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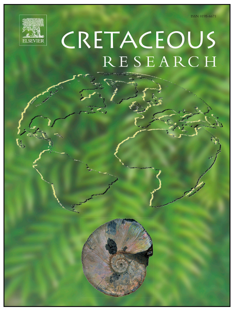

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The Cretaceous acorn barnacle *Archaeochionelasmus nekvasilovae* Kočí, Newman and Buckeridge, 2017 (Cirripedia, Neobalanomorpha) is a fragmentary rudist (Bivalvia, Mollusca)

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ABSTRACT

The unique holotype of *Archaeochionelasmus nekvasilovae* Kočí, Newman and Buckeridge, 2017, from the upper Cenomanian of the Czech Republic, supposedly an early neobalanomorph belonging to the extant family Chionelasmatidae, is compared in detail with chionelasmatids and rudist bivalves. The morphology and shell structure demonstrate that, rather than being a barnacle, it is a poorly preserved fragment of a rudist, which roughly mimics the form of an incomplete balanomorph wall.

Key words:
Cretaceous
Acorn barnacle
rudist

1. Introduction

Kočí et al. (2017) described a small calcitic fossil from Cenomanian marginal deposits at Predjob (Czech Republic) as *Archaeochionelasmus nekvasilovae* Kočí, Newman and Buckeridge, a balanomorph (acorn barnacle) belonging to the extant family Chionelasmatidae, and representing a first

Cretaceous discovery of crown-group neobalanomorphs. This find would put the first appearance of the group back by nearly 40 million years, to a time before the first occurrence of putative ancestors of the neobalanomorphs (Gale and Sørensen, 2014). The specimen was used by Kočí et al. (2017) as the basis for a reappraisal of the homologies, phylogeny and origin of the balanomorphs.

Dr Kočí kindly provided excellent images of the fossil in 2014 and one of us (ASG) expressed his doubts to him then, and to Dr Newman, as to its affinities, suggesting that it was a molluscan fragment. However, the authors believed it to be a cirripede, with eventual publication (Kočí et al., 2017). An anonymous referee for this publication also suggested that the specimen was part of a rudist. After publication of the Kočí et al. (2017) paper, ASG contacted PWS, a rudist specialist, who confirmed that it is in fact a rudist fragment. In view of the importance of the discovery of such an early neobalanomorph, we now consider it useful to publish our observations on the specimen and its affinities.

Abbreviations. NM, Narodní Muzeum (National Museum), Prague, Czech Republic; MHNH, Muséum national d'Histoire naturelle, Paris, France; UMUT, University Museum of the University of Tokyo, Japan.

2. Living chionelasmatids and related barnacles

The Chionelasmatidae is a small family of living balanomorphs, comprising one genus and four extant species: *Chionelasmus darwini* Pilsbry, 1907, *Ch. ohtai* (Yamaguchi and Newman, 1990), *Ch. paquensis* (Yamaguchi and Newman, 1997) and *Ch. crosnieri* Buckeridge, 1998. A fossil *Chionelasmus* is known from the Eocene of Tonga (Jones, 2000). *Chionelasmus darwini* is common in restricted regions of the Pacific and Indian oceans (Jones, 2000), while *Ch. ohtai* is locally common in association with hydrothermal vents in the southwest Pacific and on the East Pacific Rise (Jones, 2000).

Chionelasmatidae, illustrated here by *Ch. darwini* (Fig. 1D, E) possess six robust wall plates, the external faces of which are nearly vertical, and these surround a large kite-shaped orifice in which the operculum sits. The highest point of the capitulum is the apex of the carina. The wall plates are firmly articulated but unfused, and possess coarse ridges and grooves which diverge from the apex. Large wing-like alae are present on the carina, rostrum and carinolatus. The wall plates display conspicuous, evenly spaced growth lines, 0.7–1.0 mm apart. The presence of small imbricating plates surrounding the base of the wall are widely taken as evidence of the basal position of the family within the balanomorphs (together with waikalasmatids and catophragmids; see below).

