mesdoûr Formation, Bou Tserfine, Morocco. BT-15, coordinates 10.5/107.4.
2. *Ancyrochitina* sp. B. Daleje Formation, Kala, Czech Republic. DJE-3, coordinates 11.4/97.6.
3. *Ancyrochitina* sp. C. La Vid Group (Val Porquero Formation), La Vid, N. Spain. LP-25, coordinates 28.4/94.5.
4. *Ancyrochitina* sp. D. La Loma Member, Gustalapiedra Formation, Arbejal, N. Spain. GER-7, coordinates 12/101.7.
5. ?Chitinozoan. Choteč Formation, Škrábek Quarry, Choteč, Czech Republic. CHO-2, coordinates 13.6/107.7.
6. *Ancyrochitina* sp. E. Huergas Formation, Ciñera, N. Spain. HGSL-5, coordinates 27.3/98.8.
7. *Ancyrochitina* sp. F. Huergas Formation, Ciñera, N. Spain. HGSL-6, coordinates 29.8/100.1.
8. *Angochitina* sp. A. Black Marl Member, Oui-n-Mesdoûr Formation, Bou Tserfine, Morocco. BT-15, coordinates 23.4/109.2.
9. *Angochitina* sp. B. Huergas Formation, Ciñera, N. Spain. HGSL-4, coordinates 12.1/109.4.
10. *Angochitina* sp. C. Huergas Formation, Ciñera, N. Spain. HGSL-5, coordinates 27.9/93.7.
11. *Hoesgisphaera* sp. La Vid Group (La Pedrosa Formation), La Vid, N. Spain. LP-22, coordinates 6.4/101.
12. *Ramochitina* sp. A. Daleje Formation, Kala, Czech Republic. DJE-3, coordinates 5.1/106.
13. *Ramochitina* sp. B. La Vid Group (La Pedrosa Formation), La Vid, N. Spain. LP-21, coordinates 32/101.6.

Plate 1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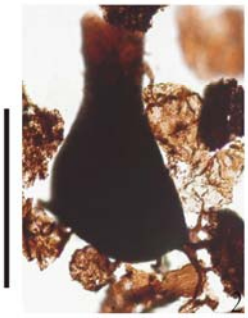
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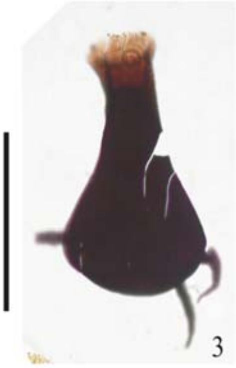
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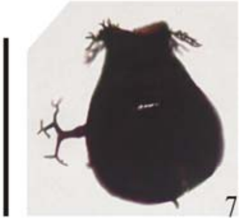
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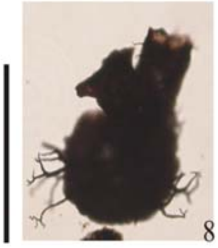
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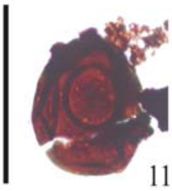
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Plate 2

Black scale bar = 50µm.
Fig. 14 = 30mm.

1. *Baltisphaeridium* sp. Huergas Formation, Ciñera, N. Spain. HGSL-1, coordinates 13.5/102.3.
2. *Duvernaysphaera* sp. Huergas Formation, Huergas, N. Spain. HG-7, coordinates 17.8/111.6.
3. *Multisplicisphaeridium ramusculosum* (Deflandre) Lister, 1970. Huergas Formation, Ciñera, N. Spain. HGSL-1, coordinates 13.2/101.6.
4. *Multisplicisphaeridium* sp. A. Huergas Formation, Ciñera, N. Spain. HGSL-1, coordinates 10.3/95.4.
5. *Multisplicisphaeridium*. sp. B. Huergas Formation, Ciñera, N. Spain. HGSL-1, coordinates 30/102.7.
6. *Navifusa bacillum* (Deunff) Playford, 1977. Huergas Formation, Huergas, N. Spain. HG-7, coordinates 14.3/110.2.
7. *Triangulina alagada* Cramer, 1964b. La Loma Member, Gustalapiedra Formation, Arbejal, N. Spain. GER-10, coordinates 41.5/106.4.
8. *Veryhachium* sp. Huergas Formation, Ciñera, N. Spain. HGSL-1, coordinates 14.5/101.8.
9. ?*Navifusa bacillum*. Trebotov Formation, Hlubočepy, Czech Republic. TREB-9, coordinates 13.6/107.2.
10. *Calyptosporites* sp. A. Naranco Formation, San Roman, N. Spain. CR-7>88µm, coordinates 33.4/111.4.
11. *Calyptosporites* sp. A. Naranco Formation, San Roman, N. Spain. CR-7>88µm, coordinates 39.5/101.5.
12. Large prasinophytes. Daleje Formation, Kala, Czech Republic. DJE-2.
13. Large prasinophytes (arrowed) and amorphous organic matter. Kačak Member, Srbsko Formation, U-Dubu, Czech Republic. KAC-1.
14. Phacopid trilobites. *Hollardops* Limestone Member, Khebchia Formation, Bou Tserfine, Morocco. Found ex-situ. Specimen prepared by Mark Hawkes, Stone Treasures of Edwinstowe. Photo courtesy of Barry Marsh, National Oceanography Centre, Southampton.

