Stalked barnacles (Cirripedia, Thoracica) from the Upper Jurassic (Tithonian) Kimmeridge Clay of Dorset, UK; palaeoecology and bearing on the evolution of living forms

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A B S T R A C T

New thoracican cirripede material from the Kimmeridge Clay (Upper Jurassic, Tithonian) is described. This includes a log, encrusted on the lower surface with hundreds of perfectly preserved, articulated specimens of *Etcheslepas durotrigensis* Gale, 2014, and fewer specimens of *Concinnalepas costata* (Withers, 1928). Some individuals are preserved in life position, hanging from the underside of the wood, and the material provides new morphological information on both species. It appears that *Martillepas ovalis* (Withers, 1928), which occurs at the same level (Freshwater Steps Stone Band, *pectinatus* Zone) attached preferentially to ammonites, whereas *E. durotrigensis* and *C. costata* used wood as a substrate for their epiplanktonic lifestyle. Two regurgitates containing abundant barnacle valves, mostly broken, and some bivalve fragments, have been found in the Kimmeridge Clay. These were produced by a fish grazing on epiplanktonic species, and are only the second example of regurgitates containing barnacle valves known from the fossil record. The evolution of modern barnacle groups is discussed in the light of the new Jurassic material as well as recently published molecular phylogenies. New clades defined herein are called the Phosphatothoracica, the Calamida and the Unilatera.

Keywords
Epiplanktonic barnacles
Kimmeridge Clay
predation

1. INTRODUCTION

Amongst the most remarkable fossils collected by Steve Etches from the Kimmeridge Clay of Dorset are articulated stalked barnacles. Articulated barnacles are extremely rare in the fossil record, because the plates separate and disperse upon decomposition of the soft tissues, and Steve has hugely improved our knowledge of Jurassic representatives of this group by collecting new material. A new genus and species, *Etcheslepas durotrigensis* was based on an articulated individual, preserved in golden iron pyrites, and on dissociated plates (Gale, 2014a). Steve has now collected a piece of fossil driftwood covered in thousands of articulated individuals of this species, some still hanging from the log in life position. Amongst these are some (about 10) articulated individuals of *Concinnalepas*, which provide new information on the morphology of this genus. Additionally, he has recovered associated clusters of fragmented cirripede valves which are interpreted as regurgitates from a barnacle-eating predator, probably a fish which browsed on epizoans attached to ammonites and wood. This is only the second known example from the fossil record of regurgitates containing barnacles.

The barnacles from Kimmeridge are not just important because some are new taxa, and others show previously unknown details of morphology, but they occur at a critical time in the evolution of the group, immediately preceding the evolution of new forms in the Early Cretaceous, some of which survive to the present day (Gale, 2014b, 2015a, b; Gale and Sørensen, 2014, 2015). The thoracican barnacles radiated during the Cretaceous and Palaeogene to produce the diversity which we find in oceans today, including in particular the acorn barnacles (balanomorphs) which are abundant intertidal organisms and caused Charles Darwin to say that we live in the "Age of Barnacles." The Tithonian barnacles from the Kimmeridge Clay include forms which are close to the common ancestors of all living, calcite-shelled barnacles, and provide phylogenetic information which can never be retrieved from analysis of the DNA of living forms.

2. The Kimmeridge barnacle log

2.1. Description of the material.

A new specimen collected recently by Steve Etches is a length (approximately 1 m x 0.2 m) of flattened lignite, associated with smaller pieces of similar material derived from the same piece of wood, from a level immediately overlying the Freshwater Steps Stone Band in the *pectinatus* Zone of Kimmeridge Bay (Cox and Gallois, 1981). The material has been deposited in the Museum of Jurassic Marine Life (MIJML) Kimmeridge, Dorset. Its lower surface is densely encrusted by articulated cirripedes, with scattered oysters (*Lopha* sp.). The present account includes a preliminary assessment of the find; a future study will examine the population structure and ontogenetic development of the material. The cirripede valves are superficially replaced by iron pyrites. Many of the cirripede specimens are partly or completely articulated, and occur in two distinct preservational modes;

1) flattened, but largely articulated (e.g. Figs. 1, 3A), with some minor displacement of the valves. This part of the lower surface of the log was evidently pressed firmly against the sea floor, flattening the individuals, long before compaction took place;

2) Articulated and erect (Figs. 2A, 3A) individuals, suspended in life position from the lower surface of the wood. This part of the log was not in contact with the sea floor, probably overlying a void, and early diagenesis (presumably sulphate reduction, forming iron pyrites) cemented the valves in place before decomposition could bring about disarticulation. Subsequent compaction simply pressed the individuals into the underlying clay.

Approximately 90 per cent of the cirripedes belong to *Etcheslepas durotrigensis*, the other 10 percent are *Concinnalepas costata*. It is notable that all the individuals of *C. costata* are large and fully grown (6-7 mm across base of capitulum), and probably represent a single recruitment, whereas *E. durotrigensis* displays a considerable size range, from about 2 to 10 mm maximum width of the capitulum. *Etcheslepas durotrigensis* was evidently actively reproducing and continually recruiting on the floating log from larval settlement.

2.2. Palaeoecology

What is also remarkable is that the cirripede fauna of the clay at the level of the Freshwater Steps Stone Band from which the log came is completely dominated by loose valves of *Martillepas ovalis*, which are abundant. A few articulated individuals were found, most attached to an ammonite (Gale, 2014a), but not a single valve of *E. durotrigensis* was recovered during five days of careful collecting by breaking up clay, from 5 m below this level to 5 m above. Indeed, I was so convinced of its absence at this level that I presumed that the material collected by Steve Etches which I described a few years ago (Gale, 2014a) had come from a higher level in the lower *pallasioides* Zone, which was not easily accessible at the time. It is therefore possible that *M. ovalis* had a preferred attachment to ammonites, which are very common at the level of the Freshwater Steps Stone Band, and that *E. durotrigensis* had a preference for floating wood. Because lignite is not common at this level, *E. durotrigensis* would also be infrequent.

 Two extant barnacle groups live epiplanktonically, the stalked lepadomorphs, and coronuloid acorn barnacles (balanomorphs) which are highly specialized ectoparasites of whales and turtles (Anderson, 1994). The former group provides the best analogy for Mesozoic epiplanktonic forms. Lepadomorphs include the well-known goose barnacles (*Lepas* spp.) which commonly wash up on shores attached to wood or flotsam. Lepadomorphs are hermaphrodites, and close individuals cross-fertilise, producing long-lived planktotrophic larvae called nauplii. These are present in most thoracican barnacles and at developmental stage VI metamorphose in a single moult to swimming cyprid larvae, which actively seek out attachment sites using complex sense organs (Southward, 2008). Once settled on a suitable site, the cyprid moults and metamorphoses into the adult barnacle. We can be sure that this sequence happened in Jurassic barnacles, because the primitive living form *Ibla*, which is a "living fossil" with origins in the Carboniferous (Pérez-Losada et al., 2008), undergoes exactly the same developmental sequence as more derived living forms.

Some living epiplanktonic cirripedes of the lepadomorph clade are notoriously unselective in their attachment sites, as shown by *Lepas* spp. (Southward, 2008) which attach indiscriminately to wood, boats and flotsam. Others, such as *Alepas parasitica* Sander-Rang, 1829 live only on two genera of medusae (jellyfish). *Dosima fascicularis* (Ellis and Solander, 1786), another common Atlantic species, secretes a vesicular float from its cement gland. There is thus a considerable range of variation in the requirements of attachment sites, but for cypris larvae to find specific genera of medusae demonstrates their ability for precision if it is required.

