**The origins of major sessile cirripede groups; a revision of Cretaceous Brachylepadomorpha and Verrucomorpha**

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The taxonomy of Cretaceous cirripedes referred to the sessile orders Brachylepadomorpha and Verrucomorpha is revised. New taxa include the brachylepadid genera *Crithmumlepas* (type species *C. hoensis* sp. nov., *C. aycliffensis* sp. nov.) and *Calvatilepas* (type species *C. recurvus* sp. nov.). The family Pycnolepadidae nov. is established (constituent genera *Pycnolepas, Faxelepas*) and *Pycnolepas batchelorum* sp. nov. is described; a new eoverrucid species, *E. barringtonensis* sp. nov. is erected. Cladistic analysis of 48 characters of 18 operational taxonomic units, including 16 in-group sessile taxa yielded a consensus tree showing the strongly supported monophyly of Brachylepadomorpha+Verrucomorpha+Balanomorpha. It is recommended that the Order Brachylepadomorpha is abandoned, and its constituent families are identified as, respectively, stem group Verrucomorpha (Pycnolepadidae) and stem group Balanomorpha (Brachylepadidae). The sister group relationship of Verrucomorpha and Balanomorpha, identified from many molecular studies, is confirmed from shell morphological data. The Neolepadoidea are shown to closely parallel the sessile adaptations of verrucomorphs and balanomorphs. The fossil record of key segments of cirripede evolution is demonstrated to be remarkably, and surprisingly, complete.

Keywords: Cretaceous; thoracican cirripedes; sessile; phylogeny

**Introduction**

The evolutionary origins of the two major groups of sessile barnacles, the Balanomorpha, which dominate Cainozoic and present day shallow marine habitats, and the dominantly deeper water Verrucomorpha, have long been a source of controversy for zoologists and palaeontologists. In his monographic studies, Charles Darwin (1851a, b, 1854, 1855) had access to only a very limited suite of fossils material, but subsequent discoveries have considerably improved our knowledge of fossil cirripedes.

Fossil evidence for the ancestry of the dominantly Cainozoic balanomorph cirripede was entirely lacking, until Woodward (1901) described an articulated specimen of *Brachylepas* from the Campanian chalk of Norwich, UK. Its lack of a peduncle, possession of low, hemiconical rostrum and carina and the presence of whorls of imbricating plates surrounding the capitulum, bore a striking resemblance to the extant primitive balanomorph *Catomerus polymerus* (Darwin, 1854); (Withers, 1912a, 1935). Newman (1987) identified numerous homologies between the wall structure of *Brachylepas* and that of basal balanomorphs. Newman (1987) and Anderson (1983) placed brachylepadids as close to the origin of both balanomorphs and verrucomorphs.

Gale and Sørensen (2014) described new material of brachylepadids from the Cretaceous of southern Sweden, and described the genera *Epibrachylepas* Gale, 2014 and *Parabrachylepas* Gale, 2014 as possessing a pair of plates between the carina and rostrum which they called marginals. They identified the marginals as homologous with the lateral wall plates of balanomorphs and argued that the balanomorph shell wall had evolved as a de novo structure from enlarged imbricating plates, (which formed marginals, carinomarginals, rostromarginals) and that homologies with lateral plates (carinolatus, rostrolatus) of pedunculate barnacles were incorrect. Their cladistic analysis (Gale and Sørensen 2014, fig. 10) showed a “ladder” of successive brachylepadid taxa leading up to the Balanomorpha, and *Epibrachylepas* as a basal balanomorph. Although these arguments have met with some acceptance (Chan et al*.,* 2021), not all workers are convinced that the new homologies are correct (e. g. Collareta et al., 2022a, b) and retain the older nomenclatorial scheme for wall plates.

In the verrucomorphs, Darwin (1854, p. 495) made the prescient observation that the moveable scuta and terga of verrucids bear a remarkable resemblance to Cretaceous species which nowadays would be assigned to the brachylepadomorphs *Fallaxlepas fallax* (Darwin, 1851a) and *Faxelepas bruennichi* (Withers, 1914a). Subsequently, Withers (1935) described *Eoverruca hewitti* from the Santonian of Suffolk, UK as a primitive verrucid, which has morphologically distinct fixed and moveable scuta and terga but possessed whorls of imbricating plates. He noted the strong similarities between the plates of *Eoverruca* and the brachylepadomorph *Pycnolepas*, to which genus he had originally assigned the carina and rostrum (Withers, 1935, p. 338).

Gale (2014b) redescribed *Eoverruca* on the basis of extensive new material and undertook a cladistic analysis of verrucomorphs to in order to determine the likely relationships between genera and with brachylepadomorphs. He used 3 brachylepadid taxa as outgroups, and the resultant tree (Gale 2014b, fig. 13) shows *Eoverruca* as basal to the verrucomorphs, and the brachylepadids *Pycnolepas* and *Faxelepas* as sister taxa to the group. In the same study, Gale (2014) demonstrated that the extant hydrothermal vent-dwelling *Neoverruca* Newman, 1989 represented a distantly related group morphologically convergent with verrucids, as suggested by previous papers (Glenner et al., 1995; Pérez-Losada et al., 2008) and subsequently confirmed by molecular studies (Kim et al*.,* 2021). Likewise, the Cretaceous genus *Proverruca* Withers, 1914b, represented another instance of parallel asymmetrical evolution with the verrucomorphs (Gale, 2014b).

Gale (2019, p.13) illustrated and discussed the highly distinctive morphology of verrucomorph terga and scuta, which, together with many brachylepadomorphs, possess a terraced structure and noded apicobasal ridges.

Although the conclusions of Gale (2014b) on verrucomorph origins, and those of Gale and Sørensen (2014) on balanomorphs are reflected in a new classification of thoracican cirripedes (Chan et al*.,* 2021), several recent papers have cast doubt on the validity of the arguments. Firstly, Koci et al*.* (2018) described a putative balanomorph from the Cenomanian of the Czech Republic (*Archaeochionelasmus* Koci, Newman and Buckeridge), which predated the then known occurrences of brachylepadids potentially ancestral to balanomorphs. Koci et al*.* (2018) also argued that the oldest balanomorph, *Pachydiadema cretacea* Withers, 1935, redescribed by Gale and Sørensen (2014) was in fact an unrelated, pedunculate barnacle with affinities to the calanticid *Scillaelepas*. Subsequently, Gale and Skelton (2019) demonstrated that the unique specimen of *Archaeochionelasmus* was actually a fragment of a rudist bivalve, negating the arguments of Koci et al. (2018) on the possible implications of the specimen for the early evolution of balanomorphs.

Secondly, Gan et al. (2022) undertook a study of the mitogenomes of diverse extant cirripedes, analysis of which placed verrucomorphs as basal to all calcareous-shelled barnacles, with an inferred origin in the Triassic (Gan et al*.,* 2022 fig. 4). They suggested that verrucomorphs descended from a 6-plated archaeolepadomorph rather than a brachylepadomorph.

Recent collecting has discovered a wide range of new material of both brachylepadomorphs, and the present paper revises the taxonomy of all Cretaceous taxa assigned to the Brachylepadomorpha and Verrucomorpha, as the basis for a detailed cladistic analysis of likely relationships between these groups.

Figure 1

**Comparative morphology of thoracican cirripedes**

**Overall form**

Plesiomorpically, the body of thoracican cirripedes is divided into a flexible stalk, called a peduncle which commonly bears rows of peduncular plates, and a capitulum (Fig. 1B) which houses the arthropodal body (soma). The capitulum is made up of a variable number of plates composed either of calcite or calcium phosphate. Plates present in all thoracicans are paired scuta and terga, a dorsal carina, and in all taxa except basal forms, a ventral rostrum (Fig. 1A-D). Cirri for feeding are extruded along the occludent margin, positioned ventrally between the scuta and terga. Other capitular plates (latera) surround the base of the capitulum and may include an upper latus (overlying the articulation between the scutum and tergum), paired carinolatera, rostrolatera, inframedian latera (Fig. 1B), and (unpaired) subrostra and subcarinae. Smaller, un-named latera are present in some groups. The upper latera are present in most pedunculate and basal sessile cirripedes (Fig. 2E-I, M-T, Fig. 3A, B, D-I) even though other lateral plates may be absent (Fig. 2E, F, M-Q, S, T).

**Peduncular/imbricating plates**

In many pedunculate thoracicans, the peduncle is armoured by alternating rows of vertically striated plates (Fig. 3B, C, J-N) which in many Mesozoic taxa possess an inwardly directed shelf (Fig. 3J-L, T-V). In sessile thoracicans, the peduncle is absent, and in some basal taxa alternating rows of imbricating plates, homologous with the peduncular plates, form a skirt around the capitulum (Fig. 1A, Fig.2C-F, M-Q, T, U). The brachylepadids plates develop a complex peg and socket articulation between imbricating plates (Fig. 3O, Q, R, S, X). The articulations between imbricating plates in catophragmid balanomorphs (Ross and Newman, 2001) are simple overlap (Fig. 3P).

**Construction of the shell wall**

In brachylepadids and balanomorphans, the capitulum maintains bilateral symmetry (Fig. 1A; Fig. 2C-F, M, N), but in verrucomorphs the shell develops asymmetrically and is made up of a fixed tergum, a fixed scutum, the carina and the rostrum (Fig. 1C, D; Fig. 2J-L). The moveable scutum and tergum form an opercular lid (Fig. 1C). Imbricating plates are present in the basal verrucomorph *Eoverruca* (Fig. 2U). The progressive development of asymmetry of the terga and scuta is shown in Fig. 4. In *Pycnolepas,* the paired scuta and terga are perfectly symmetrical (Fig. 4A-D); in *Eoverruca* (E-H) incipient development of fixed valves is shown by the broadening of the apicobasal ridges (Fig. 4F, H). In *Gibbosaverruca* (Fig. 4J, L), the ridges on the fixed terga and scuta form broad buttresses, and the moveable valves are little changed from the ancestral condition (Fig. 4I, K). In the highly modified *Verruca* (Fig. 4M-P) the fixed scuta and terga (Fig. 4N, P) have developed elongated wing-like extensions (occludent wings) which articulate with the occludent margins of the moveable valves. Again, there is little modification of the moveable valves (Fig. 4M, O).

In derived brachylepadida and balanomorphs, wall plates are present between the carina and rostrum. Although originally identified as homologous with lateral plates (Darwin 1854), Gale and Sørensen (2014) argued that these are in fact new structures called marginals, developed from modified peduncular plates. In the brachylepadids *Parabrachylepas* and *Epibrachylepas* (Fig. 2E, F) a single pair of marginal plates is present between the carina and rostrum, but in balanomorphs rostro- and carinomarginals may be present; these imbricate and articulate firmly to form the balanomorph shell wall (Fig. 1A; Fig. 2C, D).

Figures 2, 3 ,4

**Articulation between scuta and terga**

In most pedunculate cirripedes, the scutum slightly overlaps the scutal margin of the adjacent tergum with unspecialised articulation (Fig. 5A, B). In the brachylepadids, a concavity on the apical part of the scutum (tergal notch) articulates with a ridge on the occludent margin of the tergum (scutal auricle) and an upper latus inserts between the scutum and tergum (Fig. 5C-E, Fig. 6B, C, G, H). The upper latus articulates with the scutum and tergum (Fig. 5, surfaces x, y) and a narrow articular ridge is present between this surface and the scutal notch. In balanomorphs (Fig. 5F, fig. 6D, E, O-Q) the upper latus is lost, and the articulation between the tergum and scutum is deeply interpenetrant; the articular ridge on the scutum fits into an articular furrow on the tergum, the scutal auricle on the tergum fits into the tergal notch on the scutum and the scutal wall of the tergum articulates with the articular furrow on the scutum. At the same time, the scutum and tergum of each pair become angled to each other at approximately 45o.

Figure 5

In the verrucomorphs, the tergal auricle and scutal notch are also present, and the articulation between the moveable valves is characterised by the development of interpenetrant ridges and grooves (Fig. 4E, G, I, K). The articulation between the fixed valves is complex in derived verrucids, and in addition the scutal auricle/tergal notch is set within a deeper concavity which accommodates a process on the scutum (Gale, 2014, p. 11).

Changes in shape of the scuta and terga also take place in the transitions to verrucomorph and balanomorph morphologies. In verrucomorphs, the moveable terga retain a plesiomorphic rhombic outline (Fig. 4E, I, M) and the moveable scuta a triangular form (Fig. 4G, K, O). The fixed valves are highly modified (see above; Fig. 4J, N, L, P). Changes also occur in the scuta and terga of derived brachylepadids; the scuta become broader (Fig. 6F, G), and the terga kite-shaped (Fig. 6M, N).

Figure 6

**Depressor muscles**

In pedunculate cirripedes, unspecialised depressor muscles are inserted on the basal margins of the scuta and terga (Anderson, 1983; Gale and Sørensen, 2014 fig. 12a). These are absent in verrucomorphs, in which the opercular lid is closed by the scutal adductor alone. The situation on balanomorphs is very different, because three discrete depressor muscles are present, the tergal depressor (tergum), the rostroscutal and lateral scutal depressors (scutum). In the derived brachylepadid *Epibrachylepas*, insertions for all three muscles are visible (Fig.6G, N), although the tergal depressor insertion is not as sharply defined as in balanomorph taxa (Fig. 6P).

**Carinae and rostra**

The unpaired, symmetrical carina (dorsal) and rostrum (ventral) are present in almost all calcite shelled cirripedes. Typically (Fig. 2G-I, R; Fig. 7E, F) the rostrum is approximately half the height of the carina, or even very considerably smaller (Scalpellidae). In brachylepadids of the genera *Pycnolepas* and *Faxelepas* (Fig. 7A-D) the carina and rostrum are similar in shape, but in the basal verrucomorph *Eoverruca* (Fig. 7O-R) the rostrum is shorter and broader and both are slightly asymmetrical. In verrucids, the rostra and carinae are concavo-convex, asymmetrical and differ considerably in shape (Fig. 7S-V). In the brachylepadid genus *Brachylepas*, rostra and carinae are low, hemiconical and of similar shape (Fig. 7G-J) and they are also similar in the catophragmid balanomorph *Catophragmus* (Fig. 7K-N).

Figure 7

**Sculpture, shell structure**

Some brachylepadids, eoverrucids and all moveable verrucid valves have a distinctive construction, called terracing, which comprises evenly spaced, imbricating growth increments which protrude slightly on the occludent margins of scuta and terga (Gale, 2019; Fig. 4A-L). In derived verrucids, terracing is only retained on the moveable terga and scuta (Fig. 7M, O). Terracing is present on some *Brachylepas* species (e. g. *B. guascoi*, Fig. 6K) but lost on others and is not present in balanomorphs (Fig. 7K-N). Additionally, *Pedupycnolepas, Pycnolepas, Eoverruca* and Verrucidae possess noded, basally broadening apicobasal ridges on both scuta and terga (Fig. 4A-H) only present on moveable valves of verrucids (Fig. 7I, K, M, O). There are close similarities in plate structure and morphology between the pollicipedid *Etcheslepas fragilis* (Withers, 1928) and the brachylepadid *Pycnolepas scalaris* Withers, 1914a, illustrated in Fig. 8. Both display terracing on the valves, better developed in *P. scalaris*, and noded apicobasal ridges on terga and scuta, broader in *E. fragilis*. Carinae and rostra (Fig. 8K-Q) have similar shapes and sculpture.

Figure 8

**Phylogenetic analysis, evolution and classification**

Previous morphological studies of the relationships of brachylepadomorphs with verrucomorphs (Gale, 2014b) and balanomorphs (Gale and Sørensen, 2014) have supported the traditional view (e. g. Withers, 1912a, 1935; Woodward, 1901) that Cretaceous taxa such as *Pycnolepas* and *Brachylepas* are basal to, respectively, verrucomorphs and balanomorphs. A consensus tree of verrucomorph relationships (Gale, 2014b, fig. 13), based on cladistic analysis of 16 operational taxonomic units (OTUs) and 36 characters, showed *Pedupycnolepas, Faxelepas* and *Pycnolepas* species forming a paraphyletic nested ladder, basal to the Verrucomorpha, and the Cretaceous *Eoverruca* as sister taxon to all Verrucidae. A parallel study of basal balanomorph relationships (Gale and Sørensen, 2014 figs 10, 11) analysed 40 characters of 10 brachylepadid and balanomorph taxa and demonstrated that selected brachylepadids (successively, species of *Brachylepas*, *Parabrachylepas* and *Epibrachylepas*) formed a paraphyletic stem group to the Balanomorpha. In this tree, *Parabrachylepas* and *Epibrachylepas* were identified as basal balanomorphs.

Figure 10

Chan et al. (2021), in a revised classification of the thoracican cirripedes (Fig. 10C), maintained a separate Order Brachylepadomorpha, including a single family, the Brachylepadidae, which was described as (p. 44) “………paraphyletic, and includes species that form a stem group to both the Verrucomorpha and Balanomorpha.” Molecular analyses of thoracican relationships, utilising a suite of nuclear genes, consistently demonstrate the sister-group relationship between verrucomorphs and balanomorphs (e. g. Herrera et al., 2015; Lin et al., 2015; Linse et al*.,* 2013; Pérez-Losada et al., 2008, 2012, 2014). A single recent study (Gan et al*.,* 2022; Fig. 10B herein), using mitogenomes, reached a very different conclusion and placed verrucids as basal to all other calcite-shelled cirripedes and that they had evolved in the Triassic. They argued that verrucomorphs evolved from a 6-plated archaeolepadomorph.

No brachylepadomorph has survived to the present day (Fig. 9); recent molecular studies demonstrate that the living *Neobrachylepas* Newman and Yamaguchi, 1995, parallels brachylepadids morphologically, but belongs to the Order Neolepadoidea (Kim et al*.,* 2021). Likewise, extant taxa described as verrucomorphs (*Neoverruca* Newman, 1989 and *Imbricaverruca* Newman, 2000) are neolepadoids convergent with verrucomorphs (see below). Therefore, the deeper relationships of verrucomorphs and balanomorphs can only be understood from the study of fossil material.