Plate 2


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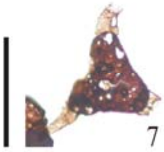
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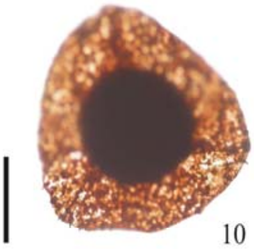
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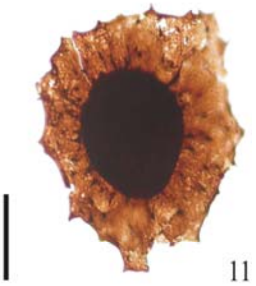
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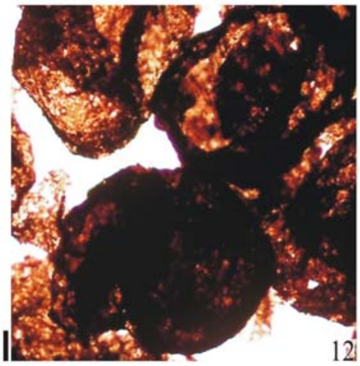
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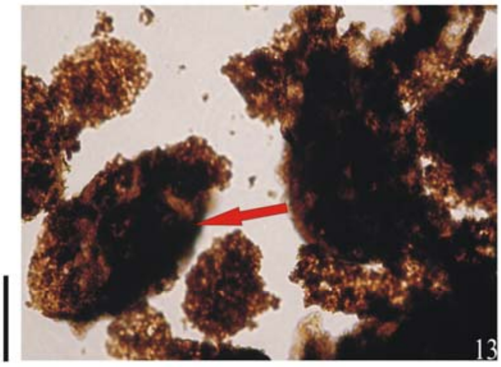
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Plate 3

Black scale bar = 55mm

1. A tainoceratid nautiloid from the *Hollardops* Limestone Member, Khebchia Formation, Bou Tserfine, Morocco. The specimen was found ex-situ and is believed to be a new genus and species. A coral resting on a spine is arrowed. Specimen prepared by Mark Hawkes, Stone Treasures of Edwinstowe. Photo courtesy of Barry Marsh, National Oceanography Centre, Southampton.

Plate 3

1

CHAPTER 7 – DISCUSSION

The original aims of this study were:

1) Validate the subsurface Devonian palynostratigraphy by comparing the subsurface data derived by the BG Group (Marshall *et al*., unpublished) with a detailed study of a continuous, unthrusted surface section (Bermejo).
2) Assess the validity of the important *E. sommeri* Epibole.
3) Improve the Devonian chronostratigraphy and constrain the age of the Huamampampa Formation.
4) Complete a detailed study of the chitinozoa at Bermejo.
5) Study the palynostratigraphy and relate this to palaeoenvironment.
6) If possible, place the palynological events and sedimentological trends in a global context by studying similar aged sections elsewhere in the world.

These aims have been realised through the generation of an extensive palynological database in Bolivia (317 samples) and 158 additional samples from non-Malvinokaffric localities. The palynology was further supplemented/supported by extensive field work and sedimentological studies.

7.1 Validation of subsurface Devonian palynostratigraphy

There have been no previous attempts to validate the subsurface Devonian palynostratigraphy by detailed investigation of surface Devonian sections. In brief, the subsurface Devonian (Mid-Late Devonian) palynology consists of a relatively impoverished Los Monos Formation marine assemblage which is replaced up-section by a phytoclast-rich interval (‘TLM’=Bermejo beds) in the lower Iquiri Formation. Above the ‘TLM’, the marine palynomorph assemblage becomes much more abundant and diverse relative to the Los Monos Formation and ‘TLM’. Also, within the subsurface Mid-Late Devonian interval are four palynomorph epiboles (oldest-youngest): *E. sommeri* Epibole (lower Los Monos), *B. bensonii* Epibole (upper Los Monos), *C. camirense* Epibole (Iquiri Formation) and the *P. connata* Epibole (Iquiri Formation).

At Bermejo, both the general palynological trends and the aforementioned palynomorph events were recognised in the same stratigraphic order. Moreover, in contrast to the subsurface, the palynology is now tied to an accurate revised lithostratigraphy. However, there are some differences between the surface and subsurface lithostratigraphies (**Fig. 7.1**):

1) The basal Los Monos Formation now includes the seldom used ‘Huamampampa Sucio siltstones/sandstones.