It is evident that some Mesozoic fossil barnacles required, or preferred, specific attachment sites. The Cretaceous family Stramentidae evidently had a preference for attachment to ammonites, which sometimes overgrew the barnacles, thus demonstrating in-life attachment (Gale, 2015a). However, in some situations they also lived benthically, attached to bivalves (Hattin and Hurt, 1991). Additionally, the zeugmatolepadid species ("*Pollicipes*") that encrust ammonites from the Tithonian Brunner Plattenkalk of southern Germany (Keupp et al., 1999) preferentially selected specific sites on the ammonite shell, immediately beneath the aperture in life position, and in an orientation facing the swimming direction of the ammonite. However, material from the Callovian Oxford Clay of Christian Malford, Wiltshire (Morris, 1845) includes *Concinnalepas concinna* attached both to ammonite shells and fossil wood (Withers, 1928), so this species did not have preferential attachment sites.

The lesson from both living and fossil epiplanktonic barnacles appears to be one of considerable variation in the specificity of attachment. Some species are highly specialized in habitat preference (e.g. *Alepas* spp.), and others attach to almost anything which floats. At present, it appears that *Martillepas* lived attached to ammonite shells, and *Etcheslepas* to wood. It is necessary to confirm this apparent substrate specificity with further finds.

2.3. Taxonomic and morphological significance

The material of *E. durotrigensis* attached to the log confirms the basic morphological description which I provided previously (Gale, 2014a), but the new specimens show much more clearly the shape and disposition of the lateral plates (Figs. 1, 2B-D). Specifically, the rostrolatera are tall and narrow, extending nearly to the tip of the rostrum (Fig. 2C), whereas the carinolatera are much shorter, reaching less than half the height of the carina (Fig. 2B). The subcarina is either tiny or absent (Fig. 2B), an unusual situation for Jurassic barnacles of this type; compare with *Concinnalepas costata* (Fig. 3B) in which the subcarina is conspicuous and approximately half the height of the carina. The new specimens (e.g. Fig. 2C, D) provide a clearer impression of the form of the capitulum, in which the numerous (about 30 on each side of the capitulum) tall, narrow lateral plates imbricate towards the peduncle, and form a buttress-like palisade against the scuta and terga. Similarities with the extant Indo-Pacific intertidal species *Capitulum mitella* (Linnaeus, 1758) (see Chan et al., 2009) (Fig. 5I herein) include overall shape, plus the tall, narrow upper latus, the presence of growth-parallel flanges on the lateral plates, and the absence of a differentiated inframedian latus. Additionally, the tips of the laterals are commonly broken off in both *Capitulum* and *Etcheslepas*. Differences are the fewer, lower lateral plates in *Capitulum*, which form a single row at the base of the capitulum, rather than a wall-like phalanx as in *Etcheslepas* and the larger subrostrum and subcarina in *Capitulum*. However, these are not major differences; suffice to say, if *Etcheslepas durotrigensis* were found alive to day, it would probably be classified as a new species of *Capitulum*. These similarities support the suggestion from molecular data (Lin et al., 2015) that *Capitulum* is basal to all living barnacles except the phosphatic Iblidae (see below).

The newly collected, articulated specimens of *Concinnalepas costata* on the log (e.g. Fig. 3B, C) provide a better impression of the form of this species than has been known hitherto from fragmentary material (Gale, 2014a). A specimen preserved in dorsal aspect (Fig. 3B) shows the paired carinolatera (cl1, cl2) and the large subcarina (sc). A specimen preserved in lateral view (Fig. 3C) demonstrates the arrangement of the numerous lower latera, which

are triangular in outline, decrease in size and imbricate towards the peduncle. The peduncular plates are also triangular, but smaller and more numerous than the lateral plates. Comparison with *Etcheslepas* (e.g. Fig. 2C, D) reveals a very similar arrangement of imbricate, triangular lateral plates which form a wall between the peduncle and scuta/terga. However, the plates are low and smooth in *Concinnalepas*, and tall, narrow and with transverse ridges in *Etcheslepas*.

3. Regurgitates of a barnacle-eating predator

Among the new material found by Steve Etches are two oval masses of fragmented shell material, most conspicuously valves and broken portions of valves of *Concinnalepas costata* (Fig. 4B, C), but including pieces of oyster shells (*Lopha* sp.), and indeterminate small fragments of calcite-shelled bivalves. Both are approximately 50 x 30 mm in dimensions. Most cirripede valves are broken, but some are largely complete, and the valves are not corroded or etched.

The specimens are interpreted as regurgitates of indigestible material, probably produced by fish browsing on epifaunal oysters and barnacles attached to floating, or possibly sunken, logs or ammonite shells. A comparable example from the Cretaceous Smokey Hill Member of the Niobrara Chalk (Turonian) of Kansas was figured and described by Hattin (1996). This was about 20 mm across, and contained both cirripede valves and actinopterygian bones, including articulated peduncular plates of cirripedes. However, in the Smokey Hill Member, the cirripedes were epibenthic (Hattin and Hirt, 1991), rather than epiplanktonic. Hattin interpreted the specimen as a regurgitate from a bottom feeding fish, possibly the selachian *Ptychodus*. The lack of corrosion of the calcite valves was taken as evidence that these had not passed through the digestive system completely. Regurgitates were also discussed by Bishop (1975), who reviewed previous literature. Regurgitates of invertebrate debris are more poorly known than

those of vertebrates, which sometimes contain partially articulated skeletons (see Thies and Hauff, 2012, for a review).

4. Thoracican barnacle evolution and the origin of the living groups

4.1. Phylogeny of thoracican barnacles.

Our understanding of the phylogeny of the thoracican cirripedes has been dominated by a model put forward by Newman (1979; see also Newman, 1987; Foster and Buckeridge, 1987), which involved the progressive addition of capitular plates through time (Figs 5, 6). Thus, in the Carboniferous, *Praelepas*, which possessed paired scuta, terga and a carina, represented a *Lepas* stage of evolution, which survived to the present. In the Triassic, *Eolepas* acquired a rostrum; *Neolepas* added an upper latus in the Early Jurassic, and a complete suite of lateral plates was developed in the Cretaceous to present day *Calantica*. The model was underpinned by the ontogenetic development of the living *Pollicipes*, which developed capitular plates in a comparable sequence (Broch, 1922) – thus, "ontogeny recapitulates phylogeny" (Fig. 6).

However, various lines of evidence do not support this model. Firstly, the discovery that *Praelepas* and *Eolepas* have phosphatic, not calcitic, shell plates (Gale, 2015b; Gale and Schweigert, 2015) indicated the existence of a fundamental mineralogical change in thoracican evolution, and supported the erection of the Thoracicalcarea, a monophyletic clade of derived thoracicans, including all living taxa except Iblidae (Gale, 2015b). Secondly, molecular phylogenies (Perez Losada et al., 2008; Lin et al., 2015; Herrera et al., 2015) consistently place the supposedly basal lepadomorphs within the more derived stalked thoracicans. This indicates that plate reduction has occurred within thoracican evolution, in this case of the rostrum and lateral plates. The loss can be achieved simply by heterochrony – paedomorphic development from pre-adult growth stages which have fewer plates, and probably occurred numerous times in thoracican evolution.