In the present study, the relationships of brachylepadomorph, verrucomorph and balanomorph taxa were investigated using a list of 48 morphological characters (Tables 1, 2) and 18 OTUs, of which 7 are extant taxa (Fig. 10A). *Capitulum* Gray, 1825 and *Polliceps* Leach, 1870 were used as an outgroup for the 16 in-group OTUs. One of the 48 characters was treated as continuous, using TNT (Goloboff and Catalano, 2016), all other characters were treated as unordered. Using the implicit enumeration tree search, both equal weights (EW) and implied weights analyses were implemented. Both analyses produced very similar single most parsimonious trees (MPT), with the only difference being the relationships between *Verruca*, *Priscoverruca*, and *Rostratoverruca*. This was to be expected because the EW MPT demonstrated very limited homoplasy, with an ensemble consistency index and retention index of 0.805 and 0.909, respectively. Herein, the 77 steps equal weights (EW) MPT and bootstrap analysis results are discussed. The data and scripts underpinning this study are openly available in the University of Southampton’s institutional repository, ePrints|Soton: <https://doi.org/10.5258/SOTON/D2700>.

The (EW) MPT and accompanying bootstrap resampled consensus tree demonstrate all three orders form a well-supported (100% bootstrap) monophyletic group, with an unresolved basal trichotomy stepwise after *Pedupycnolepas*, (Pycnolepadidae, Verrucomorpha (41%), Brachylepadidae+Balanomorpha (33%)). Thus, taxa generally identified as brachylepadomorphs fall either as basal to the Balanomorpha (paraphyletic Brachylepadidae) or Verrucomorpha (paraphyletic Pycnolepadidae).

Similarities in valve morphology and sculpture between the Tithonian (Late Jurassic) species *Etcheslepas fragilis* (Withers, 1928) and the Cenomanian (Cretaceous) *Pycnolepas scalaris* (Fig. 8) can be taken as evidence for the ancestry of the sessile clade of Balanomorpha+Verrucomorpha. Important evolutionary changes in this lineage include the loss of the peduncle and all lateral plates except the upper latus. Both of these changes can be achieved simply by paedomorphosis – accelerated development at an 8-plated stage before the peduncle has elongated.

In the verrucomorph clade, *Faxelepas* and *Eoverruca* are identified as successively nested sister taxa to crown group Verrucidae (Fig. 10A). *Faxelepas* demonstrates irregularly developed asymmetry (Gale, 2014b), and *Eoverruca* loss of the upper latus, strong morphological distinction between fixed and moveable scuta and terga, whilst plesiomorphically retaining imbricating plates (Fig. 11D). In the crown group Verrucidae, these are lost, the apicobasal ridges broaden to form buttresses and the carina and rostrum articulate (Fig. 11E). In basal verrucids (*Altiverruca, Gibbosaverruca*) the shell has an erect form and the individual plates are little modified. In derived verrucids (*Priscoverruca, Verruca*) the profile of the shell is low, plate articulations and morphologies are strongly modified and the moveable tergum and scutum form a horizontal opercular lid (Young 1998). The phylogeny of Verrucidae was analysed in detail by Gale (2014b). The fossil record of verrucomorph evolution is remarkably complete, with successive morphological changes represented by Cretaceous taxa. *Eoverruca*, which is morphologically intermediate between pycnolepadids and verrucids, forms a firm link between the two groups.

It is also interesting to observe (Fig. 10A) that the most derived verrucid genera, *Verruca* and *Priscoverruca* (Gale, 2014b) were present in the late Cretaceous upper Campanian and Maastrichtian stages (Fig. 9). Therefore, most of the evolutionary diversification of the family took place between the middle Albian (107 Ma, appearance of *Eoverruca*) and the upper Campanian (80Ma, appearance of *Priscoverruca*).

The nested successive sister taxa relationship observed in *Brachylepas* spp. is weakly supported (38%), but *Brachylepas* is found to be more closely associated with *Fallaxlepas*, in a polytomy with *Parabrachylepas*, *Epibrachylepas*+Balanomorpha (92% bootstrap) (Fig. 10A). Features uniting brachylepadids and balanomorphs are the low, hemiconical carina and rostrum and the presence of an operculum formed by the scuta and terga. The closer relationship of *Brachylepas* and *Epibrachylepas* (Fig. 11F, G) with balanomorphs is accounted for by the presence of marginal plates, the morphology of scuta and terga, and the interpenetrant articulation between scuta and terga.

The single MPT (Fig. 10A) demonstrates good stratigraphic congruence with 0.6797159 Gap Excess Ratio (GER) (Wills 1999) . For the purpose of the cladistic analysis, two more recent outgroup OTUs were used, first appearing in the Upper Cretaceous, thus the outgroup which shares a most recent common ancestor with the ingroup in the Upper Jurassic decrease the GER. With the outgroup removed, the GER is 0.757269. 1000 bootstrap replicas were employed.

The oldest balanomorph is *Pachydiadema cretacea* Withers, 1935 from the upper lower Campanian of Sweden redescribed in detail by Gale and Sørensen (2014), which possesses an 8-plated wall, incorporating rostro- and carinomarginals, absent in brachylepadids. There is thus a morphological gap, unrepresented by fossils, between the most derived brachylepadid (*Epibrachylepas*) and forms which can be referred to balanomorph groups. The purported balanomorph *Archaeochionelasmus nekvasilovae* Koci, Newman and Buckeridge, 2017, from the upper Cenomanian of the Czech Republic, is a bivalve (Gale and Skelton, 2018). The balanomorphs presumably evolved in the pre-Campanian late Cretaceous but there is no known fossil record of these.

More derived balanomorphs differ from *Pachydiadema* most importantly in the consistent overlap pattern of the wall plates in which the marginals overlap the carinomarginals and the carinomarginals overlap the carina (Fig. 11H; Gale and Sørensen, 2014 fig. 4). Taxa with this arrangement only appear in the Palaeocene.

The Pycnolepadidae essentially form the stem group of the Verrucomorpha, and the order is therefore expanded to include the pycnolepadid genera *Pycnolepas* and *Faxelepas*. Likewise, the Brachylepadidae form a basal stem group to the Balanomorpha and the Order Brachylepadomorpha is abandoned. Although the families Pycnolepadidae and Brachylepadidae are technically paraphyletic, they are useful taxonomic groupings and are therefore retained. The conclusions of Gan et al., 2022, that verrucomorphs are basal Thoracicalcareans, based on analysis of mitogenomes, is not supported by any other morphological or nuclear genetic data.

**Convergence between groups of sessile cirripedes**

New extant sessile cirripedes associated with hydrothermal vents in the Mariana Trench and Lau Back-Arc Basin in the Pacific were assigned to the Verrucomorpha (*Neoverruca, Imbricaverruca*) and Brachylepadomorpha (*Neobrachylepas*) and were identified, respectively, as the most primitive verrucomorph (*Neoverruca* – Newman, in Newman and Hessler, 1989) and a surviving brachylepadomorph (*Neobrachylepas* – Newman and Yamaguchi, 1995). *Neoverruca brachylepadiformis* Newman, 1989 (Fig. 11J), which shows slight asymmetry between the terga and scuta was identified as an intermediate form between brachylepadids and the Cretaceous verrucomorph *Eoverruca. Imbricaverruca yamaguchii* Newman, 2000 (Fig. 11K) has a primary wall composed of fixed tergum, scutum, carina and rostrum, surrounded by imbricating plates, an opercular lid formed by the moveable scutum and tergum and an upper latus. It certainly resembles a verrucid in the development of fixed and moveable valves.

Figure 11

However, the molecular phylogeny of Pérez-Losada et al. (2008, fig. 1) placed *Neoverruca* as sister group to the Scalpellomorpha, far removed from verrucids. The molecular tree of Lin et al. (2015, fig. 3) subsequently identified *Neoverruca* as sister taxon to the pedunculate neolepadids (also vent-dwellers) *Ashinkailepas, Neolepas* and *Vulcanolepas*, again closely related to scalpellomorphs. Herrera et al*.* (2014 fig. 2) undertook a detailed molecular study which placed all the known species of neoverrucid, neobrachylepadid and neolepadid in a separate clade most closely related to the Scalpellomorpha. Kim et al*.* (2022, fig. 2) undertook further molecular study which also placed all the hydrothermal vent taxa in a single clade and identified *Neobrachylepas* as basal to a neoverrucid clade (Fig. 11K). In the classification of Chan et al. (2021), the three families Neoverricidae, Neolepadidae and Neobrachylepadidae are placed in the Order Neolepadoidea.

In comparison, there has been little discussion of the morphological evolution of this group and its convergence with brachylepadids and verrucids. Gale (2014b) studied material of *Neoverruca brachylepadiformis* and noted that there were numerous differences in the morphology of the valves of this taxon and the *Pycnolepas*+Verrucomorpha clade, in valve sculpture, shape, articulation of the tergum and scutum and peduncular plates. Additionally, the apical interior of the scutum is highly distinctive in *Neoverruca*, as it carries a bifid, basally diverging structure (Fig. 11J). A similar structure is seen in the scuta of *Imbricaverruca* and *Neobrachylepas* (Fig. 11K, L). Although I have not had access to disarticulated material of these genera, it is possible to discuss similarities and differences between brachylepadids, verrucids and the convergent Neolepadoidea.

The neoverrucid clade (Fig. 11J, K) displays progressive development of asymmetry, slightly developed in *N. brachylepadiformis*, but with evolution of discrete fixed and moveable scuta and terga, the latter forming an opercular lid in *Imbricaverruca*. Differences from verrucomorphs include presence of the upper latus, the absence of any articulation between the carina and rostrum, the retention of imbricating plates and the processes on the apical interior of the scutum. The asymmetrical form is paralleled in the unrelated Cretaceous Proverrucidae, which also develops fixed and moveable terga and scuta, has an articulation between the rostrum and carina, but retains lateral plates from a scalpellomorph ancestor (Gale, 2014b). Thus, three known lineages of Thoracicalcarea independently evolved a 6-plated asymmetrical shell with incorporation of fixed scuta and terga into the primary wall, and the moveable scuta and terga formed an opercular lid.

*Neobrachylepas* is strikingly similar in overall morphology with Cretaceous brachylepadids such as *Brachylepas naissanti* in the low profile, low hemiconical carina and rostrum, upper latera and the fringe of imbricating plates (compare Fig. 11F with 11L). However, it differs importantly in the morphology of the scuta and terga. Whereas brachylepadids have a strong articulation between the terga and scuta (Fig. 6, tergal notch, scutal auricle) in *Neobrachylepas* one valve simply rests on the other as in all neolepadoids. Also, the bifid apical interior of the scutum is similar to that developed in neoverrucids. It has to be noted that without the molecular evidence of relationships, these differences are small and one can scarcely fault the original assignation of *Neobrachylepas* to the Brachylepadidae (Newman and Yamaguchi 1995). It can also be noted that *Plesiobrachylepas* Carriol, in Carriol et al., 2016 from the Eocene of Denmark, is a fossil neobrachylepadid, on the basis of similarities of the terga and scuta with those of *Neobrachylepas*. This places the radiation of the Neolepadoidea as older than 50Ma.

**Institutional abbreviations**

**BAS**, British Antarctic Survey, Cambridge, UK; **LMSU**, Department of Palaeontology, Geology Faculty, Lomonosov Moscow State University, Moscow, Russia; **MIJML**, Museum of Jurassic Marine Life, Kimmeridge, Dorset, UK; **MNSB**, Museum of Natural Sciences, Brussels, Belgium; **MSU**, Mississippi State University, Starkville, Mississippi, USA; **NCM**, Norwich Castle Museum, Norwich, Norfolk, UK; **NHMM**, Natural History Museum, Maastricht, Netherlands; **NHMUK**, Natural History Museum, London, UK; **PMC**, Catania University, Catania, Sicily, Italy; **SMNH**, Swedish Museum of Natural History, Stockholm, Sweden.

**Systematic palaeontology (by ASG)**

Order **Verrucomorpha** Pilsbry, 1916

**Amended diagnosis**. Capitulum comprises 6-8 plates, including paired scuta, terga, +-upper latera, carina, rostrum; at least some valves (moveable valves only in Verrucidae) show regularly terraced sculpture and noded apicobasal ridge.

**Included families.** Pycnolepadidae nov., Verrucidae, Darwin, 1854; Eoverrucidae, Gale, 2020a.

**Remarks**. Basal Verrucomorpha (Pycnolepadidae, some Eoverrucidae) are bilaterally symmetrical, whereas all Verrucidae and some Eoverrucidae are strongly asymmetrical, with fixed terga and fixed scuta, plus carina and rostrum, constructing the shell wall and moveable scuta and terga forming an opercular lid. Upper latus retained only in Pycnolepadidae.

Family **Pycnolepadidae** nov.

**Diagnosis**. Capitulum symmetrical, laterally compressed, upright, comprising paired scuta, terga, upper latera, carina, rostrum. Exterior of valves with regular, terraced sculpture. Noded apicobasal ridges on scuta and terga.

**Included genera**. *Pycnolepas* Withers, 1914a; *Faxelepas* Gale, 2014b; *Pedupycnolepas* Gale, 2014b.

**Remarks.** Although paraphyletic (Fig. 10A) and partially representing the stem group of the Verrucomorpha, the pycnolepadids form a distinctive group, characterised by the triangular, ventrally inclined scutum and tall upper latus. They appeared in the Hauterivian and survived into the late Pliocene or early Pleistocene in the Indian Ocean (Gale, 2020c).

Figure 12

Genus***Pedupycnolepas*** Gale, 2014b

**Diagnosis.** Short peduncle present; tergum symmetrically rhombic, not inclined ventrally; scutal region of tergum with radial sculpture.

**Remarks.** In addition to the presence of a peduncle, known only in the type species, the genus also differs from *Pycnolepas* in the shape and sculpture of the tergum, which is symmetrical, and bears radial sculpture on the scutal surface.

**Type species.** *Pycnolepas articulata* Collins, 1980.

**Included species**. In addition to the type species, *P. pulcher* Gale, 2019 and *P. lamellatus* sp. nov.

***Pedupycnolepas articulata*** (Collins, 1980)

(Fig. 2A, B)

1980 *Pycnolepas articulata* Collins; p. 22 figs 2, 3.

2014b *Pedupycnolepas articulata* (Collins); Gale: 23, fig. 1A, B, D.

2019 *Pedupycnolepas articulata* (Collins); Gale: 11 fig. 11A.

**Diagnosis**. *Pedupycnolepas* in which the relatively smooth carina bears weak apicobasal ridges, and the terga display evenly spaced ridges parallel with the lower carinal margin. Apicobasal ridges on terga sharp, narrow, weakly noded. Scutal surface of tergum with radial ridges.

**Type.** Group of 3 specimens, BAS 1657A, C, Fossil Bluff Formation, ?Lower Aptian, Alexander island, Antarctica.

**Remarks**. The possession of a short peduncle in *P. articulata* (Fig. 2B) approximately equivalent in height to the capitululm was demonstrated by Gale (2014b, fig. 1A, B, D, p. 23). *P. articulata* is distinguished from *P. pulcher* and *P. lamellatus* sp. nov. by the straight, narrow, weakly noded apicobasal ridge on the tergum and the relatively smooth carina, which bears weak apicobasal ridges (Fig. 2A). Additionally, the carinal surface of the terga of *P. articulata* possess regularly spaced ridges parallel with the lower carinal margin.

***Pedupycnolepas pulcher*** Gale, 2019

(Fig. 12E, F)

2019 *Pedupycnolepas pulcher* Gale: 11, figs 11B, F.

**Diagnosis**. Tergum with strongly noded apicobasal ridge; scutal surface bears fine nodes on individual terraces; rostrum low, equilaterally triangular, with regular flanges parallel with basal margin.

**Types.** The tergum figured by Gale (2019, fig. 11B) is holotype (NHMUK IC 1397); the rostrum figured by Gale (2019, fig. 11F) is paratype (NHMUK IC 1398). Lower Hauterivian, *Endemoceras amblygonium* ammonite Zone, Engelbostel, Hannover, Germany.

**Remarks**. *P. pulcher* is known only from a single tergum and a single rostrum. It is distinguished from its congenors by the raised, strongly noded apicobasal ridge on the tergum.

***Pedupycnolepas lamellatus*** sp. nov.

(Fig. 12A-D)

**Diagnosis**. *Pedupycnolepas* with sharply defined, imbricating terraces of equal size; sculpture of radial, elongated nodes which are prolonged basally to form a low apicobasal ridge separating rostral and tergal surfaces.

**Types.** The scutum figured here (Fig. 12A, B) is holotype (NHMUK PI In 64815). Two carinae (Fig. 12C, D) are paratypes (NHMUK PI In 64816, 64817). Basal West Melbury Formation, Cambridge Greensand Member, lower Cenomanian *Neostlingoceras carcitanense* ammonite subzone, Barrington, Cambridgeshire, UK.

**Material.** A scutum and 2 carinae, from the basal West Melbury Formation, Cambridge Greensand Member, lower Cenomanian *Neostlingoceras carcitanense* ammonite subzone Barrington, Cambridgeshire, UK.

**Derivation of name**. After the conspicuous, lamellate terracing on the exterior of the scutum.

**Description**. Scutum (Fig. 12A, B) kite-shaped, weakly inclined dorsally; lateral margin slightly convex, tergal margin concave, basal margin straight. External surface with evenly spaced, sharply demarcated co-marginal terraces which bear basally directed nodes, best developed on occludent surface; weakly defined apicobasal ridge comprises enlarged nodes. Interior of scutum with flat occludent platform, narrowing to basal margin; tergal notch weak, shallow. Scutal adductor scar large, rounded. Carinae (Fig. 12C, D) tall, weakly convex, bearing evenly spaced, noded transverse ridges conjoined by weak apicobasal ribs.

**Remarks.** *P. lamellatus* sp. nov. is referred to *Pedupycnolepas* on the striking similarity of terraced sculpture on the scutum with that on the tergum of *P. pulcher* (Fig. 12F). It differs from that species in its very weakly developed apicobasal ridge, comprising a column of basally directed nodes; in comparison, the apicobasal ridge in *P. pulcher* is elevated and sharply defined.

Genus ***Pycnolepas***Withers, 1914a

**Diagnosis**. Capitulum bilaterally symmetrical, peduncle absent; tergum inclined ventrally; interior of scutum bears narrow occludent surface.

**Type species.** *Pollicipes rigidus* J. de C. Sowerby, 1836.

**Included species.** *P. scalaris* Withers, 1914a*; P. industriosa* Jagt, 2007*; P. batchelorum* sp. nov.

**Remarks.** *Pycnolepas orientalis* Kolosváry, 1966, from the Upper Cretaceous of Azerbaijan is a nomen dubium (Jagt *et al.* 2007). *Pycnolepas landenica* Withers, 1953 from the Selandian of Belgium and *Pycnolepas ignabergensis* Carlsson, 1953, from the Campanian of Ignaberga, southern Sweden, are transferred to *Faxelepas*. *P. industriosa* Jagt, 2007, is based on a single rostrum from the Maastrichtian of Belgium. Additionally, *Pycnolepas tithonica* Withers, 1912b and *P. fimbriata* Withers, 1912b from the Berriasian of the Czech Republic have been transferred to the eolepadid genus *Eolepas* (Koci et al., 2014).