2) The Los Monos/Iquiri Formation contact is now defined sedimentologically (appearance of sandstone channels), resulting in the originally palynologically defined 'TLM' interval being placed in the Iquiri Formation.

3) The 'TLM' has been renamed the Bermejo beds due to its new stratigraphic position.

Based on the revision of the Los Monos/Iquiri Formation boundary, the *B. bensonii* Epibole is now located in the basal Iquiri Formation.

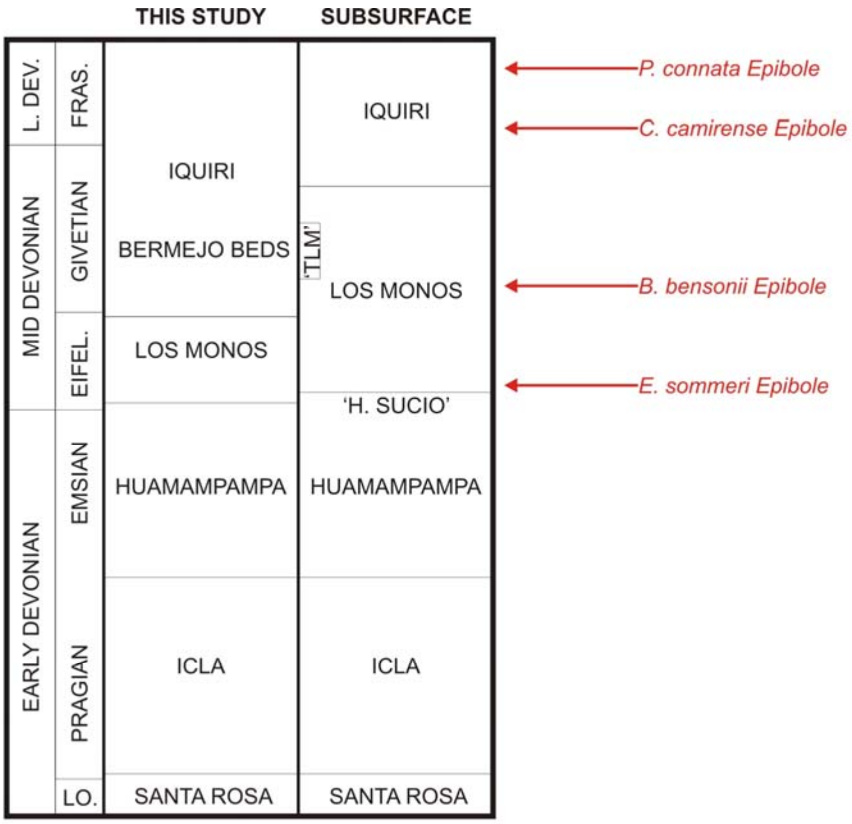

Fig. 7.1. Surface and subsurface stratigraphies in the southern Subandean.

The integrated biostratigraphic and lithostratigraphic data from Bermejo provides an opportunity to establish a reliable palynologically based Devonian stratigraphy for Bolivia as demonstrated at Cha-Kjeri and Campo Redondo where the Devonian lithostratigraphy has been revised. The subsurface biostratigraphic framework has now also been validated and refined. The data from Bermejo recently assisted in the recognition of tectonic repetition in the subsurface which may have been missed previously due to insufficient resolution in the biostratigraphic and seismic data.

7.2 The validity of the *E. sommeri* Epibole

The *E. sommeri* Epibole is the most important palynomorph event since it is found immediately above the Huamampampa Formation reservoir, in the basal Los Monos Formation in subsurface sections. This epibole is a single, stratigraphically short-lived event. Furthermore, *E. sommeri* is restricted to the latest Emsian/Eifelian interval which is also supported by data from Campo Redondo and Cha-Kjeri where it is found associated with the same palynomorph assemblage. In the Parnaíba Basin, NE Brazil, *E. sommeri* is found with a similar palynomorph assemblage in the basal Pimenteira Formation suggesting that this acritarch and probably the *E. sommeri* Epibole are geographically widespread in South America. Attempts to find *E. sommeri* in the Emsian/Eifelian of Euramerica and Siberia were unsuccessful and it seems likely the *E. sommeri* Epibole is restricted to the Malvinokaffric Realm.

Although, the *E. sommeri* Epibole is associated with a marine transgression at the base of the Los Monos Formation (as is the type material of *E. sommeri* in the Pimenteira Formation), its precise meaning is unclear. The *E. sommeri* Epibole occurs during an interval which is relatively impoverished in terms of marine palynomorphs and since the epibole is related to a marine transgression, *E. sommeri* could be a ‘disaster’ species that took advantage of stressed environmental conditions. Prasinophytes (leiospheres, in particular) have been noted to exhibit such behaviour in anoxic shales associated with marine transgressions (Tappan, 1980). Alternatively, the epibole may be an artefact of some peculiarities in algal cyst production (i.e. other taxa not producing cysts) which may also explain the relatively impoverished marine palynomorph assemblage (aside from cool water) in the Los Monos Formation. In terms of sequence stratigraphy, the *E. sommeri* Epibole can be interpreted as being the maximum flooding surface of the basal Los Monos Formation transgression. Consequently, the increase in abundance of *E. sommeri* could be the result of condensation.