The Waikalasmatidae Ross and Newman, 2001 are similar to the Chionelasmatidae in overall morphology, but possess eight wall plates rather than six. *Waikalasma boucheti* Buckeridge, 1996 (Fig. 2A-C) is known from only three specimens (Jones, 2000). The genus is also represented by a fossil species, *W. juneae* Buckeridge, 1983, from the Lower Miocene (Aquitainian) of New Zealand.

The family Catophragmidae Utinomi, 1968 comprises three genera (*Catomerus* Pilsbry, 1916, *Catophragmus* Sowerby, 1826 and *Catolasmus* Ross and Newman, 2001) all of which possess eight wall plates, and like chionelasmatids, all have alae and basal imbricating plates surrounding the wall. The molecular phylogeny of Pérez-Losada et al. (2014, fig. 1) indicates that the chionelasmatids, catophragmids and pachylasmatids are very closely related and all fall within a single clade, which probably also includes *Waikalasma*.

The nomenclature of lateral plates has traditionally followed Darwin (1854) in identifying homologous plates in both pedunculate forms (e.g. scalpellids) and balanomorphs. Thus, six-plated balanomorphs, such as *Chionelasmus* (Fig. 1D,E; Fig. 2D,E,F) are usually described as having a rostrolatus (RL) and a carinolatus (CL); eight-plated forms such as *Waikalasma* (Fig. 2A-C) possess an additional pair of plates, identified by Yamaguchi and Newman (1990) as a "replicated" carinolatus, CL2. Gale and Sørensen (2014) argued that the lateral plates of balanomorphs had evolved as *de novo* structures, and proposed a new nomenclature based on evidence from both inferred phylogeny and Cretaceous fossil forms. The centrally positioned lateral wall plate is called a marginal (M), the plate between this and the rostrum a rostromarginal (RM), and the plate between the marginal and the carina a carinomarginal (CM). Both interpretations are provided in Figure 2.

3. The Czech fossil

The unique type specimen of *Archaeochionelasmus nekvasilovae* (Fig. 1A–C) comprises a curved portion of calcite wall, approximately 25 by 15 mm. The exterior surface is smooth, but in detail is seen to bear very fine transverse ridges. The exterior surface is divided into three portions by low ridges which run from the apex to the base. Two shell layers are apparent; an inner one made of calcite spar, and a thin outer one of fibrous brown calcite.

4. Comparative morphology

Overall morphology. The shape of the capitulum in chionelasmids is fairly consistent across the known species. In lateral profile, the alar margin of the carina forms the tallest point, higher than the tip of the rostrum (Figs. 1D, E, 2A–F). The lateral plates are lower and are situated in between the rostrum and carina. The opercular plates, the scuta and terga, form a prominence rising anteriorly to a maximum height above the carina (Fig. 1D, E). In dorsal view, the capitulum has a rounded, kite-shaped outline, and the acuminate carinal margin is formed entirely by the carina. The wall plates of chionelasmatids overlap and articulate only loosely, and detach readily upon decomposition of the soft tissues. By contrast, the boundaries of the “valves” of *A. nekvasilovae* are very low ridges flush with the external surface of the object and do not represent fundamental divisions of the shell.

Orifice. The opercular opening of balanomorphs is a kite-shaped rhomb, with the rostral dimension slightly shorter than the carinal one (Figs. 1D, E, 2A–F). The articulated scuta and terga fit precisely within it. The “orifice” of *A. nekvasilovae* is irregularly oval (Fig. 1A, C), and it is difficult to see how an operculum could ever fit into this space.

Alae. Extant chionelasmatids are all characterized by large alae, lateral extensions of the parietal plates, which in the carina and rostrum are set nearly at right angles to the parietal external surface (Figs. 1D, E, 2A–F). These are also present in catophragmids, waikalasmatids and pachylasmatids (Jones, 2000). Alae infill the gaps between plates generated by diametric growth (Anderson, 1994). The ala on the rostral margin of the carinomarginal ("CL2" of Kočí et al., 2017) is large in *Chionelasmus*. The alae display conspicuous regular growth lines, approximately 0.7–1 mm apart. *Archaeochionelasmus nekvasilovae* completely lacks any structures which might be interpreted as alae.