A further problem is what can be called the "*Ibla* gap", which is the absence of any living taxa which record the evolutionary transition between the archaic, extant, phosphatic Iblidae, and *Capitulum*, the most basal calcite-shelled living barnacle (Lin et al., 2015). Therefore, molecular studies provide no evidence at all of the phylogenetic history for a crucial episode in thoracican evolution, involving fundamental changes in mineralogy and plating development (Gale, 2015b; Gale and Schweigert, 2016). The new Jurassic and Cretaceous fossil record partly fills this gap, and new finds enable the development of an evolutionary scenario, which leads up to the appearance of extent groups by the end of the Cretaceous (Gale and Sørensen, 2014; Gale, 2014b, 2015a). This story is outlined in the following section.

4.2 Phosphatothoracica (new clade) and the phosphate to calcite transition

The phosphatic shelled thoracicans (here called Phosphatothoracica, new clade) survived from the Carboniferous, and *Eolepas* (Fig. 5A, 6, 7) existed from the Triassic (Rhaetian) and continued to occur in shallow-water nearshore facies throughout the Jurassic, into the Valanginian of the Lower Cretaceous (Withers, 1928; Gale, 2015b; Gale and Schweigert, 2015; Kocí et al., 2015). *Eolepas* gave rise to calcite-shelled barnacles, the Thoracicalcarea Gale, 2015, by a change in mineralogy, probably during the Early Jurassic, and these constitute almost all of the living forms. Only the small living *Ibla* and its close relatives (Buckeridge and Newman, 2006) have phosphatic valves, and are survivors from the Palaeozoic. The phosphatic barnacle *Toarcolepas,* from the Toarcian of southern Germany, is the oldest form known which had an epiplanktonic lifestyle, attached to floating wood (Fig. 5B; Gale and Schweigert, 2015).

4.3. Calamida (new clade): basal thoracicalcareans and plate multiplication

The stalked thoracicalcareans are here referred to the new clade Calamida, from the Latin *calamis*, meaning stalked.

The most primitive calcite-shelled barnacle are *Archaeolepas* and the closely related *Loriolepas* Gale, 2015b (Fig. 5C,D), which ranged from the Callovian to the Tithonian (Fig. 5C, D, 6; Withers, 1928; Gale, 2015b). These have a simple structure, with paired scuta, terga, a carina, a scutum and lacked any lateral plates. *Archaeolepas* has a relatively small number (10) of large, robust peduncular plate columns. Descendants of these survived into the Cretaceous (*Bosquetlepas* and *Myolepas*), specializing in living intertidally, and developed powerful retractor muscles to hold themselves down on rocky substrates (Gale and Sørensen, 2015).

The next evolutionary stage in the Jurassic saw a progressive increase in the number of lateral plates, with the addition of an upper latus overlying the suture between the scutum and tergum, and a carinolatus between the tergum and carina. This condition is represented by the Stramentidae, a Late Cretaceous family of largely epiplanktonic cirripedes which attached to ammonites (Fig. 5E; Gale, 2015b).

The final stage of plate addition saw the formation of a rostrolatus, between the scutum and rostrum, and numerous smaller, triangular laterals in alternating rows beneath the upper plates (Fig.5F,G,H). These have been assigned to the family Zeugmatolepadidae Newman, 1996 (emend. Newman, 2004), a group characterized by the presence of numerous rows of small lateral plates, decreasing in size towards the peduncle and including at least one subrostrum and subcarina, and two carinolatera (Figs. 5G, H). They first appear in the early Bathonian, and continue into the Eocene (Withers, 1935, 1953). All of the Kimmeridge Clay fossils belong to this group. Gale (2014a) reviewed the fossil record of the Zeugmatolepadidae, and recognized two subfamilies, the Jurassic-Cretaceous Martillepadinae and the Cretaceous Zeugmatolepadinae including a total of five genera (Fig. 5G, H). He placed *Etcheslepas* Gale, 2014a in the extant family Pollicipedidae, which includes the extant genera *Capitulum* and *Pollicipes*, now known to both extend back to the Cretaceous (Gale and Sørensen, 2015; Kocova Veleská et al., 2015).

However, there is a problem with this classification scheme, because it does not appear possible to separate the families Zeugmatolepadidae and Pollicipedidae using firm morphological characters. Actually, the family diagnoses of Gale (2014a) are very similar, both forms having numerous small lower lateral plates, including subcarinae and subrostra (see above). Additionally, a similar condition is found in some species of the Calanticidae such as the New Zealand intertidal form *Smilium spinosa* (Quoy and Gaimard, 1834; see Foster, 1978, fig. 23), in which the lateral plates are hugely variable in number and size. The problems of adequately diagnosing the Calanticidae were discussed by Jones and Hosie (2009), who commented that the genus can possess between nine and 60 lateral plates. All the other diagnostic characters, such as the presence of numerous lateral plates, subrostra and subcarinae, are actually plesiomorphic (i.e. primitive) for stalked cirripedes. Classifications should not the based upon primitive characters, because this results in the creation of paraphyletic taxa (Kitching et al., 1998) which are not natural groups.

The geologically early occurrence (predominantly Bathonian-Tithonian) and the plesiomorphic morphology of zeugmatolepadids makes it likely that they share a common ancestor with all living calcite-shelled barnacles (Fig. 7).

4.4. Secondary plate loss

The post-zeugmatolepadid evolutionary history of the barnacles involves importantly a reduction in shell plate numbers. The thoracicalcareans evidently diverged into two separate groups during the Late Jurassic. A lineage leading to the Cretaceous to present-day Scalpellidae (Fig. 8) involved reduction to a consistent number of 14 plates, probably from an ancestor close to the Cretaceous (Barremian-Maastrichtian) genus *Cretiscalpellum* (Withers, 1935; Gale, 2015a), plus the evolution of a lateral plate called the inframedian latus (Fig. 8). There is now evidence of transition from the zeugmatolepadids to a new genus from the Tithonian of Germany (Fig. 8). This change involved:

1) loss of the subrostrum, and decrease of the height of the rostrum
2) differentiation of an inframedian latus
3) loss of all but three lower lateral plates (CL 2, plus 2 plates adjacent to the inframedian latus)
4) development of a low rostrolatus
5) development of elongated peduncular plates

The transformation from this form to *Cretiscalpellum* involved only the loss of the two lower laterals adjacent to the inframedian latus. The earliest scalpellids, *Virgiscalpellum* Withers, 1935 and *Arcuatoscalpellum* Gale, 2015a, are found in the lower Aptian. The transition from *Cretiscalpellum* to the Scalpellidae (Gale, 2015a) involved:

1) loss of the subcarina
2) loss of the lower pair of carinolatera (CL2)

The lepadomorph barnacles (e.g. the common goose barnacle, *Lepas*), which have only five plates (carina and paired scuta and terga) appear to branch from the lineage leading to the scalpellids, according to the molecular tree. This probably occurred by paedomorphic evolution, because stalked barnacles such as calanticids and pollicipedids undergo an ontogeny which involves the progressive addition of plates from the five primordial valves (Broch, 1922; Gale, 2015b; Gale and Schweigert, 2015). Thus, precocious development at the five-plated stage would lead to the *Lepas*- like morphology. However, lepadomorphs do not appear until the Eocene (Withers, 1945), whereas the scalpellids were already present in the Lower Cretaceous.

