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Cirripedes (Crustacea) from the Pliocene (Piacenzian) Rushmere Member, Yorktown Formation of North Carolina, USA

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ABSTRACT:

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Abundant cirripedes of Pliocene age (Piacenzian Stage) are described from two localities in North Carolina. These include seven species, of which the most abundant are the large balanids *Arossia glyptopoma* (Pilsbry, 1916), previously known from the Pliocene of Florida and Virginia, and *Chesaconcavus proteus* (Conrad, 1834), known from the Pliocene of Virginia and Florida. Abundant material of the scalpellid *Scalpellum multangulatum* (Lea, 1843) permits the first description of all the plates of this species and allows a reconstruction to be made. A new species of *Membranobalanus* Hoek, 1913, *M. distortus* sp. nov., a genus which has an obligate relationship with clionaid sponges, represents only the second fossil record of this extant genus. New records of the extinct whale barnacle *Coronula bifida* Bronn, 1931 are the first from the Atlantic Coastal Plain of the eastern USA and indicate that the migration paths of humpback whales in the Pliocene ran close to the palaeocoastline. The material includes the only known juvenile specimens of the species and allows reconstruction of the ontogeny of *C. bifida*. We report the second and third North American occurrences of the verrucid barnacle *Verruca stroemia* (O.F. Müller, 1778) and the second known record of *Fistulobalanus multiseptatus* (Ross, 1964). The barnacle assemblage represents a warm water fauna, brought into the region during the Mid-Piacenzian Warm Period by the basal Rushmere Member transgression at 3.25 Ma. Only 1 of the 7 species recorded is still extant.

Key words: Cirripedes; Pliocene; Piacenzian; North Carolina.

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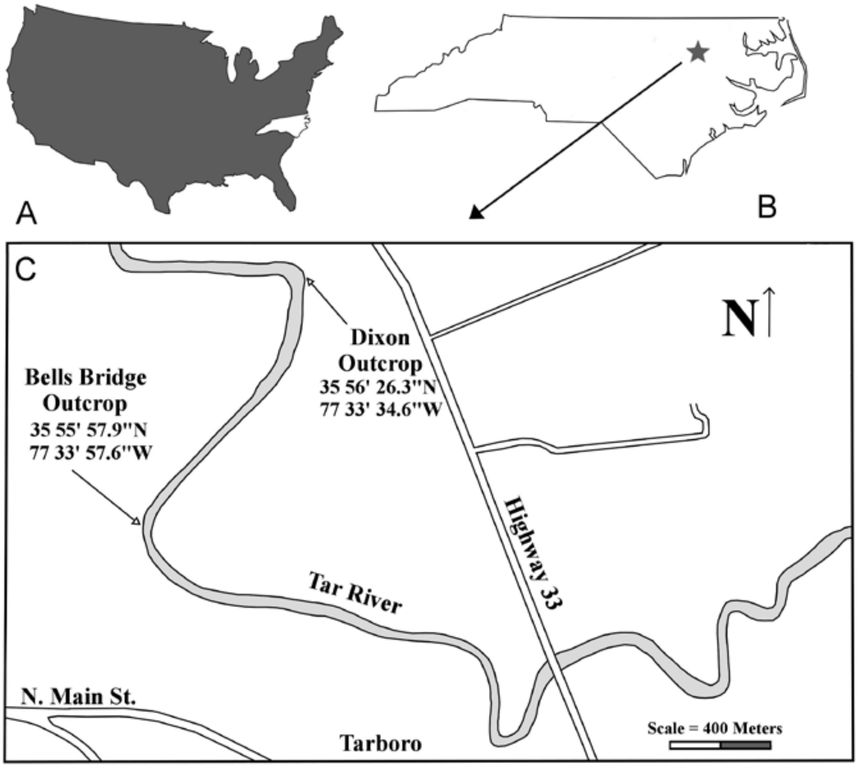
INTRODUCTION

Barnacles of Pliocene age are locally common in the Atlantic and Floridian Coastal Plains of the USA, particularly in the Yorktown Formation of Virginia (Ross 1964) and South Carolina (Zullo 1986) and the correlative Jackson Bluff and upper Tamiami formations of Florida (Ross 1964, 1965a, b; Zullo 1986). However, in a review of the faunas Zullo (1986, table 1) listed only 3 barnacle species from the Pliocene of North Carolina, including the chelonibiid *Chelonibia testudinaria* (Linnæus, 1758) from the Yorktown Formation at New Bern, Craven County (Zullo 1982) and, without locality details, the balanids *Concavus glyptopoma* (Pilsbry, 1916) and *Fistulobalanus multiseptatus* (Ross, 1964) from the upper Yorktown Formation. Subsequently, Zullo (1992) described a new species, *Arossia aurae* from the lower Yorktown



Text-fig. 1. Locality maps. Map of the USA (A), showing the location of North Carolina (B) and locations of outcrops of the Rushmere Formation (C) on the Tar River, Edgecombe County, North Carolina, USA.