***Pycnolepas rigida***(J. de C. Sowerby, 1836)

(Fig. 13A-Q)

 1836 *Pollicipes rigidus* J. de C. Sowerby: 335, pl. 11 fig. 6.

 1851 *Pollicipes rigidus* J. de C. Sowerby; Darwin : 73, pl. 4 figs 7a-f.

 1855 *Pollicipes rigidus* J. de C. Sowerby ; Darwin : 638.

p.1914a *Pycnolepas rigida* (J. de C. Sowerby) ; Withers : 170, pl. 7 figs 16-19, pl. 8 figs 1-3

 only

p.1935 *Pycnolepas rigida* (J. de C. Sowerby); Withers: 352, pl. 46 figs 1-16, pl. 47 figs 1-5

 only.

 2007 *Pycnolepas rigida* (J. de C. Sowerby); Jagt et al.: 36.

 2014b *Pycnolepas rigida* (J. de C. Sowerby); Gale: 23, figs 4H, K-T.

**Diagnosis**. Large *Pycnolepas* lacking secondary ridges on the occludent surface of the tergum; rostrum low, triangular, bearing fine apicobasal ridges intersecting with transverse terracing.

Figure 13

**Type.** The scutum figured by J. de C. Sowerby, 1836, pl. 9 fig. 6 was selected as lectotype by Withers (1914). This probably came from the Albian Gault Clay at Folkestone, Kent. Whereabouts unknown.

**Material.** Withers (1935, p. 354) recorded 478 specimens in the NHMUK collection, which come from the Gault Clay Formation of Kent and Bedfordshire. The JSH Collins collection (NHMUK) includes more than 300 additional specimens.

**Remarks.** The species has been described in detail by Withers (1935, pp.352-359). It is important to note that the Cenomanian scuta and terga which he referred to this species (p. 355; pl. 47 fig. 6) actually belong to *P. scalaris* (see below). *P. rigida* differs from *P. scalaris* in the shape and sculpture of the rostrum, which is relatively low, evenly convex and bears fine apicobasal ribs and evenly spaced terracing (fig. 13K, L, Q), whereas the rostrum of P. scalaris (Fig. 14I, K-P) is taller, narrower and has 3 noded apicobasal ridges. *P. rigida* differs from *P. batchelorum* sp. nov. in the consistently greater size and absence of secondary ridges on the occludent surface of the tergum.

**Occurrence**. Middle and upper Albian Gault Clay of southern England (*A. intermedius* to *M.* *inflatum* ammonite zones); middle Albian clays (*L. lyelli* to *M. inflatum* zones) of Aube, France.

***Pycnolepas scalaris*** Withers, 1914a

(Fig. 14A-U)

p.1914a *Pycnolepas scalaris* Withers: 187, pl. 8 figs 7-10 only.

p.1935 *Pycnolepas*(?) *scalaris* Withers; Withers: 364, pl. 47 figs 16-18 only.

 2007 *Pycnolepas scalaris* Withers; Jagt et al*:* 38.

**Diagnosis**. *Pycnolepas* in which the rostrum and upper latus bear noded apicobasal ridges.

**Holotype**. Rostrum figured by Withers (1914a, pl. 8 fig. 7a, b; 1935, pl. 47 fig. 16). NHMUK I.16679. “Chalk Marl” (lower part of West Melbury Formation), lower Cenomanian, *Neostlingoceras carcitanense* ammonite subzone, near Cambridge, UK.

**Material**. 6 rostra (NHMUK I.16679, I.16680), upper latus (I.16681), 2 scuta (I.16646, I.16647), 6 terga (I.16650-1), 6 carinae (I.16648-9, I.13450), Chalk Marl (lower Cenomanian, *N. carcitanensis* Subzone), Cambridge, U.K. 100+ valves from the middle Cenomanian *T. acutus* ammonite subzone and *A. jukesbrownei* ammonite zone of Dover, Kent (NHMUK PI In 64851-64870).

**Remarks.** Withers (1914a) based the species on 2 rostra, a single upper latus and a scutum from the Chalk Marl of Cambridge. The taxon is common in the middle Cenomanian *T. acutus* Subzone at Dover, Kent, where over 70 valves have been picked from residues. These demonstrate that the rostrum characteristic of the species co-occurs with scuta, terga, upper latera and carinae from the lower Cenomanian assigned to *P. rigida* by Withers (1935). The scutum figured by Withers (1935, pl. 47 fig. 19) as *P. ? scalaris* is from a *Proverruca* sp. *P. scalaris* can now be confidently redescribed on the basis of the new material from Dover. The species differs from the Albian *P. rigida* in the small size and the noded sculpture of the rostrum and upper latus.

Figure 14

**Occurrence**. Present in the Cambridge Greensand and basal 1-2 m of the Chalk Marl (lower Cenomanian, *M. mantelli* Zone) and common in the middle Cenomanian, *T. acutus* ammonite subzone, at the level of 46.4 m (Kennedy and Gale 2006, fig. 2), Samphire Hoe, west of Dover, Kent, UK. The species ranges from the basal Cenomanian *N. carcitanense* ammonite subzone to the middle Cenomanian *A. jukesbrownei* ammonite zone.

***Pycnolepas batchelorum*** sp. nov.

(Fig. 13R-Z)

**Diagnosis.** Small *Pycnolepas* in which the scuta and terga carry strong, raised apicobasal ridges; secondary ridges present on terga; upper latus smooth.

**Types.** A tergum figured here (Fig. 13T) is holotype (NHMUK Pi In 64844), and the other figured scuta and terga are paratypes (Fig. 13U-X) are paratypes (NHMUK PI In 64842, 64843, 64845-64850). Upper Aptian Bargate Formation, Littleton, Surrey, UK.

**Material.** Over 100 valves, mostly abraded and encrusted with sand grains, from the Upper Aptian Bargate Formation of Compton and Littleton, Surrey, UK.

**Derivation of name**. After Trevor and Rita Batchelor of Redhill, who collected the type material by painstakingly picking washed sand residues from the Bargate Formation.

**Description**. Terga (Fig. 13T-V) rhomboidal to kite-shaped, bearing strong, slightly curved raised apicobasal ridge which broadens basally. One to several secondary ridges run from the apex to the upper part of the lateral margin on the occludent surface of the plates, separated from the scutal auricle by a groove. Scuta (Fig. 13W, X) rhombic, occludent margin straight to weakly convex; external surface bears strong, rounded, noded apicobasal ridge and weak, fine apicobasal ribbing. Upper latera (Fig. 13R, S) tall, narrow, slightly inclined dorsally; external surface smooth, internal surface bearing central ridge. Plates which are either carinae or rostra (Fig. 13Y, Z) hemiconical, height equal or slightly greater than breadth, displaying weak terracing.

**Remarks.** The tiny valves, a few millimetres in maximum dimension, were found to be common in bulk samples of the Bargate Formation of northern Surrey. I had originally assigned these to *Eoverruca* on account of the secondary ridges on the terga but the eventual discovery of upper latera demonstrated correct placement in *Pycnolepas*. The species differs from all other *Pycnolepas* in the presence of secondary ridges on the occludent surface of the terga, and the rounded, raised apicobasal ridges on terga and scuta. The poor preservation of the material is frustrating, because the terga bear a striking resemblance to those of *Eoverruca* in the development of secondary ridges on the terga (see Fig. 3E), separated from the scutal auricle by a groove; the material of *P. batchelorum* sp. nov. does not permit detailed description of these structures. *P. batchelorum* sp. nov., like *Eoverruca hewitti*, is very small and may fall close to the evolutionary origin of Eoverrucidae.

**Occurrence**. Upper Aptian, lower *Parahoplites nutfieldensis* Zone, Bargate Formation, Littleton and Compton, Surrey, UK.

Genus***Faxelepas*** Gale, 2014b

**Diagnosis.** Pycnolepadids which display variable asymmetry in slanting of rostra and carinae and breadth of apicobasal ridges on scuta and terga; tergal notch on scuta deep, elongated ; broad, flat occludent surface on interior of scuta extends to basal margin.

**Type species**. *Pycnolepas bruennichi* Withers, 1914a.

**Included species**. *Pycnolepas bruennichi* Withers, 1914a, *Pollicipes paronai* De Alessandri, 1895, *Pycnolepas landenica* Withers, 1953, *Pycnolepas ignabergensis* Carlsson, 1953.

**Remarks.** Although I founded *Faxelepas* for Wither’s *P. bruennichi,* *Pollicipes paronai* De Alessandri, 1895 also belongs in the genus, as pointed out by Hoffmann et al*.* (2021). The latter species, which occurs from the Miocene to the early Pleistocene (Gale, 2020c) does not appear to show asymmetry of the valves, but possesses a tall, deep tergal notch and a broad occludent surface on the interior of the scuta (Fig. 15D, E) similar to features developed in *F. bruennichi* (Fig. 15L, S).

Figure 16

***Faxelepas bruennichi*** (Withers, 1914a)

(Fig. 15L-X)

1914a *Pycnolepas bruennichi* Withers: 181, pl. pl. 7 figs. 5-9, pl. 8 fig. 6.

1935 *Pycnolepas bruennichi* Withers; Withers: 359, pl. 47 figs. 7-15.

2007 *Pycnolepas bruennichi* Withers; Jagt et al: 40.

2014b *Faxelepas bruennichi* (Withers); Gale: 23, figs 4A, C, F, G; 6A, B, N, 7M, N, 8M, N, 9M, N

**Diagnosis**. *Faxelepas* in which the valve sculpture comprises fine apicobasal ribbing, transvered by regular terracing on the scuta and terga, irregularly spaced on the carinae and rostra. Imbricating plates with internally directed ledge.

**Types.** The scutum figured by Withers (1935, pl. 47 fig. 5) is lectotype (NHMUK I. 16625). This comes from the Middle Danian of Faxe, Denmark.

**Remarks**. *F. bruennichi* is a variably asymmetrical taxon, in which the carinae are sometimes slanted (Fig. 15P) and the breadth of the apicobasal ridge on the scuta varies from broad (Fig. 15Y) to narrow (Fig. 15S). The imbricating plates (Fig. 15U-X) bear an inwardly directed shelf, like those of *Pycnolepas rigida* (compare Fig. 13 D-H) and an irregular external sculpture of weakly defined ridges and irregular transverse growth lines.

**Occurrence**. Lower and Middle Danian of Denmark and Sweden, northeast Belgium, southeastern Netherlands (Jagt and Collins, 1989) and the Crimean Peninsula, Ukraine (Jagt et al*.*, 2007).

***Faxelepas ignabergensis*** (Carlsson, 1953)

1953 *Pycnolepas ignabergensis*, Carlsson: 23, pl. 5 fig. 10, pl. 6 figs 1, 2.

2007 *Pycnolepas ignabergensis*, Carlsson; Jagt et al: 39.

**Diagnosis**. *Faxelepas* in which the apicobasal ridge on the tergum is very narrow; terracing on scutum closely spaced.

**Types**. The scutum figured by Carlsson, 1953, pl. 6 fig. 2 is holotype (SMNH AR 8742). Upper lower Campanian, Ignaberga, Skåne, Sweden.

**Remarks**. Carlsson (1953) had 3 scuta and a tergum of this species, all from Ignaberga; no further material has been collected. The strong dorsal curvature of the scuta, and variable width of the apicobasal ridges, warrant inclusion in *Faxelepas*. The species differs from the closely related *F.* *bruennichi* in the very narrow apicobasal ridge on the tergum (Carlsson, 1953, pl. 5 fig. 10) and the more numerous, closely spaced terracing on the scutum.

***Faxelepas landenica*** (Withers, 1953)

(Fig. 15, Y-A2)

 1953 *Pycnolepas landenica* Withers: 348, pl. 60 figs 1-6.

 2007 *Pycnolepas landenica* Withers: Jagt et al.: 40.

**Diagnosis.** *Faxelepas* in which the commarginal (transverse) ridges on all valves are weak and irregularly spaced.

**Type.** The scutum figured by Withers, 1953 pl. 60 fig. 2 is holotype. MSNB, material not located in March 2022, presumed lost.

**Material.** Withers (1953, p. 348) examined 24 valves of this species, all from the base of the “Landenian Sands” (nowadays Heers Formation, basal Orp Sand Member) Wansin, NE of Saumur, Belgium. Mid- Selandian, NP5. Four of these specimens are now in the NHMUK (In. 38043-38046) and several are figured here (Fig. 15Y-A2).

**Remarks**. *F. landenica* is referred to *Faxelepas* on account of the broad based apicobasal ridge on the scuta (compare Fig. 10Y with Fig. 10F, R); it differs from other species of the genus in the weak sculpture of the valves.

***Faxelepas paronai*** (De Alessandri, 1895)

(Fig. 15A-K)

1895 *Pollicipes paronai* De Alessandri: 260, pl. 3 figs 8a-f.

1906 *Pollicipes paronai* De Alessandri; De Alessandri: 248, pl. 13 figs 1-9.

1914a *Pycnolepas paronai* (De Alessandri); Withers: 184, pl. 7 figs 1-4.

1953 *Pycnolepas paronai* (De Alessandri) ; Withers : 350, pl. 60 figs 7-10.

2007 *Pycnolepas paronai* (De Alessandri) ; Jagt et al : 41.

2020c *Pycnolepas paronai* (De Alessandri) ; Gale : 192, pl. 2 figs 1-11.

2021 *Faxelepas paronai* (De Alessandri); Hoffmann et al*.,* 2021: 17, fig. 12A-I.

**Diagnosis.** Large species, apex of scutum strongly incurved dorsally. Scuta flat, interior surface adjacent to occludent margin broad; intricate sculpture of regularly spaced ridged growth increments intersecting with fine apicobasal ridges.

**Type.** Lectotype, designated by Withers (1914, p.185), is an unregistered scutum, illustrated by De Alessandri (1895, pl. 3, fig. 8a, b), contained in the Luigi Di Rovasenda Collection (now at the Museo Regionale di Scienze Naturali, Torino). Chieri, southeast of Torino, northern Italy; lower Miocene (Aquitanian, c. 20-23 Ma).

**Description.** See Gale (2020c p. 192)

**Remarks.** The absence of any peduncular plates in residues obtained from samples yielding capitular valves (Gale, 2020c; Hoffmann et al., 2021) provides negative evidence that this species may have lacked these. The species occurs in the Miocene, early Messinian, Abad Member of Turre Formation, Carboneras, southern Spain, Miocene, Aquitanian, of the Torino Hills, northern Italy, early Pleistocene, bathyal, Rodrigues Ridge, Indian Ocean.

Family **Eoverrucidae** Gale, 2020a

**Diagnosis.** Basal verrucomorphs, in which the rostrum and carina do not articulate; imbricating plates surround the shell wall, of which the most basal are fused with the calcified basis; upper latus absent.

**Included genera**. *Eoverruca* Withers, 1935.

**Remarks.** Withers (1935) identified the species *Eoverruca hewitti* Withers, 1935, from the Santonian chalk of Suffolk, UK, as ancestral to all other verrucomorphs, a conclusion supported by a detailed reappraisal of the species based on new material (Gale, 2014b). In this genus, the upper latus has been lost, peduncular scales are present, and there is incipient differentiation into fixed and moveable scuta and terga, resulting in the development of slight asymmetry. Jagt et al. (2008) recorded *E. hewitti* from the Upper Campanian of Poland. Subsequently, Gale (2020a) described two further species of *Eoverruca, E. aubensis* from the Middle Albian of the Aube (based on a single scutum), France, and *E. symmetrica* from the Upper Campanian of Norwich, Norfolk, UK. Recent processing of bulk chalk yielded abundant material of *E. hewitti* from the upper Santonian *Uintacrinus socialis* Zone of the UK, France and Poland, and a new species of *Eoverruca*, *E. barringtonensis* sp. nov. from the lower Cenomanian of Cambridge, UK.

Genus ***Eoverruca*** Withers, 1935

**Diagnosis.** As for family.

**Type species**. *Eoverruca hewitti* Withers, 1935.

**Included species.** *E. aubensis* Gale, 2020a, *E. symmetrica* Gale, 2020a, *E. barringtonensis* sp. nov.

**Remarks.** *Eoverruca* is extremely rare in Cretaceous samples, and two of the species (*E. aubensis, E. barringtonensis* sp. nov.) are only known from single valves. However, the genus occurs in thin, very widespread horizons of abundance in the Santonian and Campanian (see Jagt et al., 2007 and below). In its retention of imbricating whorls of plates, combined loss of upper latera and development of fixed and moveable scuta and terga, *Eoverruca* provides a link between pycnolepadids and verrucids. Indeed, the transition to basal Verrucidae involves simply loss of imbricating plates, broadening of apicobasal ridges and formation of an articulation between the carina and rostrum (see above). The genus is characterised also by the presence of a calcified basis which incorporates the lower whorls of imbricating plates (Fig. 16A-F; fig. 18L-N); the upper whorls are free (Fig. 16G-M).

Figure 17

***Eoverruca hewitti*** Withers, 1935

(Fig. 16A-X; Fig. 18F-K)

1935 *Eoverruca hewitti* Withers: 338, figs 37, 38, pl. 44 figs 9-18.

2008 *Eoverruca hewitti* Withers; Jagt et al: 62 figs 2, 3.

2014b *Eoverruca hewitti* Withers; Gale: 24, fig. 4B, D, E, I, J, 6E, F, fig. 7I, J, Fig. 8I, J, fig. 9I, J, fig. 17A-K, fig. 18A-P, fig. 19A-O.

2020a *Eoverruca hewitti* Withers; Gale: 273, fig. 14D-F, H, N-R.

**Diagnosis.** *Eoverruca* in which there is a marked asymmetry between fixed and moveable terga and scuta; fixed valves possess broader apicobasal ridges; tergal surface of fixed valves narrow.

**Types.** The holotype is a fixed scutum from the Santonian *Uintacrinus socialis* crinoid zone, East Harling, Norfolk, UK (NHMUK In. 27598; Withers, 1935).

**Material.** Many hundred valves from the *Uintacrinus socialis* zone of Suffolk, Norfolk, Sussex and Kent, UK, and the same level at Sens, France and Biocieniec, Poland (Fig. 17).

**Description.** See Gale, 2014b, p. 24.

**Remarks.** *E. hewitti* differs from *E. symmetrica* in its development of markedly asymmetrical scuta and terga and in the shape of these valves. It differs from *E. aubensis* in the narrower tergal surface of the fixed scutum, and from *E. barringtonensis* sp. nov. in the better defined apicobasal and secondary ridges on the moveable terga, plus the smaller tergal auricle.