Compared to the younger epiboles, the *E. sommeri* Epibole is the most significant not only as a stratigraphic marker but also in terms of environment. The *B. bensonii* Epibole occurs during a time of general regression/increased continental input and the environmental importance of this event requires further study. Irrespective, *B. bensonii* dominates the acritarch flora at this level. While *C. camirense* and *P. connata* are distinctive palynomorphs and useful stratigraphic markers, the acmes of the species may not be important in terms of environmental context. The palynomorph assemblage at the level at which these taxa are found is relatively diverse and there are probably acmes of other short-lived, distinctive elements that could also be described as ‘epiboles’ e.g. chitinozoa such as *Lagenochitina* spp.

7.3 Age of the Huamampampa Formation

A goniatite (as yet unidentified) was found at Campo Redondo in the basal Huamampampa Formation, 15m above the level from which another goniatite (*Tornoceras bolivianum*) was reported by Hünicken *et al.* (1980). Due to the scarcity of Devonian goniatites in South America, *T. bolivianum* was considered to be important in terms of chronostratigraphy and the Huamampampa Formation was often assigned to the Mid-Devonian or younger based on the presumed age of *T. bolivianum*. However, both goniatite levels at Campo Redondo are now redated as Emsian in age based on palynomorphs. This negates the previous Mid/Late Devonian assignments for *T. bolivianum* and permits the age of the Huamampampa Formation to be constrained mainly to the Emsian (uppermost Lower Devonian) rather than Middle Devonian. If the findings of this study are accepted, then the range of tornoceratid goniatites is extended into the Lower Devonian. This is significant because in Euramerica, Lower Devonian tornoceratids are currently unknown (Becker *pers. comm.*, 2004; Brett *pers. comm.*, 2006). Further investigation of the spore flora at Campo Redondo is currently being undertaken by Dr. John Marshall (National Oceanography Centre, Southampton).

7.4 Chitinozoa

Many of the chitinozoa identified at Bermejo have short stratigraphic ranges (less than a stage). The chitinozoan fauna is directly comparable to Brazil although the ranges in Brazil for some taxa, e.g. *Ancyrochitina langei* and *Ramochitina ramosi* are somewhat extended. As some of the Brazilian data come from widely spaced subsurface samples (often cuttings), the stratigraphic resolution provided in this study is generally lacking in Brazil. Consequently, it is probable that specimens have been assigned to the wrong taxon resulting in longer stratigraphic ranges, e.g. *Ancyrochitina* sp.1 (restricted to the early-mid Eifelian) to *A. langei* (mid-late Givetian). Higher density sampling is required through Devonian sections with good lithostratigraphic control in Bolivia and other South American countries before a high resolution sequence of inceptions/zonal scheme can be developed.

There is a high degree of endemism in the chitinozoan fauna throughout the Devonian in Bolivia (and Brazil). This endemism is particularly pronounced when comparing time equivalent sections to the Los Monos Formation in Euramerica which were sampled and yielded different faunas.

7.5 Palaeoenvironment

During Emsian Huamampampa times, Bermejo was located proximally in a nearshore sand-dominated environment. A subsequent early Eifelian marine transgression in basal Los Monos Formation (associated with the *E. sommeri* Epibole) resulted in shale deposition in an offshore shelf environment below storm wave base. Following this transgression, there was a general regression into a storm influenced inner shelf environment in the upper Los Monos Formation with deposition becoming more proximal in the Bermejo beds. Apart from two marine flooding events in the mid/late Givetian and early Frasnian which were deposited in a more oxygen-deficient outer shelf environment compared to the lower Los Monos Formation (higher TOC content and more abundant AOM), Bermejo remained a storm-dominated inner shelf environment throughout the upper Los Monos-Iquiri Formation interval. The three marine flooding events are interpreted as 3rd order events in terms of sequence stratigraphy.

The presence of higher order cyclicity (>3rd order) cannot be discounted in Bolivia, although there is insufficient biostratigraphic control to correlate these at present.

7.6 Global context

7.6.1 South America

The Devonian of Bolivia closely resembles that of the Paraná Basin of southern Brazil, eastern Paraguay and NE Argentina, suggesting that most of this region was generally stable and cratonic in nature (Sempere, 1990). This is consistent with the transgressive events found at Bermejo being identifiable elsewhere in the subsurface of Bolivia and N. Argentina. An early Eifelian flooding event associated with *E. sommeri* is recorded in the basal Pimenteira Formation, NE Brazil (Melo, 1988). Data on the Givetian transgression is generally lacking although it may be represented by part of the black shale package between 150-205m depth (São Domingos Formation) in Well RSP-1-MT in the Paraná Basin, southern Brazil based on available chitinozoan data (Grahn *et al.*, 2002). There is a widespread development of black shales across Brazil during the Frasnian which is thought to be related to high global sea-levels (Melo, 1988). It is likely that the Frasnian transgression is represented by part of the condensed radioactive shales (lower Barreirinha Formation) in the Caima Ph-2 well, Amazonas Basin, northern Brazil based on spore and chitinozoan data (Grahn & Melo, 2002; Le Hérissé, 2001; Loboziak *et al.*, 1997a).

