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# Cirripedes (Crustacea) from the Neogene and Pleistocene of Lee Creek Mine, Beaufort County, North Carolina, USA

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ABSTRACT:

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Seven species of balanomorph cirripedes are recorded from the Miocene to Pleistocene succession exposed in a phosphate mine in North Carolina; although collected loose, most probably originated from the Pliocene Yorktown Formation. Four of the species belong to the balanid subfamily Concavinae, i.e., *Chesaconcavus proteus* (Conrad, 1834), *Arossia aurae* Zullo, 1992, *Paraconcavus talquinensis* (Wiesbord, 1966), *P.* cf. *prebrevicalcar* (Ross, 1964), and one to the subfamily Amphibalaninae, i.e., *Fistulobalanus multiseptatus* (Ross, 1964). A chelonibiid (turtle barnacle), *Protochelonibia collaretai* sp. nov. is new, and the living balanine *Balanus calidus* (Pilsbry, 1916) is recorded from the Pleistocene (Calabrian) James River Formation.

**Key words:** Cirripedes; Neogene; Pleistocene; North Carolina.

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## INTRODUCTION

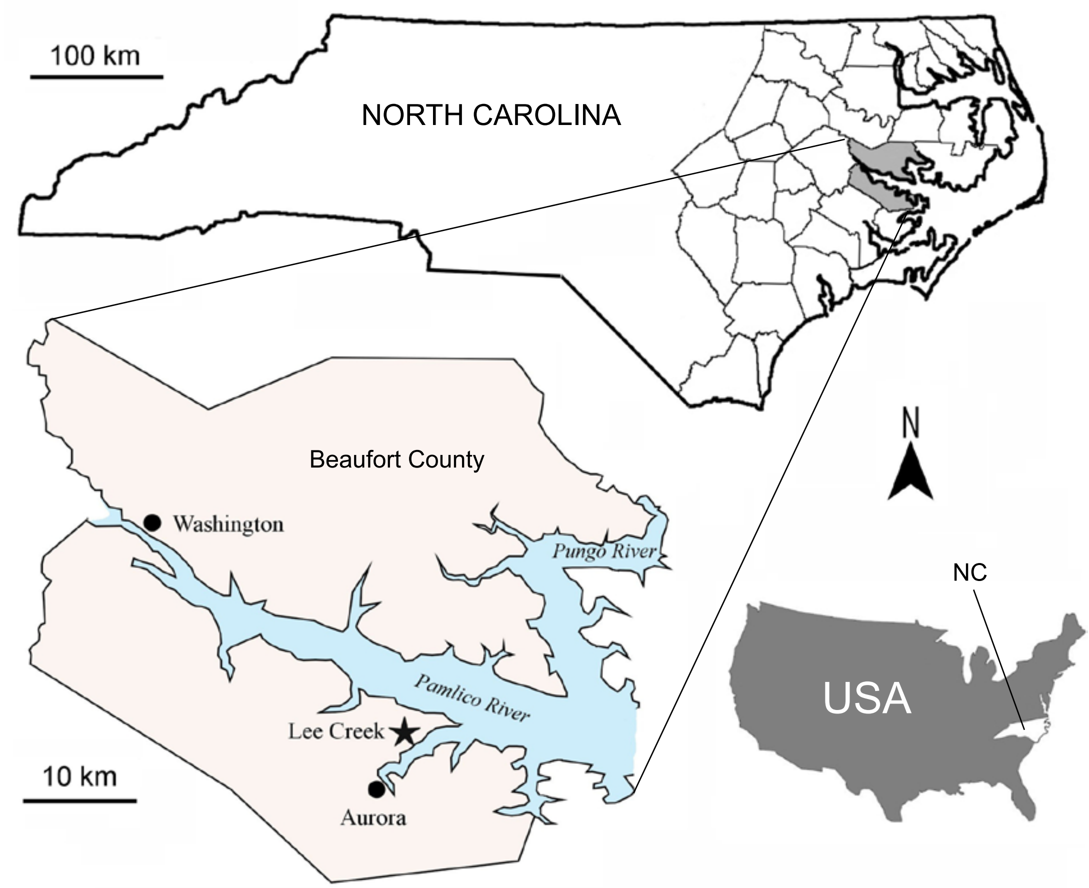
The Lee Creek phosphate mine, near the town of Aurora, in Beaufort County, NC (Text-fig. 1) commenced working Miocene phosphates from the Pungo River Formation in 1965. This involved removal of approximately 25 m of Pliocene and Pleistocene overburden, in order to access the underlying 12 m of phosphate-bearing sediment (Ward 2007). All formations are fossiliferous, and have yielded diverse marine vertebrate and invertebrate faunas, including cirripedes (Zullo 1984, 1992; Zullo and Miller 1986). Most material has been collected *ex situ*, from the extensive spoil piles of overburden, and access to the walls of the mine was largely prohibited for safety reasons.

The present account is large based on two collections of cirripedes made from the spoil heaps — one by ES, the other by David Ward. Sediment extracted from the matrix of these specimens was dated using calcareous nannofossils. The results tend to confirm that most of the material is derived from the Pliocene Yorktown Formation. Other descriptions of Neogene cirripedes from various localities in North Carolina were made by Zullo (1984, 1992), Zullo and Miller (1984), and Gale and Sadorf (2025a, b).

## STRATIGRAPHY (Text-fig. 2)

### Pungo River Formation

The Pungo River Formation is the oldest exposed formation at the Lee Creek Mine. Kimrey (1964) described the Pungo River Formation as interbedded phosphatic sands, silts and clays, diatomaceous clays,




Text-fig. 1. Map to show position of Lee Creek Mine in Beaufort County, North Carolina, USA.

and phosphatic and non-phosphatic limestones. Drill cores indicate a thickness of around 28 m for the Pungo River Formation near Aurora (Gibson 1983). A summation of age data for the formation indicates an Aquitanian to Langhian age (Early to Middle Miocene; Boessenecker 2019).

**Yorktown Formation**

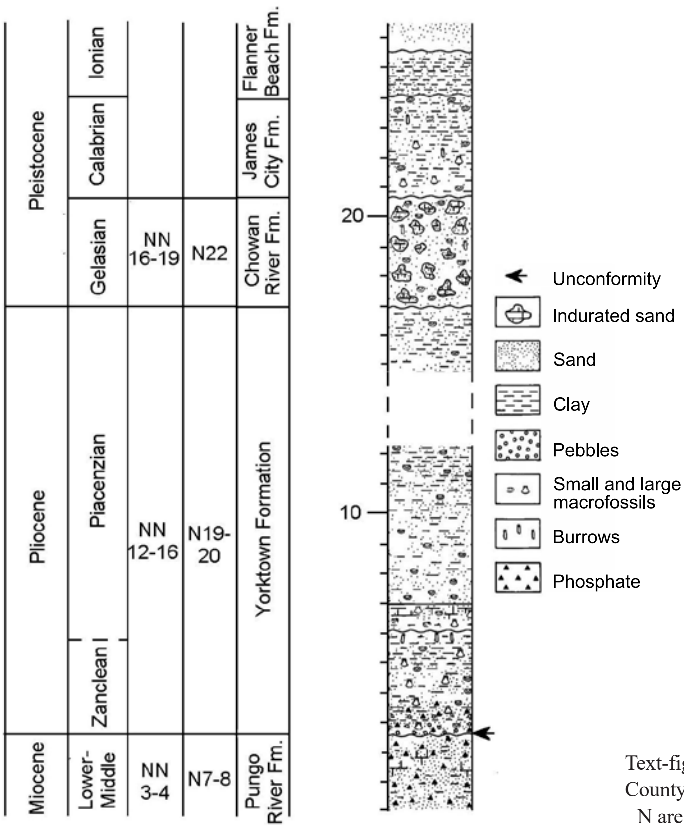
The Pliocene Yorktown Formation lies unconformably above the Pungo River Formation. It is approximately 14 m thick at Lee Creek and contains four members, which are, in ascending order: the Sunken Meadow, the Rushmere, the Morgarts Beach and the Moore House (Ward and Blackwelder 1987; Ward 2007). The Yorktown Formation consists of a basal, pebbly, coarse-grained sand; a shelly fine-grained sand; a very fine-grained sandy clay; and an upper sandy shell hash (Ward and Blackwelder 1980). At Lee Creek, unlike other localities, aragonitic invertebrates within the Yorktown Formation are poorly preserved or only preserved as moulds and casts (Ward 2007). The Yorktown Formation is of Late Pliocene (Piacenzian) age (Dowsett *et al*. 2021).

**Chowan River Formation**

The Pleistocene Chowan River Formation unconformably overlies the Yorktown Formation (Blackwelder 1981; Ward *et al.* 1991). At Lee Creek, it is 2 to 3 m thick and consists of partially indurated olive-grey coarse sand that is bedded, burrowed, mottled, and partly leached (Ward and Blackwelder 1987; Ward *et al.* 1991; Ward 2007). The formation is divided into two members: a lower Edenhouse Member and an upper Colerain Beach Member (Blackwelder 1981).

**James City Formation**

The Pleistocene James City Formation unconformably overlies the Chowan River Formation. At Lee Creek the thickness varies from 2.5 to 3.5 m and




Text-fig. 2. Stratigraphical succession in Lee Creek Mine, Beaufort County, North Carolina, modified after Hazel (1983, fig. 2). NN and N are two alternative zonations based on calcareous nannofossils.

is composed of shelly sands with a diverse molluscan assemblage dominated by subtropical species (Ward and Blackwelder 1987). There are at least two beds of different ages at Lee Creek, representing at least two marine highstands (Ward *et al.* 1991).

**Flanner Beach Formation**

The Pleistocene Flanner Beach Formation at Lee Creek is a 4.3 m thick poorly-sorted, fine, muddy sand (Ward 2007). Most exposures at Lee Creek are leached of fossils or did not contain them but some yielded an assemblage of molluscs and other invertebrates, including balanomorph cirripedes (Ward 2007).

**Institutional abbreviations**

ANSDU – Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, USA.
NHMUK – The Natural History Museum, London, UK.
PRI – Paleontological Research Institute, Ithaca, New York, USA.
RGM – Naturalis Biodiversity Center [formerly Rijksmuseum van Geologie en Mineralogie], Leiden, the Netherlands.
USNM – United States National Museum, Washington D.C., USA.

## SYSTEMATIC PALAEONTOLOGY

Superfamily Coronuloidea Leach, 1817

DIAGNOSIS: The shell wall is composed of eight (the rostral plate is sometimes discernibly tripartite), six or four plates. The plates are tubiferous; the tubes are formed between the inner and outer laminae, between internal buttresses or between external ribs. The radii are solid and the basis is membranous or weakly calcareous.

Family Chelonibiidae Pilsbry, 1916

REMARKS: Harzhauser *et al.* (2011) created the subfamily Protochelonibiinae to accommodate their genus *Protochelonibia* Harzhauser and Newman in Harzhauser *et al.*, 2011. Furthermore, molecular studies (Pérez-Losada *et al.* 2014) place only two extant genera in the Chelonibiidae, *Chelonibia* Leach, 1817 itself and *Stephanolepas* Fischer, 1886, a small barrel -shaped taxon which embeds in turtles and was previously referred to the Platylepadidae (e.g., Hayashi 2013). Therefore, we provisionally leave all three taxa as Chelonibiidae without any subfamilial designation.