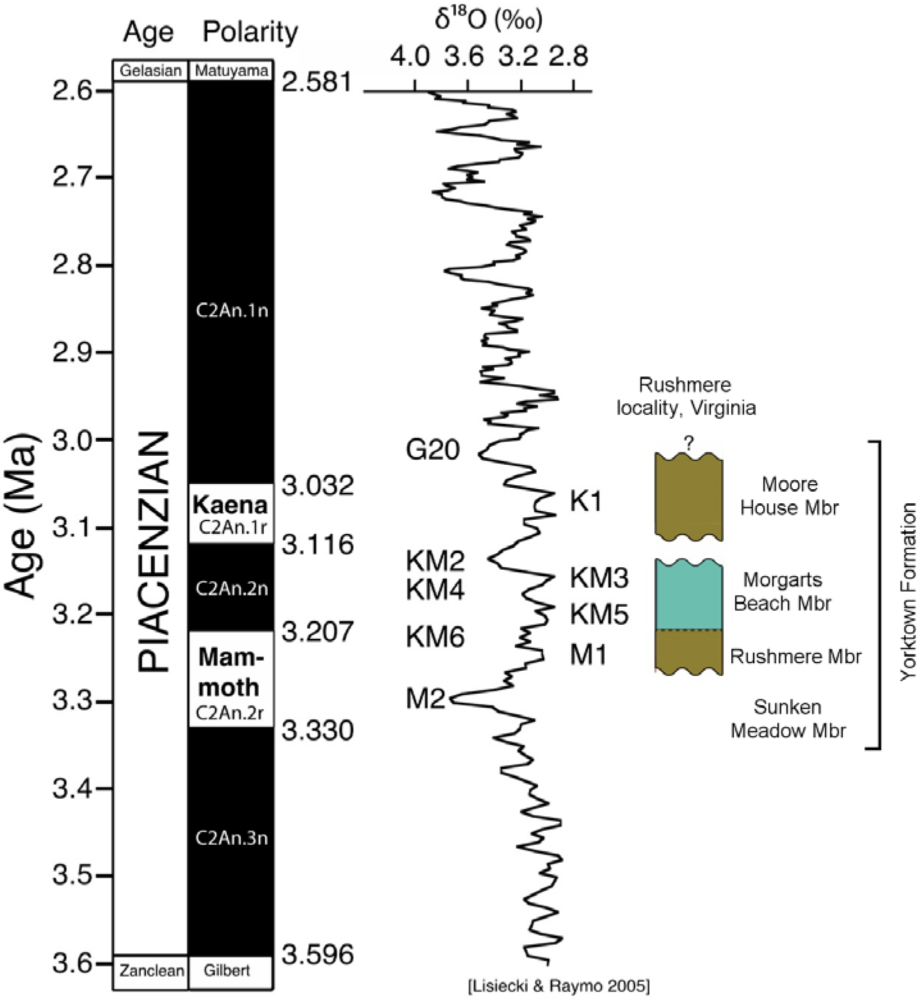
Formation of Lee Creek Mine, Beaufort County, NC. Gale and Sadorf (2025) recorded abundant material of the verrucid species *Verruca stroemia* (O.F. Müller, 1776) from the Rushmere Member of the Yorktown Formation at Martin-Marietta Fountain Quarry near the town of Fountain, North Carolina, representing the first occurrences of this species in North America. Recently, one of us (ES) discovered localities containing abundant cirripedes in the Pliocene (Piacenzian) Rushmere Member in Edgecombe County, North Carolina (Text-fig. 1), which form the subject of this paper.

LOCALITIES

The barnacles for this investigation were obtained primarily from bulk samples collected from two different localities on the Tar River in Edgecombe County, North Carolina (Text-fig. 1). The Bells Bridge Locality is located northwest of Tarboro, just beyond the town on the right bank of the Tar River (35º55’57.9” N, 77º33’57.6” W). Shells beds with well-preserved molluscs were present at the site. Bulk samples were collected from a greenish layer that is exposed during low water conditions. The Dixon Locality is situated approximately 800 m upstream (north) of the Bell Bridge Locality on the left bank of the Tar River (35º56’26.3” N, 77º33’34.6” W). Bulk sampling was done during low water conditions and collected at and below the water level. These localities have also yielded extensive teleost otolith faunas (Stringer *et al.* 2022).

STRATIGRAPHY

The Yorktown Formation was long considered to be of Miocene age, but the discovery of planktonic foraminifera (Akers 1972) placed it within Pliocene zones N19–20. Subsequent more detailed studies (e.g., Dowsett *et al.* 2019, 2021) demonstrated that the formation falls within the Mid-Piacenzian Warm Period (3.264–3.025 Ma), and the Rushmere Member represents the interglacial transgression equivalent to the M1 oxygen isotope event in the ocean basins (Dowsett *et al.* 2021). It lies within the upper part of the Mammoth reversed magnetochron C2An.2r (Text-fig. 2).



Text-fig. 2. Stratigraphy and age of the Yorktown Formation, based on data obtained from the James River composite section, Virginia (Dowsett *et al*. 2021, modified after their fig. 6). The oxygen isotope curve is taken from the LR04 oxygen isotope stack of Lisiecki and Raymo (2005) with Marine Isotope Stages M2-G60 labelled.