Plate shape. The parietal wall plates of chionelasmids are highly distinctive. The rostrum and carina are U- to V-shaped in cross section, the triangular non-alar parietal wall forming the base, the alar extensions forming the processes (Figs. 1D, E, 2A–F). The apex of the carina is directed anteriorly. The lateral plates are triangular, tapering apically. All plates are robust and slightly convex exteriorly. The irregularly shaped "carina" of *A. nekvasilovae*, in contrast, has an apex directed posteriorly. The "CL" and "RL" are slightly concave, triangular, and higher than the "carina".

External sculpture. All extant chionelasmids have a similar plate sculpture pattern, comprising a small number of weakly defined radially arranged ribs and grooves, and quite regularly spaced growth lines, about 0.7–1 mm apart (Figs. 1D, E, 2A–F). The holotype of *A. nekvasilovae* (e.g., Kočí et al., 2017, pl. 2f, h) is essentially smooth, and shows very fine 40-50 μm radial ridges, and irregular transverse lineation, also very fine. Similar growth patterns are not found on any cirripede.

Symmetry. Chionelasmids, and balanomorphs in general, are symmetrical about the sagittal plane, in order to ensure an excellent fit of the operculum within the orifice/parietal sheath (Figs. 1D, E, 2A–F). The purported "carina" (C) of *A. nekvasilovae* is markedly asymmetrical, one side (left in Fig. 1A) is strongly inflected, the other (right) is almost flat.

Microstructure. Calcareous thoracican barnacle plates are composed of a dense felt of tiny calcite crystals, a few microns in diameter, which are extraordinarily resistant to recrystallization. Even in rocks which have been strongly affected by diagenesis, they invariably preserve their original structure. In contrast, the wall of the sole specimen of *A. nekvasilovae* has two layers. The inner one has a coarse blocky calcite fabric (Fig. 1B, marked ‘x’), the outer one (y) is a thin encrustation with a finely striated surface. These are unlike anything ever seen in a cirripede.

Scales. The chionelasmatids, catophragmids and waikalasmids all possess a skirt of one to several rows of small scale-like plates which surround the base of the wall, homologous with the peduncular plates of ancestral pedunculate forms (Figs. 1D, E, 2A–F). Although Kočí et al. (2017, pl. 1D, E) claim that there are impressions made by such scales present in *A. nekvasilovae*, we are unable to identify these in their excellent photographs.

5. Interpretation

The unique type specimen of *A. nekvasilovae* is a fragmentary rudist bivalve. The blocky calcite layer (Fig. 1A,B - x) is the originally aragonitic *inner shell layer*, now entirely replaced by calcite spar, and the pale brown crust (Fig. 1A - y) is where the fibrillar calcite *outer shell layer* has spalled away, leaving just the striated pattern (and colour) on the outer surface. This preservation style, with the inner shell replaced by calcite spar, and the outer shell spalling off, was a common taphonomic accident among rudists, all of which originally had a fibrillar calcite outer shell layer and an aragonitic inner shell (Skelton, 2013). This preservation is seen in countless rudists. The present specimen is the basal portion of a right valve, of which the umbonal region is broken off, giving the impression of an orifice.

Počta (1889) and Frič (1911) illustrated numerous rudists from the Cenomanian of the Czech Republic, and some of these look similar to the type of *A. nekvasilovae*. The specimens figured as *Caprotina* (Počta’s pl. 2, fig. 2, reproduced here as Fig. 3B, D) appears to have lost the outer shell layer (as described above) and, as a result, the invaginated ligamentary seam is visible. Rudists are common at Předboj (Žítt et al., 1999), the type locality of *A. nekvasilovae*, and were listed by Zelenka (1990).