*Protochelonibia* Harzhauser and Newman in Harzhauser *et al*., 2011

DIAGNOSIS: Shell wall made up of 8 plates, unfused rostrum and rostromarginals; profile low, sides straight to weakly concave; articular sutures between compartments simple; septa thin, do not reach basal margin. Inner lamina absent.

TYPE SPECIES: *Protochelonibia submersa* Harzhauser and Newman in Harzhauser *et al*., 2011 (=*Chelonibia capellinii* De Alessandri, 1895).

ASSIGNED SPECIES: In addition to the type species: *Chelonibia melleni* Zullo, 1982, *Protochelonibia starnesi* Perreault, Collareta and Buckeridge, 2022; *Protochelonibia hermani* Gale in De Schutter *et al*., 2023; *Protochelonibia collaretai* sp. nov.

REMARKS: There is some uncertainty as to the number of species of *Protochelonibia* and precisely how these are diagnosed. Harzhauser *et al*. (2011) used the 'depressed profile' as a diagnostic character of *P. submersa* as distinguishing it from the higher profile of *P. capellinii*. However, as the type material of *P. submersa* is flattened by compaction (see Harzhauer *et al*. 2011, fig. 2), the valves are broken and some separated, this is not really a valid argument. Harzhauser *et al*. (2011) also stated that the internal ribbing in *P. submersa* showed irregular development, as compared to the regular primary, secondary and tertiary ribbing in *P. capellinii*; however, a further specimen of *P. capellinii* figured by De Alessandri (1906, pl. 18, fig. 4) shows similar ribbing to both *P. submersa* and the holotype of *P. capellinii*. Both species are of Early Miocene age, and were found approximately 600 km apart, no great distance for cirripedes attached to swimming sea turtles. For these reasons, *P. submersa* is here treated as a junior synonym of *Chelonibia capellinii*.

Zullo (1982) described *Chelonibia melleni* from the Lower Oligocene of Mississippi, USA, on the basis of 5 isolated compartments, including a carina, a rostrum, two rostromarginals, and a marginal or carinomarginal plate. This species was subsequently referred to *Protochelonibia* (Collareta and Newman 2020), and *P. melleni* was later identified from the Oligocene (Rupelian) of Germany, on the basis of a crushed colony (Collareta *et al.* 2022a) and specimens attached to a turtle (Collareta *et al*. 2022b) from the Rauenberg Lagerstätte in southern Germany. Collareta and Newman (2020) argued that *Protochelonibia* differed from *Chelonibia* in the unfused rostrum-rostromarginals, and in the acutely triangular apices of these compartments. They also considered that *P. melleni* and *P. submersa* differed primarily in the presence of a corrugated basal compartmental margin on a single plate of *P. melleni* (Zullo 1982, figs 1, 2). Recently, Perreault *et al.* (2022) described a new species of *Protochelonibia*, *P. starnesi*, from the Early Oligocene of Mississippi, USA, from which they also recorded and figured a well preserved carinomarginal of *P. melleni* (Perreault *et al*. 2022, fig. 3).

The nature of the articulations between compartments provides valuable characters for the distinction between species of *Protochelonibia* (Text-fig. 3; see also Gale in De Schutter *et al*. 2023). The termination of the dorsally projecting radius is an elongated, narrow ridge (R) which bears irregular, denticulate ridges diverging from the central axis; this structure fits precisely into a corresponding groove (G) on the articulating adjacent plate, immediately adjacent to the ala (Text-fig. 3C, D, G, H, K, L). The lateral surfaces of the parietes bear rugosities and shallow depressions (R/D) which serve to strengthen the articulation.

*Protochelonibia collaretai* sp. nov.
(Text-figs 3I–L, 4H–M)

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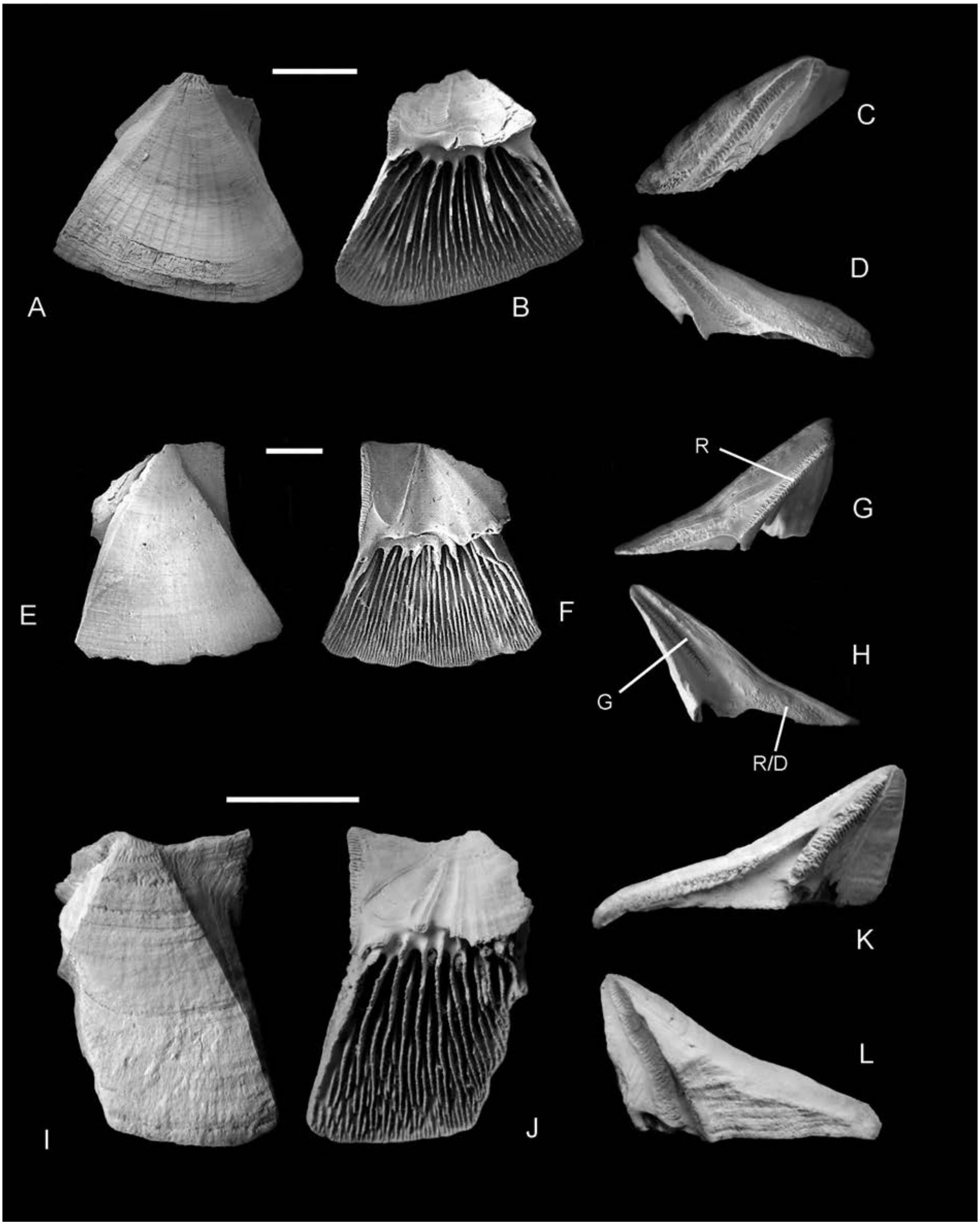
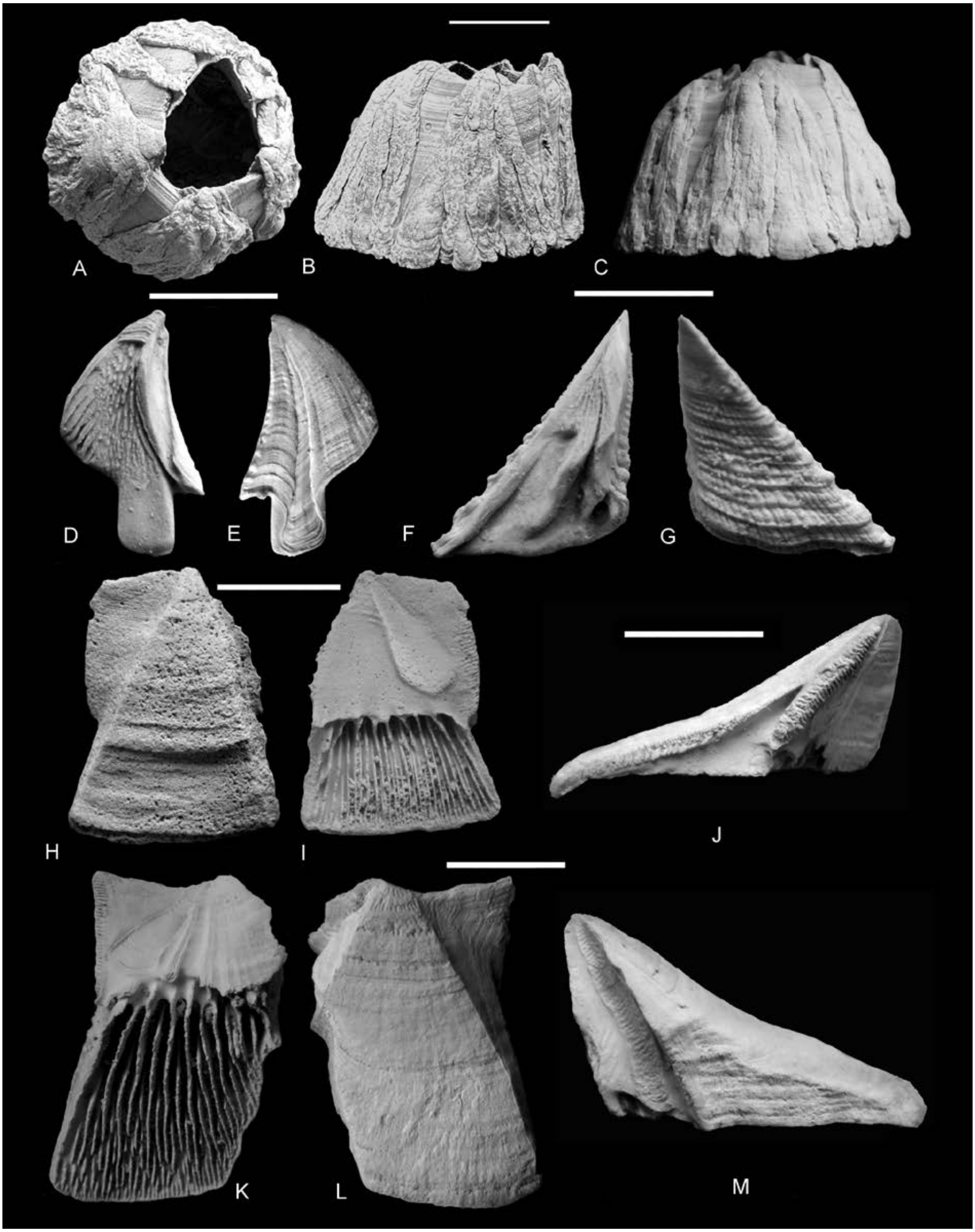
DIAGNOSIS: *Protochelonibia* in which the marginal compartments are relatively broad and short, and the short, coarsely rugose dorsal termination of the radius is angled to the basal margin at 40–45°.