**Occurrence.** *E. hewitti*occurs most commonly in the middle part of the *Uintacrinus socialis* Zone (upper Santonian) in the UK (Kent, Sussex, Suffolk, Norfolk), France (Sens) and Poland (Biocieniec), as shown in Fig. 17. It is also common in the lower Campanian of Jezowska, southern Poland (Jagt et al., 2008).

Figure 18

***Eoverruca aubensis*** Gale, 2020a

(Fig. 18A, B)

2020a *Eoverruca aubensis,* Gale: 273, fig. 14I, J.

**Diagnosis.** *Eoverruca* in which the fixed scutum possesses a broad tergal surface and a curved apicobasal ridge.

**Type.** A unique scutum from the middle Albian *Anahoplites intermedius* ammonite zone, Pogains, Department of Aube, France (NHMUK IC 1557).

**Description.** See Gale 2020a, p. 273.

**Remarks**. By comparison with material of *E. hewitti*, the sole specimen of *E. aubensis* is a fixed scutum (compare fig. 16O, P with fig. 18A, B) because it has a broad apicobasal ridge. The species differ in the greater curvature of the apicobasal ridge and broader tergal surface in *E. aubensis*.

***Eoverruca symmetrica*** Gale, 2020a

(Fig. 18L-A4)

2020a *Eoverruca symmetrica* Gale: 273, fig. 14A-C, G, I-M, fig. 15A-P

**Diagnosis.** *Eoverruca* in which the paired scuta and terga are symmetrical. Scutum in form of isosceles triangle, terga rhomboidal; apicobasal ridge on scuta poorly defined.

**Type.** The scutum figured by Gale (2020a, fig. 14K) is holotype (NHMUK IC 1553). Paratypes include scuta, terga, carinae, rostra and a calcified basis (NHMUK IC 1554-6, 1557-1573). Upper Campanian, *Belemnitella mucronata* belemnite zone, uppermost Weybourne Chalk, Catton Grove, Norwich, Norfolk, UK.

**Material.** 150 loose valves from the type locality and horizon.

**Remarks**. *E. symmetrica* differs from its congenors in the symmetry of the scuta and terga and the shape of the scuta of which form an isosceles triangle, the poor definition of the apicobasal ridge on the scuta (Fig. 18S, X, Y) and the confluence of the apicobasal ridge and the secondary ridge on the terga (Fig. 18Q, T, U).

**Occurrence.** *E. symmetrica* is only known from its type locality and horizon.

***Eoverruca barringtonensis*** sp. nov.

(Fig. 18A5)

**Diagnosis.** *Eoverruca* in which the occludent margin of the moveable tergum is short and convex, the scutal auricle broad and the secondary ridge poorly defined.

**Type.** A moveable tergum (NHMUK PI In 64882) from the basal West Melbury Formation, Cambridge Greensand Member, lower Cenomanian *Neostlingoceras carcitanense* ammonite subzone, Barrington, Cambridgeshire, UK.

**Description**. Tergum kite-shaped, occludent margin short, convex. Apicobasal ridge weakly noded, sharply demarcated on occludent side, poorly defined on lateral/scutal margin; secondary fold and groove apical to this weakly defined; scutal auricle large, protrudes from margin of valve.

**Remarks.** This species differs from the corresponding valve of *E. hewitti* in the shorter, more convex occludent margin and the poorly defined secondary ridge and groove. It differs from *E. symmetrica* in the broader scutal auricle and the strong demarcation between the apicobasal ridge and the secondary fold.

Family **Verrucidae** Darwin, 1854

**Diagnosis.** Verrucomorphs in which there is an articulation between the carina and rostrum, and in which there is strong asymmetry between the fixed and moveable scuta and terga. Imbricating plates absent.

**Included genera**. *Verruca* Schumacher, 1817, *Rostratoverruca* Broch, 1922, *Cameraverruca* Pilsbry, 1916, *Altiverruca* Pilsbry, 1916, *Metaverruca* Pilsbry, 1916, *Newmaniverruca* Young, 1998, *Gibbosaverruca* Young, 2002, *Cristallinaverruca* Young, 2002, *Brochiverruca* Zevina, 1993, *Spongiverruca* Zevina, 1978, *Globuloverruca* Young, 2004, *Priscoverruca* Gale, 2014b, *Youngiverruca* Gale, 2014b.

**Remarks**. Verrucids are a widespread and diverse group of present day marine benthos, which occur dominantly in bathyal settings. However, *Verruca* occurs commonly in shallow water, subtidal environments.

Genus ***Rostratoverruca*** Broch, 1922

**Diagnosis.** Shell box-like, elongated along dorsal-ventral line; opercular lid parallel with base, occludent wing large. Fixed scutum trapezoidal to triangular, occludent margin convex.

**Type species.** *Verruca nexa* Darwin, 1854, by subsequent designation of Zevina (1987).

**Remarks.** The taxonomy of *Rostratoverruca* was discussed in some detail by Gale (2020b; Gale et al., 2021). The most recent of these papers concluded that *Costatoverruca* Young, 1998 is a synonym of *Rostratoverruca*. There are numerous extant species (e. g. Young, 2002), but the only Cretaceous taxon which can be ascribed to the genus is *Verruca pusilla* Bosquet, 1857.

Figure 19

***Rostratoverruca pusilla*** (Bosquet, 1857)

(Fig. 19Q)

1857 *Verruca pusilla* Bosquet: 3, pl. i fig. 3.

1935 *Verruca pusilla* Bosquet; Withers: 346, pl. 45 fig. 13.

**Diagnosis.** *Rostratoverruca* in which the fixed tergum and scutum bear rather few, strong apicobasal ridges.

**Lectotype**. Withers (1935, p. 346) selected the rostrum figured by Bosquet (1857, pl. 1 fig. 3A) as lectotype. Maastrichtian, St. Petersburg, Geulhem, and Limbourg, Netherlands; near Nédercanne, Belgium. John Jagt (pers. comm.) noted that the material he saw was labelled as coming from St. Pierre, Netherlands, and that the lectotype rostrum could not be located.

**Material.** Bosquet (1857) stated that the had a great number of valves of this species, but it has not been collected subsequently. John Jagt (pers comm., Feb 2022) kindly provided me with his notes on the material in the Bosquet collection in the MHNB. The material could not be located during my visit to the museum, so the redescription is based on Bosquet’s figures and John Jagt’s notes.

**Description.** Fixed scutum trapezoidal, bearing 5 broad apicobasal ribs, occludent wing broad, margin concave (Fig. 19QS). Articular surface for rostrum has 4 fine ribs with intervening grooves. Fixed tergum robust, bearing 3 broad apicobasal ribs, occludent wing short, margin straight (Fig. 19QT’). I am not convinced that the valves figured by Bosquet (fig. i3A, B) as carina (A) and rostrum (B) are different; they are nearly identical, and it is likely that both are rostra (Fig. 19QA, B). Rostrum broad, rather flat, weakly ribbed, nearly symmetrical, with prominent commarginal ridges. 6 narrow ridges and intervening grooves extend from the body of the plate to form an interpenetrant articulation with the carina; 3 shorter ribs form the articulation surface with the fixed scutum. Moveable tergum rhombic, robust, apicobasal ridge broadening basally, secondary ridge weak (Fig. 19QT).

**Remarks.** The form of the fixed scutum, bearing a broad, well demarcated occludent wing, the ribbed articulation of the rostrum and fixed scutum and the numerous interpenetrant ribs and grooves on the rostral margin are typical of *Rostratoverruca* species (compare with Fig. 19L, M, N). The morphology of the rostrum is quite similar to that of *R. nexa* (Fig. 19PA) except that the ribs do not extend onto the upper interior of the plate (compare Fig. 19P with Fig. 19Q). The numerous interpenetrant ribs on the articulation between the rostrum and carina are also seen in the Plio-Pleistocene *R. crebricosta* (Seguenza, 1873; see Gale et al., 2021 fig. 7.1). It can be concluded that *V. pusilla* is a *Rostratoverruca*, with closest affinities to the extant, Caribbean *R. nexa* and the Plio-Pleistocene to Recent *R. crebricosta*. It differs from these species in the coarse, broad apicobasal ridges on the fixed valves. The presence of a species of this genus in the Maastrichtian is further evidence of a Cretaceous radiation of verrucids, of which some genera are still extant.

Genus ***Youngiverruca*** Gale, 2014b

**Diagnosis.** Fixed scutum robust, buttress broad, flat, triangular, occludent wing small. Fixed tergum bears long declined occludent wing.

**Remarks.** The structure of the fixed scutum distinguishes this genus from all other verrucids, most notably in the diminuitive occludent wing (Fig. 19A-C) and very broad, flat buttress. The relationships of the genus are uncertain.

***Youngiverruca ruegenensis*** Gale, 2014b

(Fig. 19A-C, F-H)

2014b *Youngiverruca ruegenensis,* Gale: 28 fig. 20A-D, J-L.

**Diagnosis**. As for genus.

**Types**. The fixed tergum (NHMUK In. 16224) is holotype, a fixed tergum and fixed scutum (NHMUK IC 1n. 16222, In. 16225) are paratypes. All from lower Maastrichtian, Rügen, Germany.

**Remarks.** This species is only known from 3 valves, one of which had previously been figured by Withers (1935, pl. 45 fig. 13) as *Verruca prisca* (Fig. 19F-H). The most distinctive features of the genus are shown by the fixed scutum, which differs from those of all other known verrucids.

Genus ***Priscoverruca*** Gale, 2014b

**Diagnosis.** Capitulum twice as broad as high, carina and rostrum not inflexed; buttresses of fixed tergum and scutum, rostrum and carina not inflexed, surfaces smooth, imperforate; occludent margin of free scutum incurved at apex.

**Type species.** *Verruca prisca* Bosquet, 1854.

**Included species.** In addition to the type species, *P. elongatum* Gale, 2014b.

**Remarks.** *Priscoverruca* is closest to *Verruca* but differs in the higher shell profile (compare Fig. 20X with Fig. 22C, I), lack of inflection of the wall plates, a smaller, shorter myophore (compare Fig. 20A-E with Fig. 22L), the absence of apicobasal ridges and imperforate shell plates. Additionally, the occludent wings on the fixed scuta and terga are shorter, do not terminate acutely and are not widely separated from the body of the plates (compare Fig. 20H, I, L, M with Fig. 22K-M). The genera share a number of features, including the nature of the articulation of the fixed scutum and tergum, and a ridge on the carina which articulates with the moveable tergum (Fig. 20X, Fig. 22A, J; Gale 2014b, p. 30). The occurrence of *Priscoverruca* in the upper Campanian provides evidence that much of the morphological diversity displayed by verrucids had evolved by this time.

***Priscoverruca prisca*** (Bosquet, 1857)

(Fig. 20A-Y; Fig. 21A-F)

 1854 *Verruca prisca* Bosquet : 14, pl. i figs1-7, 7’

 1855 Verruca Prisca Bosquet; Darwin: 43, pl. 2 figs 10a-c.

p1923 *Verruca prisca* Bosquet; Withers: 36 fig, pl. 2 figs 40-45, 50 only.

P1935 *Verruca prisca* Bosquet; Withers: 341, pl. 45 figs. 7-12, 14 only.

 1989 *Verruca prisca* Bosquet; Jagt and Collins: 190 fig. 4d, e, g.

 2014b *Priscoverruca prisca* (Bosquet); Gale: 30 figs 3F, 20E-I, M, N, P, 21A-C, I, J, L, M, 23E, F.

**Diagnosis**. *Priscoverruca* in which the height of the fixed tergum is only slightly greater than its maximum breadth.

**Types**. The moveable scutum figured by Bosquet (1854, pl. I fig. 2a, b; reproduced here as Fig. 21G 2a, b) was selected by Withers (1935, p. 46 as lectotype. Unfortunately, this specimen could not be found among Bosquet’s type series, illustrated here in Fig. 21A-F. The new images show the veracity of Bosquet’s illustration albeit drawn with some artistic licence.

**Material**. 3 complete shells from the upper lower Maastrichtian Vijlen Member (Gulpen Formation), CPL quarry, Haccourt, NE Belgium (NHMUK In. 63639, 63640, 62170). Abundant valves from the upper Campanian *Belemnitella mucronata* belemnite zone of Norwich.

**Description**. See Gale (2014b, p. 30). The new material from Norwich (Fig. 20A-T) provides evidence for both morphological variation, ontogeny and valve morphology. The smallest fixed scuta (Fig. 20A, B) possess a short myophore; larger valves show considerable variation in shape, from those elongated on the rostral side (Fig. 20D, I) to short, tall forms (Fig. 20 E, J). The fixed terga (Fig. 20L-Q) are less variable in outline, but the presence of an internal cavity extending up to the apex (Fig 20N) is only present on some specimens and absent on many (e. g. Fig. 20Q). This is noteworthy, because the genus *Cameraverruca* Pilsbry, 1907 (type species *Verruca euglypta* Pilsbry, 1907) is characterised by the presence of such cavities. The moveable terga and scuta (Fig. 20F, G, P) display no significant variation in morphology, but the interior of the moveable scutum (Fig. 20K) has a triangular tergal notch, set in the valve of the valve, whereas in *Verruca stroemia* (Fig. 22G) this is angled obliquely.

**Remarks.** *P. prisca* differs from *P. elongata* in the lower form of the shell and the broader fixed terga.

**Occurrence.** Upper Campanian and Maastrichtian of UK, Belgium, Netherlands and Denmark.

Figure 20

***Priscoverruca elongata*** Gale, 2014b

(Fig. 19D, E, J, K)

2014b *Priscoverruca elongata* Gale: 30, fig. 22A-E.

**Diagnosis**. *Priscoverruca* in which the fixed terga are tall and narrow and possess a very short occludent wing.

**Types**. The holotype is a large fixed tergum (NHMUK In. 16224), the paratype a smaller fixed tergum (NHMUK In. 16225), both from the lower Maastrichtian of Rügen, Germany.

**Description**. See Gale 2014b, p. 31.

**Remarks.** The species can be distinguished from *P. prisca* by the very tall, narrow, fixed tergum and the short occludent wing.

**Occurrence**. Lower Maastrichtian of Rügen, Germany.

Genus ***Verruca*** Schumacher, 1817

**Diagnosis.** Shell with form of low dome, basal parts of wall inflexed, myophore forms horizontal sheet. Growth lines irregular and convoluted forming irregular lobes. Shell perforated by tiny pores.

**Type species.** *Lepas strömia* (sic), Müller, 1776

**Included species**. *V. spengleri* Darwin, 1854, *V. jago* Buckeridge, 1997, *V. cookei* Pilsbry, 1927, *V. jagti* Gale, 2014b, *V. laevigata* G. B. Sowerby, 1827, *V. galegoedertae* Perrault and Buckeridge, 2019 and *V. sorrellae* Perrault and Buckeridge, 2019.

**Remarks**. Numerous species, from the Cretaceous to the present day, have been referred to *Verruca*, but the concept of the genus has progressively narrowed, as species have been referred to other genera in the Verrucidae (e. g. Young 1998, 2002); there remain a residue of living and fossil species for which the generic affinities remain uncertain. Correct placement of these will depend upon an agreed definition of the genus *Verruca*. The definition of Perrault and Buckeridge (2019, p. 37), which follows Buckeridge (1997, p. 128), states “Verrucid with shell form depressed; apices of rostrum and carina marginal; operculum parallel to base.” However, this definition covers a very wide range of verrucids, including species referred to *Metaverruca*. The definition used here follows Gale (2014b, p. 32) also includes the presence of pores, a horizontal myophore and irregular, lobed growth lines (e. g. *V. stroemia*, Fig. 22E-N). This latter definition covers the extant species *V. stroemia, V. spengleri, V. jago, V. laevigata* and *V. cookei*, and some species described by Perrault and Buckeridge (2019) from the Paleogene of North America, including *V. galegoedertae* and *V. sorrellae*. It is important to note that the pores are not always visible on the exterior of the shell, as in. *V. stroemia* (Young et al., 2003 fig. 1), but in this species they are clearly seen on the interior (Fig. 22H). Additionally, as noted by Perrault and Buckeridge (2019, p. 37) they may be obscured by diagenesis in fossils. Future work needs to establish agreed diagnoses of *Verruca, Metaverruca* and *Priscoverruca*.

 *Verruca tasmanica* Buckeridge, 1983 was recorded as occurring in the Cretaceous of Australasia, but these records are not documented and the only specimens figured appear to be from the Oligocene (Buckeridge, 1983 figs 43, 44). Gale (2014b) suggested that *V. sauria* Buckeridge, 2011, from the Maastrichtian of Canterbury, New Zealand, *V. punica* Buckeridge and Jagt, in Buckeridge et. al., 2008, from the Danian of Tunisia, and *V. digitali* Buckeridge, in Buckeridge and Finger (2001) from the Miocene of California, USA, may belong to *Priscoverruca*, but, in my view, their generic placement remains uncertain.

Figure 21

***Verruca jagti*** Gale, 2014b

(Fig. 22A-D)

2014b *Verruca jagti* Gale: 33, fig. 21G, H, 23A, B.

**Diagnosis**. *Verruca* in which the pores in the shell wall are irregularly distributed; shell lacks apicobasal ribbing.

**Type**. The complete shell figured by Gale (2020, fig. 21G, H) is holotype (NHMM JJ 13472). Complete individual from the ENCI-Heidelberg Cement Quarry, Maastricht, south Limburg, Netherlands. Meerssen Member (Maastricht Formation, latest Maastrichtian), top 10cm of subunit IVf-1 (hardground).

**Material**. A further specimen (NHMM JJ 13456) from the Meerssen Member, top IVf-1, ENCI-Heidelberg Cement Quarry, may also belong to this species, but is coated with calcite and all details are not visible.

**Remarks**. This species differs from all described species of *Verruca* in the absence of apicobasal ridges, particularly on the rostrum and carina, and the irregular distribution of pores in the shell. This is the oldest species certainly belonging to *Verruca*.

Figure 22

Order **Balanomorpha** Pilsbry, 1916

**Diagnosis.** Symmetrical sessile cirripedes in which the rostrum and carina are of similar size, and the terga and scuta form an operculum positioned in an orifice. There is a strong articulation between the terga and scuta.

**Remarks.** The definition of the order is modified to include the Brachylepadidae.

Family **Brachylepadidae** Woodward, 1901

**Modified diagnosis**. Capitulum low, carina and rostrum short, hemiconical; primary wall surrounded by imbricating plates conjoined by peg-and socket articulations. Rostro- and carinomarginals absent.