7.6.2 Comparison with the Euramerican sea-level curve (Johnson *et al.*, 1985)

Without conodonts and goniatites, it is difficult to apply an accurate chronostratigraphic framework to the Devonian in Bolivia and compare the transgressive events to the Johnson *et al.* (1985) sea-level curve with the precision possible in Euramerica. However, a comparison of the transgressive events at Bermejo with the Euramerican sea-level curve is still possible using the palynomorph data generated in this study, albeit with the assumption that these flooding events could be eustatic based on their widespread geographic distribution in South America. Some of the cosmopolitan palynomorphs identified at Bermejo have conodont-constrained inceptions in Euramerica, and using these it is possible to broadly recognise stage boundaries or positions within stages during the Mid-Late Devonian in Bolivia.

During the latest Emsian through mid Givetian, the Johnson *et al.* (1985) curve **(Fig. 1)** records a gradual deepening in contrast to surface and subsurface data (Marshall *et al.*, in prep.) from Bolivia which records a general regression. Following deposition of the Bermejo beds there is an increase in the abundance and diversity of marine palynomorphs relative to the Lower Iquiri and Los Monos Formations and these could be interpreted as representing increasingly marine conditions. An increased marine influence would be consistent with progressive deepening from the end of the Givetian into the early-mid Frasnian interval which represents the time of highest sea-level in the Devonian according to Johnson *et al.* (1985).

The basal Los Monos Formation transgression is early Eifelian or older based on the inception of *Alpenachitina eisenacki* in CGH 46 with this chitinozoan first appearing in the *partitus* Conodont Zone in the USA (Wright, 1980). Furthermore, the appearance of abundant large camerate and zonate spores in the lower Los Monos Formation (relative to the underlying Huamampampa and Icla Formations) would support a latest Emsian/early Eifelian age in terms of spore evolution (Richardson & McGregor, 1986). The Eifelian/Givetian boundary is easily identifiable based on the inception of *G. lemurata* in CGH 77 and crucially, there is no palynological or sedimentological evidence for a major transgression around this level (Kačák Event). Precise dating of the Givetian transgression is problematical. The cosmopolitan spores, *Cristatisporites triangulatus* and *Chelinospora concinna*, can be used for correlation but the sequence of their inceptions is not always the same.

Apart from one inception dated as late early Givetian by conodonts in the Eifel region of Germany (Loboziak *et al.*, 1991), the inceptions of *C. triangulatus* are otherwise consistently mid Givetian (middle-upper *varcus* Conodont Zone) as are those of *C. concinna* (Turnau, 1996; Turnau & Rackii, 1999 and references therein). Only one specimen of *C. concinna* was found at Bermejo in CGH 106. Assuming the mid-Givetian age assignments for the inception of *C. triangulatus* are correct, CGH 108 (= inception of *C. triangulatus* at Bermejo) could be equivalent to a level within the middle-upper *varcus* Zone (= *ansatus* and *semialternans* Zones). The early Frasnian is recognisable in CGH 117; 208m above CGH 108 therefore a mid-late Givetian age for the Givetian shales (CGH 113-CGH 114) is reasonable. The inception of *Verrucosisporites bulliferus* is in CGH 117 and in Europe this inception may occur in either the *punctata* or *transitans* Zones (Streel *et al.*, 2000), i.e. early Frasnian. Since the top of the Iquiri Formation is probably not much younger than mid-Frasnian, the Frasnian shales (CGH 127-CGH 132) are early-mid Frasnian.

A possible candidate for the early Eifelian flooding event in the lower Los Monos Formation is in TR (transgressive-regressive) cycle Ic of Johnson *et al.* (1985). Within TR cycle Ic **(Fig. 7.2)**, a marine transgression within the *partitus* Zone may be broadly consistent with the age assignment for the lower Los Monos Formation. In Euramerica, this transgression is apparently widespread and is manifested by a facies change, i.e. the onset of dark coloured or black sediments referred to as the Choteč Event (Walliser, 1996).