4.5 Unilatera (new clade)

The other clade of calcite-shelled thoracicans which evolved during the Jurassic are here called the Unilatera, because they are plesiomorphically characterized by possession of a single lateral plate, the upper latus. The most basal unilaterans are the vent-dwelling, deep-sea Neolepadidae, which do not occur before the Pleistocene, but this may be a consequence of non-

preservation of these very specialized deep-sea habitats. The other major clade of living barnacles, the Sessilia, also involved lateral plate reduction to a paired tall upper latus (Gale & Sørensen 2014; Gale, 2014b), prior to formation of a new wall structure in the balanomorph clade (Fig. 7). In the verrucomorph clade (Fig. 7), one each of the paired scuta and terga, plus the carina and rostrum, form an asymmetrical shell wall, and the free tergum and scutum form an opercular lid (Fig. 7; Gale, 2015b).

5. Conclusions

Well-preserved cirripedes from the Kimmeridge Clay provide a unique window into a critical period of the history of the group, as they immediately precede a major Cretaceous radiation leading to the forms which dominate in present-day oceans. The Late Jurassic barnacles thus represent a stem group from which all living forms were ultimately derived. Only one possible survivor of this stage in cirripede evolution is extant – the Cretaceous to present-day genus *Capitulum*. Jurassic cirripedes therefore fill a gap in our knowledge of the group which can never be obtained from molecular data of living forms, as we have only the phosphatic *Ibla*, a Palaeozoic survivor, and the descendants of the Cretaceous radiation. Integrating the Jurassic fossils with the molecular trees is a major challenge, which requires the resolution of conflicts between trees and morphological data provided by fossils.

The new finds from Kimmeridge also provide a fascinating glimpse into the palaeoecology of Late Jurassic barnacles and their predators. It appears that all were epiplanktonic, some taxa apparently preferring ammonite shells as substrates, others floating wood. The floating, or sunken, aggregates provided a food source for durophagous fish.

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CAPTIONS

Fig. 1. Individuals of *Etcheslepas durotrigenis* Gale, 2014 attached to the underside of a log. Note the variety of sizes, reflecting active recruitment of

juveniles by settling. Freshwater Steps Stone Band, *pectinatus* Zone, Tithonian, Kimmeridge. MIJML coll, Kimmeridge. Scale bar equals 5 mm.

Fig. 2. *Etcheslepas durotrigensis* Gale, 2014. A, portion of underneath of log to show specimens of different sizes in pendant life position. B, dorsal view of specimen to show carina (c) and carinolatus (cl). C, D, lateral aspects of well-preserved individuals to show plates in original positions;note rostrum (r), rostrolatus (rl), scutum (s) and upper latus (ul). See reconstruction in Fig. 5F. Freshwater Steps Stone Band*, pectinatus* Zone, Tithonian, Kimmeridge. MIJML coll, Kimmeridge. Scale bars equal 5 mm (A) and 2 mm (B, C).

Fig. 3. A, portion of underside of log, showing *E. durotrigensis* in original pendant life position. B, C, *Concinnalepas costata* (Withers, 1928), individual in (B) dorsal aspect to show carina (c), subcarina (sc) and carinolatera (Cl1, 2). C, individual in lateral aspect; note numerous small lateral plates (see Fig. 5G for reconstruction). Freshwater Steps Stone Band*, pectinatus* Zone, Tithonian, Kimmeridge. MIJML coll, Kimmeridge. Scale bar equals 5 mm.

Fig. 4. A, undersurface of log to show density of *Etcheslepas*, here flattened. Compare with Figs. 2A and 3A, in which the specimens are still pendant and intact. Note single example of *Concinnalepas costata* (*C.c.*) in the centre left. B, C, masses of broken cirripede valves, with oyster and other bivalve fragments, interpreted as regurgitates produced by a fish which grazed upon epifauna on driftwood and/or ammonite shells. Freshwater Steps Stone Band*, pectinatus* Zone, Tithonian, Kimmeridge. MIJML coll, Kimmeridge. Scale bars equal 5 mm (A) and 10 mm (B, C).

Fig. 5. A-H, Selected Jurassic and Cretaceous barnacles in lateral aspect. A, *Eolepas* (Rhaetian-Valanginian), widespread. B, *Toarcolepas*, Toarcian, southern Germany. C, *Archaeolepas*, Tithonian, southern Germany. D, *Loriolepas,* Tithonian, France, E, *Stramentum*, Late Cretaceous, widespread. F, *Etcheslepas,* Tithonian, UK. G, *Concinnalepas*, Bathonian-Berriasian, widespread. H, *Martillepas*, Tithonian, UK. I, *Capitulum mitella*, Recent, Hong Kong. Note the similar construction to *Etcheslepas*. Scale bar equals 10 mm.

Fig. 6. Figure 5. Diagram to illustrate the thoracican phylogeny proposed by Newman1979, and modified from his Fig. 5, demonstrating how ontogeny reflects phylogeny, and how successive taxa appear in the correct stratigraphical order. At the bottom are the successive ontogenetic stages of the living *Pollicipes polymerus*, after Broch 1922, showing the progressive acquisition of plates after metamorphosis. *Praelepas* is interpreted as representing the stage with only scuta, terga and carina; *Eolepas* has acquired a rostrum; *Neolepas* has an upper latus, and finally, *Calantica* has a full compliment of plates. The problems of this model are discussed in the text. See fig. 5 for colour key to plates.

Fig. 7. Proposed Mesozoic to present-day phylogeny of thoracican barnacles, based upon a combination of molecular data (Pérez-Losada et al., 2008; Herrera et al., 2015; Lin et al., 2015) and fossils (Gale, 2014a, 2015a; Gale, herein; Gale and Schweigert, 2015). The Phosphatothoracica (new clade) include the living *Idioibla* and the fossil (Triassic-Cretaceous) *Eolepas*. A calcite shell evolved in the Late Triassic or Early Jurassic in taxa close to *Archaeloepas* and *Loriolepas*, which possess a simple plate construction, comprising paired scuta, terga, a rostrum and a carina. Progressive addition of lateral plates led to forms close to *Capitulum*, *Etcheslepas* (see Figs. 1, 2) and zeugmatolepadids (see Fig. 5 herein) in which numerous rows of laterals are present; *Capitulum* survives to the present day as a representative of the group. Subsequent thoracican evolution involved loss of lateral plates. In the Unilateria (new clade) only a single lateral (i.e., upper latus) was retained; this clade eventually gave rise to the Sessilia by loss of the peduncle, including the balanomorphs with well-developed, new wall plates (Gale and Sørensen, 2014) and asymmetrical, 6-plated verrucomorphs (Gale, 2014b). The more derived Calamida (new clade) display progressive loss of lateral plates, from the condition in Calanticidae, to the 14 plate arrangement in Scalpellidae (see Fig. 8). Lepadomorphs probably evolved by paedomorphic loss of all laterals and the rostrum. See fig. 5 for colour key to plates.

Fig. 8. Morphological trends in Jurassic-Early Cretaceous stalked barnacles. A, *Concinnalepas costata* (Kimmeridge Clay, Tithonian); B, new genus, Tithonian, Germany; C, *Cretiscalpellum aptiensis* (Lower Greensand, Aptian, UK); D, *Arcoscalpellum michelottianum,* Recent. Evolutionary trend involves reduction and loss of lower lateral plates (A, B; pale green), formation of inframedian latus (B-D; dark pink), reduction in number of carinolatera and subcarinae (A-D; purple, pale red), loss of one rostrolatus and change in shape of plate to horizontal orientation (A-D; olive green). Although this may not represent an actual phylogenetic sequence, it illustrates the changes which must have taken place in the evolution of the modern fauna (se Fig. 5 for key).