METHODS AND MATERIAL

The barnacles for this study were obtained from bulk sampling at the two localities by one of the authors (ES). Approximately 30 kg of sediment was collected from each site. The bulk samples were processed offsite by thoroughly drying the samples before wet screening with water. A small subsample of each bulk sample (approximately 2 kg) was screened using a 30-mesh sieve (US Sieve with 0.60-mm openings). After wet screening, the residue was dried, and barnacle plates were extracted using a stereomicroscope. The remaining sediment was screened using a an 18-mesh sieve (US Sieve with 1.00-mm openings). The residue was dried, and barnacle plates were extracted under magnification. Shells and isolated plates were cleaned with an ultrasonic tank before imaging with an iphone 14, a USB microscope or an SEM as appropriate to the size of specimens. Some were sprayed with ammonium chloride to enhance features.

Institutional abbreviations

ANSDU – Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, USA;
MFM – Mizunami Fossil Museum, Mizunami, Japan;
NCSM – North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA;
NHMUK – The Natural History Museum, London, UK;
USNM – United States National Museum, Washington D.C., USA.

SYSTEMATIC PALAEONTOLOGY

Family Scalpellidae Pilsbry, 1907

DIAGNOSIS: Scalpellomorphs which possess a maximum of 14 plates (carina, rostrum, paired scuta, terga, upper latera, carinolatera, rostrolatera inframedian latera), rarely 13, by secondary loss of the rostrum.

INCLUDED SUBFAMILIES: Amigdaloscalpellinae Gale, 2015; Brochiinae Zevina, 1978; Meroscalpellinae Zevina, 1978; and Scalpellinae Pilsbry, 1907.

Subfamily Scalpellinae Pilsbry, 1907

DIAGNOSIS: Scalpellids in which the rostrolatus is broad, low, strap-like and gently incurved. The rostrum is broader than high, rectangular, trapezoidal or triangular, and large triangular lateral surfaces contact the interior of the rostrolatus. The articulation surface between the rostrum and rostrolatus extends over the entire height of both plates (Gale 2015).

Genus *Scalpellum* Leach, 1817

TYPE SPECIES: *Lepas scalpellum* Linnæus, 1767, by subsequent designation of Leach (1825).

DIAGNOSIS: Derived scalpellines in which the carinal and scutal umbones are subapical, the carinolatus has a horn-like projection, often recurved, extending beyond the carinal margin, the inframedian latus is rectangular to trapezoidal, with a low umbo, and the upper latus is rhomboidal with a subapical umbo. The rostrum is rectangular and pyramidal with large subumbonal surface (modified after Gale 2015).

Scalpellum multangulatum (Lea, 1843)

(Text-figs 3, 4A, E, F)

1843. *Avicula multangulata* Lea, p. 5.
1843. *Patella acinaces* Lea, p. 5.
1888. *Scalpellum magnum* Darwin; Meyer, p. 138, figs 11, 12.
part ?1965b. *Scalpellum gibbum* Pilsbry; Ross, p. 219, fig. 1B only.
part 1988. *Scalpellum multangulatum* (Lea, 1843); Campbell and Zullo, p. 479, fig. 1.1–5 only.

DIAGNOSIS: *Scalpellum* in which the capitulum is broad, possessing a low, broad rostrolatus which does not extend ventrally beyond the scutum, and a strongly recurved, crescentic carinolatus. The tergum is not notched to receive the apical tip of the carina.

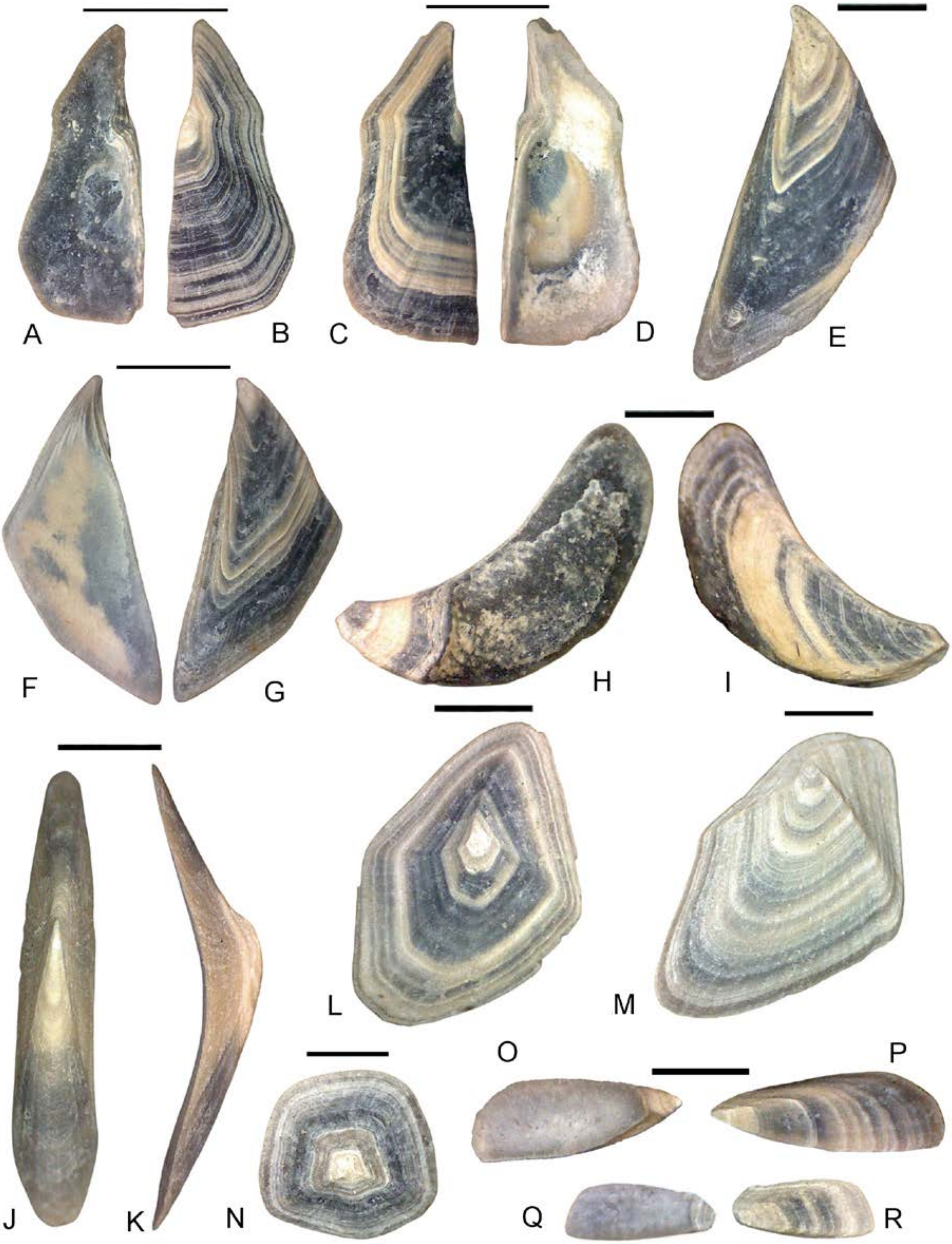
TYPE: A carina from Lea's original material was selected as lectotype by Campbell and Zullo (1988, p. 479). This is in the collection of ANSDU (no. 3312), from the Yorktown Formation, Petersburg, Virginia, USA.