6. Conclusions

The fossil record is full of small shelly objects of dubious affinity, which may resemble skeletal elements of most animal phyla. The history of fossil barnacle study contains a number of examples of mistaken identity, whereby a molluscan fragment, usually a pectinid auricle, is identified and figured as a cirripede valve. These include the great Charles Darwin, who illustrated a pectinid auricle as a carinal latus of *Scalpellum solidum* (Darwin, 1851, pl. 1, fig. 8f). Discovery of the first true Cretaceous acorn barnacle has become something of a holy grail, after Bosquet's specimen of *Chthamalus darwini* (Bosquet, 1857) turned out to be a modern contaminant (Jagt and Carriol, 2008). Moreover, the calibrated molecular phylogeny of cirripedes provided by Pérez Losada et al. (2014) actually predicts that neobalanomorphs should be present by the Cenomanian. The reality is that Cretaceous shoreline facies, representing marine habitats most likely to be occupied by the group, yield only *Brachylepas* and its close relatives (Gale and Sørensen, 2014), often in extraordinary abundance (see also Zullo et al., 1987).

The specimen described as *Archaeochionelasmus nekvasilovae* by Kočí et al. (2017) is certainly not a chionelasmatid and does not have the morphology, symmetry, microstructure or growth pattern of any cirripede. It is a part of a poorly preserved rudist shell, which by chance, roughly mimics the form of an incomplete balanomorph wall. The morphological, phylogenetic and palaeoecological conclusions based upon the specimen are therefore invalid, and the taxon *Archaeochionelasmus nekvasilovae* should be considered as a rudist *incertae sedis.*

The assertions by Kočí et al. (2017) that the Cretaceous species *Pachydiadema cretacea* (Withers, 1935), from the Upper Cretaceous of southern

Sweden, is not a sessile barnacle, and that it was incorrectly reconstructed by Gale and Sørensen (2014) are without any foundation.

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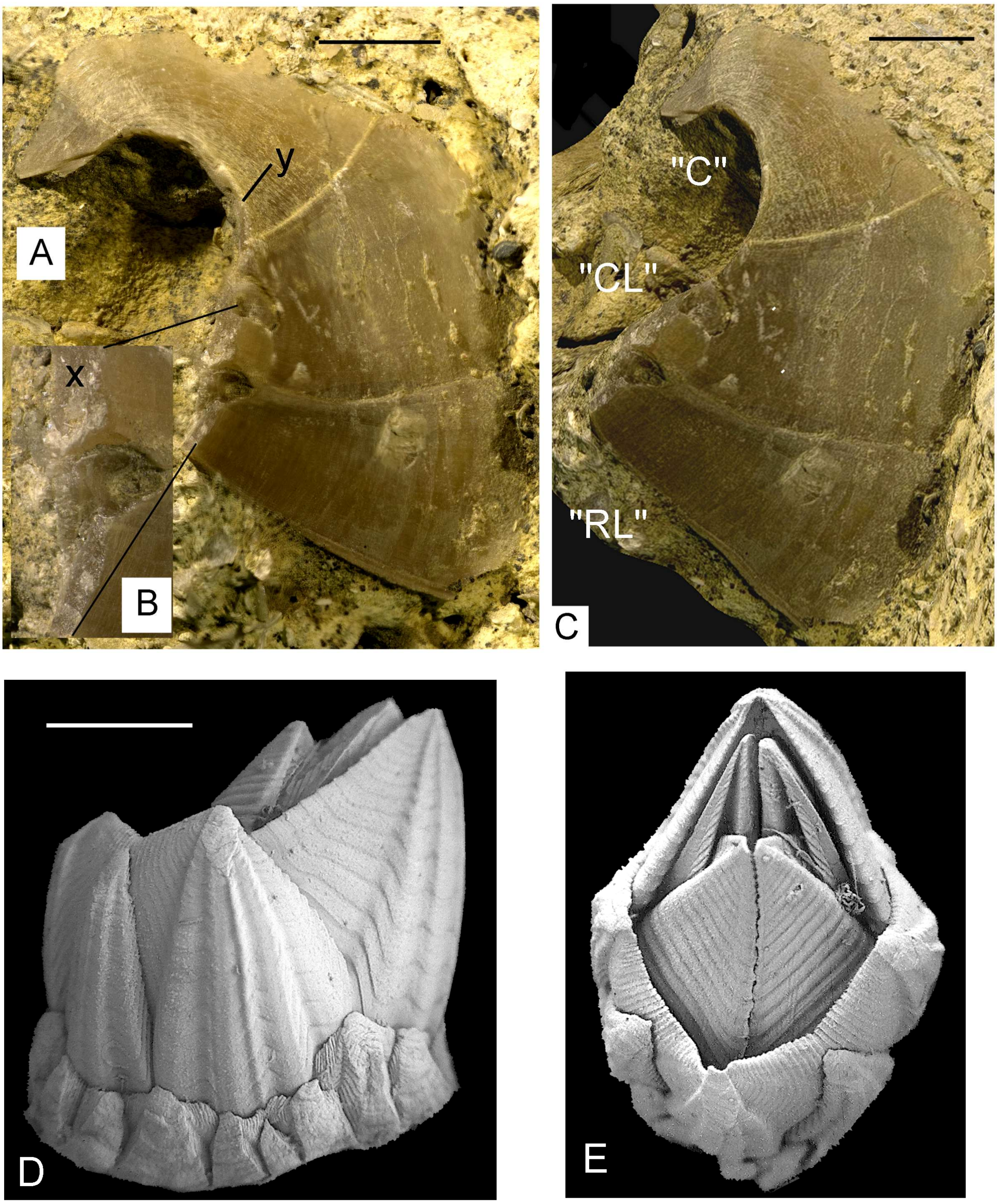
Captions