TYPES: The well-preserved marginal compartment is the holotype (NHMUK PI In 66687), the other specimen (NHMUK PI In 66688) is paratype. Probably from the Yorktown Formation, Lee Creek Mine, Beaufort County, North Carolina, USA.

MATERIAL: Two marginal compartments, from the type locality.




Text-fig. 3. Comparative morphology of *Protochelonibia* spp. A–H – *Protochelonibia capellinii* (De Alessandri, 1895); A–D – RGM 1440134, marginal plate in external (A), internal (B), dorsal (C), and ventral (D) views; Middle Miocene, Miste, near Winterswijk, the Netherlands; E–H – NHMUK In.27570, marginal plate in external (E), internal (F), dorsal (G), and ventral (H) views; Tortonian, Kalksberg, Vienna, Austria. I–L – *Protochelonibia collaretai* sp. nov., NHMUK PI In 66687, holotype marginal plate in external (I), internal (J), dorsal (K), and ventral (L) views; Neogene, probably Pliocene, Piacenzian, Lee Creek Mine, Beaufort County, North Carolina. Expanations: R – termination of radius, G – corresponding groove, R/D – ridges and depressions. Scale bars equal 10 mm.




Text-fig. 4. Cirripedes from Lee Creek Mine, Beaufort County, North Carolina, USA. A–G – *Arossia aurae* Zullo, 1992, NHMUK PI In 66689; A–C – shell with opercular plates in apical (A), lateral (B), and rostral (C) views; D, E – tergum in internal (D) and external (E) views; F, G – scutum in internal (F) and external (G) views. H–M – *Protochelonibia collaretai* sp. nov.; H, I – NHMUK PI In 66688, paratype marginal in external (H) and internal (I) views; J–M – NHMUK PI In 66687, holotype marginal in dorsal (J), internal (K), apical (L), and ventral (M) views. Scale bars equal 10 mm (A–C, H–M) and 5 mm (D–G).

DERIVATION OF NAME: For Alberto Collareta, in recognition of his work on turtle and whale barnacles.

DESCRIPTION: Marginals broad and relatively short, outer surface concave. Sheath occupies between a half and a third of the interior surface. Radius broad and triangular, angled at 40–45° to basal margin, dorsal margin ridged and coarsely denticulate. Ala short, with deep overlying groove to accommodate the dorsal margin of radius. Articular surface of lateral parietal margin with narrow zone of fine rugosities and depressions. Interior of parietes bear weakly crenulate septa of variable length, most of which do not reach the sheath; minor septa of variable length increase in number towards the lateral margin. Exterior of parietes nearly smooth, with irregularly spaced commarginal growth lines and weak apicobasal ribbing.

REMARKS: *Protochelonibia collaretai* sp. nov. differs from the Miocene–Pliocene European species *P. capellinii* (Text-fig. 3A–H) in its broader, shorter shape and in the nature of the articulation between the parietes. The coarsely rugose, shorter, dorsal termination of the radius (R) has a relatively high angle to the basal margin (40–45°) in *P. collaretai* sp. nov. (Text-fig. 3K), whereas in *P. capellinii* (Text-fig. 3C, G) the angle is lower (30°), the ridge is narrower, more elongated and the rugosities are finer. Additionally, the articulating rugosities on the lateral margins of the compartments are coarser in the former species. *Protochelonibia collaretai* sp. nov. differs from *P. melleni* and *P. starnesi* in lacking a crenulate basal margin.

Zug (2001) recorded 11 species of turtles from the Yorktown Formation of Lee Creek Mine, which would have provided numerous opportunities for colonisation by chelonibiids. It is therefore surprising that only 2 specimens have been recorded.

Superfamily Balanoidea Leach, 1817

INCLUDED FAMILIES: Balanidae Leach, 1817; Pyrgomatidae Gray, 1825.

DIAGNOSIS: Wall composed of rostrum, carina and one to two pairs of marginals, or wholly concrescent; parietes solid or tubiferous; radii solid or tubiferous; basis commonly calcareous, solid or permeated by tubes, rarely membranous; when basis is calcareous, internal surfaces of compartments commonly with uniform ribs which interdigitate with margins of basis.

REMARKS: Molecular analysis of numerous balanoids (Pérez-Losada *et al.* 2014, fig. 1) recovered only two monophyletic clades, the Balanidae and the Pyrgomatidae.

Family Balanidae Leach, 1817

INCLUDED SUPERFAMILIES: Archaeobalaninae Newman and Ross, 1976; Wanellinae Chan, Dreyer, Gale, Glenner, Ewers Saucedo, Pérez-Losada, Kolbasov, Crandall and Høeg, 2021; Acastinae Kolbasov, 1993; Amphibalaninae Pitombo, 2004; Balaninae Leach, 1817; Bryozobiinae Ross and Newman, 1996; Concavinae Zullo, 1992; Hexacreusiinae Zullo in Newman, 1996; Megabalaninae Newman, 1979.

DIAGNOSIS*:* Monophyletic by molecular analysis. Wall of six or four plates; parietes tubiferous or solid; tubiferous shell, with tubes basally in a single uniform row formed between inner and outer laminae, although supplementary tubes can form in the same basal region; interlaminate figures complex, arborescent; radii either solid or tubiferous; basis commonly calcareous and tubiferous or membranous (Chan *et al.* 2021, p. 48).

REMARKS: Derived balanomorphs have traditionally been divided into a more basal Archaeobalanidae, characterised by a relatively simple parietal structure (rarely tubiferous, with solid radii) and a more derived Balanidae, in which the wall structure is more complex and the radii are commonly tubiferous (Newman and Ross 1976). Pitombo (2004) undertook a cladistic analysis of character distribution in genera of the Balanidae and identified four monophyletic subfamilies; the Megabalaninae Newman, 1979, Concavinae Zullo, 1992, Balaninae Leach, 1817 and the Amphibalaninae Pitombo, 2004. His most parsimonious trees (Pitombo 2004, figs 12, 13) placed the Megabalaninae and Concavinae as sister taxa, crownward of, respectively, the Amphibalaninae and the Balaninae.

Gale (2021) undertook a cladistic analysis of 24 morphological characters for eleven Balanomorpha genera. This tree shows the Archaeobalanidae as a paraphyletic stem group to the Balanidae, in which successive genera form a ladder leading crownward. *Vectibalanus* Gale, 2021 appears as either a basal balanid or the most crownward archaeobalanid. The first stratigraphical occurrence of the balanomorph genera is broadly congruent with this tree. However, on the basis of recent molecular studies, there is no consistent separation of even the Archaeobalanidae and Balanidae in the genera studied (Pérez-Losada *et al.* 2014; Chan *et al.* 2017), and it appears that the families represent grades rather than clades; none appears to be a monophyletic entity. Thus, genera included within the derived subfamilies Megabalaninae, Concavinae and Amphibalaninae by Pitombo (2004, figs 12, 13) appear in different clades in the molecular tree of Pérez-Losada *et al.* (2014, figs 12, 13). It is clear that resolving the phylogeny of the Balanoidea is not a simple matter. For the present, the families Archaeobalanidae and Balanidae are used informally.

### Genus *Balanus* Da Costa, 1778

TYPE SPECIES: *Lepas balanus* Linnæus, 1758, by subsequent designation (Pilsbry 1916).

INCLUDED SPECIES: In addition to the type species, *Balanus balanus*, *B. crenatus* Bruguière, 1789, *B. spongicola* Darwin, 1854 and over 30 additional species (see list in Pitombo 2004, appendix 1A).

DIAGNOSIS: Balaninae in which the radii are solid, and transverse septa are present in the parietal tubes. The parietal structure includes interlaminate figures.

REMARKS: The genus *Balanus* is very difficult to diagnose precisely; essentially, it comprises an assemblage of species which lack many of the derived characters found in the subfamilies Concavinae, Amphibalaninae and Megabalaninae (Pitombo 2004). These include the absence (in many) of tubiferous radii, the absence of incomplete septa between the primary septa and multi-layered bases.

### *Balanus calidus* (Pilsbry, 1916)
(Text-figs 5K–N, 6)

1854. *Balanus spongicola*, var. Darwin, p. 225, pl. 4, fig. 1d.
1916. *Balanus calidus* Pilsbry, p. 118, pl. 25, figs 1–1c, text-fig. 32a–f.
1976. *Balanus calidus* Pilsbry; Newman and Ross, p. 65.
1986. *Balanus calidus* Pilsbry; Zullo and Miller, p. 729, fig. 4f–j.

DIAGNOSIS: Shell conical, parietes strongly ribbed; radii rather narrow, summits slightly oblique. Scutum thick, exterior bears numerous growth ridges and radial striae. Tergum with short beak and relatively broad spur (modified from Pilsbry 1916, pp. 118, 119).

TYPE: USNM 48193, Gulf of Mexico, southwest of Cape San Blas, western Florida.

MATERIAL: Over 50 shells, some with opercular valves, many attached to external surface of crepidulid gastropods or oysters. The material probably comes from the James River Formation (Calabrian).