The Givetian flooding event can be assigned to either TR cycle If or IIa **(Fig. 7.2)**. Placing this event in IIa is inconsistent with the presumed late early Eifelian inception of *C. triangulatus* in South America (Melo & Loboziak, 2003) based on its range in Germany (Loboziak *et al.*, 1991). However, given the inception of *C. triangulatus* is generally mid

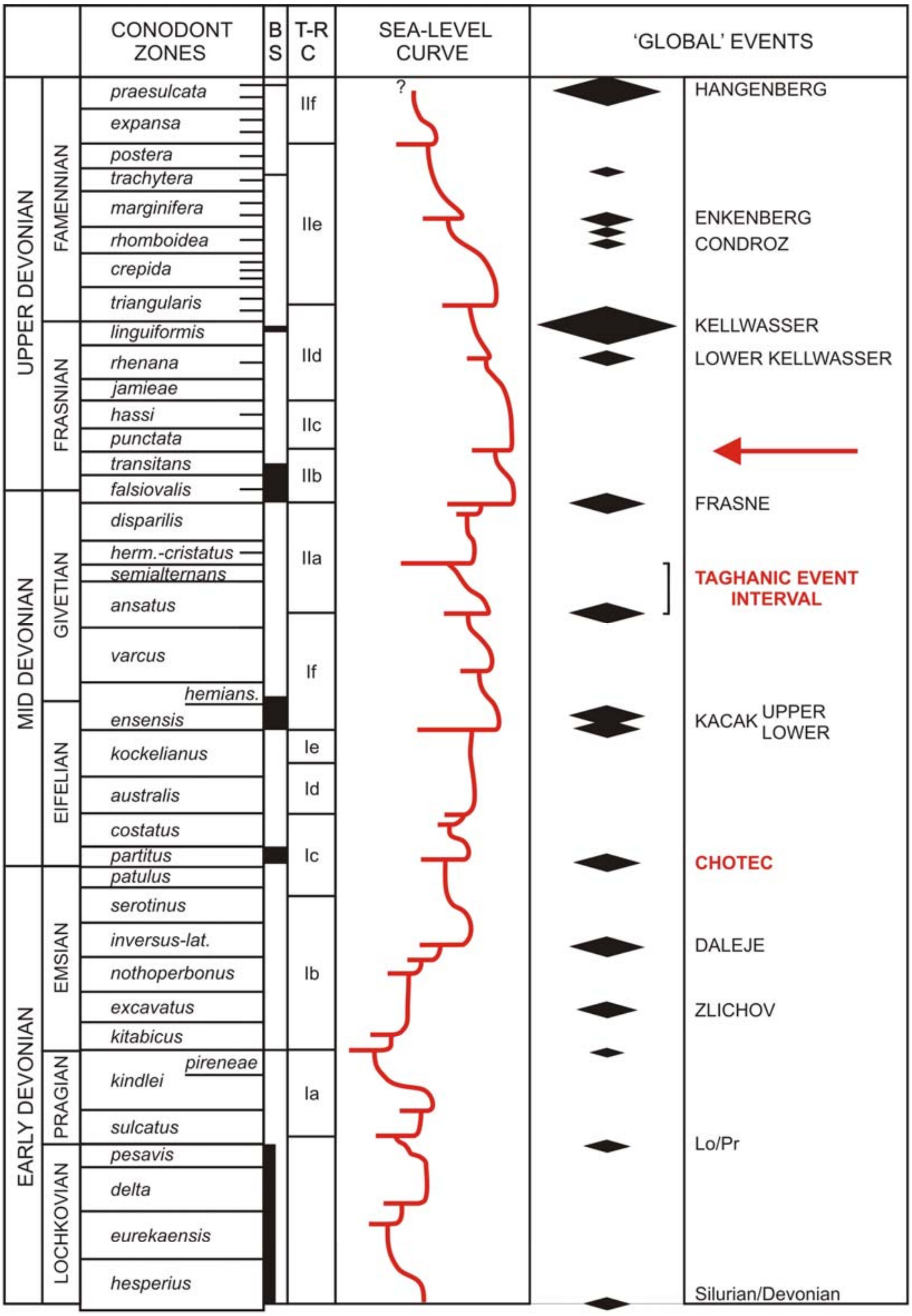

Fig. 7.2. The Devonian Euramerica sea-level curve (Johnson *et al*., 1985) and 'global events' (Walliser, 1996) with modifications to the conodont biozonation from Aboussalam (2003) and Sandberg (2002). Possible candidates for the three flooding events marked at Bermejo are highlighted in red.

Givetian (specifically mid-upper *varcus* Zone = *ansatus* and *semialternans* Zones) apart from in Germany, then this event could be placed in TR cycle IIa. Although tenuous, this would be supported by the single specimen of *C. concinna* in CGH 106. If accepted, the Givetian flooding event could be related to the Taghanic Event Interval of Aboussalam (2003) which is detectable throughout North America, North Africa and Europe.

In the early-mid Frasnian, there is one transgression at the boundary between TR cycles IIb and IIc **(Fig. 7.2)** which also corresponds to the *transistans*/*punctata* conodont Zone boundary. The next transgression is in the late Frasnian (Lower Kellwasser Event; Becker, 1993b), although this can be discounted as a likely candidate since the top of the Iquiri Formation is no younger than the mid Frasnian. On this basis, the Frasnian event may represent the transgression at the base of TR cycle IIc (=Rhinestreet of House, 1985).