Fig. 1A–C. Holotype (NM-07615) of *Archaeochionelasmus nekvasilovae* Kočí, Newman and Buckeridge, 2017. A. "apical" view; B. "lateral" view; C. enlargement of fractured surface, to show calcite spar structure. "CL", carinolatus, "RL", rostrolatus, "C" carina. Note asymmetry of "carina", absence of alae, coarse calcite structure of inner shell wall (x) and thin, fibrillar structure of outer wall (y), NM-07615, Předboj near Prague; upper Cenomanian (Korycany Member), Bohemian Basin, Czech Republic. Photographs kindly provided by Dr Tomáš Kočí. D, E. *Chionelasmus darwini* (Pilsbry, 1907), individual in lateral view (D), apical view (E). Note robust, convex plates bearing large alae, with coarse growth lines and radial sculpture; large kite-shaped orifice in which the operculum fits, and tip of carina forming anterior extremity. Present day, off Rodrigues Ridge, Indian Ocean (collected A.S. Gale, 1987).

Fig. 2. Drawings of living chionelasmids and supposed fossil species. A–C, *Waikalasma boucheti* Buckeridge, 1996, in lateral (A) and apical (B) aspects and (C) with opercular plates removed. D, E. *Chionelasmus darwini* (Pilsbry, 1907), in lateral aspect with opercular plates (D) and without them (E). F, *Chionelasmus ohtai* (Yamaguchi and Newman, 1990) in slightly oblique lateral aspect. Note the similar construction of living chionelasmids, with large alae (blue) and symmetrical, kite-shaped orifices, into which the opercular plates fit tightly. Note tall carina, with posteriorly extended alae, slightly lower rostrum, with anteriorly extending alae. Two lateral plates present in *W. boucheti,* one in *Ch. darwini* and *Ch. ohtai*. Note also the similar construction and sculpture of plates, with weak radial ridges and grooves and prominent, evenly spaced growth increments. The plates are unfused and disaggregate easily. G, H. *Archaeochionelasmus nekvasilovae* Kočí, Newman and Buckeridge, 2017.