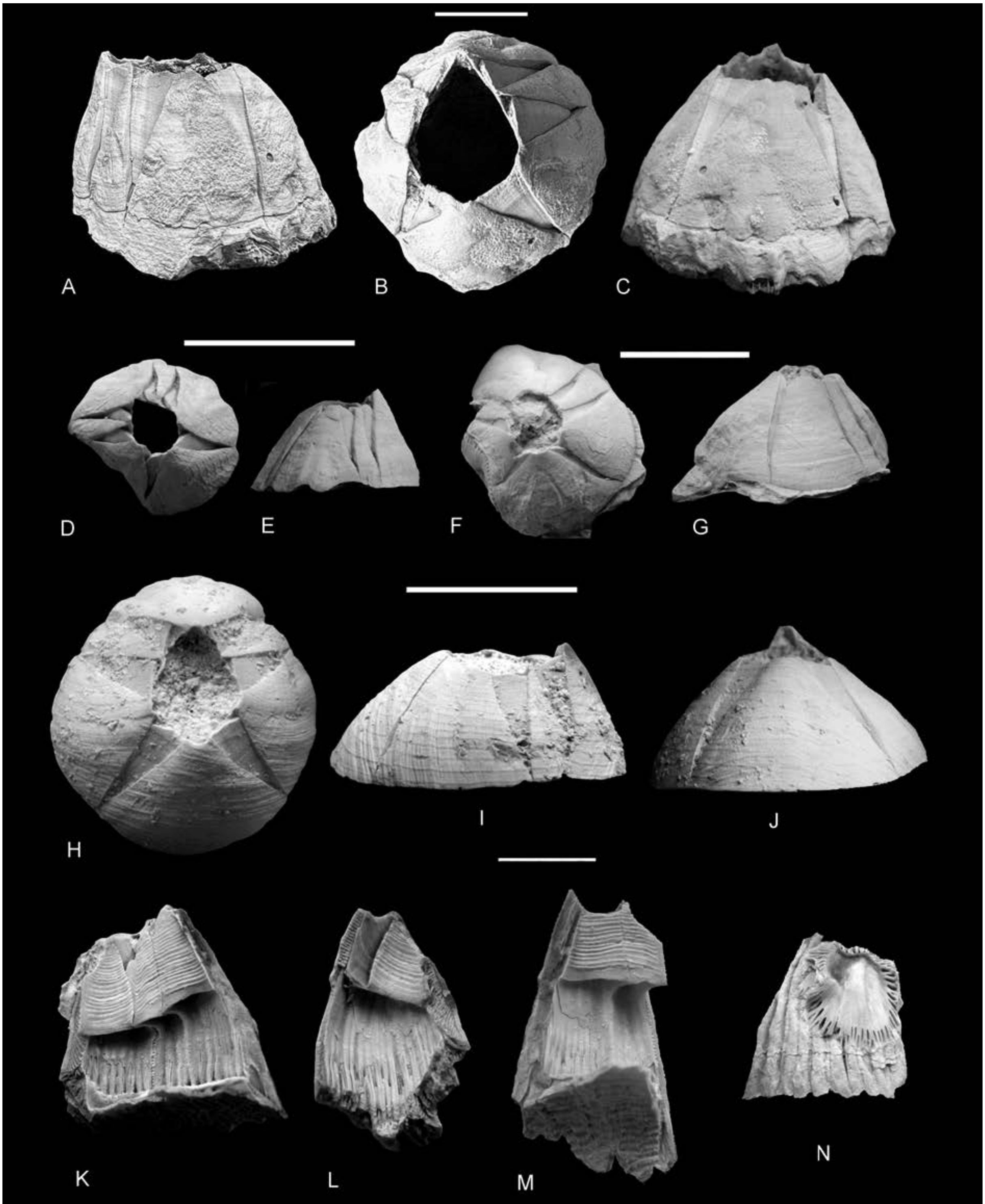
REMARKS: The morphology of the scuta and terga compare closely with those of present day specimens from Florida (Text-fig. 6H, J, K; compare with Text-fig. 6D–F). We also illustrate the interiors of compartments of this species (Text-fig. 5K–N); these show that the sheath occupied between one third and one half of the height of the shell, and that the interiors of the parietes are smooth. The basis is tubiferous, and the sutural edges of the radii bear rather coarse, transverse denticles. The species is closely related to *Balanus spongicola* Brown, 1827 (from the eastern Atlantic, Mediterranean and Indian Oceans, also recorded from Brazil and Venezuela) as Darwin (1854) originally recorded *B. calidus* as a variant of this species. In *B. spongicola*, the lower interior parts of the parietes are ribbed, and the exterior surfaces lack ribbing (see Gale 2026, text-fig. 122). There are also small but significant differences in the opercular plates noted by Pilsbry (1916, pp. 118, 119). The species ranges from the Miocene to Pleistocene in the Eastern American Coastal Plain, and at the present day extends through the Caribbean, the Gulf of Mexico, and as far north as North Carolina.

Many of the specimens of *B. calidus* which we have examined from the Lee Creek Mine are attached to the external surfaces of a crepidulid gastropod (Text-fig. 6A, C, I), some of which are densely crowded with individuals. This is possibly in-life attachment, because they are never attached to the interiors. Gale (2021) recorded the Eocene balanid *Vectibalanus* attaching around the apertures of gastropod shells which were probably occupied by hermit crabs. Attachments of this type would enable the sessile cirripedes some degree of movement.

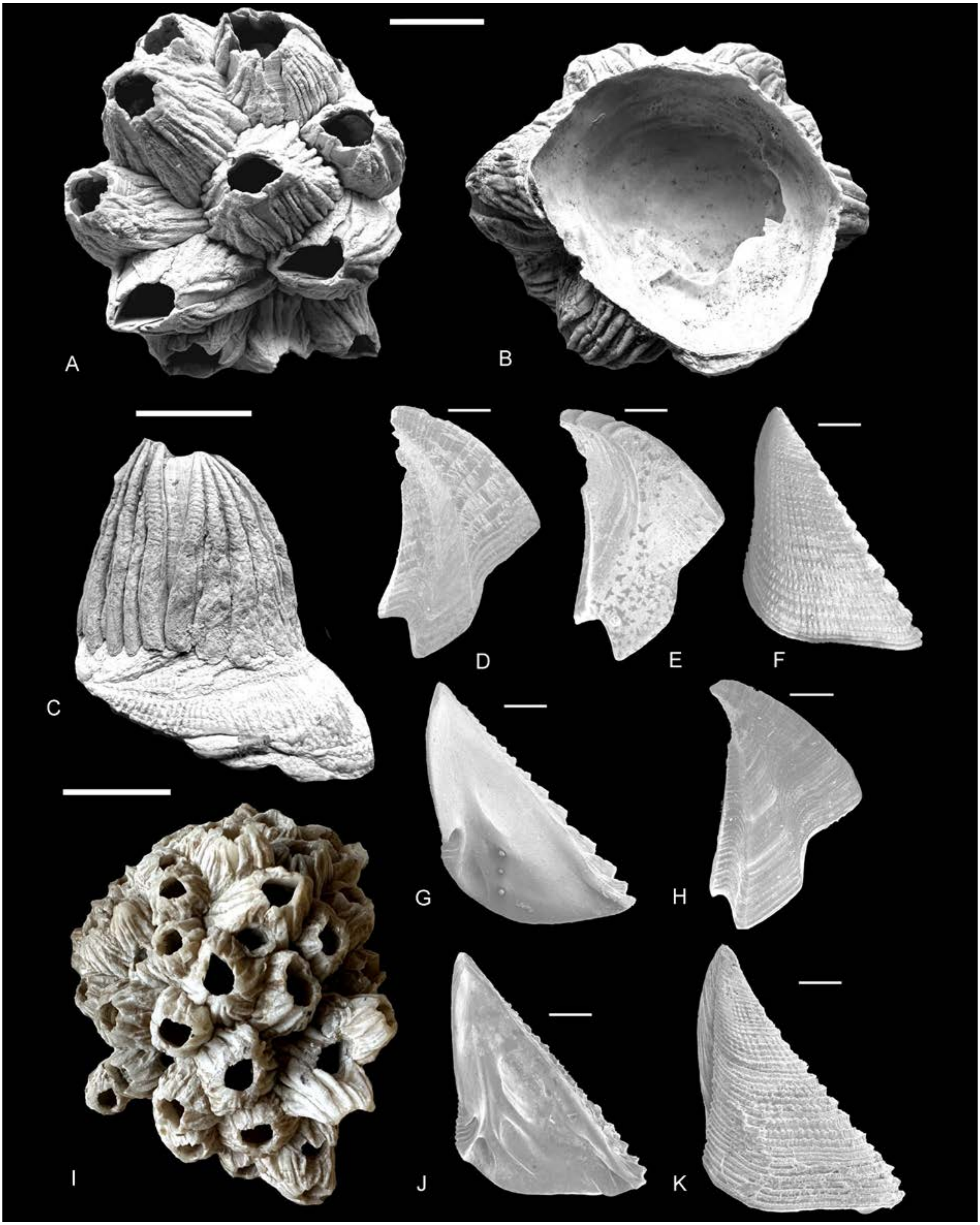
### Subfamily Amphibalaninae Pitombo, 2004

INCLUDED GENERA: *Amphibalanus* Pitombo, 2004; *Fistulobalanus* Zullo, 1984; *Tetrabalanus* Cornwall, 1941.

DIAGNOSIS*:* Wall of six or four plates, relatively small, smooth or lightly ribbed, with one or more rows of parietal tubes, commonly with transverse septa. Radii solid, transverse teeth on sutural edge with denticles on lower side only; alae not cleft; lateral margin of sheath not extending over the adjacent ala, with or without calcareous vesicles. Basis tubiferous, tubes in single layer. Scutum with a conspicuous adductor ridge. Tergum with spur and furrow




Text-fig. 5. Cirripedes from Lee Creek Mine, Beaufort County, North Carolina, USA. A–C – *Arossia aurae* Zullo, 1992, NHMUK PI In 66690, shell in lateral (A), apical (B) and ventral (C) views. D–G – *Paraconcavus talquinensis* (Weisbord, 1966); D, E – NHMUK PI In 66696, small shell in apical (D) and lateral (E) views; F, G – NHMUK Pi In 66697, shell in apical (F) and lateral (G) views. H–J – *Fistulobalanus multiseptatus* (Ross, 1964), NHMUK PI In 66706, shell in apical (H), lateral (I), and ventral (J) views. K–N – *Balanus calidus* Pilsbry, 1916, NHMUK PI In 66707, morphology of compartments in internal (K–M) and internal (N) views; N with basis of a further individual attached. Provenance: A–J are probably from the Yorktown Formation, Piacenzian; K–L are from the James City Formation, Calabrian. Scale bars equal 10 mm (A–J); 5 mm (K–N).




Text-fig. 6. *Balanus calidus* Pilsbry, 1916. A, B – NHMUK PI In 66708, cluster of shells attached to crepidulid gastropod; C – NHMUK PI In 66709, large shell in lateral view; D, E, H – terga in external (D, H) and internal (E) views; D, E, from specimens figured in A, B; H from specimen figured in C; F, G, J, K – scuta in external (F, K) and internal (G, J) views; F, G from specimens figured in A, B; J, K from specimen figured in C; I – NHMUK PI In 66710, cluster of shells on crepidulid gastropod. Provenance: A–G are probably from the James City Formation, Gelasian, Lee Creek Mine, Beaufort County, North Carolina, USA; H, J, K are from present day of Florida, USA. Scale bars equal: 5 mm (A–C, I) and 0.5 mm (D–H, J–K).

margins coincident, basal margin with well-developed depressor muscle crests projecting beyond border (Pitombo 2004, p. 264).

REMARKS: *Tetrabalanus* is clearly distinguished by its 4-plated shell, but it is not clear from the diagnoses of Zullo (1984) and Pitombo (2004) how *Amphibalanus* and *Fistulobalanus* differ. The scuta and terga of at least some species are remarkably similar; for example, those of *Amphibalanus venustus* (Darwin, 1854) are closely similar in detail to those of *Fistulobalanus multiseptatus* (Text-fig. 7A–H). The most important differences appear to be in the presence of external, coloured apicobasal stripes in *Amphibalanus* which are situated in the outer lamina between the septa (Text-fig. 7I). These preserve in fossil material, sometimes retaining the original colour (e.g., Menesini and Casella 1988, pl. 1, figs 6, 7). Zullo's (1984, p. 1330) description of the parietal structure in *Fistulobalanus* ("parietal tubes in two or more rows; larger, primary parietal tubes arranged in single row against inner lamina of shell wall; smaller, irregularly arranged, subsidiary rows of parietal tubes between primaries and outer lamina…..") was illustrated in a compartment of *Fistuloblastus klemmi* (Zullo 1984, pl. 7F).