Figure 1
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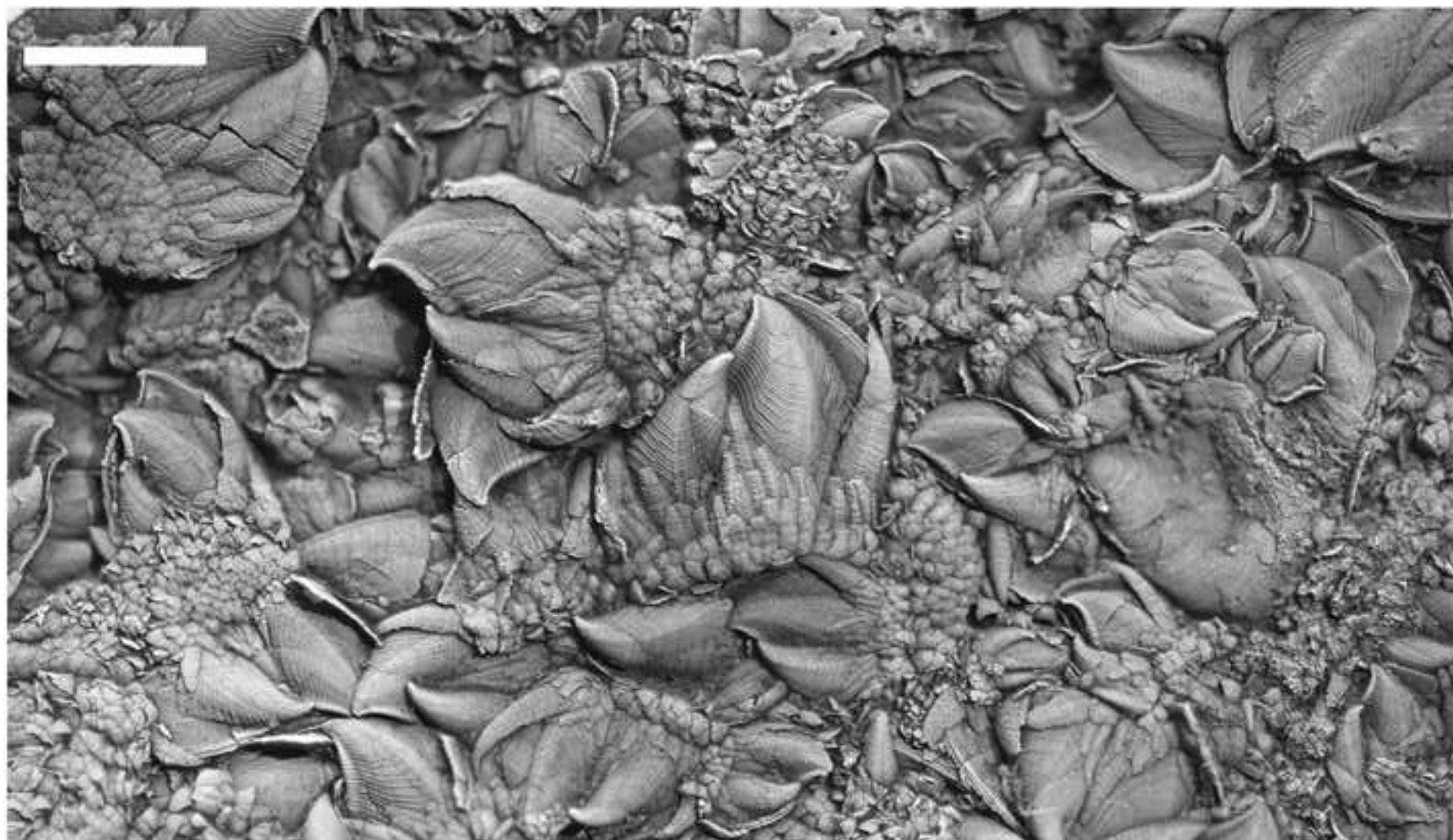
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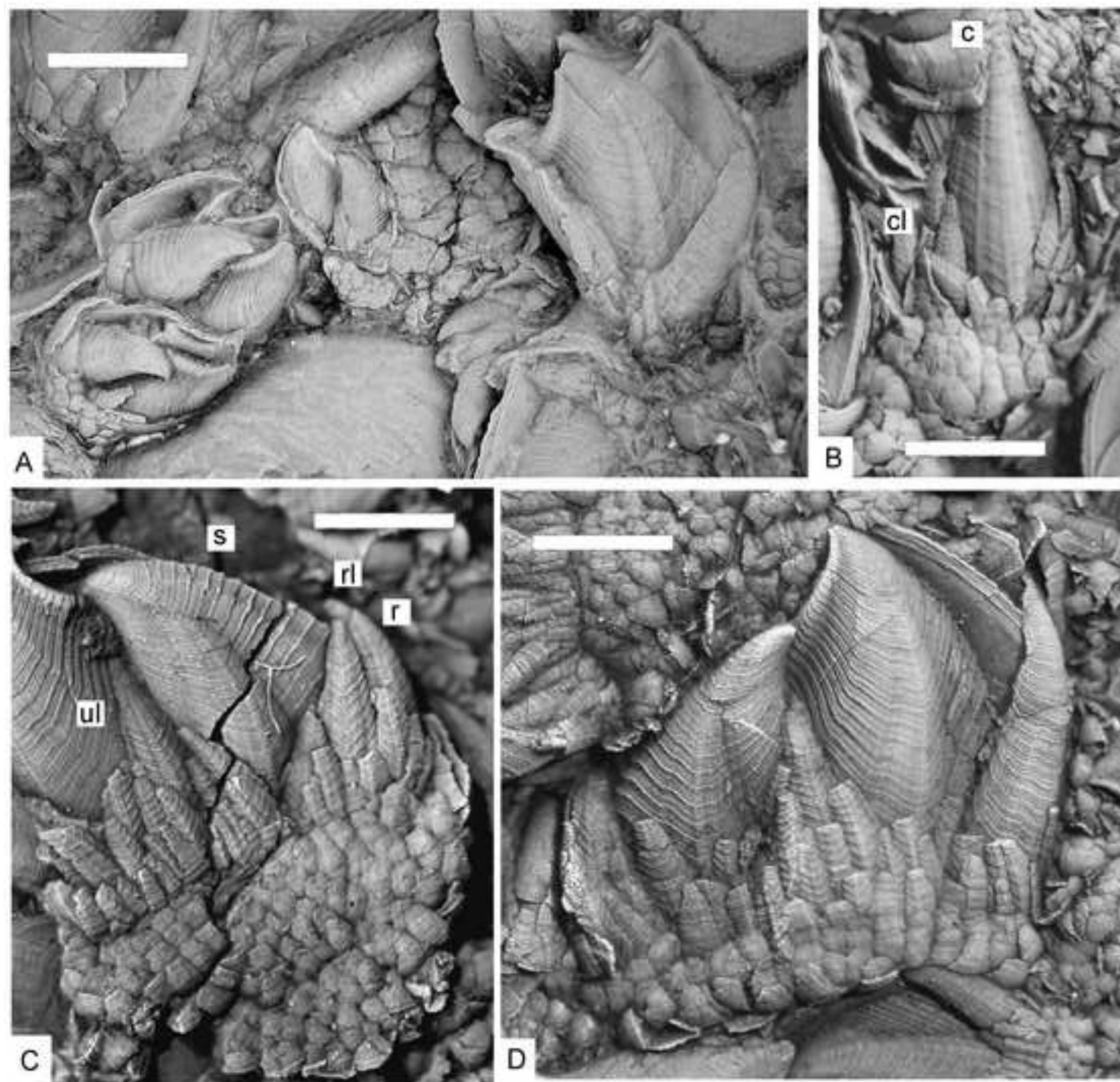
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