6.3 Implications for the breakdown of the Malvinokaffric Realm

The Eifelian/Givetian boundary Kačák Event is considered to have had a profound effect on the Malvinokaffric Realm. According to May (1996) the Kačák transgression caused a sudden lowering of the global climatic gradient and a corresponding world-wide warming which resulted in the breakdown of the Malvinokaffric Realm (Boucot, 1988, 1990b; Schöne, 1997). This assertion was made despite the recognition that there is no lithological evidence for the Kačák Event in South America (Boucot, *pers. comm. in*: May, 1996; Melo, 1988). At the type locality of the Kačák Event (U Dubu) in the Czech Republic there is an abrupt change from limestone to dark calcareous claystones and mudstones and these yielded abundant AOM and prasinophytes. This lithological and palynological evidence would support a marine transgression. In contrast, the Eifelian/Givetian boundary interval at Bermejo is characterised by a general marine regression based on palynology (an increase in phytoclasts plus AOM and prasinophytes are not abundant) and sedimentology.

The breakdown of the Malvinokaffric Realm is thought to have commenced near the Eifelian/Givetian boundary based on the first appearances of the brachiopod *Tropidoleptus* in Bolivia and 'Tornoceratid' goniatites, particularly *Tornoceras bolivianum*. This is further supported by the appearance of another brachiopod, *Rhipidothyris*, a Givetian circum-Atlantic genus in the Mid Devonian of Bolivia and South Africa (Isaacson, 1974; Boucot & Theron, 2001). Both *Tropidoleptus* and *Tornoceras* are cosmopolitan and long-ranging genera, but *Tornoceras* is a Mid-Late Devonian genus and this originally provided a Givetian/Frasnian age for *Tropidoleptus*-bearing beds and the Huamampampa Formation in Bolivia (Isaacson & Perry, 1977; Hünicken *et al.*, 1980). Some authors cited this association in Bolivia along with Mid-Devonian occurrences of *Tropidoleptus* in NW Argentina, South Africa and Brazil (Melo, 1988 and references therein) as signalling the Mid-Devonian breakdown of the Malvinokaffric Realm.

However, more recently it has been recognised that palynomorphs provide more reliable correlations in the Malvinokaffric Realm (Boucot, 1999, Racheboeuf *et al*., 1993). Using spores it has been demonstrated that *T. bolivianum* is Emsian and the earliest known Bolivian occurrence of *Tropidoleptus* in the Carinatus Shale at Cha-Kjeri (Issacson, 1977a) is early Eifelian. The Carinatus Shale at Cha-Kjeri was originally considered to be Givetian (Isaacson & Perry, 1977) but this age was emended to Eifelian by Issacson & Sablock (1988) based on spore work by McGregor (1984). This study supports an Eifelian age due the presence of *E. sommeri* and *A. eisenacki* in this unit. *Tropidoleptus* dominated assemblages are also found in the basal Pimenteira Formation (as is *E. sommeri*) in the eastern Parnaíba Basin, NE Brazil which is early Eifelian according to Melo (1988). The brachiopod and goniatite data presented herein do not support a Kačák Event-related breakdown of the Malvinokaffric Realm.

If the Malvinokaffric Realm broke down in the Eifelian, based on the available data, *Tropidoleptus* would be expected to have a more continuous range than it has after the early Eifelian since it is not recorded again until the Givetian/Frasnian in Bolivia (Issacson, 1977a; Racheboeuf *et al.,* 1993). In the Parnaíba Basin, *Tropidoleptus* also appears in the Eifelian and in common with Bolivia is not observed again until the Givetian/Frasnian (Melo, 1988). While this could be coincidental and/or a collecting bias, goniatites have a similarly sporadic stratigraphic distribution in Bolivia, although most records are from the Mid/Late Devonian (Babin *et al*., 1991; Racheboeuf *et al*., 1993; Becker, pers. comm., 2005). Furthermore, conodonts are only currently known from the Late Devonian of the Amazonas Basin (Hünicken *et al*., 1988).

The stratigraphic distribution of these groups coupled with mainly endemic chitinozoa (this study) throughout the Mid-Late Devonian does not necessarily support a complete Mid-Devonian breakdown of the Malvinokaffric Realm, the evidence for which is based largely on the appearance of only two extra-Malvinokaffric brachiopod genera. Instead, the restricted occurrences of the aforementioned groups may represent short-lived incursions from lower latitudes coincident perhaps with marine transgressions. Relating the palynology and sedimentology of these events to Bermejo could be used to test this hypothesis in the future.

The recognition of only three major Mid-Late Devonian transgressive events in Bolivia suggests that this interval on the Euramerica sea-level curve has limited application in the Malvinokaffric Realm. However, this could be an artefact of the poorer biostratigraphic control and lack of detailed sedimentology in Bolivia making identification and correlation of any smaller scale sea-level cyclicity difficult.