Genus *Fistulobalanus* Zullo, 1984

DIAGNOSIS: Scutum with a conspicuous adductor ridge. Tergum with spur having abrupt change in the direction of growth lines, and spur and furrow margins coincident, basal margin with well-developed depressor muscle crests projecting beyond border (Pitombo 2004, p. 264).

TYPE SPECIES: *Balanus pallidus* Darwin, 1854.

*Fistulobalanus multiseptatus* (Ross, 1964)
(Text-figs 5H–J, 8)

1964. *Balanus* (*Megabalanus*) *multiseptatus* Ross, p. 485, pl. 71, figs 1–6.
1976. *Megabalanus multiseptatus* (Ross); Newman and Ross, p. 68.
1984. *Fistulobalanus klemmi* Zullo, p. 1331, fig. 7A–Z.
1986. *Fistulobalanus multiseptatus* (Ross, 1964); Zullo, table 1.
2025b. *Fistulobalanus multiseptatus* (Ross, 1964); Gale and Sadorf, p. 13, text-fig. 5D–G.

DIAGNOSIS: Shell small, low, conical, smooth, radii narrow, sunken. Parietal tubes with numerous, evenly spaced transverse septa. Radii with coarsely septate sutural margins. Scutum triangular, with short adductor ridge, striated apical callus and a deep articular furrow. Tergum elongate, with short, rounded spur and shallow spur furrow.

TYPES: The small shell figured by Ross (1964, pl. 71, fig. 1) is the holotype (USNM 648117) from the Yorktown Formation, Rice's Pit, Hampton, Elizabeth City County, Virginia, USA. According to Vélez-Juarbe and Pyenson (2011) Rice's Pit exposed the upper part (9–10 m) of the Morgarts Beach Member of the Yorktown Formation, which is approximately 100 kyr younger than the Rushmere Member (Dowsett *et al*. 2021).

MATERIAL: 4 complete shells, 3 of which contained the opercular valves, probably from the Yorktown Formation, Lee Creek Mine, Beaufort County, North Carolina, USA.

REMARKS: The new material includes the first large shells available; Ross' material included only small individuals with a maximum rostrocarinal length of approximately 10 mm, whereas the Lee Creek mine individuals reach up to 20 mm. The shells are subrhombic to oval in outline, the length is slightly greater than the breadth. In lateral profile, they are low and conical, with the height less than half the length. The orifice is rhombic and represents half the length of the shell; it is strongly toothed, with the apex of the slightly recurved carina marking the highest point. The parietes are smooth (apart from xenomorphic imprint from the substrate), although one specimen shows evenly spaced commarginal growth increments. The radii broaden apically and the summits are horizontal to slightly oblique.

The scuta and terga are very similar in detail to those figured by Ross (1964, pl. 71, figs 2, 3). On the scutum, the adductor ridge is short and passes upwards into a striated callus (Text-fig. 8D–I). The articular furrow is broad and deep, the articular ridge short and erect. The external face shows evenly spaced growth ridges and weak apicobasal striae on the tergal portion of the surface. *Fistulobalanus klemmi* Zullo, 1984, also from the Yorktown Formation of Lee Creek Mine (not the Pungo River Formation as stated; see Ward 2007) does not differ in any important features from *F. multiseptatus* and is therefore placed in its synonymy.

Subfamily Concavinae Zullo, 1992

DIAGNOSIS: The scutum is radially striate with adductor and lateral depressor ridges. The tergum has a spur furrow and long to moderately long spur, with nearly parallel sides. The outer parietal lamina has secondary, incomplete septa between the primary septa. The radii are solid or imperfectly tubiferous, the basis is tubiferous often with an underlying vesicular layer (modified after Zullo 1992, p. 3).

INCLUDED GENERA: *Alessandriella* Carriol and Cahuzac, 2001; *Arossia* Newman, 1982; *Chesaconcavus* Zullo, 1992; *Concavus* Newman, 1982; *Menesiniella* Newman, 1982; *Paraconcavus* Zullo, 1992; *Zulloconcavus* Carriol, 2000. Pitombo (2004) added the genus *Perforatus* Pitombo, 2004 to the Concavinae and demonstrated numerous morphological similarities between *Perforatus* and *Concavus*.

### Genus *Arossia* Newman, 1982

DIAGNOSIS: Alar sutural edge simple, either smooth or denticulate; parietal tubes with numerous, closely spaced transverse septa or secondarily filled; external radial striae of scutum deeply incised, forming prominent nodes at intersection with growth ridges; tergal segment of scutum narrow, markedly inflected, partially infolded over depressor muscle pit; adductor and lateral depressor ridges of scutum not confluent; tergum usually with incipient beak; tergal spur furrow narrowly to broadly open, rarely closed; tergal spur short, rather broad, basally truncate or subtruncate, less than own width from basiscutal angle (after Zullo 1992, p. 25).

TYPE SPECIES: *Balanus panamaensis* Rogers, 1948.

INCLUDED SPECIES: *Arossia aurae* Zullo, 1992; *Arossia newmani* Zullo, 1992; *Arossia rubra* Zullo, 1992; *Balanus concavus glyptopoma* Pilsbry, 1916; *Balanus sendaicus* Hatai, Masuda and Noda, 1979; *Concavus ashleyensis* Zullo, 1986; *Concavus* (*Arossia*) *henryae* Newman, 1982.

REMARKS: *Arossia* occurs globally from the middle Miocene to the Pliocene and at the present day survives on the western coasts of Southern, Central and North America (Zullo 1992, fig. 14).

### *Arossia aurae* Zullo, 1992
(Text-figs 4A–G, 5A–C)

1992. *Arossia aurae,* Zullo, p. 28, figs 17.1–17.9.

DIAGNOSIS: Parietes smooth to irregularly folded, numerous closely spaced transverse septa present. Radii broadening apically, bearing fine transverse ridges, with horizontal summits, orifice subrhombic. Scutum with elongated adductor ridge separated from articular ridge by narrow, deep groove. Tergum broad with incipient beak, spur furrow open (modified from Zullo 1992, p. 28).

TYPE: Shell with 1 scutum and 2 terga, Lower Yorktown Formation, Lee Creek Mine, Beaufort County, North Carolina (USNM 459029), original of Zullo (1992, fig. 17.1–17.6, 17.9.

MATERIAL: 2 shells, one with 1 tergum and 1 scutum from the type locality.

REMARKS: The specimens agree moderately well with Zullo's (1992) account of the species, particularly in the morphology of the scutal interior (long adductor ridge, separated from articular ridge by a deep, narrow groove) and the tergum (broad, spur short, spur furrow open). However, the sculpture of the external surface of the scutum is very different to that of Zullo's material, which had conical nodosities. Our specimen, this consists of blunt, slightly elongated nodes separated by raised growth increments.

### Genus *Chesaconcavus* Zullo, 1992

DIAGNOSIS: External radial striae of scutum not deeply incised; tergal segment the of scutum narrow, partially inflected; adductor and lateral depressor ridges of scutum not confluent; tergum with simple apex; tergal spur furrow closed or narrowly open; tergal spur long, placed a distance equal to at least its own width from the basiscutal angle (after Zullo 1992, p. 12).

TYPE SPECIES: *Balanus concavus chesapeakensis* Pilsbry, 1916, by original designation.

INCLUDED SPECIES: *Balanus proteus* Conrad, 1834; *Balanus tamiamiensis* Ross, 1965; *Concavus belgradensis* Zullo, 1984; *Chesaconcavus myosulcatus* Zullo, 1992; *Chesaconcavus rossi* Zullo, 1992; *Chesaconcavus santamaria* Zullo, 1992.

REMARKS: Gale and Sadorf (2025b, p. 22) noted that the construction of the sheath in *C. proteus* is distinctive. It is triangular, narrow and tall, and both ventral and dorsal margins are slightly raised and apicobasally striated. In the carinomarginal, the ventral part of the sheath bears raised transverse bars. A similar structure can be seen in *Chesaconcavus myosulcatus* (Zullo 1992, fig. 11.11).

*Chesaconcavus proteus* (Conrad, 1834)
(Text-fig. 9A–K, N)

1834. *Balanus proteus* Conrad, p. 134.
1842. *Balanus proteus* Conrad, pp. 184, 187.
1845. *Balanus proteus* Conrad, p. 77, pl. 44, fig. 1.
1916. *Balanus concavus proteus* Conrad; Pilsbry, p. 103, pl. 22, figs 3–3c.
1964. *Balanus concavus proteus* Conrad; Ross, p. 486, pl. 71, fig. 20, pl. 72, fig. 1, text-fig. 2.
1976. *Balanus concavus proteus* Conrad; Newman and Ross, p. 61.
1986. *Concavus proteus* (Conrad); Zullo, p. 3.
1992. *Chesaconcavus proteus* (Conrad); Zullo, p. 21, figs 12.9–12.17, 13.1–13.4, 13.10.
2025b. *Chesaconcavus proteus* (Conrad); Gale and Sadorf, p. 20, text-figs 5H–K, 11A–F, L, 12A–M.

DIAGNOSIS: Shell sharply and regularly ribbed, orifice moderately toothed, upper margins of radii oblique, scutum narrow. Adductor ridge long, tergal furrow narrowly open throughout length, tergal spur elongated (abbreviated from Zullo 1992, pp. 21, 22).

LECTOTYPE: A complete shell (ANSDU no. 18813) from the Yorktown Formation, James River, Suffolk County, Virginia, USA.

MATERIAL: Ten complete shells, and numerous isolated compartments; 2 shells with terga and scuta, probably from the Yorktown Formation, Lee Creek mine.

REMARKS: The species is particularly characterised by the strong, irregular ribbing on the parietes. The opercular valves conform closely with those figured by Zullo (1992, fig. 13.1–13.7). Note that some specimens have a very low, conical form (Text-fig. 9D, N); one of these was confirmed as belonging to *C. proteus* from the opercular plates.

OCCURRENCE: Pliocene (Piacenzian) of North Carolina and Virginia, USA.

Genus *Paraconcavus* Zullo, 1992

DIAGNOSIS: Sheath solid; alar sutural edge simple, inconspicuously denticulate; parietal tubes without transverse septa; external radial striae of scutum not deeply incised; tergal segment of scutum narrow, partially inflected; adductor and lateral depressor ridges of scutum not confluent; tergum with simple tergal spur furrow narrowly to broadly open; tergal spur long (modified from Zullo 1992, p. 32).

TYPE SPECIES: *Balanus concavus pacificus* Pilsbry, 1916.

INCLUDED SPECIES: *Balanus concavus mexicanus* Henry, 1941; *Balanus concavus prebrevicalcar* Ross, 1964; *Balanus talquinensis* Wiesbord, 1966; *Balanus neusensis* Zullo and Miller, 1986; *Paraconcavus margaritatus* Zullo, 1992.