**Included genera**. *Brachylepas* Woodward, 1901, *Fallaxlepas* Gale, 2020a, *Epibrachylepas* Gale, in Gale and Sørensen, 2014, *Parabrachylepas* Gale, in Gale and Sørensen, 2014.

**Remarks**. The restricted family, admittedly paraphyletic, is demarcated by the low profile of the capitulum and the highly specialised articulation (peg and socket) between the alternate rows of imbricating plates (Fig. 8S, X). The family is exclusively Upper Cretaceous, extending from the lower Cenomanian to the Maastrichtian. *Neobrachylepas* Newman and Yamaguchi 1995, which is morphologically convergent with the brachylepadidae, is now placed in the superfamily Neolepadoidea, subfamily Neobrachylepadinae (Chan et al., 2021 and above). *Plesiobrachylepas* Carriol, in Carriol et al., 2016 is transferred to the Neobrachylepadidae (see above).

Figure 23

Genus ***Brachylepas*** Woodward, 1901

**Diagnosis**. Marginal plates absent, rostrum and carina of similar shape, low, hemiconical; tergal surface of scutum set at 90o to occludent surface; terga rhombic, scutal auricle prominent.

**Type species**. *Emarginula (?) naissanti* Hébert, 1855.

**Included species**. *Mitella guascoi* Bosquet, 1857, *Brachylepas angulosus* Collins, 1973, *Brachylepas americana* Zullo, Russell and Mellen, 1987, *Brachylepas hantonensis* Gale, 2020a, *Brachylepas thieli* Gale, 2020a.

**Remarks**. *Brachylepas* ranges from the lower Cenomanian to the Maastrichtian and only occurs abundantly in shallow, near shore facies associated with a rocky coastline (*B. guascoi, B. americana*; Zullo et al., 1987; Gale and Sørensen, 2014, 2015). *B. naissanti* is common in the upper Campanian and Maastrichtian basinal chalk facies of northwest Europe, but other species of the genus are extremely rare. *Brachylepas solida* Zullo, 1987, is correctly referred to the archeolepadomorph genus *Myolepas* Gale, in Gale and Sørensen, 2015.

***Brachylepas naissanti*** (Hébert, 1855)

(Fig. 23A-S)

1855 *Emarginula* (?) *Naissanti*, Hébert: 374, pl. 29 fig. 10.

1865 *Pyrgoma cretacea* Woodward:321.

1868 *Pyrgoma cretacea* Woodward: 258, pl. 14 figs 1, 2.

1901 *Brachylepas cretacea* Woodward: 150, pl.8 figs 3, 4.

1912 *Brachylepas naissanti* (Hébert); Withers: 323, pl. 20 figs 1-18.

1923 *Brachylepas naissanti* (Hébert); Withers: 37, pl. 2 figs 28-39.

1935 *Brachylepas naissanti* (Hébert); Withers: 375, pl. 49 figs 1, 2, text-figs 44-62.

1953 *Brachylepas naissanti* (Hébert); Carlsson: 26, pl. 6 fig. 7.

1987 *Brachylepas cretacea* Woodward; Newman: 27, fig. 7A-C.

2009 *Brachylepas naissanti* (Hebert); Alekseev: 31, pl. 4 fig. 23.

2014 *Brachylepas naissanti* (Hébert); Gale and Sørensen: 20 fig. 17M-O.

2015 *Brachylepas naissanti* (Hébert); Gale and Sørensen: 238, fig. 15N-P.

**Diagnosis**. *Brachylepas* in which the robust carina and rostrum bear coarse, regularly spaced apicobasal ridges, separated by pitted grooves.

**Type.** The carina from the upper Campanian chalk of Meudon, Paris, France, figured by Hébert 1955 pl. 29 fig. 10 is lectotype (Withers, 1935 p. 375). Whereabouts unknown.

**Material.** For the present study, specimens from the upper Campanian of Norwich, Norfolk, UK were used (Withers, 1935 p. 376-378), including the articulated specimen figured by Woodward (1901).

**Remarks**. This species is separated from all congenors by the strongly ribbed carina and rostrum (Fig. 23E, F, H, I, L, M). The terga (Fig. 23K), scuta (Fig. 23N, O) and upper latera (Fig. 23C, D, G, J) are almost smooth, bearing only weak growth lines. The imbricating plates (Fig. 23P-S) have a centrally positioned ridge. The articulated rostrum and carina, with in situ imbricating plates (Fig. 23A, B) is the only articulated brachylepadid which has been found.

**Occurrence.** The species is locally common in the upper Campanian and Maastrichtian chalk of the UK, France, Germany and Denmark and occurs more rarely in the shallow water facies of Skåne, southern Sweden (Carlsson, 1953; Gale and Sørensen, 2014, 2015). It is also present in the Maastrichtian of Mangyschlak, Kazakhstan (Alekseev, 2009).

***Brachylepas guascoi*** (Bosquet, 1857)

(Fig. 24H-Z)

1857 *Mitella guascoi* Bosquet: 11, pl.1 figs 8, 9 only.

1857 *Mitella lithotryoides* Bosquet: 23, pl. 3 figs 6-9 only.

1906 *Brachylepas lithotryoides* (Bosquet); Woodward: 339 figs 1-4.

1914 *Brachylepas lithotryoides* (Bosquet);Withers: 169.

1935 *Brachylepas guascoi* (Bosquet); Withers: 383, pl. 49 figs 3-14.

1953 *Brachylepas guascoi* (Bosquet); Carlsson: 26, pl. 6 figs 8-10.

2014 *Brachylepas guascoi* (Bosquet); Gale and Sørensen: 16, fig. 14A-P, fig. 16A-R.

2015 *Brachylepas guascoi* (Bosquet), Gale and Sørensen, p. 238, fig. 15A-M.

**Diagnosis**. *Brachylepas* in which the carina is rounded and lacks an apicobasal ridge; basi-occludent angle of scutum acute.

**Types**. The scutum figured by Bosquet (1857 fig. 8) was selected as lectotype by Withers (1935, p. 384). Brussels Museum, not found in Feb. 2022.

**Material.** Abundant valves from the upper lower Campanian of Ivö Klack, Skåne, southern Sweden.

**Remarks**. This species is close to *B. americana* from the Campanian of Arkansas, USA; Zullo et al. (1987) noted a number of differences, including the presence of a median ridge on the carina (less noticeable on the rostrum) on *B. americana* (Fig. 25K, L), absent on *B. guascoi* (Fig. 24J-N); the basi-occludent angle is more acute in *B. guascoi* (Fig. 23O, P) than in *B. guascoi* (Fig. 25E, F). However, some of the other differences noted by Zullo et al. (1987), notably those in the terga, actually represent parallel variations within respective species, as demonstrated by examination of a larger sample set of *B. guascoi*. It is remarkable that such closely related species occupied near-shore habitats in the Campanian, separated by a distance of approximately 7,000 km. As noted by Zullo et al. (1987), it appears likely that *Brachylepas* populations extended along the entire northern margins of the North Atlantic. It is evident that brachylepadids were widespread and locally abundant in Late Cretaceous marginal marine environments.

**Occurrence**. The species occurs at a number of localities in the upper lower Campanian of the Kristianstad Basin, Skåne, southern Sweden (Carlsson, 1953) and in the Maastrichtian of Belgium and the Netherlands (Withers, 1953).

Figure 24

***Brachylepas hantonensis*** Gale, 2020a

(Fig. 24D, E)

2020a *Brachylepas hantonensis* Gale: 275, fig. 16C, D.

**Diagnosis**. Carina as tall as broad, apex acuminate, dorsal margin weakly concave; sculpture of closely spaced, imbricate terraces.

**Type.** The unique holotype (NHMUK IC 1575) is from the Lewes Chalk Formation, *Plesiocorys planus* Zone of Froxfield, Hampshire, UK, pit no. 112 of Brydone (1912).

**Remarks**. This species is most closely related to *B. guascoi* and *B. americana*, from which it differs in the more closely spaced terracing and the greater length of the ventrally directed wings.

***Brachylepas thieli*** Gale, 2020a

(Fig. 24F, G)

2020a *Brachylepas thieli* Gale: 275, fig. 16A, B.

**Diagnosis**. *Brachylepas* in which the rostrum is low, bears irregular growth lines and has a weak apicobasal striation.

**Type**. A unique rostrum (NHMUK IC 1574) from the lower Cenomanian (*Neostlingoceras carcitanense* Subzone) of Kassenberg, Mülheim-Ruhr, Germany.

**Remarks**. *B. thieli* differs from all other known *Brachylepas* rostra in its very low profile, irregular growth increments and weak apicobasal striation. This is the oldest known brachylepadid and was found in association with a rocky shoreline in an erosional pocket cut into Carboniferous sandstones (Gale and Thiel, 2023).

Figure 25

***Brachylepas americana*** Zullo, 1987

(Fig. 25A-A1)

1987 *Brachylepas americana* Zullo, Russell and Mellin: 105, figs 6, 7.

**Diagnosis**. Robust *Brachylepas* in which the carina bears a weak median ridge; basi-occludent angle of scutum obtuse.

**Type**. A carina, MSU 3313, from the basal Brownstown Formation, Campanian, Friendship, Hot Springs County, Arkansas, USA. Paratypes MSU 3314-3323, same locality.

**Material**. Over 3,000 valves from the type locality (Zullo et al., 1987).

**Remarks**. As discussed above (under *B. guascoi*), *B. americana* is closely related to *B. guascoi* and differs only in minor aspects of carinal and scutal morphology. The species is known only from the type locality, where it occurs in a basal conglomerate which rests on an irregular unconformity overlying Carboniferous sandstones (Zullo et al., 1987).

***Brachylepas angulosa*** Collins, 1973

(Fig. 25A2-A5)

1973 *Brachylepas angulosa* Collins: 380, pl. 5 fig. 16.

1987 *Brachylepas angulosa* Collins; Zullo, Russell and Mellin: 104, fig. 5.8-10.

**Diagnosis**. *Brachylepas* in which the tall rostrum is angled at 90o about a strong apicobasal ridge; irregular sculpture of growth increments and 6 weak, discontinuous, apico-basal ridges.

**Type**. Unique holotype, NHMUK In. 64479. Barr Pasture, Oktibbeha County, Mississippi, USA. Ripley Formation, Maastrichtian.

**Remarks**. The rostrum differs from all other species of *Brachylepas* in its 90o angulation and distinctive sculpture of ridges and growth increments. It is only known from the type specimen.

Genus ***Fallaxlepas*** Gale, 2020a

**Diagnosis**. Rostrum and carina tall, cylindrical, tapering apically, often with slight lateral slanting; rostrum, carina and imbricating plates smooth or with weakly defined commarginal growth lines; scuta, terga and upper latera with sharply defined, closely spaced terracing.

**Type species**. *Pollicipes fallax* Darwin, 1851a.

**Included species**. *Brachylepas nervosa* Alekseev, 2009.

**Remarks**. The tall, subcylindrical carinae (dorsally reclined) and rostra (Fig. 2O, Fig. 26G) distinguish this genus from *Brachylepas* in which the rostra and carinae are low and blunt apically (Fig. 2P, Q). Cladistic analysis (Fig. 10A) did not resolve a polytomy between *B. naissanti, Fallaxlepas* and more derived brachylepadids, However, in its possession of tall rostra and carinae, the shape of the scuta and terga, and the strong, even terracing on the scuta and terga, *Fallaxlepas* appears to be closer to the pycnolepadids than do other brachylepadids. Indeed, Withers (1914a, 1923) originally placed *Pollicipes fallax* in the genus *Pycnolepas* (see Withers, 1935, p. 372).

Figure 26

***Fallaxlepas fallax*** (Darwin, 1851a)

(Fig. 26A-U)

1851a *Pollicipes fallax* Darwin: 75, pl. 4 fig. 8a, b.

1857 *Mitella fallax* (Darwin); Bosquet: 17, pl. 2 figs 1-12, pl. 3 figs 1, 2.

1878 *Pollicipes fallax* Darwin; Kafka: 19, pl. 3 figs 2r, 3 a, b only.

1887 *Pollicipes fallax* Darwin; Fritsch and Kafka: 10, fig. 17.

1906 *Brachylepas (Pollicipes) fallax* (Darwin); Woodward: 340, figs 5-18, 21-24.

1914a *Pycnolepas fallax* (Darwin); Withers: 175, pl. 7 figs 10-14, pl. 8 fig. 5.

1923. *Pycnolepas fallax* (Darwin); Withers: 35, pl. 2 fig. 27.

1935 *Brachylepas fallax* (Darwin); Withers: 367, pl. 48 figs 1-24.

2014 *Brachylepas fallax* (Darwin); Koci et al: 227, pl. 3 figs 1,2, pl. 4 figs 1-8.

2020a *Fallaxlepas fallax* (Darwin); Gale: 277 fig. 15J, K.

**Diagnosis**. *Fallaxlepas* in which the rostrum and carina are smooth or bear only weak growth lines; secondary ridge on tergum weakly developed or absent.

**Types.** A scutum figured by Darwin (1851a, pl. 1 fig. 8a) was selected as lectotype by Withers (1912c). The specimen is from the upper Campanian chalk of Norwich, Norfolk, UK (NCM 2153).

**Remarks**. There is considerable variation in the valve morphology of this species. The carinae show variable asymmetry (compare Fig. 26F and Fig. 26G) and some forms are broad and proportionately low (Fig. 26M). Most only carry irregular growth lines (Fig. 26F, M) whereas others bear weak apicobasal ridges (Fig. 26U). The rostra (Fig. 26N, Q-T; compare with Fig. 26G) vary significantly in shape, as do the terga (compare Fig 26E, 26P).

**Occurrence**. Turonian to Maastrictian in the UK; Campanian and Maastrictian of southern Sweden, Denmark, Germany, Netherlands, Belgium (Jagt and Collins, 1989); Turonian to Campanian, Czech Republic (Kafka, 1878; Fritsch and Kafka, 1887; Koci et al., 2014).

***Fallaxlepas nervosa*** (Alekseev, 2009)

(Fig. 24A-D)

2009 *Brachylepas nervosa* Alekseev: 34, pl. 4 figs 16-21.

2014 *Brachylepas nervosa* Alekseev; Koci et al: 227.

**Diagnosis**. *Fallaxlepas* in which the carinae and rostra carry regularly spaced transverse ridges; terga with marked secondary ridge on scutal surface.

**Types**. The tergum figured by Alekseev (2009, pl. 4 fig. 21a, b) comes from the lower Maastrichtian of Beshkosh Mountain, southwestern Crimea, Ukraine. Moscow, LMSU no. 270, no. 9026.

**Material**. Alekseev (2009) recorded 151 valves from the Lvow area, Crimea (Ukraine) and Russia (Volga River, northern Caucasus, and Mangyschlak (Kazakhstan). All Maastrichtian.

**Remarks**. *F. nervosa*, from the Maastrichtian of Crimea (Ukraine), Russia and Kazakhstan, is very closely related to *F. fallax* from northwest Europe and I am not convinced that they represent separate species, because there is considerable variation in valve morphology in material of *F. fallax* which I have examined. For example, the shape of the terga varies significantly between forms which possess a broad scutal surface (Fig. 26P) and those in which this feature is rather narrow with a concave scutal margin (Fig. 26E). *F. nervosa* differs principally in the more regular transverse, slightly swollen growth increments on the rostra and carinae (Fig. 24B-D) and the presence of a better defined secondary ridge adjacent to the scutal auricle on the tergum (Fig. 24A). Alekseev (2009) suggested that some of the material from northwest Europe actually belongs to *F. nervosa*. Without access to the Mangyschlak material it is not possible make detailed comparisons.

Genus ***Parabrachylepas*** Gale, in Gale and Sørensen, 2014

**Diagnosis**. Tergum subrectangular, carinal margin single, large scutal auricle present; Upper latus low, broad based. Marginals present between carinae and rostra. External sculpture of commarginal ridges, replaced in adult by weak reticulate sculpture.

**Type species**. *Calantica (Scillaelepas) ifoensis* Withers, 1935.

**Remarks**. Although Withers (1935, p. 128) assigned this species to the pedunculate calanticid *Calantica (Scillaelepas),* the subsequent discovery of low, hemiconical rostra and carinae, bearing identical sculpture to the scuta and terga (Fig. 27N, O, S-U) and imbricating plates (Fig. 27L, M, Q, R, V) served to identify its brachylepadid affinity (Gale and Sørensen, 2014). The presence of marginal plates, set between the carina and rostrum (Fig. 27I, J) indicated that it is a derived brachylepadid. The reconstruction (Fig. 2E) shows that it had a low, compact morphology.

Figure 27

***Parabrachylepas ifoensis*** (Withers, 1935)

(Fig. 27A-V)

 1935 *Calantica (Scillaelepas) ifoensis* Withers: 128, pl. 10 figs 1-6

 p1935 *Pachydiadema cretacea* Withers: pl. 50 figs 4, 5 only.

 1953 *Calantica (Scillaelepas) ifoensis* Withers; Carlsson: 12, pl. 2 figs 3, 10-12.

 2014 *Parabrachylepas ifoensis* (Withers); Gale and Sørensen: 24, figs 18, 19.

 2015 *Parabrachylepas ifoensis* (Withers); Gale and Sørensen: 239, fig. 17A-V.

**Diagnosis**. As for genus.

**Type**. A tergum figured by Withers (1935, pl. 10 fig.4) is holotype (NHMUK In. 29410). upper lower Campanian, Ivö Klack, Skåne, southern Sweden.

**Material**. Several hundred valves from the upper lower Campanian, Ivö Klack, Skåne, southern Sweden.

**Description**. See Gale in Gale and Sørensen 2014, p. 24.

**Remarks**. *Parabrachylepas ifoensis* possessed distinctive and unusually shaped terga which are rectangular with a single carinal margin (Fig. 27E, F) and have scars on the interior basal and scutal margins for insertion of tergal depressor muscles (Fig. 27E). The species is known only from Ivö Klack.

Genus ***Epibrachylepas*** Gale, in Gale and Sørensen, 2014

**Diagnosis**. Scutum low, triangular, tergal notch deep, articular ridge present. Tergum kite-shaped, bearing large scutal auricle, tergal depressor scars on interior of lower carinal margin; reticulate sculpture on all plate exteriors. Marginal plate triangular, robust.

**Type species**. *Epibrachylepas newmani* Gale, in Gale and Sørensen, 2014.

**Included species**. *Mitella smeetsi* Bosquet, 1857.

**Remarks**. *Epibrachylepas* is the most derived brachylepadid known; the shape of the scutum, the interpenetrant articulation between the scutum and tergum (Fig. 6E; Fig. 28D-F) and the presence of discrete tergal retractor scars on the lower carinal margin of the tergum approach the condition in seen in balanomorphs (compare Fig. 6E, F). A pair of marginal plates are present (Fig. 28I, J). The reconstruction (Fig. 2F) shows a low profile and bears a resemblance to basal balanomorphs such as *Catophragmus* (Fig.2C, D) which retain imbricating plates.