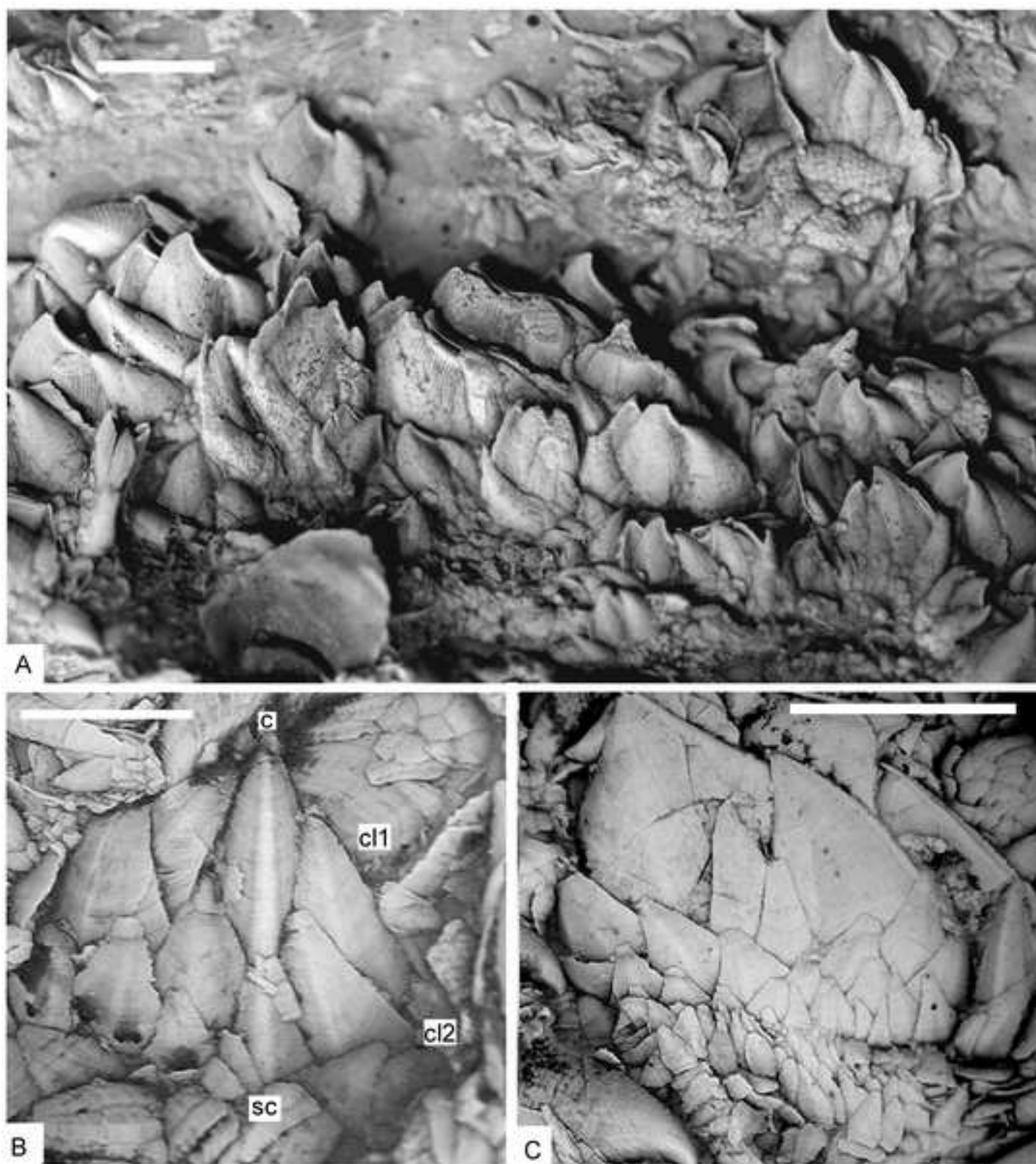
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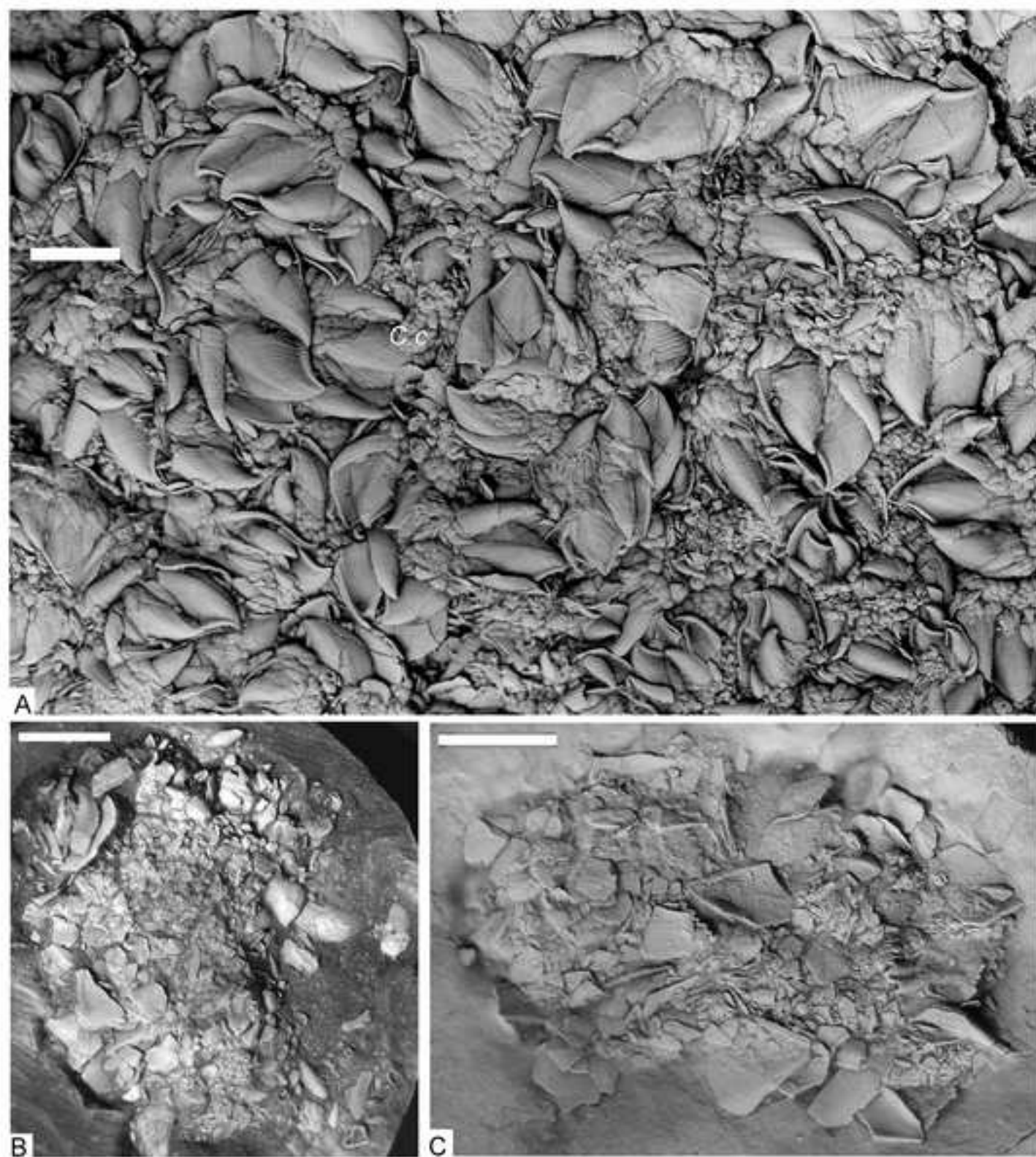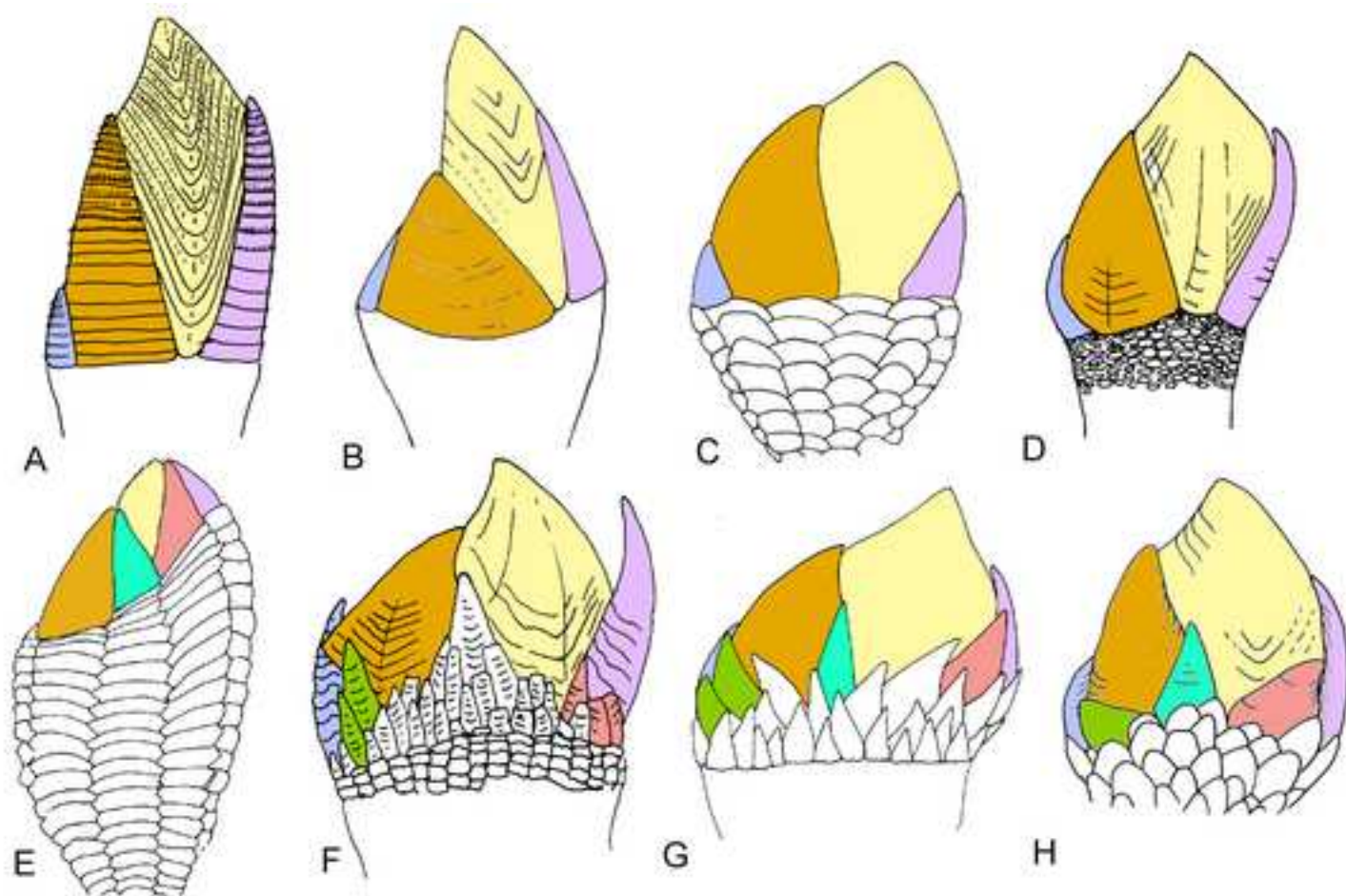**Click here to download high resolution image**