CHAPTER 8 - CONCLUSIONS

1. This study is the first in Bolivia to undertake a detailed analysis of an unthrusted surface section (Bermejo) and compare the data obtained to a regional subsurface dataset. The major achievement of this work has been establishing the foundations for a stable palynology-based stratigraphy by validating the cuttings-based Mid-Late Devonian biostratigraphic framework developed in the subsurface of central/southern Bolivia and northern Argentina by the BG Group.

2. Cosmopolitan spore taxa have been used to underpin the Devonian chronostratigraphy herein through the Huamampampa-Iquiri Formation interval (Emsian-Frasnian). The chitinozoan *Alpenachitina eisenacki*, which has a Euramerican-calibrated early Eifelian inception, is important in the Los Monos Formation. An assumption is made that these cosmopolitan taxa have similar stratigraphic ranges globally; consequently the inception of *A. eisenacki* provides an early Eifelian age constraint for the *E. sommeri* Epibole in the basal Los Monos Formation. Therefore the underlying Huamampampa Formation is pre-early Eifelian in age.

3. The *E. sommeri* Epibole is a distinctive, short-lived pulse in abundance of the acritarch *Evittia sommeri* and is found in the basal Los Monos Formation. *E. sommeri* is restricted to the Eifelian as demonstrated herein and is also present at Campo Redondo, Cha-Kjeri and in the basal Pimenteira Formation, NE Brazil, associated with the same palynological assemblage.

4. Attempts to find the *E. sommeri* Epibole in the early Eifelian of Euramerica and Siberia were unsuccessful, suggesting that it is probably endemic to the Malvinokaffric Realm. A high degree of endemism is also demonstrated by the chitinozoa throughout the Devonian in Bolivia, particularly the Eifelian fauna, which is completely dissimilar to a coeval chitinozoan assemblage collected in Spain (Euramerica).

5. Palaeoenvironmentally, deposition at Bermejo is interpreted as having taken place in a stable shallow marine environment consistent with the overall palaeogeographic reconstructions of Bolivia as an epicontinental seaway for much of the Devonian. Deposition of the Huamampampa Formation occurred in a nearshore environment. This was abruptly terminated by the deposition of the Los Monos Formation in a deeper, more distal shelf environment followed by a regression into a more proximal environment below storm wave base in the upper Los Monos/Iquiri Formations. The palynologically defined Bermejo beds

(Givetian) represent the period of most proximal deposition during the Los Monos/Iquiri Formation interval since it is dominated by abundant spores and large phytoclasts suggesting increased terrestrial input.

6. Superimposed on this broad scale trend outlined in (**5**) at Bermejo are three 3rd order marine transgressions. The basal Los Monos Formation transgressions (early Eifelian) is particularly important since it contains the *E. sommeri* Epibole.

7. In terms of hydrocarbon source rocks, the shales deposited during the mid-late Givetian and early Frasnian transgressions in the Iquiri Formation are interesting since they have overall higher TOCs (>1%) and more abundant AOM relative to the basal Los Monos Formation, thus constituting potential petroleum source rocks.

8. Geographically, the early Eifelian transgression is detectable in the Parnaíba Basin, NE Brazil and the Frasnian event is manifested by part of the condensed Barreirinha Formation shales in the Amazonas Basin in northern Brazil.

9. High resolution biostratigraphic data are currently insufficient to precisely identify the Givetian flooding event outside of Bolivia, although its presence is probable in the Paraná Basin, SE Brazil.

10. Euramerican candidates for the flooding events identified in Bolivia are the Choteč Event (basal Los Monos Formation transgression), the Taghanic Event (Givetian transgression) and the transgression at the *transistans*/*puncata* Zone boundary (Frasnian transgression) referred to as Rhinestreet in New York State, although the assignment to the latter two events is somewhat tenuous at present.

11. The absence of a major flooding event around the Eifelian/Givetian boundary (Kačák Event) in Bolivia and South America generally is notable.

12. The Kačák Event has been implicated in the breakdown of the Malvinokaffric Realm based on the appearances of a supposed *Tornoceras* goniatite (*T. bolivianum*) in Bolivia and the brachiopods *Tropidoleptus* and *Rhipidothyris* in the Mid-Late Devonian of South America and South Africa. All three genera are cosmopolitan at lower palaeolatitudes, i.e. extra-Malvinokaffric Realm. The stratigraphic distribution of these brachiopods, *T. bolivianum* and other Bolivian goniatites is discontinuous and sporadic during the Mid-Late Devonian in the

Malvinokaffric Realm while other major marine groups present in Euramerica remain rare/absent. Consequently, the available evidence does not support a full breakdown of the Malvinokaffric Realm in relation to the Kačák Event and instead, the appearance of these cosmopolitan taxa may be related to short-lived incursions from lower palaeolatitudes associated with marine transgressions.

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