MATERIAL: Several hundred isolated valves from the Rushmere Member, Pliocene (Piacenzian), Bells Bridge and Dixon, North Carolina, USA.

DESCRIPTION: The first full description of this species is provided here. The material is exceptionally well preserved, displaying variably coloured fine growth increments in grey-blue and cream hues which may possibly be original pigment. The scuta (Text-fig. 3A–D) are triangular, with height slightly exceeding maximum breadth, and the apex is acuminate. The slightly prominent subapical umbo is positioned between a third and a quarter of the total occludent height beneath the apex. The occludent margin is straight to slightly sinusoidal and the tergal margin is short and straight. The basal margin is straight and subtends the straight inframedian margin by 50º.

The margin and valve surface between the tergal and inframedian latus margins are weakly concave. The interior of the scuta has a large, oval, slightly subcentral adductor scar. Apical to this, the occludent margin is inflexed to provide a shallow notch to accommodate dwarf males. The terga (Text-fig. 3E–G) are elongated, triangular and the length is slightly twice the maximum breadth. The carinal margin is long and straight, the occludent margin short, and the upper latus and scutal margins are poorly differentiated. The apex of the tergum is slightly hooked dorsally, especially in large specimens. The carina (Text-fig. 3J, K) is oval in dorsal view, elongated, with the maximum breadth (at the top of the basal margin) representing a quarter to a fifth of the height. The umbo is positioned slightly above the centre of the ventrally inclined valve. The basal margin is rounded, the tectum is convex and poorly differentiated from the narrow parietes. The intraparietes are broad and extend from the apex to the top of the basal margin.

The upper latus (Text-fig. 3L, M) is rhombic and its height is slightly greater than its breadth. The umbo is subapical to subcentral in position, and ridges run from the umbo to the lateral margins. The inframedian latus (Text-fig. 3N) is flat and pentag-



Text-fig. 3. *Scalpellum multangulatum* (Lea, 1843). A–D – scuta, in internal (A, C) and external (B, D) views (NHMUK PI In 66588, 66522); E–G – terga, in external (E, G) and internal (F) views (NHMUK PI In 66523, 66524); H, I – carinolatus, in internal (H) and external (I) views (NHMUK PI In 66525); J, K – carina, in dorsal (J) and lateral (K) views (NHMUK PI In 66526); L, M – upper latera, external views (NHMUK PI In 66527, 66528); N – inframedian latus, external view (NHMUK PI In 66529); O–R – rostrolatera, in external (P, R) and internal (O, Q) views (NHMUK PI In 66530, 66531). All specimens are from the Rushmere Member, Pliocene, Piacenzian, Dixon, North Carolina, USA. Scale bars equal 2 mm (A–N) and 1 mm (O–R).

onal with subequal margins and an umbo close to the basal margin. The carinolatus (Text-fig. 3H, I) is crescentic in outline with a strongly convex inframedian latus margin, and a concave carinal margin; it projected beneath the carina. The paired carinolatera articulated across the sagittal plane by means of a short, triangular surface. The rostrolatera (Text-fig. 3O–R) are triangular to trapezoidal in outline, broad and low, with the maximum height representing one third of the breadth. They taper ventrally to a blunt or short apex. On the ventral interior surface there is small concave surface for articulation with the rostrum.