Drawings of holotype, NM 07615, Prague, upper Cenomanian, Korycany Member, Předboj, Bohemian Basin, Czech Republic. G, “lateral” view, H, “apical”. Note asymmetrical “carina”, complete absence of alae, lack of evidence of separate valves on broken margin (pink). A–C after Buckeridge (1996, fig. 1c, f; holotype of *W. boucheti*, MHNH c12428, Vannatu, SW Pacific). D, E. *Ch. darwini*, after Newman (1987, fig. 4A, no locality information). F. after Yamaguchi and Newman (1990, fig. 2A; holotype of *Ch. ohtai*, UMUT RA-18631, North Fiji Basin, Southwest Pacific). Scale bars equal 5 mm. Abbreviations/letters: T, tergum; S, scutum, IP, imbricating plates; C, carina; R, rostrum; AL, alae; wall plates, “CL1”, “CL2”, “carinolatera; “RL”,” rostrolatus”(interpretation of Yamaguchi and Newman 1990). CM, carinomarginal; M, marginal; RM, rostromarginal, after Gale and Sørensen’s (2014) proposed new homologies and names for the wall plates in balanomorphs.

Fig. 3. A–D, Reproduction of Plate 2, figures 1, 2 and 4 from Počta (1889); 1, *Cryptaulia triangularis* Počta; 2a, b, 4, *Caprotina sodalis* Počta, both from the Cenomanian of Korycany, Czech Republic. Note the fine, transverse fibrillar surfaces of the specimens shown in Figures 2 and 4, like those in *A. nekvasilovae*. The invaginated ligamentary seam (ils) is marked; it corresponds to one of the supposed valve boundaries in the type of *A. nekvasilovae,* which is the basal portion of the right valve of a comparable specimen. E–G, reproduction of Figures 224-6 from Frič (1911). E, *Caprotina vadosa* Počta. F, *Caprotina perplexa* Počta. G, *Cryptaulia paradoxa* Počta. E and F are from Radovesnice, while G is from Skuč, Czech Republic. Scale bar equals 10 mm.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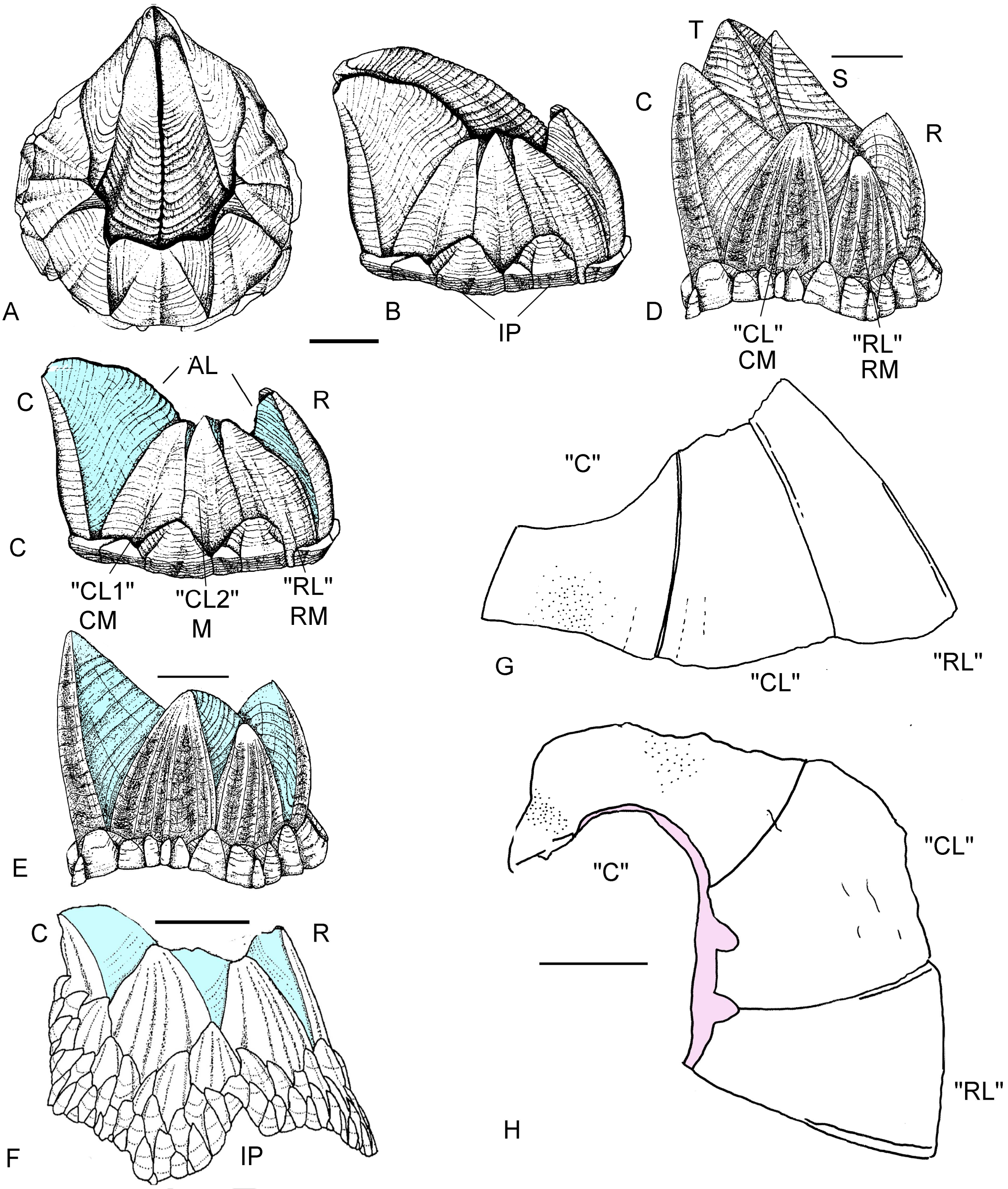
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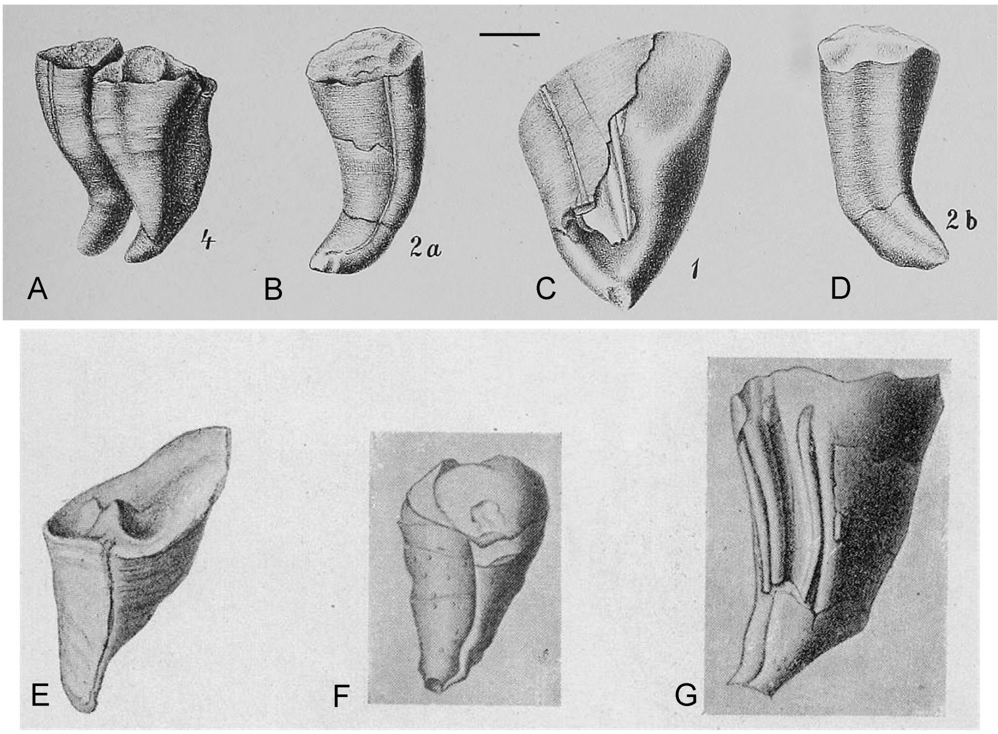
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