*Paraconcavus talquinensis* (Weisbord, 1966)
(Text-figs 5D–G, 10A–E, G–J, 11)

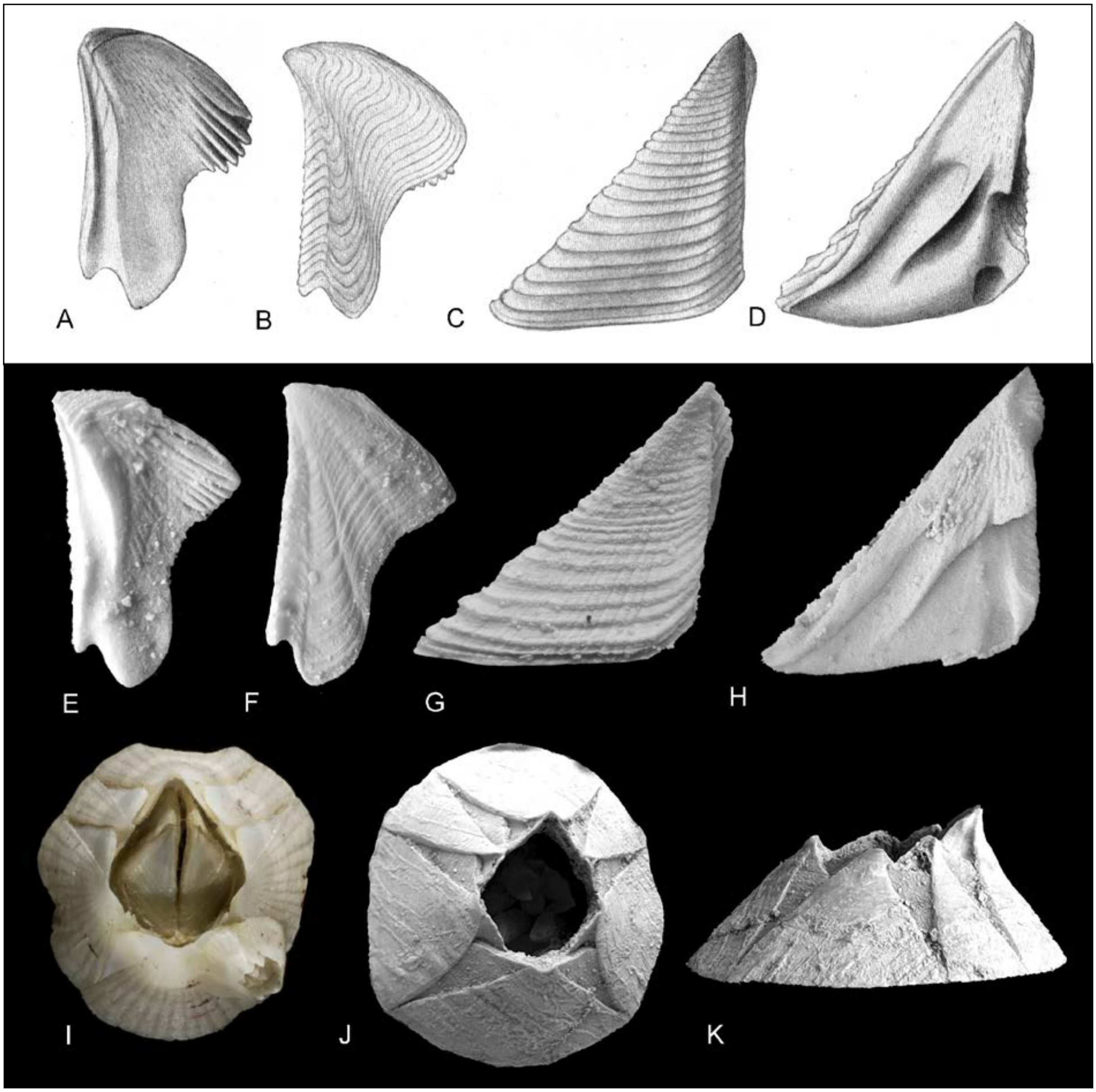
1966. *Balanus talquinensis* Weisbord, p. 37, pl. 8, figs 1–13.
1976. *Balanus talquinensis* Weisbord; Newman and Ross, p. 61.
1977. *Balanus talquinensis* Weisbord; Spivey, p. 127.
1986. *Balanus talquinensis* Weisbord; Zullo, p. 3.
1992. *Paraconcavus talquinensis* (Weisbord); Zullo, p. 38, fig. 21.1–21.5.

DIAGNOSIS: Shell tall, conical, orifice rhombic, small, strongly toothed. Apical margin of shell slopes ventrally from tall carina. Radii narrow, with oblique summits. Interior of parietes smooth. Tergum broad, apex acuminate, interior bears coarse rugosities and striae. Occludent margin of scutum denticulate.

TYPE: A shell from the Jackson Bluff Formation, Jackson Bluff, Leon County, Florida (PRI no. 27374).

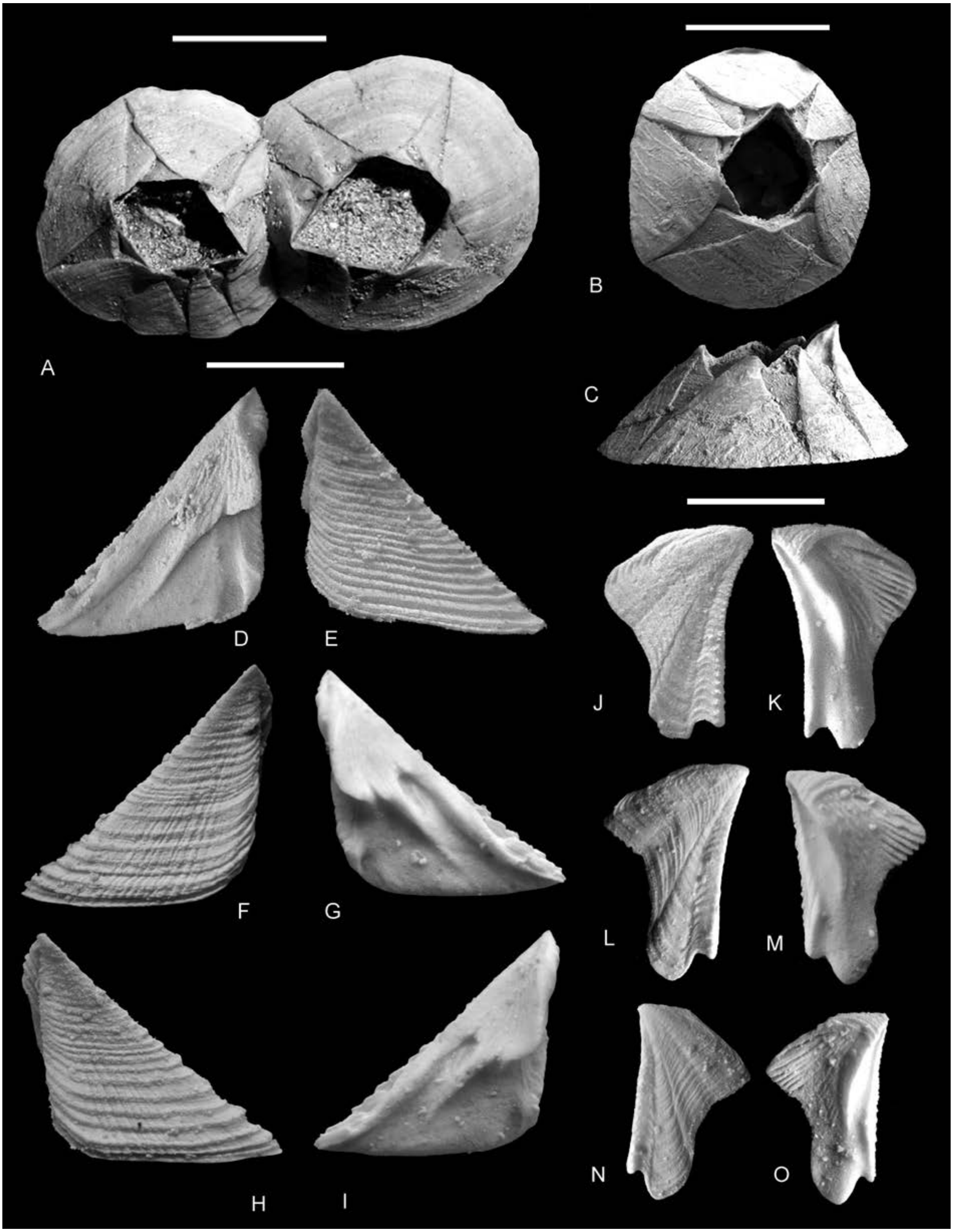
MATERIAL: 20 shells, 3 of which contain opercular plates, from the Yorktown Formation, Lee Creek Mine, Beaufort County, North Carolina. This is the most extensive material of the species known, and the only record from anywhere except that from the Jackson Bluff Formation, Jackson Bluff, Leon County, Florida (Weisbord 1966; Zullo 1992).

DESCRIPTION: Shells tall, conical, orifice relatively small, representing less than half the rostrocarinal dimension. Orifice strongly toothed, diamond-shaped. Apical margin sloping ventrally from tall carina to lower rostral plate. Radii narrow, broadening apically,