Figure 5
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Figure 5

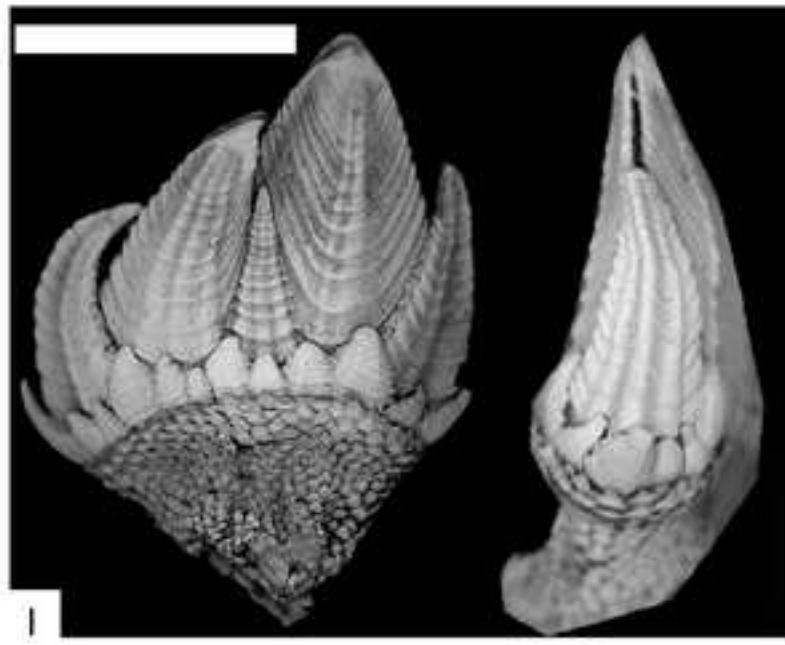|	
inframedian latus	rostrum
tergum	carinolatus
scutum	upper latus
carina	rostrolatus