Figure 28

***Epibrachylepas newmani*** Gale, in Gale and Sørensen, 2014

(Fig. 28A-X)

2014 *Epibrachylepas newmani* Gale, in Gale and Sørensen: 21, fig. 16A-R, fig. 17A-L.

2015 *Epibrachylepas newmani* Gale; Gale and Sørensen: 238, fig. 16A-N.

**Diagnosis**. *Epibrachylepas* in which the articular region of the scutum which contacts the tergum is short and angled to the surface of the valve.

**Types**. A well preserved tergum (Fig. 16E of Gale, in Gale and Sørensen, 2014) is holotype (NHMUK IC 858). The other valves figured by Gale, in Gale and Sørensen (2014) are paratypes (NHMUK IC 825, 830, 831, 855-868). All are from the upper lower Campanian, Ivö Klack, Skåne, southern Sweden.

**Material**. Several hundred valves from the upper lower Campanian, Ivö Klack, Skåne, southern Sweden.

**Remarks**. *E. newmani* differs from *E. smeetsi* in the nature of the articular region of the interior of the scutum (see below).

***Epibrachylepas smeetsi*** (Bosquet, 1857)

(Fig. 28V, W)

1857 *Mitella smeetsi* Bosquet: 28, pl 3 figs 11a-c.

1935 *Proverruca (?) smeetsi* (Bosquet); Withers: 336, pl. 45 fig. 6.

2014 *Epibrachylepas smeetsi* (Bosquet); Gale, in Gale and Sørensen: 20.

**Diagnosis**. *Epibrachylepas* in which the internal articular region with the tergum forms a broad, concave surface, largely in the plane of the valve’s surface.

**Types**. A lectotype scutum (Bosquet 1857, pl. 3 figs 11a-c) was selected by Withers (1935 p. 337), described as being in the collection of J. Smeets, whereabouts unknown. A second poorly preserved scutum in the Bosquet collection was in the NHMB but cannot be located (Feb. 2022). Maastrichtian, between Vilt and Sibbe, Limbourg, Netherlands.

**Material**. 2 scuta, both apparently lost. No further material has been found (J. Jagt, pers. comm).

**Description**. This is based on Bosquet’s original figure (1857 pl. 3 figs 11a-c), reproduced here (Fig. 28V, W). Scutum small (total length 7.5 mm, *fide* Withers 1935, p. 337), robust, triangular with elongated, gently convex basal margin. Occludent margin convex, tergal margin slightly concave, short. External sculpture reticulate, comprising weak apicobasal striations intersecting with stepped growth increments. Interior of valve with flattened region parallel with occludent margin and very large, oval scutal adductor scar, extending nearly to basal margin. Large, concave articular surface for tergum, comprising tergal notch confluent with articular furrow; articular ridge low, weakly defined.

**Remarks**. The shape and external sculpture of the scutum of *E. smeetsi* are similar to those of *E. newmani,* but the interior region articulating with the tergum is very different. In *E. smeetsi*, the articular furrow, articular ridge and tergal notch (see Fig. 6 for detailed nomenclature) form a broad (nearly half the length of the valve), concave, triangular region in which a low articular ridge separates the furrow and the notch. In contrast, in *E. newmani* the tergal notch, articular ridge and furrow form a short tergal margin (Fig. 28D, E).

Genus ***Crithmumlepas*** nov.

**Diagnosis**. Carina hemiconical, tall, reclined dorsally; rostrum low, triangular; terga rhombic to kite shaped; outline of scuta isosceles triangle; sculpture of evenly spaced rows of commarginal beads.

**Type species**. *Crithmumlepas hoensis* sp. nov.

**Included species**. *Crithmumlepas aycliffensis* sp. nov.

**Derivation of name**. After Samphire Hoe, Dover, the type locality; the generic name of Rock Samphire is *Crithmum*.

**Remarks**. *Crithmumlepas* gen. nov. is included in the brachylepadids on account of the tall, hemiconical, dorsally reclined carinae and possession of a strong apicobasal ridge on the terga. The carinae and terga bear some resemblance to those of *Fallaxlepas* in shape (compare Fig. 26E, G with Fig. 29C-E, O, P, T-V), but the rostra are low. The highly distinctive sculpture of all valves separates the genus from all other genera. Imbricating plates and upper latera are unknown.

Figure 29

***Crithmumlepas hoensis*** sp. nov.

(Fig. 29O-X)

**Diagnosis**. *Crithmumlepas* in which the apicobasal ridge of the tergum is narrow and bears a single column of nodes.

**Types**. The tergum figure here (Fig. 29V) is holotype (NHMUK PI In 64911), all other figured valves are paratypes (NHMUK PI In 64912-64920). Grey Chalk Subgroup, Zig Zag Formation, middle Cenomanian, *Turrilites acutus* ammonite subzone (46.4 m on log of Kennedy and Gale, 2006 fig. 2), Samphire Hoe, west of Dover, Kent, UK.

**Material**. 58 valves, including rostra, carinae, scuta and terga. All from the type locality and horizon.

**Derivation of name**. After Samphire Hoe, Dover, the type locality.

**Description**. Terga rhombic to kite-shaped (Fig. 29O, P, T-V), scutal margin weakly concave, occludent margin straight to slightly convex. Apicobasal ridge curved ventrally, comprises a raised region carrying irregularly developed elongated nodes. Scutum (Fig. 29W) fragmentary, outline triangular, sculpture comprises evenly spaced, commarginal, rows of beaded nodes, weak apicobasal ridges present adjacent to occludent margin. Height of carinae (Fig. 29Q, R-S) 1.5 times maximum breadth, tapering apically, hemiconical, with reticulate external sculpture. Upper latus and imbricating plates unknown.

**Remarks**. The species differs from the later *C. aycliffensis* sp. nov. in the narrower apicobasal ridge on the tergum, which carries a single column of nodes.

**Occurrence**. The species is only known from the middle Cenomanian at Dover, Kent and is relatively common at the 46.4 m level in the *T. acutus* ammonite subzone (Kennedy and Gale, 2006 fig. 2), but rarely ranges up to 52 m in the same unit at Dover. It is replaced at 56 m (*Acanthoceras jukesbrownei* ammonite zone) by *C. aycliffensis* sp. nov.

***Crithmumlepas aycliffensis*** sp. nov.

(Fig. 29A-N)

**Diagnosis**. *Crithmumlepas* in which the apicobasal ridge of the tergum is broad and carries regularly spaced bands of 4-6 beaded nodes.

**Types**. A well preserved tergum (Fig. 29A) is holotype (NHMUK PI In 64927); the other figured valves are paratypes (Fig. 29B-N; NHMUK PI In 64921-64926, 64928-64929). The holotype and some paratypes (Fig. 29B-F, H-N) come from the *Calycoceras guerangeri* ammonite zone at Aycliff, west of Dover, Kent, UK. A paratype tergum (Fig. 29G) comes from the lower Coniacian of Cuckmere, Sussex, UK.

**Material**. 14 valves (terga, scuta, carinae, rostra) from the middle Cenomanian *Acanthoceras jukesbrownei* to the Upper Cenomanian *Calycoceras guerangeri* ammonite zones at Dover, Kent (56-72.5m on the log of Kennedy and Gale 2006, fig. 2). A single tergum from the lower Coniacian Lewes Chalk Formation at Cuckmere, Sussex, UK.

**Derivation of name**. After the community of Aycliff, west of Dover, Kent, where the type material was collected.

**Description**. Terga (Fig. 29A, B, G, H, J) kite shaped, occludent and upper carinal margins shorter than lower carinal and scutal margins; basal angle rounded. Apicobasal ridge flat-topped, broadens basally, carries evenly spaced transverse rows of 4-6 beaded nodes. Scutal and carinal surfaces bear evenly spaced, commarginal rows of nodes which coalesce into ridges on some specimens (Fig. 29H) and protrude from the upper carinal margin. Scuta with isosceles triangular outline (Fig. 29K, L), occludent margin longer than basal and tergal margins. Sculpture of evenly and widely spaced rows of commarginal nodes, conjoined by weak apicobasal striations. Interior of scutum (Fig. 29L) with large, central, scutal adductor scar, and shelf along occludent margin. Carina (Fig. 29C-E) hemiconical, reclined dorsally, height greater than maximum breadth, tapering evenly to apex. Sculpture of numerous, transverse, evenly spaced nodes and weak, fine, apicobasal ridges. Rostrum (Fig. 29M, N) triangular, as broad as high, with reticulate sculpture.

**Remarks**. This species differs from the older *C. hoensis* sp. nov. in the flat-topped, basally broadening apicobasal ridge on the tergum, and the rounded basal angle of the tergum.

**Occurrence**. The species occurs uncommonly in the middle Cenomanian *Acanthoceras jukesbrownei* Zone and the upper Cenomanian *Calycoceras guerangeri* Zone west of Dover, Kent. A single tergum was collected from the lower Coniacian at Cuckmere, Sussex, UK.

Genus ***Calvatilepas*** nov.

**Diagnosis**. Scuta strongly inclined dorsally, convex occludent margin bears raised strip parallel to edge; carinae tall, strongly recurved dorsally; imbricating plates with internal shelf and flat-topped apicobasal ridge.

**Type species**. *Calvatilepas recurvus* sp. nov. by monotypy.

**Derivation of name**. Calvatia, latin meaning bald, with reference to the smooth exterior of the plates.

**Remarks**. I had originally assigned the scuta of this species to the stramentid *Loriculina*, but the discovery of diverse other valves, including rostra, carinae and imbricating plates indicates that it is correctly placed in the Brachylepadidae. The tall, dorsally recurved carinae (Fig. 12M, U) are broadly similar in shape, if not in sculpture, to those of *Crithmumlepas* gen. nov., and the imbricating plates, which possess an internal shelf like those of *Brachylepas* species (compare Fig. 12I, J with Fig. 23Q-S and Fig. 26H, I) and an external apicobasal ridge support the provisional assignation to Brachylepadidae.

***Calvatilepas recurvus*** sp. nov.

(Fig. 12G-Z)

**Diagnosis**. As for genus

**Types**. A scutum (Fig. 12G, H) is the holotype (NHMUK PI In 64818), from the upper Cenomanian *C. guerangeri* ammonite zone, west of Dover, Kent, UK. The other illustrated valves (Fig. 12I-Z) are paratypes (NHMUK PI In 64819-64834).

**Material**. 35 valves (scuta, carinae, rostra, tergum, imbricating plates) from Grey Chalk Subgroup, Zig Zag Formation, upper Cenomanian *Calycoceras guerangeri* ammonite zone, at Shakespeare Cliff, west of Dover, Kent, UK (68-72 m, log of Kennedy and Gale, 2006 fig. 2). A single scutum from the West Melbury Chalk Formation, Cambridge Greensand Member, *Neostligoceras carcitanense* ammonite subzone, Barrington, Cambridgeshire, UK.

**Derivation of name**. Recurvus, recurved, with reference to the recurved, reclined carina.

**Description**. Scuta (Fig. 12G, H, N, V-Z) triangular, strongly inclined dorsally, occludent margin evenly convex, basal margin straight. A raised rim parallels the occludent margin; large, obliquely directed primordial valves form the apices of the scuta. Along the apicobasal line a poorly defined, slightly elevated region is present, extending to the basiscutal margin. Surface of scuta with weak growth lines; interior of scuta (Fig. 12H, Y) with internal shelf along occludent margin, scutal adductor scar not clearly marked. Tergum (Fig. 12L) triangular, exterior smooth. Height of carinae 2-3 times greater than maximum breadth (Fig. 12K, M, O, U); carinae strongly recurved dorsally (Fig. 12M), external surface with weak apicobasal line. Rostra (Fig. 12Q-T) variable in height, externally strongly convex, some inclined laterally (Fig. 12U). Imbricating plates (Fig. 12I, J) rhombic, bearing flat apicobasal ridge and interior basal shelf.

**Remarks**. This unusual species is common in the *Calycoceras guerangeri* ammonite zone at Dover and is also known from the lower Cenomanian *Neostlingoceras carcitanense* ammonite subzone at Barrington, Cambridgeshire, UK.

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**Figure Captions**

**Figure 1.**

Comparative morphology of thoracican cirripedes. **A**, balanomorph *Chionelasmus darwini* (Pilsbry, 1907) in lateral view. **B, C**, verrucid *Altiverruca quadrangularis* (Hoek, 1883), lateral views. **D**, scalpellid *Amigdaloscalpellum mamillatum* (Aurivillius, 1898), lateral view. **Abbreviations:** **MT, MS**, moveable scuta and terga; **FS, FT**, fixed scuta and terga; **ped**, peduncular. Not to scale.

**Figure 2.**

Comparative morphology of cirripedes. **A, B, S**, *Pedupycnolepas articulata* (Collins, 1980); **A**, cast of group of 3 specimens; **B**, reconstruction of peduncle; **S**, reconstruction. **C, D**, balanomorph *Catophragmus pilsbryi* Broch, 1922, in apical (**C**) and lateral (**D**) views. **E**, brachylepadid *Parabrachylepas ifoensis* (Withers, 1935), reconstruction in lateral view. **F**, brachylepadid *Epibrachylepas newmani* Gale, 2014b, reconstruction in lateral view. **G-I, R,** *Etcheslepas durotrigensis* Gale, 2014a, lateral views of articulated individuals (**G-I**); **R**, reconstruction. Note peduncle and presence of numerous lateral plates. **J-L**, Verrucid *Gibbosaverruca* sp., note loss of peduncle and 6 plated shell with strong asymmetrical differentiation of fixed and moveable scuta and terga (see also Fig. 3I-L). **M, N, Q**, shell of *Brachylepas naissanti* (Hébert, 1855) in lateral (**M**) and apical (**N**) views; **Q**, reconstruction, lateral view. Note large, hemiconical rostrum and carina and whorls of surrounding imbricating plates. **O-Q**, reconstructions of brachylepadids in lateral view. **A**, *Fallaxlepas fallax* (Darwin, 1851a). **B**, *Brachylepas guascoi* (Bosquet, 1854). **C**, *Brachylepas naissanti* (Hébert, 1855). **T**, *Pycnolepas rigida* (J. de C. Sowerby, 1836), reconstruction in lateral view. **U**, *Eoverruca hewitti* Withers, 1935, reconstruction in lateral view. A, B, Aptian, Antarctic Peninsula; C, D, Recent, Panama; E, F, P, based on material from Campanian of Ivö Klack, Sweden; G-I, R, Tithonian, Kimmeridge Clay, Dorset, UK; J-L, Recent, Indian Ocean off Madagascar; M, N, O, upper Campanian, Norwich, Norfolk, UK; O, based on material from Maastrichtian, Rügen, Germany; T, based on material from Upper Albian, UK; U, based on material from Santonian, Suffolk, UK. Reconstructions (E, F, O-U not to scale. Colour key as in Fig. 1. **Abbreviations: c**, carina; **r**, rostrum; **rl**, rostrolatus; **s**, scutum; **ul**, upper latus. Scale bars equal 5mm.

**Figure 3.**

Morphology of upper latera and peduncular/imbricating plates. **A-C**, *Etcheslepas durotrigensis* Gale, 2014; **A**, exterior view of upper latus; **B**, upper latus and other lateral plates on capitulum; **C**, peduncular plates. **D, E, J-N**, *Pycnolepas rigida* (J. de C. Sowerby, 1836); upper latus in external **(D**) and internal (**E**) views; **J-N** peduncular plates. **F, G, O, S**, *Brachylepas naissanti* (Hébert, 1855), upper latus in external (**F**) and internal (**G**) views; external (**O**) and internal (**S**) views of imbricating plates. **H, I, Q, R**, *Parabrachylepas ifoensis* (Withers, 1935), upper latus in external (**H**) and internal (**I**) views; **Q, R**, imbricating plates. **T-W**, *Eoverruca hewitti* Withers, 1935; imbricating plates. **P**, *Catophragmus pilsbryi* Broch, 1922; interior view of imbricating plates. **X**, *Brachylepas americana* Zullo, Russell and Mellen, 1987, interior view of articulating imbricating plates. Scale bars equal (B, D, E, P) 5 mm; A, C, X, 1 mm; all others, 0.5 mm.

**Figure 4**

Terga and scuta of selected verrucomorph cirripedes, to show asymmetrical development and progressive differentiation of fixed and moveable valves. See text for discussion. **A-D**, *Pycnolepas rigida (*J. de C. Sowerby, 1836), terga (**A, B**) and scuta (C, D). **E-H**, *Eoverruca hewitti* Withers, 1935, slight but distinct asymmetry of terga (**E, F**) and scuta (**G, H**). **I-L**, *Gibbosaverruca* sp., Strong asymmetry of terga (**I, J**) and scuta (**K, L**). **M-P**, *Verruca stroemia* (O. F. Müller, 1776), note major differences in structure of fixed and moveable valves in terga (**M, N**) and scuta (**O, P**). A-D, upper Albian, Gault Clay, Kent, U.K. E-H, upper Santonian chalk, Suffolk, U.K. I-L, Recent, Indian Ocean, off Madagascar. M-P, Recent, Donegal, Republic of Ireland.. **Abbreviations: abr**, apicobasal ridge; **ow**, occludent wing. Scale bars equal A-D, I-L, 5 mm; E-H, M-P, 0.5 mm.

Figure 5.

Nature of scutal-tergal articulations in thoracican cirripedes. **A**, *Calantica* sp. (Calanticomorpha); **B**, *Capitulum* sp*.* (Pollipedimorpha); **C**, *Faxelepas bruennichi* (Withers, 1914a) – Brachylepadomorpha, Pycnolepadidae); **D**, *Brachylepas guascoi* (Bosquet, 1854) – Brachylepadidae); **E**, *Epibrachylepas newmani* Gale, 2014b – Brachylepadomorpha, Brachylepadidae); **F**, *Octomeris sulcata* (Darwin, 1854) – Balanomorpha, Chthalamidae).

Plesiomorphically (A, B), the scutum simply rests on the tergum, a weak tergal notch (tn, green) rests upon a poorly defined scutal auricle (sa, green). The upper latus infills the gap between scutum and tergum, and articulates with both (brown, x, y). In more derived forms (C, D, E), the scutal auricle and tergal notch become better defined and the articulation is more precise. In balanomorphs (F) the upper latus is lost, and the articulation between scutum and tergum is interpenetrant, and a prominent articular ridge (ar) on the scutum fits into an articular furrow (af) on the tergum. The scutal auricle and tergal notch are retained, and the regions of the scutum and tergum which previously articulated with the upper latus become a further articulation, the scutal wall (sw) and tergal wall (tw). Not to scale.