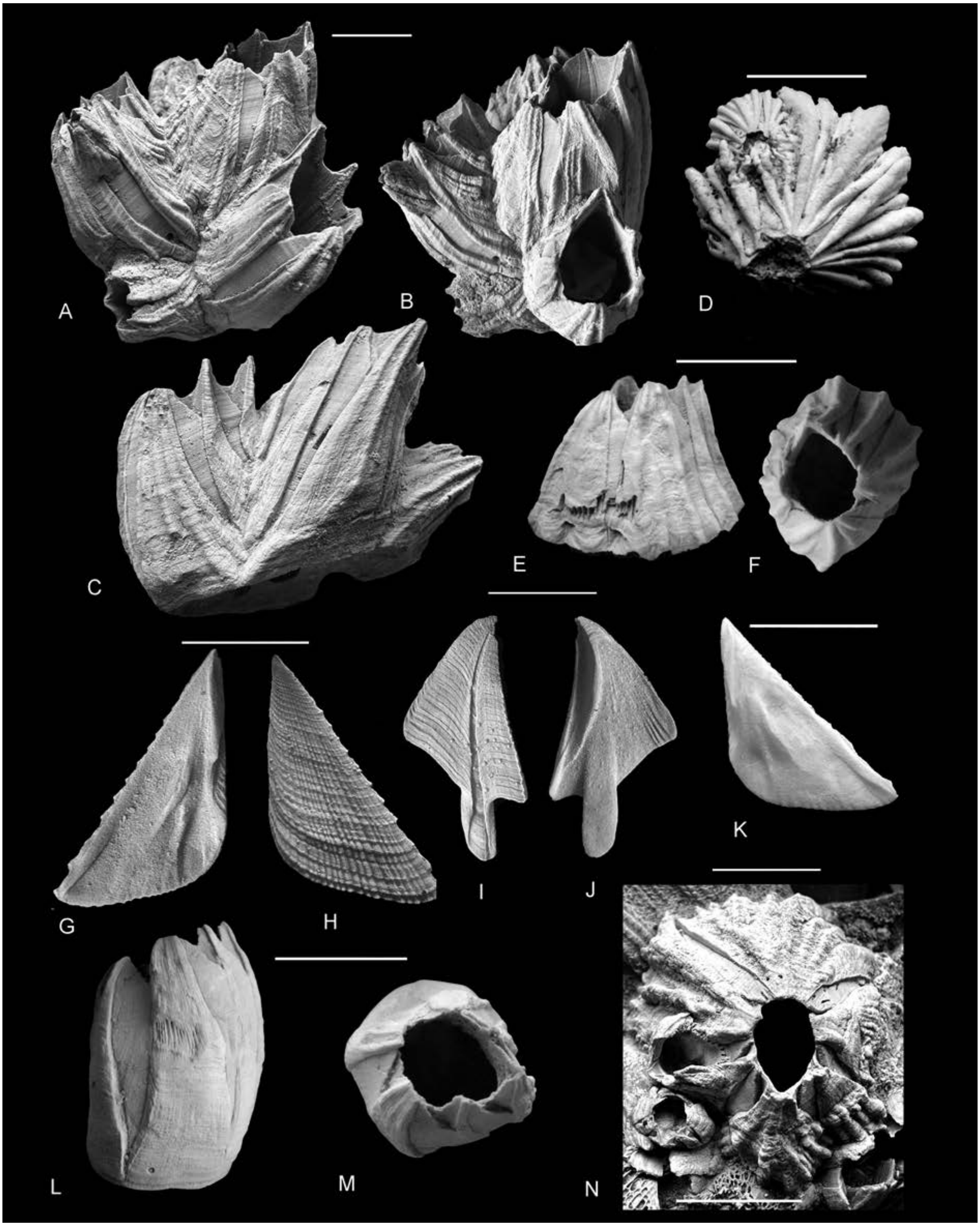



Text-fig. 7. Comparative morphology of species of *Amphibalanus* Pitombo, 2004 and *Fistulobalanus* Zullo, 1984. A–D, I – *Amphibalanus venustus* (Darwin, 1854); A–D – opercular plates, figured after Pilsbry (1916, pl. 19, figs 1=A; fig. 1d=B; fig. 1b=C; fig. 1e=D); A, B – terga in internal (A) and external (B) views; C, D – scuta in external (C) and internal (D) views; I – shell with opercular plates in apical view. E–H, J, K – *Fistulobalanus multiseptatus* (Ross, 1964), NHMUK PI In 66705; E, F – tergum in internal (E) and external (F) views; G, H – scutum in external (G) and internal (H) views; J, K – shell in apical (J) and lateral (K) views. Provenance: A–D are from the present day of Florida, USA; I is from the present day of northwest or tropical Atlantic; E–H, J, K are from the Neogene, probably Pliocene, Piacenzian, of the Lee Creek Mine, Beaufort County, North Carolina, USA. Not to scale.

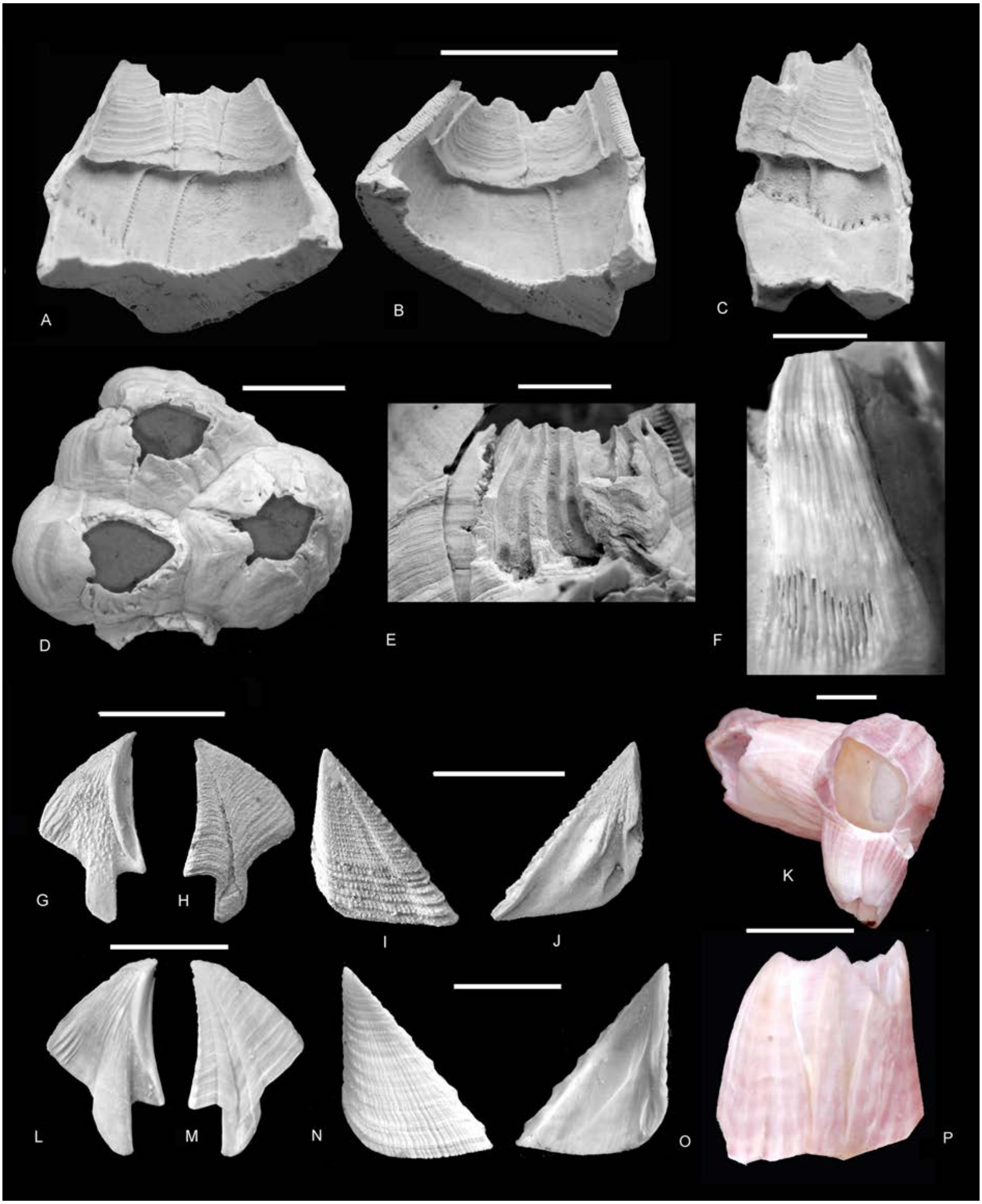
with oblique summits. External sculpture of parietes variable, from virtually smooth (Text-fig. 11D), or weakly striate (Text-fig. 11A), to ribbed forms (Text-fig. 11E, F) in which 5–7 broad, rounded apicobasal ribs extend from the base to the apex. Transverse septa are absent in the parietes (Text-fig. 10E). The interiors of the compartments (Text-fig. 10A–C) smooth and the basis is thin and perforate. The tergum (Text-fig. 11K, L) is broad with an acuminate apex, a short, truncated tergal spur and a narrow, nearly closed spur furrow; the interior is striated next to the occludent surface, and strongly rugose except on the tergal spur. The scutum



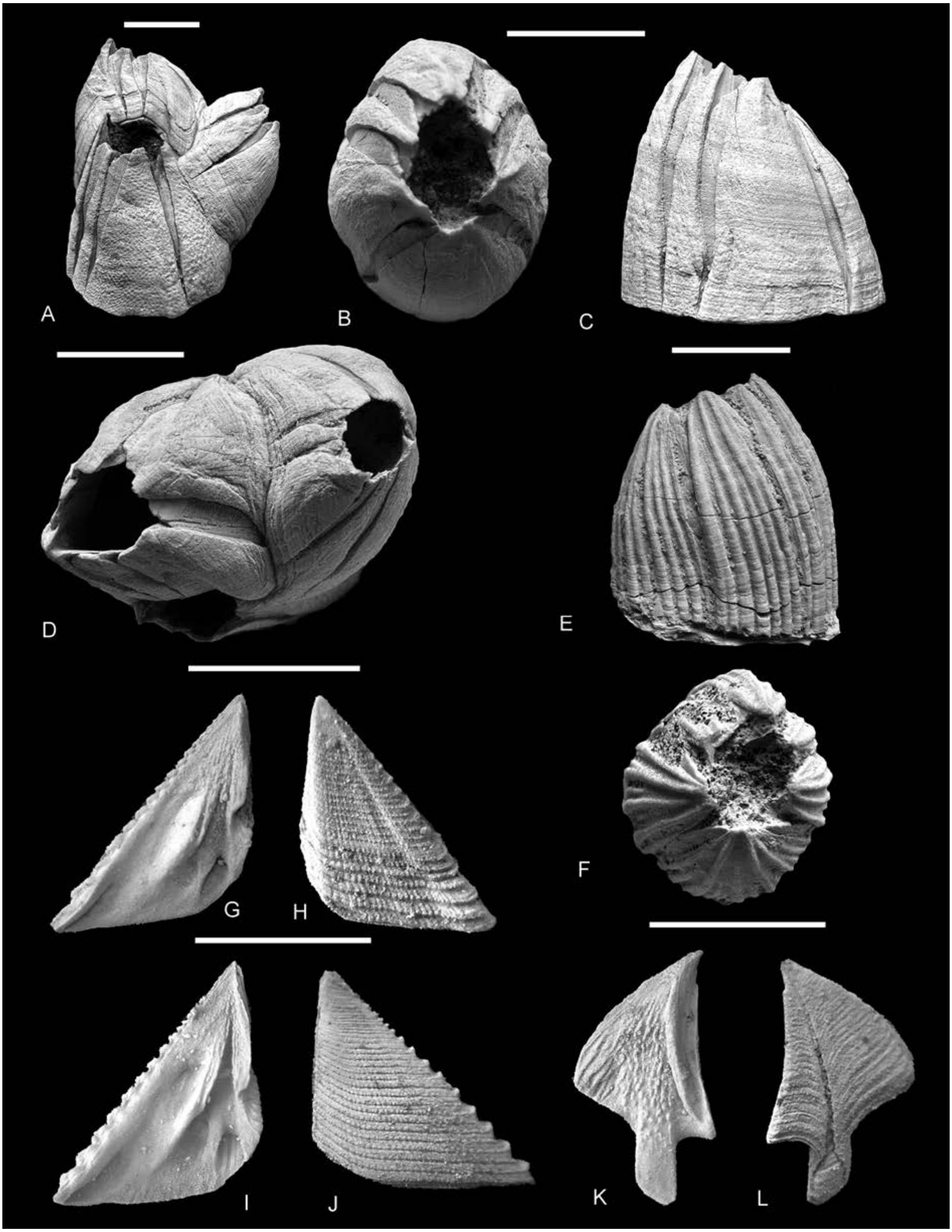

Text-fig. 8. *Fistulobalanus multiseptatus* (Ross, 1964) probably from the Yorktown Formation, Piacenzian, Lee Creek Mine, Beaufort County, North Carolina, USA. A – NHMUK PI In 66704, two conjoined shells in apical view; B, C – NHMUK PI In 66705, shell in apical (B) and lateral (C) views; D–I – scuta in external (E, F, H) and internal (D, G, I) views; D, E belong to specimen B, C; F–I belong to specimen A; J–O – terga in external (J, L, N) and internal (O) views; J, K belong to specimen B, C; L–O belong to specimen A. Scale bars equal: 10 mm (A–C) and 5 mm (D–O).