REMARKS: *Scalpellum multangulatum* is a true *Scalpellum,* as the inframedian latus is pentagonal with a basal umbo (see Text-fig. 4G); forms with a tear-drop shaped inframedian latus were separated off as *Lacrymascalpellum* Gale, 2025a. The presence of a low, broad rostrolatus and a recurved carinolatus suggest affinities with the living Indo-west Pacific *Scalpellum stearnsi* (Text-fig. 4G), and Old World Miocene taxa such as *Scalpellum pfeifferi* Weithofer, 1887 from Austria, which, unlike this species, lacks a pit for dwarf males.

Campbell and Zullo (1988) resurrected the taxa originally described by Lea (1843) from the Neogene of Virginia as a bivalve and a gastropod, which Meyer (1888) correctly identified as, respectively, the scutum and carina of a *Scalpellum*. Campbell and Zullo (1988) chose *Avicula multangulata* Lea, 1843 (scutum), by page precedence, as the correct name for the *Scalpellum* species which occurs in the Miocene and Pliocene of the Atlantic Coast states of the USA. They chose a carina figured by Lea as a lectotype, and also synonymised the living species *Scalpellum gibbum* Pilsbry, 1907 with the fossil taxon.

However, there are problems with these courses of action. Firstly, carinae are poorly diagnostic for species of *Scalpellum* (Withers 1953) and cannot be used to separate some taxa; instead, the shapes and orientations of carinolatera, rostrolatera terga and scuta are widely used to characterise species. The above description and illustrations (Text-fig. 3) of all plates (except the rostrum) of the *Scalpellum* present in the Pliocene (Piacenzian) of North Carolina permit reconstruction of the morphology of the species (Text-fig. 4A). This is quite different to the form of *Scalpellum gibbum* (Text-fig. 4B), in its possession of a low, broad rostrolatus and the dorsal projection of the carinolatus. Additionally, in *S. gibbum* the upper dorsal margin of the tergum is notched to accommodate the tip of the carina, not present in *S. multangulatum*. Importantly, the interior of the scutum of *S. gibbum* (Text-fig. 4D) has a large circular pit, apical to the adductor scar, to accommodate dwarf males; this is absent in *S. multangulatum* (Text-fig. 4F) and *S. scalpellum* (Text-fig. 4I). A rather similar pit is present in the Indo-West Pacific species *S. stearnsi* Pilsbry, 1890 (Text-fig. 4G, H).

In conclusion, we are not convinced that *S. multangulatum* is the correct name for all the Neogene *Scalpellum* recorded from the Atlantic coast states of the USA. Re-examination of the type series of Lea's material is required, as is a reappraisal of material from different localities and ages.

Order Verrucomorpha Pilsbry, 1916
Family Verrucidae Darwin, 1854

Genus *Verruca* Schumacher, 1817

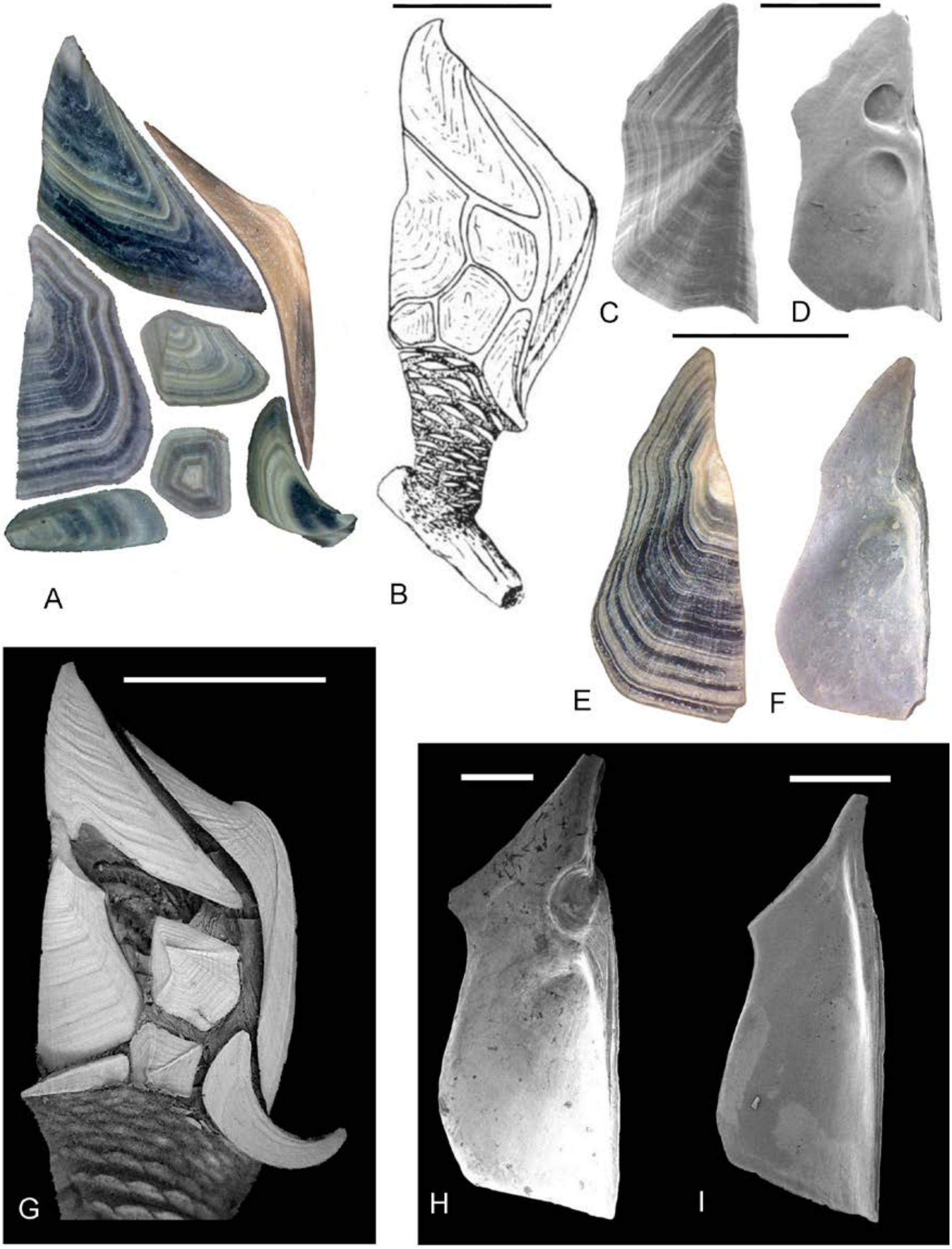
TYPE SPECIES: *Lepas stroemia* O.F. Müller, 1776.