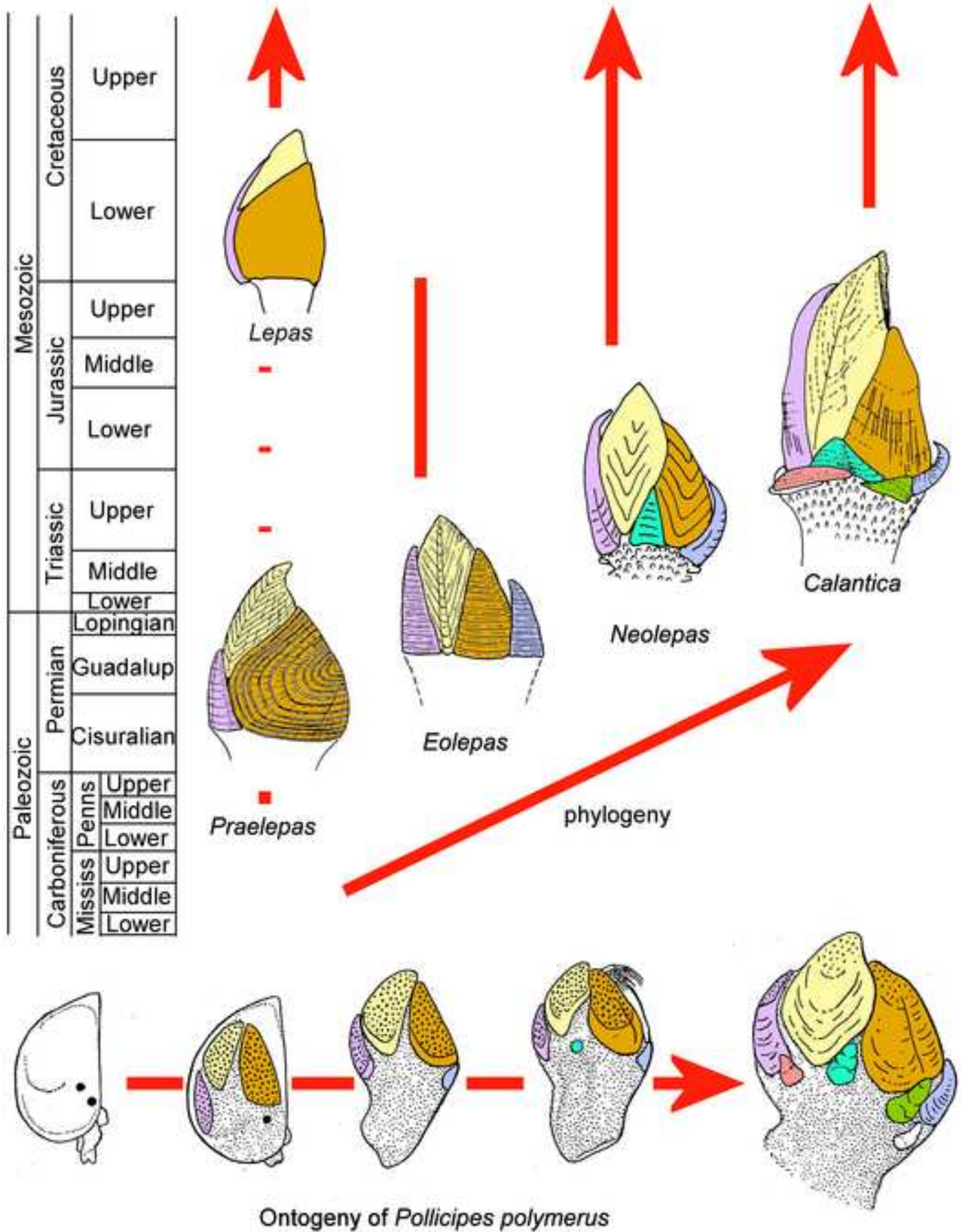**Figure 6**
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Ontogeny of *Pollicipes polymerus*
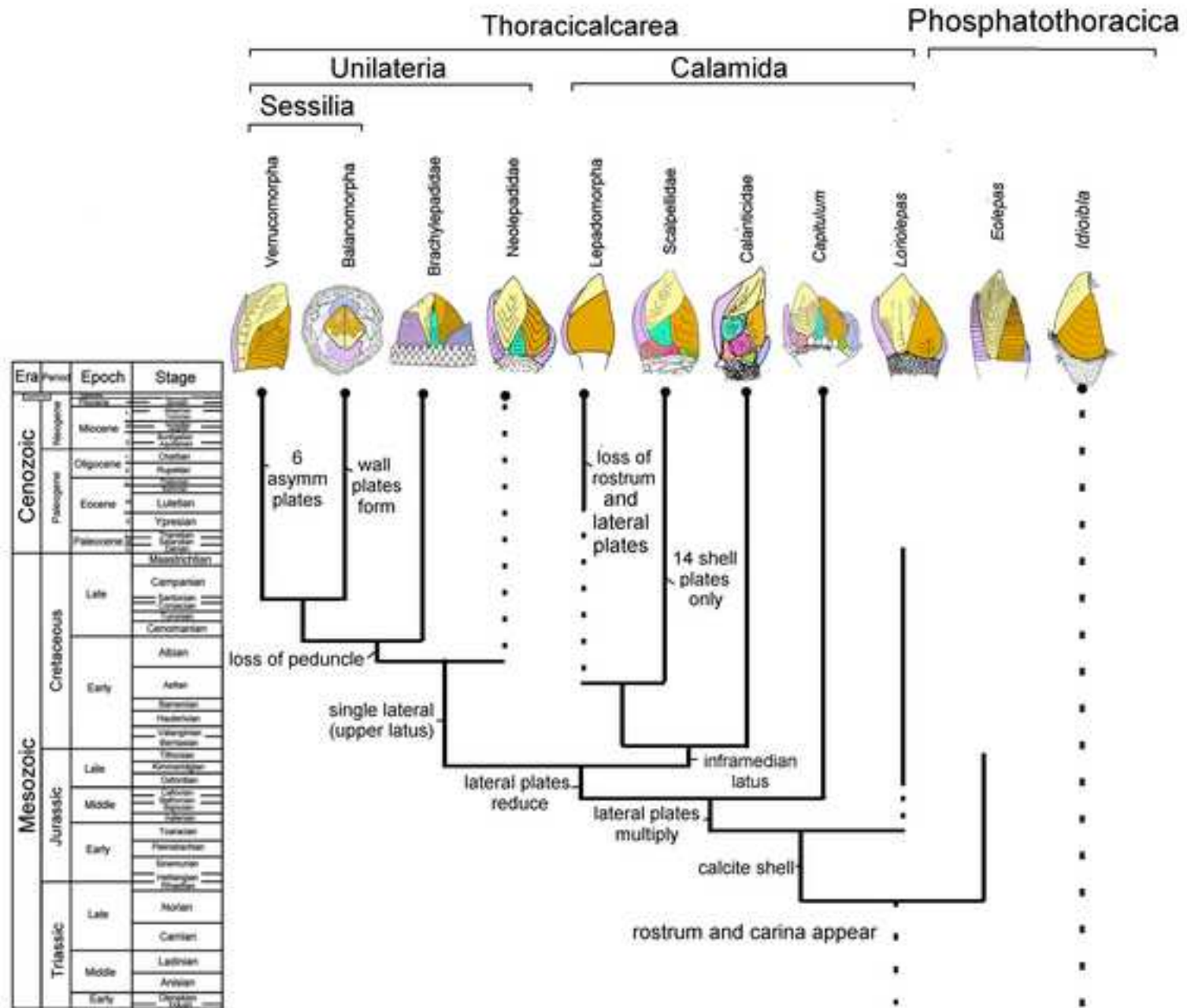
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Figure 7

Figure 8
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A
B
C
D