Text-fig. 9. Cirripedes from the Yorktown Formation (probably), Piacenzian, Lee Creek Mine, Beaufort County, North Carolina, USA. A–K, N – *Chesaconcavus proteus* (Conrad, 1834); A–C – NHMUK PI In 66691, cluster of shells; D – NHMUK Pi In 66692, small shell with low profile in apical view; E, F – NHMUK PI In 66693, shell in lateral (E) and apical (F) views; G, H – scutum in internal (G) and external (H) views from specimen figured in A–C; I, J – tergum in external (I) and internal (J) views from specimen figured in A–C; K – scutum in internal view from specimen figured in A–C; N – NHMUK PI In 66694, shell with low profile in apical view. L, M – *Paraconcavus* cf. *prebrevicalcar* (Ross, 1964), NHMUK PI In 66695, shell in lateral (L) and apical (M) views. Scale bars equal: 10 mm (A–C, L–M) and 5 mm (D–K).




Text-fig. 10. Morphology of living and fossil species of *Paraconcavus* Zullo, 1992. A–E, G–J – *P. telquinensis* (Weisbord, 1966); A–C – NHMUK PI In 66702, internal views of parietes; D, E – NHMUK PI In 66703, cluster of shells, with enlargement of parietal tubes (E); G, H – tergum of same specimen in internal (G) and external (H) views; I, J – scutum of same specimen in external (I) and internal (J) views. F – *Paraconcavus* cf. *prebrevicalcar* (Ross, 1964), NHMUK PI In 66695, external view to show tubes lacking transverse septa. K–P – *Paraconcavus pacificus* (Pilsbry, 1916), K – group of shells; L, M – tergum in internal (L) and external (M) views; N, O – scutum in external (N) and internal (O) views; P – shell in lateral view. Provenance: A–J, L–O are probably from the Yorktown Formation, Piacenzian, Lee Creek Mine, Beaufort County, North Carolina, USA; K, P are from present day of California, USA. Scale bars equal: 10 mm (A–D, K, P) and 5 mm (E–J, L–O).




Text-fig. 11. *Paraconcavus talquinensis* (Weisbord, 1966) from the Yorktown Formation (probably), Piacenzian, Lee Creek Mine, Beaufort County, North Carolina, USA. A, D – NHMUK PI In 66698, cluster of shells; B, C – NHMUK PI In 66699, large shell in apical (B) and lateral (C) views; E, F – NHMUK PI In 66701, large, ribbed shell in lateral (E) and apical (F) views; G–J – scuta in internal (G, I) and external (H, J) views; K, L – tergum in internal (K) and external (L) views; opercular plates from specimen D. Scale bars equal: 10 mm (A–F) and 5 mm (G–L).

(Text-fig. 11G–I) has the form of an isosceles triangle, with a long, straight occludent margin which carries short denticles. The interior shows a long adductor ridge, separated from the articular structures by a deep cleft. The lateral depressor muscle scar is deep and impressed.

REMARKS: This species has previously only been recorded from the Jackson Bluff Formation of Florida, so its discovery in North Carolina was unexpected. The material is closely similar to specimens figured by Weisbord (1966, pl. 8, figs 1–13, pl. 9, figs 1–6) and Zullo (1992, fig. 21.1–5), particularly in the broad tergum, with a nearly closed tergal furrow and strongly striated and rugose interior (compare Text-fig. 11K, L with Zullo 1992, fig. 21.2, 21.4). Additionally, the scutum bears short denticles along the occludent margin (compare Text-fig. 11G–J with Zullo 1992, fig. 21.2, 21.5). The species differs from other *Paraconcavus* (e.g., *P. pacificus*; Text-fig. 10K–P) in its small, strongly toothed orifice, the strongly sculptured interiors of the opercular plates and the denticulate occludent margin of the scutum.

*Paraconcavus* cf. *prebrevicalcar* (Ross, 1964).
(Text-figs 9L, M, 10F)

1964. *Balanus concavus prebrevicalcar* Ross, p. 488, pl. 72, figs 2–16.
1964. *Balanus oppidieboraci* Ross, p. 490, pl. 72, figs 16–30.
1986. *Balanus oppidieboraci* Ross; Zullo, p. 3, 8, pl. 2, figs F–L, pl. 3, figs A–I.
1992. *Paraconcavus prebrevicalcar* (Ross); Zullo, p. 38, fig. 21.13–21.26.

DIAGNOSIS: Conical to high conical shell, smooth to irregularly plicate; orifice subtriangular, toothed, radii broad with steeply sloping summits; interiors of opercular plates rugose, scutum broad, with deeply incised radial striae; tergum moderately broad to broad, spur furrow narrowly open, spur short, relatively narrow (modified from Zullo 1992, p. 38).

TYPE: The holotype is a shell with opercular plates (USNM 648121) from the upper Yorktown Formation, Rice's pit, Hampton, Elizabeth City County, Virginia, USA.

MATERIAL: A single well-preserved shell, probably from the Yorktown Formation, Lee Creek Mine, Beaufort County, North Carolina.

REMARKS: The shell, which lacks opercular plates (Text-fig. 9L, M) is cylindrical to slightly fusiform in lateral profile. The orifice is broad and strongly toothed, the radii broad with very oblique summits. The exterior of the shell is smooth, and the interior ribbed. The parietal tubes lack transverse septa (Text-fig. 10F), the absence of which places the specimen in *Paraconcavus*. It differs from *P. talquinensis* (see above) in its cylindrical shell, broad orifice and the internal ribbing on the parietes. Its shape is similar to that of specimens referred to *P. prebrevicalcar* (Zullo 1992, fig. 21.26), but in the absence of opercular plates the identification is uncertain.

## DISCUSSION

The exceptionally well-preserved cirripede assemblage recovered from the Lee Creek Mine (Table 1) includes seven species of balanomorphs, of which two are known only from this locality (*Protochelonibia collaretai* sp. nov., *Arossia aurae*). Most of these records, although collected loose, probably originate from the Yorktown Formation (Pliocene, Piacenzian; Zullo 1992) and the matrix of these (fine sand, silt) supports this. *Balanus calidus* probably comes from the James River Formation, from which the species has been recorded from various localities in North Carolina (Zullo and Miller 1986).

*Fistulobalanus multiseptatus*, *Chesaconcavus proteus* and *Paraconcavus prebrevicalcar* are known from the Yorktown Formation of Virginia (Ross 1964) and North Carolina (Zullo 1984, 1992; Gale and Sadorf 2025b). *Paraconcavus talquinensis*, one of the most common Lee Creek Mine species, was previously known only from the Pliocene Jackson Bluff Formation, Jackson Bluff, Leon County, Florida (Weisbord 1966; Zullo 1992). Chelonibiids (turtle barnacles) are uncommon fossils in the Cenozoic of the eastern USA, previously known from the Oligocene of Mississippi (Zullo 1982; Perreault *et al.* 2022) and the Miocene to Pleistocene of Florida (Ross 1963). *Protochelonibia collaretai* sp. nov., probably from the Yorktown Formation (Pliocene) adds a further record of the family.

It is interesting that, of the eight species recorded from Lee Creek mine, only *Balanus calidus* is extant, presently distributed along the east coast of the Americas, from North Carolina to Brazil, and invasive in the eastern central Pacific (Smithsonian Institution https://invasions.si.edu/panama/species_summary).

The concavine taxa, dominant in the Mio- and Pliocene, disappeared from the northwest Atlantic region during the early Pleistocene (Zullo 1992; Gale and Sadorf 2025b).

| numbers | family | genus | species | author and year | figured herein | type | age | formation |
|---|---|---|---|---|---|---|---|---|
| NHMUK PI In 66687 | Chelonibiidae | *Protochelonibia* | *collaretai* | Gale and Sadorf, 2026 | Text-fig. 4J–M | holotype | Pliocene | Yorktown |
| NHMUK PI In 66688 | | | | | Text-fig. 4H, I | paratype | | |
| NHMUK PI In 66689 | Concavinae | *Arossia* | *aurae* | Zullo, 1992 | Text-fig. 4A–G | | | |
| NHMUK PI In 66690 | | | | | Text-fig. 5A–C | | | |
| NHMUK PI In 66691 | | *Chesaconcavus* | *proteus* | (Conrad, 1834) | Text-fig. 9A–C, I, J | | | |
| NHMUK PI In 66692 | | | | | Text-fig. 9D | | | |
| NHMUK PI In 66693 | | | | | Text-fig. 9E, F | | | |
| NHMUK PI In 66694 | | | | | Text-fig. 9N | | | |
| NHMUK PI In 66695 | | *Paraconcavus* | cf. *prebrevicalcar* | (Ross, 1964) | Text-fig. 9L, M | | | |
| NHMUK PI In 66696 | | | *talquinensis* | (Weisbord, 1966) | Text-fig. 5D, E | | | |
| NHMUK PI In 66697 | | | | | Text-fig. 5F, G | | | |
| NHMUK PI In 66698 | | | | | Text-fig. 11A | | | |
| NHMUK PI In 66699 | | | | | Text-fig. 11B, C | | | |
| NHMUK PI In 66700 | | | | | Text-fig. 10G–J | | | |
| NHMUK PI In 66701 | | | | | Text-fig. 11E, F | | | |
| NHMUK PI In 66702 | | | | | Text-fig. 10A–C | | | |
| NHMUK PI In 66703 | | | | | Text-fig. 10D, E | | | |
| NHMUK PI In 66704 | Amphibalaninae | *Fistulobalanus* | *multiseptatus* | (Ross, 1964) | Text-fig. 8A, F–I, L–O | | | |
| NHMUK PI In 66705 | | | | | Text-fig. 7E–H, J, K; 8B–E, J, K | | | |
| NHMUK PI In 66706 | | | | | Text-fig. 5H–J | | | |
| NHMUK PI In 66707 | Balaninae | *Balanus* | *calidus* | (Pilsbry, 1916) | Text-fig. 5K–N | | Pleistocene | James City |
| NHMUK PI In 66708 | | | | | Text-fig. 6A, B, D–G | | | |
| NHMUK PI In 66709 | | | | | Text-fig. 6C, H, J, K | | | |
| NHMUK PI In 66710 | | | | | Text-fig. 6I | | | |

Table 1. List of specimens from Lee Creek Mine, North Carolina, USA, illustrated herein.

## Acknowledgements

We are particularly grateful to David Ward for donating his collection of Lee Creek Mine barnacles for this study. Also, to Dona Dickinson for donating specimens from the same locality. We thank Dr Richie Howard (NHMUK) for assistance with registration, and to the referees (Tomáš Kočí and John Buckeridge) for their useful comments.

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