**Figure 6.**

Comparative morphology of terga and scuta. **A-C**, pycnolepadid *Pycnolepas rigida* (J. de C. Sowerby, 1836), **A, B**, external and internal views of scutum; **C**, external view of tergum. **F**, **G, H, M, N**, brachylepadid *Epibrachylepas newmani* Gale, in Gale and Sørensen, 2014; external (**F**), internal (**G**), tergal (**H**) views of scuta, note presence of articular ridge (ar); **M**, **N**, external and internal views of terga; insertion sites for tergal depressor muscle indicated (td). **D, E, O-Q**, balanomorph *Octomeris brunnea* (Darwin, 1854); D, E, external (D) and tergal (E) views of scutum, note articular ridge (ar) and furrow (af); O-P, tergum, in external (O), internal (P) and scutal (Q) views of tergum; note scutal auricle (sa) and articular furrow (af). I-L, brachylepadid *Brachylepas guascoi* (Bosquet, 1854); internal (I) and external (J) views of terga; K, L, external (K) and internal (L) views of scutum. **Abbreviations: ar**, articular ridge; **af,** articular furrow; **td**, tergal depressor muscle site; **sa**, scutal auricle; **tn**, tergal notch. Scale bars equal A-C, I-L, 5 mm; all others 1 mm.

**Figure 7.**

Morphological features of the rostrum and carina in brachylepadomorphs, verrucomorphs and balanomorphs. **A-D**, *Faxelepas paronai* (De Alessandri, 1895 - Pycnolepadidae); **A**, ventral view of rostrum, **B**, lateral view of rostrum; **C**, dorsal view of carina, **D**, interior view of carina. **E, F**, *Etcheslepas durotrigensis* Gale, 2014a; external views of rostrum (**E**) and carina **(F). G-J,** *Brachylepas naissanti* (Hébert, 1855); ventral view (**G**) and internal view (**H**) of rostrum; dorsal view (**I**) and internal view (**J**) of carina. **K-N**, *Catophragmus pilsbryi* Broch, 1922 – Catophragmidae, Balanomorpha). Ventral **(K**) and internal (**L**) views of rostrum; dorsal (**M**) and internal (**N**) views of carina. **O-R**, *Eoverruca hewitti* Withers, 1935 – Eoverrucidae); ventral (**O**) and internal (**P**) views of rostrum; dorsal (**Q**) and internal (**R**) views of carina. **S, U**, *Gibbosaverruca* sp. (Verrucidae); external views of rostrum (**S**) and carina (**U**). **T, V**, *Verruca stroemia* (O. H. Müller, 1776); external views of rostrum (**T**) and carina (**V**). Scale bars equal A-D, 10 mm; E-N, 5 mm; S-V, 5mm; O-R, 0.5 mm.

**Figure 8.**

Comparative morphology of capitular plates of pollicipedid *Etcheslepas fragilis* (Withers, 1928; **A, B, F, G, J-L, O, P**) and pycnolepadid *Pycnolepas scalaris* (Withers, 1914a; **C-E, H, I, M, N, Q**). External views of terga (**A-D**), scuta (**F, I**), upper latera (**E, J**), carinae (**K-N**) and rostra (**O-Q**). The overall structural and sculptural similarity of the valves can be viewed as evidence of close phylogenetic relationship. However, *E. fragilis* possesses numerous lateral plates, absent in *P. scalaris*. A, B, F, G, J-L, O, P, upper Kimmeridge Clay, Tithonian, *Pavlovia pallasioides* ammonite zone, Portland, Dorset, UK. C-E, H, I, M, N, Q, Grey Chalk subgroup, Middle Cenomanian *Turrilites acutus* ammonite subzone, Dover, Kent, UK. Scale bars equal; A, B, F, G, J, K, L, O, P, 0. 5 mm; all others 0.2 mm.

**Figure 9.**

Stratigraphical distribution of taxa discussed in this paper.

**Figure 10.**

**A**, consensus cladogram (MPT) based on analysis of 48 morphological characters (Tables 1, 2) and 18 OTUs, of which 7 are extant taxa. *Capitulum* Gray, 1825 and *Pollicipes* Leach, 1870 were used as an outgroup for the 16 in-group OTUs. One of the 48 characters was treated as continuous, using TNT (Goloboff & Catalano 2016), all other characters were treated as unordered. Using the implicit enumeration tree search, both equal weights (EW) and implied weights analyses were implemented. Both analyses produced very similar single most parsimonious trees (MPT). GER, Gap Excess Ratio (Wills, 1999).

**B**, molecular tree based on mitogenome analysis, which shows Verrucomorpha as basal to all other Thoracicalcarea (after Gan et al., 2022 fig. 4). All other molecular and morphological studies place balanomorphs and verrucomorphs as sister groups.

**C**, thoracican cirripede classification and inferred phylogeny, based on nuclear genes and morphology, after Chan et al. (2021, fig. 10). Note the close relationship of verrucomorphs and balanomorphs.

**Figure 11.**

Parallel evolution to sessile mode of life between the balanomorph-verrucomorph clade (left) and the neolepadoid clade (right).

Verrucomorph-balanomorph clade; **A**, *Etcheslepas durotrigensis* Gale, 2014a; **B**, *Pedupycnolepas articulata* (Collins, 1980); **C**, *Pycnolepas rigida* (J. de C. Sowerby, 1836); **D**, *Brachylepas naissanti* (Hébert, 1855); **E**, *Eoverruca hewitti* Withers, 1935; **F**, *Epibrachylepas newmani* Gale, 2014b; **G**, *Altiverruca quadrangularis* (Hoek, 1883); **H**, *Catomerus polymerus* Darwin, 1854. Neolepadoid clade; **I**, *Ashinkailepas seepiophila* Yamaguchi, Newman and Hashimoto, 2004; **J**, *Neoverruca brachylepadiformis* Newman, 1989; **K**, *Imbricaverruca yamaguchii* Newman, 2000; **L**, *Neobrachylepas relica* Newman and Yamaguchi, 1995. Each lineage begins with pedunculate forms, and both subsequently give rise to asymmetrical forms with progressive differentiation of fixed and moveable valves (Verrucomorpha, Neoverrucidae) and symmetrical, low-profile forms with hemiconical carinae and rostra surrounded by imbricating plates (Balanomorpha, Neobrachylepadidae). Important differences between the two lineages include the distinctive paired processes on the apical interior of the scuta (Neolepadoidea, J-L) absent in the balanomorph-verrucomorph lineage. Additionally, molecular data consistently places the lineages in separate clades (see text). **Abbreviations: MT, MS**, moveable scuta and terga; **FS, FT,** fixed scuta and terga.

**Figure 12.**

**A-D**, *Pedupycnolepas lamellatus* sp. nov. **A, B**, holotype scutum (NHMUK PI In 64815) in internal (**A**) and external (**B**) views. **C, D**, carinae (NHMUK PI In 64816, 64817) in dorsal view. **E, F**, *Pedupycnolepas pulcher* Gale, 2019. **F**, holotype tergum in external view, original of Gale (2019, fig. 11B; NHMUK IC 1397). **E**, paratype rostrum, ventral view, original of Gale (2019 fig. 11F; NHMUK IC 1398). **G-Z**, *Calvatilepas recurvus* gen et sp. nov. **G, H, V-Z,** scuta (NHMUK PI In 64818, 64831-64834) in external (**G, N, V-X, Z**) and internal (**H, Y**) views. **G, H**, is holotype (NHMUK PI In 64818), all other specimens are paratypes**. I, J**, peduncular plate (NHMUK PI In 64819) in external (**I**) and internal (**J**) views. **K, M, O, Q, S, U**, carinae (NHMUK PI In 64820, 64822, 64824, 64826, 64828, 64830) in dorsal (**K, O, S, U**), lateral (**M**) and internal (**Q**) views. **P, R, T**, rostra (NHMUK PI In 64825, 64827, 64829) in ventral views. **L**, possible tergum, in external view (NHMUK PI In 64821). A-D, Grey Chalk Group, Cambridge Greensand Member, lower Cenomanian, *Neostlingoceras carcitanense* ammonite subzone, Barrington, Cambridge, UK. E, F, G-Z, Grey Chalk Group, Zig Zag Formation, upper Cenomanian *Calycoceras guerangeri* ammonite Zone, 70-72m, Shakespeare Cliff, west of Dover, Kent, UK (Kennedy and Gale, 2006, fig. 2). E, F, Lower Hauterivian *Endemoceras amblygonium* ammonite zone, Engelbostel, near Hannover, Germany. Scale bars equal; F, 1 mm; E, 0.5 mm; A-D, G, H, K, L, N-V, X-Z, 0. 2 mm; M, W, 0.1 mm

**Figure 13.**

**A-Q,** *Pycnolepas rígida* (J. de C. Sowerby, 1836). **A-C,** scuta, in external (**A, C**) and internal (**B**) views (A, B, NHMUK PI In 64835, B, 64835a). **D-F**, peduncular plates, originals of Gale (2014b, fig. 4K-O; NHMUK In. 3224-9). **I**, tergum external view, original of Gale (2014b, fig. 4I; NHMUK IC 1032). **J,** carina, dorsal view (NHMUK PI In 64837). **K, L, Q,** rostra; **Q**, ventral view, original of Gale (2020, fig. 4T; NHMUK IC 1035); **K, L**, external ventral (**L**) and internal (**K**) views (NHMUK PI In 64838). **M-P**, upper latera; M, N, original of Gale (2014b, fig. 4R; NHMUK IC 1033). **O, P** (NHMUK PI In 64840) in external (**N, P**) and internal (**M, O**) views. **R-Z**, *Pycnolepas batchelorum* sp. nov. R, S, paratype upper latera (NHMUK PI In 64842, 64843) in internal (**R**) and external (**S**) views. **T-V**, terga (T, holotype, NHMUK PI In 64844, U, V, paratypes NHMUK PI In 64845, 64846) in external views. **W, X**, paratype scuta (NHMUK PI In 64847, 64848) in external views. **Y, Z,** paratype carinae (NHMUK Pi In 64849, 64850) in dorsal views. A, B, J, O, P, Gault Formation, upper Albian, *Hysteroceras orbignyi* ammonite Subzone, Ford Place, Wrotham, Kent, UK. I, M, N, Q, *Hysteroceras varicosum* ammonite subzone, Naccolt, near Wye, Kent, UK. C, middle Albian, Argiles à Tegulines, *Lyelliceras lyelli* ammonite zone, Aube, France. D-H, basal Gault Formation, lower Albian, 21 Acre Pit, Miletree Farm, Leighton Buzzard, Bedfordshire, UK. K, L, basal Gault Formation, lower Albian, Munday’s Hill, Leighton Buzzard, Bedfordshire, UK. R-Z, Bargate Formation, upper Aptian, Guildford, Surrey, UK. Scale bars equal; A-C, I-N, O-Q, 5 mm; D-H, 1 mm; R-Z, 0.3 mm.

**Figure 14.**

**A-U**, *Pycnolepas scalaris* (Withers, 1914a). **A-C**, external views of terga (NHMUK PI In 64851-64853). **D, E, T, U**, carinae (NHMUK PI In 64854, 64855, 64869,) in external (**D, E, U**) and internal (**T**) views. **F-H, J,** scuta (NHMUK PI In 64856-64858, 64860) in (**F-H)** external and (**J**) internal views. **I, K-P**, rostra (NHMUK PI In 64862-64866) in ventral (**I, K, L, N, P**), lateral (**M**) and internal (**O**) views. **Q-S**, upper latera (NHMUK PI In 64867-64869) in external (**Q, S**) and internal (**R**) views. All from Grey Chalk Group, Zig Zag Formation, middle Cenomanian *Turrilites acutus* ammonite Subzone, 46.4 m (Kennedy and Gale, 2006, fig. 2), Samphire Hoe, west of Dover, Kent, UK. Scale bars equal 0.2 mm.

**Figure 15**.

**A-L**, *Faxelepas paronai* (De Alessandri, 1895). **A, B,** Upper latus, in exterior (**A**) and interior (**B**) views, original of Gale (2020c, pl. 2 fig. 5; NHMUK IC 1826). **C-F**, scuta, in external (**C, F**) and internal (**D, E**) views. Originals of Gale (2020c, pl. 2 figs 2-4; NHMUK IC 1823-1825). **G, H**, rostrum, in ventral (**G**) and internal (**H**) views (original of Gale 2020c pl. 2 fig. 11; NHMUK IC 1831). **I, J,** carina, in dorsal (**I**) and internal (**J**) views, original of Gale (2020c pl. 2 fig. 9; NHMUK IC 1829). **K**, external views of tergum, original of Gale (2020 pl. 2 figs 6; NHMUK IC 1827). **L-W**, *Faxelepas bruennichi* (Withers, 1914a). **M, N**, upper latus, in external (**M**) and internal (**N**) views (NHMUK PI In 64871). **O**, carina, in dorsal view (NHMUK PI In 64872). **P**, carina in dorsal view, original of Gale (2014b, fig. 4A; NHMUK IC 1022). **Q**, ventral view of rostrum (NHMUK PI In 64873). **L. R, S,** scuta, in internal (**L, S**) and external (**R**) views (NHMUK PI In 64875-64877). **T**, tergum in external view (NHMUK Pi In 64878). **U, V, W, X**, imbricating plates, in external (**V, W**), lateral (**X**) and internal (**U**) views (NHMUK PI In 64879-64881). **Y-A2**, *Faxelepas landenica* (Withers, 1953). **Y, Z**, external and internal views of scutum (NHMUK In. 38043). **A1**, rostrum, ventral view (NHMUK In. 38046). **A2**, tergum, external view (NHMUK In. 38045). A-K, Plio-Pleistocene, Rodrigues Ridge, Indian Ocean. L-X, middle Danian, Faxe, Denmark. Y-A2, Selandian, Heers Formation, Wansin, NE of Namur, Belgium. Scale bars equal; C-L, 10 mm; A, B, M-S, Y-A1, 5 mm; T-V, W, X, 0.4 mm.

**Figure 16.**

**A-X**, *Eoverruca hewitti* Withers, 1935. **A-F**, calcified basis, incorporating imbricating plates, in basal (**A, E, F**), apical (**B**) and lateral (**C, D**) views, originals of Gale 2014b, fig. 17A-F (NHMUK IC 1066). **G-N**, imbricating plates, in external (**H, I-K, M, N**) and internal (**G, L**) views, originals of Gale 2014b, fig. 18A-H (NHMUK IC 1070-1076). **O, P**, fixed scutum in internal (**O**) and external (**P**) views, original of Gale 2014b fig. 19K, L (NHMUK IC 1061). **Q-U**, imbricating plates, originals of Gale 2014b fig. 17G-K (NHMUK IC 1060, 1067, 1068). **V**, moveable scutum, original of Gale 2014b fig. 19J (NHMUK IC 1065). **W**, moveable tergum, original of Gale 2014b, fig. 19A (NHMUK IC 1063). **X**, fixed tergum, external view (NHMUK IC 1064). Upper Santonian, *Uintacrinus socialis* Zone, Hinderclay Lane, Wattisfield, Suffolk, UK. Scale bars equal 0.5 mm.

**Figure 17.**

Distribution of *Eoverruca hewitti* in the upper Santonian *Uintacrinus socialis* zone across Europe, from Biocieniec, near Warsaw, Poland (5) through the Anglo-Paris Basin (1-4). The species occurs commonly within the lower part of the range of the zonal crinoid.

**Figure 18.**

**A, B,** *Eoverruca aubensis* Gale, 2020a, holotype scutum in internal (**A**) and external (**B**) views, original of Gale (2020a fig. 14I, J; NHMUK IC 1566). **C-K**, *Eoverruca hewitti* Withers, 1935. **C**, small moveable scutum, original of Gale, 2014b, fig. 19M (NHMUK IC 1089). **D, F-H,** carinae, in internal (**D**), dorsal (**F, H**) and lateral (**G**) views, originals of Gale, 2014b, fig. 18I-L (NHMUK IC 1057, 1077, 1078). **E, I-K**, rostra, in internal (**E**), ventral (**I, K**) and lateral (**J**) views, originals of Gale 2014b, fig. 18M-P (NHMUK IC 1058, 1080-1082). **L-A4**, *Eoverruca symmetrica* Gale, 2020a, paratypes. **L-N,** calcified basis incorporating imbricating plates, original of Gale 2020a, fig. 14A-C (NHMUK IC 1552). **O, Q, R, T-V**, external views of terga, originals of Gale, 2020a, fig. 15, A, C, D, F-H (NHMUK IC 1557, 1559, 1561, 1563-1565). **P, S, X, Y,** scuta, in internal **(P**) and external (**S, X, Y**) views, originals of Gale, 2020a, fig. 15B, E, I, J (NHMUK IC 1558, 1562, 1566, 1567). **Z-A4**, carinae or rostra, in external (**Z, A4**), internal (**A1, A3**) and apical (**A2**) views, originals of Gale, 2020a, fig. 15L-P (NHMUK IC 1570-1573). **A5**, *Eoverruca barringtonensis* sp. nov. holotype, moveable tergum, external view (NHMUK PI In 64882). A, B, middle Albian, *Anahoplites intermedius* ammonite Subzone, Pogains, Aube, France. C-K, upper Santonian, *Uintacrinus socialis* Zone, Hinderclay Lane, Wattisfield, Suffolk, UK. L-A4, upper Campanian, *Belemnitella woodi* belemnite zone, uppermost Weybourne Chalk, Catton Grove, Catton, Norwich, Norfolk, UK. A5, Cambridge Greensand, lower Cenomanian, *Neostlingoceras carcitanense* ammonite Subzone, Barrington, Cambridgeshire, UK. Scale bars all equal 0.5 mm.