DIAGNOSIS: Shell depressed, breadth 3 to 4 times height, opercular plates proportionately small (Text-fig. 4A, B). All plates bearing 5–10 µm diameter circular pores, arranged in regular rows on edges of imbricate growth increments. Apical ridge (r1 in Text-fig. 5B, C) on moveable scutum prominent, strongly ridged; tergal notch very short and shallow. Fixed scutum bearing large, triangular, alate occludent wing (Text-fig. 6C); myophore borne on horizontal flange confluent with proximal articular ridge, forming V-shaped structure overlying cavity; tergal notch forming horizontal prominence. Articulation of fixed scutum and fixed tergum specialised, strongly interpenetrant. Prominent, alate, triangular occludent wing on fixed tergum (Text-fig. 6A, B); scutal auricle forming depression (after Gale and Sadorf 2025).

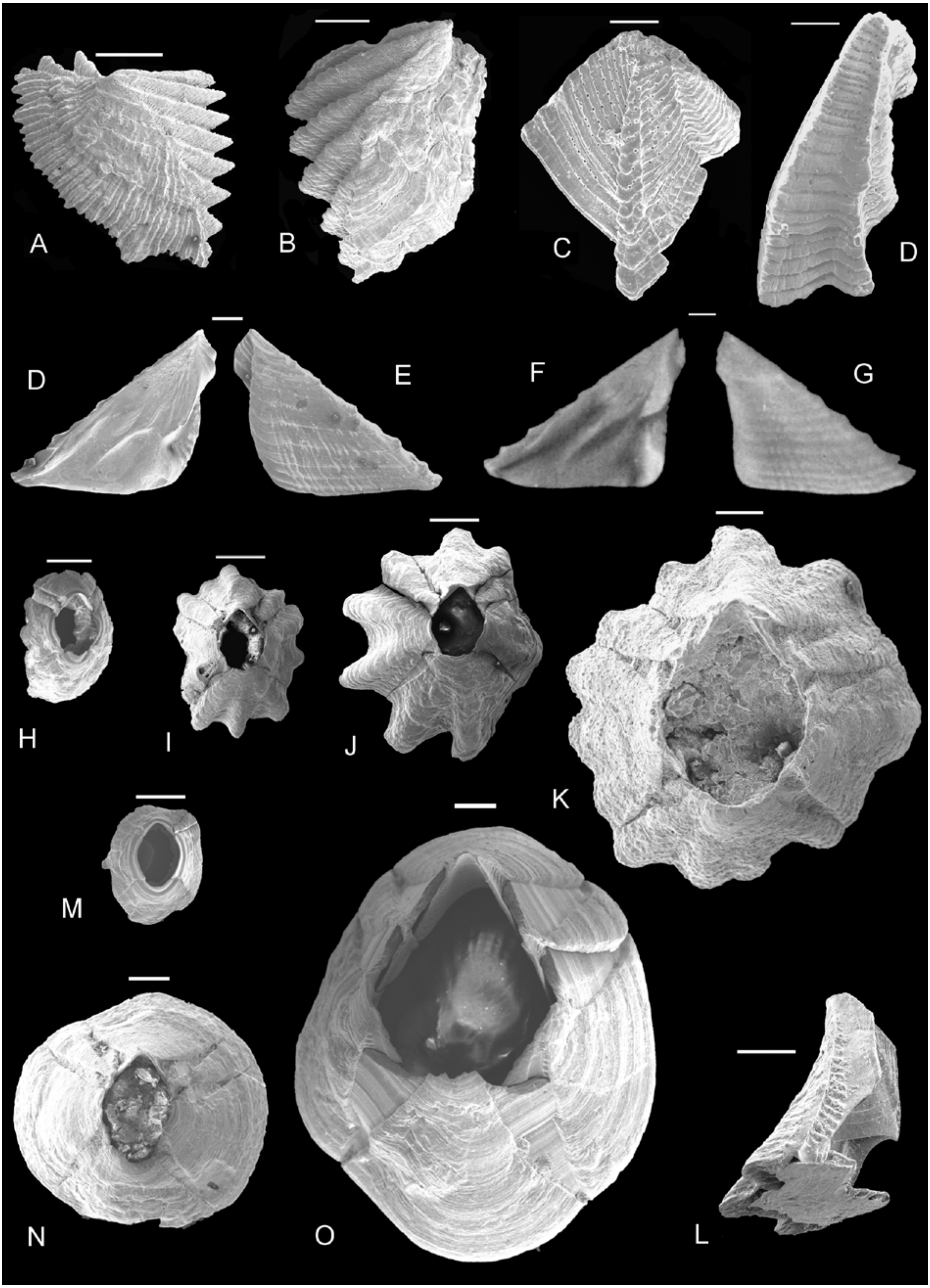
INCLUDED SPECIES: In addition to the type species, the following extant forms: *Clitia laevigata* G.B. Sowerby, 1827; *Verruca cookei* Pilsbry, 1927; *Verruca jago* Buckeridge, 1997; *Verruca minuta* Young, 2000; *Verruca spengleri* Darwin, 1854.