**Figure 19.**

**A-C, F-H**, *Youngiverruca ruegenensis* Gale, 2014b. **A-C**, paratype fixed scutum, in external (**A**), internal (**B**) and oblique (**C**) views, original of Gale (2014b, fig. 20J-L (NHMUK I. 6222), original of Withers 1923, pl. 2 figs 46a, b). **F-H**, holotype fixed tergum in external (**F**), lateral (**G**) and internal (**H**) views, original of Gale, 2014b, fig. 20F-H, Withers 1923, pl. 2 fig. 48 and Withers, 1935, pl. 45 fig. 13 (NHMUK In. 16224). **D, E, I-K** *Priscoverruca elongata* Gale, 2014b. **D, E,** paratype fixed scutum, in lateral (**D**) and internal (**E**) views, original of Gale, 2014b, fig. 22D, E (NHMUK 16225). **I-K,** holotype fixed tergum in external (**I**), lateral (**J**) and internal (**K**) views, original of Gale, 2014b, fig. 22A-C (NHMUK 16224). **L, M,** *Rostratoverruca baxteri* Gale, 2020b, holotype fixed scutum in external (**L**) and internal (**M**) views, original of Gale, 2020b, pl. 14 figs 1a, 1b (NHMUK IC 1768). **N, O**, *Rostratoverruca romettensis* (Seguenza, 1873). **N**, apical view of shell, original of Gale et al., 2021 pl. 5 fig. 7b. (PMC I. I. R. CIR-45). **O**, fixed tergum, external view, original of Gale et al*.,* 2021 pl. 5 fig. 11 (PMC R. I. Cal. CIR-49). **P**, *Rostratoverruca nexa* (Darwin, 1854), figured after Darwin, 1854, pl. 21 fig.5. **Q**, *Rostratoverruca pusilla* (Bosquet, 1857), figured after Bosquet, 1857 pl. 1 fig. 3. Specimens not found. Withers (1935) selected the rostrum (B) as lectotype. A-K, lower Maastrictian, Rügen, Germany. L, M, Plio-Pleistocene, Rodrigues Ridge, Indian Ocean. N, Recent, Mediterranean, off Sicily, Italy. O, Pliocene, Scoppo, near Messina, Sicily, Italy. P, Recent, West Indies. Q, Maastrichtian, locality uncertain, localities listed for species are St. Pietersburg, Guelhem, and between Vilt and Sibbe, Limburg, Netherlands. **Abbreviations: FT**, fixed tergum; **FS**, fixed scutum; **MS**, moveable scutum; **MT**, moveable tergum; **R**, rostrum; **C**, carina. Scale bars equal; A-C, F-H, L-O, 0.5 mm; D, E, I-K, 1 mm; P, Q, 2mm.

**Figure 20.**

**A-Y**, *Priscoverruca prisca* (Bosquet, 1854). **C-E, H-J**, fixed scuta, in internal (**A-E**) and external (**H-J**) views (NHMUK PI In 64883-64887). **F, G, K**, moveable scuta, in external **(F, G**) and internal (**K**) views (NHMUK PI In 64888-64890). **L-O, Q**, fixed terga, in external (**L, M**), lateral (**0**) and internal (**N, Q**) views (NHMUK PI In 64891, 64892). **P**, moveable tergum, external view (NHMUK PI In 64893). **R**, rostrum, oblique apical view (NHMUK PI In 64894). **S, T**, carina in external (**S**) and internal (**T**) views (NHMUK PI In 64895). **U**, apical view of complete shell, original of Withers (1913 fig. 2a, b; Withers, 1935 p. 342, figs 41, 42; Gale, 2014b fig. 3F (NHMUK In. 27156). **V, X, Y**, interior (**V**), apical (**X**) and lateral (**Y**) views of complete shell, original of Jagt and Collins 1989, fig. 4d (NHMUK In. 62170). **W**, interior view of entire shell, original of Jagt and Collins, 1989, fig. 4 (NHMUK In. 62171). A-T, upper Campanian, lower *Belemnitella mucronata* belemnite zone, Cringleford, Norwich, Norfolk, UK. U, upper Campanian, *Belemnitella mucronata* Zone, pit 154, Whitlingham, Norwich, Norfolk, UK. V-Y, upper lower Maastrichtian, Haccourt, Belgium. Scale bars all equal 0.5 mm.

**Figure 21.**

**A-F**, Bosquet’s type material of *Verruca prisca* Bosquet, 1854. **A, B**, fixed scutum, **A**, external, **B**, internal views, original of Bosquet, 1854, pl. 1 figs 1a, 1b. **C**, moveable tergum, original of Bosquet, 1854, pl. 1 fig. 3a. **D**, moveable tergum, not figured by Bosquet. **E, F**, fixed tergum, internal (**E**) and external (**F**) views, original of Bosquet, 1854, pl. 1 fig. 5. Material in the Brussels Natural History Museum, all from Maastrichtian of St. Pietersberg, Maastricht, Netherlands. G, reproduction of the upper part of plate 1 of Bosquet, 1854. Scale bars equal 0.5 mm.

**Figure 22.**

**A-D**, *Verruca jagti* Gale, 2014b. Holotype (NHMM JJ 13472), original of Gale, 2014b fig. 23A, **B**, a complete individual in internal (**B**), apical (**D**), lateral (**C**) views, with enlargement of moveable valves (**A**). **E-M**, *Verruca stroemia* (O. F. Müller, 1776), for comparison with fossil species. **E**, external view of moveable tergum; **F, G**, external and internal views of moveable scutum. **H**, internal view of shell; **I**, lateral view of shell; **J**, apical view of shell; **K**, oblique view of fixed tergum; **L, M,** fixed scutum, in internal (**L**) and external (**M**) views. A-D, from the ENCI-Heidelberg Cement Group quarry, Maastricht, southern Limburg, the Netherlands; Meerssen Member (Maastricht Formation, latest Maastrichtian), top 10 cm of subunit IVf-1 (hardground surface). E-M, Recent, Murvagh beach, County Donegal, Republic of Ireland. Scale bars equal; B-D, H-I, 1 mm; A, E-G, K-M, 0.5 mm.

**Figure 23.**

**A-S**, *Brachylepas naissanti* (Hébert, 1855). **A, B**, lateral (**A**) and apical (**B**) views of capitulum, original of Woodward, 1901, pl. 8 fig. 4; Withers, 1935, pl. 49 figs 1a, 1b; Gale and Sørensen, 2014, fig. 3A-D (NHMUK In. 27160). **C, D, G, J,** upper latera, external (**C, J**) and internal (**D, G**) views (NHMUK PI In 64896, 64900, 64901). **E, F, H, I**, carinae, in dorsal (**E, H**) and internal (**F, I**) views (NHMUK PI In 64897, 64898). **K**, tergum, external view (NHMUK PI In 64902). **L, M,** rostrum, in ventral (**L**) and internal (**M**) views (NHMUK PI In 64899). **N, O**, scutum, in external (**N**) and internal (**O**) views (NHMUK PI In 64903). **P-S**, imbricating plates, in external (**P-R**) and internal (**S**) views (NHMUK PI In 64904-64907). A, B, White Chalk Subgroup, *Belemnitella mucronata* belemnite zone, upper Campanian, pit 153, Thorpe, Norwich, UK. C-S, White Chalk Subgroup, lower *Belemnitella mucronata* belemnite zone, upper Campanian, Cringleford, Norwich, UK. Scale bars equal; A, B, 5 mm; all others 0.5 mm.

**Figure 24.**

**A-D**, *Fallaxlepas nervosa* (Alekseev, 2009). **A**, tergum, original of Alekseev 2009 pl. 4 fig. 20A; **B, C**, carina, in dorsal (**B**) and lateral (**C**) views, original of Alekseev 2009 figs 16A, 16B. **D**, rostrum in ventral view, original of Alekseev, 2009, fig. 15A. **E, F,** *Brachylepas hantonensis* Gale, 2020a. Holotype carina, original of Gale (2020a, fig. 16C, D) in apical (**E**) and lateral (**F**) views (NHMUK IC 1575). **G, H**, *Brachylepas thieli* Gale, 2020a, holotype carina, original of Gale (2020a, fig.16A, B) in apical (**G**) and lateral (**H**) views (NHMUK IC 1574). **I-Z**, *Brachylepas guascoi* (Bosquet, 1857). **I, J**, rostrum in internal (**I**) and ventral (**J**) views, original of Gale and Sørensen, 2014, fig. 15E, F (NHMUK IC 842). **K-M**, carina, in dorsal (**K**), lateral (**L**) and internal (**M**) views, original of Gale, in Gale and Sørensen, 2014, fig. 15A-C (NHMUK IC 841). **N, O**, apical views of small carinae, originals of Gale, in Gale and Sørensen, 2014, fig. 14O, P (NHMUK IC 839, 840). **P, Q,** scutum in external (**P**) and internal (**Q**) views, original of Gale, in Gale and Sørensen, 2014, fig. 14A, B (NHMUK IC 827). **R**, tergal view of scutum, original of Gale, in Gale and Sørensen 2014, fig. 14E (NHMUK IC 823). **S,** external view of tergum, original of Gale, in Gale and Sørensen, 2014, fig. 14C (NHMUK IC 825). **T-V**, upper latera, in oblique lateral (**T**), external (**U**) and internal (**V**) views, originals of Gale, in Gale and Sørensen, 2014, fig. 14I-K (NHMUK IC 826, 824, 836). **W-A1**, imbricating plates, in external (**W, X, Z**) and internal (**Y, A1**) views. Originals of Gale, in Gale and Sørensen, 2014, fig. 15J, K (NHMUK IC 909, 910) X (NHMUK IC 913). A-D, Maastrichtian, Beshkosh Mountain, southwest Crimea, Ukraine. E, F, Lewes Chalk Formation, upper Turonian, Froxfield, pit no. 112 of Brydone, 1912, Hampshire, UK. G, H, lower Cenomanian, Kassenberg, Mülheim-Broich, Germany. I-A1, upper lower Campanian, Ivö Klack, Skåne, Sweden. Scale bars equal; I-S, 5 mm; T-A1, 1 mm; E-H, 0.5 mm.

**Figure 25.**

**A-A1,** *Brachylepas americana* Zullo, Russell and Mellen, 1987. **A, B**, carina, in dorsal (**A**) and internal (**B**) views (NHMUK In. 62268a). **C**, scutum, view of tergal surface (NHMUK In. 62268b). **D-F**, scutum in tergal view (**C**), external (**D**) and internal (**E**) views (NHMUK In. 62268c). **G, H**, carina, in dorsal (**G**) and (**H**) internal views (NHMUK In. 62268d). **I, J,** scutum, in external (**J**) and internal (**K**) views (NHMUK In. 62268e). **K, L,** carina, in dorsal (**K**) and lateral (**L**) views (NHMUK In. 62268f). **M-O**, external views of terga (NHMUK In. 62268g-i). **P-R, X, Y**, imbricating plates, in external (**P, R, Y**) and internal **Q, X**) views (NHMUK In. 62268g-k). **Z, A1**, upper latera, in external (**Z**) and internal (**A1**) views (NHMUK In. 62268l, m). **S-W**, rostra, in ventral (**S, V**), apical (**T**) and internal (**U, W**) views (S-U, In. 62268n, V, W, In. 62268o). **A2-A5**, *Brachylepas angulosa* Collins, 1973. Holotype carina (NHMUK In. 64479), original of Collins, 1973 (pl. 3 fig. 16a-c) and Zullo et al. (1987, fig. 5 8-10). Apical (**A2**), dorsal (**A3**), lateral (**A4**) and internal (**A5**) views. A-Z, A1, basal Brownstown Formation, mid-Campanian, Friendship, Hot Spring County, Arkansas, USA. A2-5, Ripley, Formation, Maastrichtian, Oktibbeha County, Mississippi, USA. Scale bars equal; A-O, S-A5, 5 mm; P-R, X-A1, 0.5 mm.

**Figure 26.**

**A-K**, *Fallaxlepas fallax* (Darwin, 1851b). **A, B**, large scutum, external (**A**) and internal (**B**) aspects, original of Withers (1935, pl. 48 fig. 2; NHMUK In. I. 14466). **C, D**, upper latus, external (**C**) and internal (**D**) views, original of Woodward (1906, fig. 21) and Withers (1935, pl. 48 fig. 3; NHMUK In. 30121). **E,** tergum, external view (NHMUK I. 15766). **F**, carina, dorsal view (NHMUK IC 1578). **G**, associated valves, showing carina (c), rostrum (r) and scutum (sc), original of Gale (2020a, fig. 16J; Kutscher collection, Munich). **H, I**, imbricating plate, external (**H**) and internal (**I**) views (NHMUK PI In 64908). **J, K,** imbricating plate, external (**J**) and internal (**K**) views (NHMUK PI In 64909). **L**, tergum, external view (Kutscher collection, Munich). M, large carina, dorsal view (NHMUK In. 30125). **N**, rostrum, ventral view (NHMUK In. 30126). **O**, scutum, external view (NHMUK In. 30017). **P**, tergum, external view (NHMUK In. 30015). **Q, R**, large rostrum, external (**Q**) and internal (**R**) views (NHMUK In. 30129). **S, T,** rostrum, internal (**S**) and external (**T**) views (NHMUK In. 30130). **U**, small carina, dorsal view (NHMUK PI In 64910). A, B, D, F, H-K, U, Upper Campanian, *Belemnitella mucronata* belemnite zone, Norwich, Norfolk, UK. G, L, lower Maastrichtian, Rügen, Germany. E, Maastrictian, Benzenrathof, near Heerlen, Netherlands. C, D, M-T, lower Maastrichtian, *Belemnella sumensis* belemnite zone, Trimingham, Norfolk, UK. **Abbreviations**: **c**, carina; **r**, rostrum; **sc,** scutum. Scale bars equal ; A-G, L-T, 5 mm; H-K, U, 1 mm.

**Figure 27.**

**A-V***, Parabrachylepas ifoensis* (Withers, 1935). **A, B, G, H**, scuta, in external (**A, H**) and internal (**B, G**) views, originals of Gale, in Gale and Sørensen, 2014, fig. 18A-D (NHMUK IC 881, 883). **C, D**, upper latus, in external (**C**) and internal (**D**) views, originals of Gale, in Gale and Sørensen, 2014, fig. 18N, O (NHMUK IC 890). **E, F**, tergum, in internal (**E**) and external (**F**) views, originals of Gale, in Gale and Sørensen, 2014, fig. 18F, G (NHMUK IC 855). **I, J, K,** marginal plates in external (**I, K**) and internal (**J**) views, originals of Gale, in Gale and Sørensen, 2014, fig. 18I, J, K (NHMUK IC 887, 889). **N, O, S, U**, rostra, in dorsal (**N**), internal (**O**) lateral (**U**) and apical (**S**) views, originals of Gale, in Gale and Sørensen, 2014, fig. 19B, C, E, G (NHMUK IC 893, 894, 895, 896). **T**, carina in apical view, originals of Gale, in Gale and Sørensen, 2014, fig. 19A (NHMUK IC 892). **L, M, P-R, V**, imbricating plates in external (**M, P, R**) and internal (**L, Q, V**) views, originals of Gale, in Gale and Sørensen, 2014, fig. 19N-R (NHMUK IC 902-906). All from upper lower Campanian, Ivö Klack, Skåne, Sweden. Scale bars equal; A-H, I-K, N, O, S-U 1 mm; L, M, P-R, V, 0.5 mm.

**Figure 28.**

**A-U**, *Epibrachylepas newmani* Gale, in Gale and Sørensen, 2014. **A-E**, paratype scuta, in external (**A-C**), tergal (**D**) and internal (**E**) views, originals of Gale, in Gale and Sørensen, 2014, fig. 16A-D (NHMUK IC 855-857, 825) E, original of Gale, in Gale and Sørensen, 2014, fig. 17I (NHMUK IC 876). **F-H**, terga, in external (**F, G**) and internal (**H**) views. F, holotype, original of Gale, in Gale and Sørensen, 2014, fig. 16E (NHMUK IC 858). G, H, paratypes, originals of Gale, in Gale and Sørensen, 2014, fig. 16F, H (NHMUK IC 859, 861). **I, J**, marginal plate in external (**I**) and internal (**J**) views, original of Gale, in Gale and Sørensen, 2014, fig. 17A, B (NHMUK IC 869). **K, L,** upper latera, in external (**K**) and internal (**L**) views, originals of Gale, in Gale and Sørensen, 2014, fig. 16I-K (NHMUK IC 830, 831). **O, P**, rostra, in internal (**P**) and apical (**O**) views, originals of Gale, in Gale and Sørensen, 2014, fig. 16M, N (NHMUK IC 864, 865). **T, U,** carinae, in apical (**T**) and internal (**U**) views, originals of Gale, in Gale and Sørensen, 2014, fig. 16L, O (NHMUK IC 863, 866). **M, N, Q-S,** imbricating plates, in external (**N, Q, R, S**) and internal (**M**) views, originals of Gale, in Gale and Sørensen, 2014, fig. 17C, G, H, J-L (NHMUK IC 870, 874, 875, 877-9). **V, W**, *Epibrachylepas smeetsi* (Bosquet, 1857) lectotype scutum, figured after Bosquet (1857, pl. 3 figs 11a-c), specimen presumed lost. A-U from upper lower Campanian, Ivö Klack, Skåne, Sweden. V, W, Maastrichtian, between Vilt and Sibbe, Limburg, Netherlands. Scale bars equal 1 mm.

**Figure 29.**

**A-N,** *Crithmumlepas hoensis* gen. et sp. nov. **A, B, G, H, J**, terga in external view (NHMUK PI In 64911, 64912, 64915, 64916, 64918); **A** is holotype (NHMUK PI In 64911), all other figured valves are paratypes. **C-E**, carina, in dorsal (**C**), lateral (**D**) and internal (**E**) views (NHMUK PI In 64913). **I, K, L**, scuta, in external (**I, K**) and internal (**L**) views (NHMUK PI In 64917, 64919). **F, M, N**, rostra, in ventral (**F, N**) and internal (**M**) views (NHMUK PI In 64914, 64920). **O-X**, *Crithmumlepas aycliffensis* gen et sp. nov. **O, P, T-V**, terga, in external views (NHMUK PI In 64921, 64922, 64925, 64927); **V** (NHMUK PI In 64927) is holotype all other figured valves are paratypes. **Q-S, X**, carinae, in dorsal (**Q, S, X**) and lateral (**R**) views (NHMUK PI In 64923, 64924, 64929). **W**, scutum, in external view (NHMUK PI In 64928). I-F, H-J, Grey Chalk Group, Zig Zag Formation, upper Cenomanian *Calycoceras guerangeri* ammonite Zone, 70-72m (Kennedy and Gale, 2006, fig. 2), Shakespeare Cliff, west of Dover, Kent, UK. O-X, Grey Chalk Group, Zig Zag Formation, middle Cenomanian *Turrilites acutus* ammonite Subzone, 46.4 m (Kennedy and Gale, 2006, fig. 2), Samphire Hoe, west of Dover, Kent, UK. G, White Chalk Group, Lewes Formation, Coniacian, upper *Micraster cortestudinarium* Zone, Hope Gap, Seaford, Sussex, UK. Scale bars equal; C-E, 0.3 mm, all others 0.2 mm.