Verruca stroemia (O.F. Müller, 1776)
(Text-fig. 5A–D)

*1776. *Lepas strömia* O.F. Müller, p. 251.
1854. *Verruca strömia* Darwin, p. 518, pl. 21, fig. 1a–f.
1855. *Verruca strömia* Darwin, p. 42, pl. 2, fig. 9a, b.



Text-fig. 4. Selected species of *Scalpellum* Leach, 1843. A, E, F – *Scalpellum multangulatum* (Lea, 1843); A – reconstruction in lateral view, based on isolated plates; E, F – external and internal views of scutum, respectively (NHMUK PI In 66521). B–D – *Scalpellum gibbum* Pilsbry, 1907; B – lateral view of holotype, figured after Pilsbry (1907, fig. 4a); C, D – external and internal views of scutum, respectively, figured after Campbell and Zullo (1988, fig. 1.7, 1.8). G, H – *Scalpellum stearnsi* Pilsbry, 1890; G – lateral view of capitulum; H – internal view of scutum. I – *Scalpellum scalpellum* (Linnæus, 1767), internal view of scutum. A, E, F are from the Rushmere Member, Pliocene (Piacenzian), Dixon, North Carolina, USA; B–D are present day of the Atlantic Ocean, off east coast of Florida (B) and Georgia (C, D); G, H are present day of the Philippines; I is present day of Dorset, UK. A is not to scale. Scale bars equal 10 mm (G), 2 mm (B, E, F, H, I) and 1 mm (C, D).


A
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1916. *Verruca strömia* (O.F. Müller); Pilsbry, p. 24.
1943. *Verruca alaskana* Pilsbry in MacNeil *et al*., p. 95, pl. 15, figs 8, 9.
2003. *Verruca stroemia* (O.F. Müller); Young *et al*., p. 91, fig. 1A, B.
2006. *Verruca koikei* Tanaka, Kawase, Narita and Karasawa in Koike *et al*., p. 1, figs 1.1–1.7.
2009. *Verruca stroemia* (O.F. Müller); Marquet *et al*., p. 55, pl. 4, figs 5–7.
2025. *Verruca stroemia* (O.F. Müller); Gale and Sadorf, p. 9, text-figs 4, 5A–C, 6A–C, 11A–T.

TYPE: Unspecified, 'North Sea'.

DIAGNOSIS: *Verruca* with moveable scutum lacking an adductor ridge; moveable tergum kite shaped, height greater than breadth; carina and rostrum articulating by 5 or fewer ridges and intervening grooves.

MATERIAL: Over 50 plates, mostly carinae and rostra, bur including moveable scuta and terga, from the Rushmere Member at Bells Bridge and Dixon, Edgecombe County, North Carolina. USA.

REMARKS: The plates are typical of the species, discussed in detail in Gale and Sadorf (2025). These constitute the second and third records of the species from North Carolina and from the USA.

Order Balanomorpha Pilsbry, 1916

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

Family Coronulidae Leach, 1817

DIAGNOSIS: The wall is composed of six plates which lack a median longitudinal sulcus. The terga are vestigial and opercular plates are lacking in *Xenobalanus* Steenstrup, 1852. The borders of the mantle form a hood over the cirri. A single row of wall tubes is formed by infoldings of the outer lamina against the sheath.

Genus *Coronula* Lamarck, 1802

DIAGNOSIS: The shell comprises six compartments of equal size; the walls are thin, deeply folded and the folds form cavities which are open basally. The radii are wide and the body chamber is relatively small and cup-shaped. The paired terga and scuta are small and do not articulate. The orifice of the body chamber is wider than the basal opening and the basis is membranous.

TYPE SPECIES: *Lepas diadema* Linnæus, 1767, by subsequent designation of Pilsbry (1916).

INCLUDED SPECIES: *Coronula aotea* Fleming, 1959; *Coronula bifida* Bronn, 1831; *Coronula intermedia* Buckeridge, 1983; *Coronula reginae* Darwin, 1854.

REMARKS: All species are parasitic on the epidermis of whales. There has been considerable discussion as to the number of species which can be recognised. Here, we follow Buckeridge *et al.* (2018, p. 4) in recognising the fossil species, *C. bifida*, which existed from the mid-Pliocene to the early Pleistocene (Gelasian Stage). Its probable descendant, *C. diadema* subsequently appeared in the early Pleistocene Calabrian Stage (Dominici *et al*. 2011) and exists today on the humpback whale, *Megaptera novaeangliae* (Borowski, 1781). *Coronula* differs from *Cetopirus* Ranzani, 1817 (which attaches to right whales of the family Balaenidae) in numerous morphological features, reviewed in detail by Collareta *et al.* (2016, p. 5). *Cetopirus* is known as a fossil from the Gelasian of southern Italy (Collareta *et al.* 2016).

ONTOGENY: The ontogeny of *Coronula* parietal plates was described, but only partly figured, by

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← Text-fig. 5. SEM images of selected cirripedes. A–D – *Verruca stroemia* (O. F. Müller, 1778); A – carina, external view (NHMUK PI In 66532); B – rostrum, external view (NHMUK PI In 66533); C – moveable tergum, external view (NHMUK PI In66534); D – moveable scutum, external view (NHMUK PI In 66535). D–G – *Fistulobalanus multiseptatus* (Ross, 1964); D, E – scutum, in internal and external views, respectively (NHMUK PI In 66536); F, G – scutum, in internal and external views, respectively, paratype, original of Ross (1964, pl. 71, figs 2, 3; USNM 648118). H–L – *Chesaconcavus proteus* (Conrad, 1834); H–K – apical views of juvenile shells (NHMUK PI In 66537–66540); L – lateral view of carina (NHMUK PI In 66541). M–O – *Arossia glyptopoma* (Pilsbry, 2016), apical views of juvenile shells (NHMUK PI In 66542–66544). A–E and H–L are from the Rushmere Member, Pliocene (Piacenzian), Dixon, North Carolina, USA; F, G are from the Morgarts Beach Member, Pliocene (Piacenzian), Rice's Pit, Hampton, Virginia, USA. Scale bars equal 1 mm (A), 0.5 mm (H–L), 0.4 mm (B, C, D) and 0.2 mm (C, D).

Seilacher (2005, pp. 28, 29), who noted that the early stages are strongly allometric. He observed (p. 28) "In the second stage, four radial (i.e., growth normal) folds develop on each mural plate. As they get more accentuated, they become T and L-shaped in cross-section and eventually fuse with their neighbors." Our discovery of a carina from the North Carolina Pliocene, at this developmental stage (5.5 mm breadth, Text-fig. 5A, B), prompted a review of the ontogeny of the extinct species *Coronula bifida* (Text-fig. 5), based on the carinae. The earliest known stages (Text-figs 6A–C, 7A–C) show the four separated processes, each with an internal groove. At a maximum breadth of about 10 mm, the processes fuse (Text-fig. 6D, E) and the grooves become three oval cavities on the interior of the plate. New cavities develop by the formation of apically upturned walls at the central bases of these, with the eventual formation of 6 structures in the fully grown plate (Text-fig. 6F, G).

Coronula bifida Bronn, 1831

(Text-figs 6 and 7)

1831. *Coronula bifida* Bronn, p. 126.
1854. *Coronula barbara* Darwin, p. 421, pl. 15, fig. 6.
1855. *Coronula barbara* Darwin, p. 38 pl. 2, fig. 8a–e.
1951. *Coronula dormitor* Pilsbry and Olsson, p. 202.
1968. *Coronula bifida bifida* Menesini, p. 387, pl. 1, figs 1–4, pl. 2, figs 1–3, pl. 3, figs 1, 2, pl. 4, figs 1, 3.
1968. *Coronula bifida barbara* Menesini, p. 395, pl. 3, figs 3–5, pl. 4, figs 2, 4, 6.
2016. *Coronula bifida* Bronn; Collareta *et al*., p. 15, fig. 5a–h.
2018. *Coronula bifida* Bronn; Buckeridge *et al*., p. 4, figs 3–5.
2023. *Coronula barbara* Darwin; Karasawa, p. 5, pl. 1, figs 4–7, pl. 2, figs 1, 2.
2023. *Coronula bifida* Bronn; Karasawa, p. 5, pl. 2, figs 3–9.
2025b. *Coronula bifida* Bronn; Gale, pl. 74, figs 3–8.

DIAGNOSIS: The shell is globose, with apicobasal convex parietal ribs that often bifurcate and possess strong transverse ridges. The radii are moderately thick, displaying a roughly constant width (or slightly widening basally) in the upper two-thirds of the shell and narrowing basally in their lowermost third. The body chamber is relatively shallow, sub-cylindrical and the sheath is less than half of the total height of the shell (modified after Collareta *et al.* 2018, p. 15).

TYPE: The whereabouts of Bronn's (1831) original material is unknown.

MATERIAL: 2 carinae, a juvenile from the Rushmere Member at Bells Bridge, North Carolina, USA (NHMUK PI In 66545) and a large broken specimen from Dixon, North Carolina, USA (NHMUK PI In 66546). A large, complete marginal plate from the Rushmere Member at Martin-Marietta Fountain Quarry near the town of Fountain, Pitt County, North Carolina, USA (NCSM 13785).

REMARKS: The significance of the juvenile carina is discussed above. *Coronula bifida* differs from the younger *C. diadema* (later Calabrian to present day) in numerous features (Buckeridge *et al.* 2018; Collareta *et al.* 2018; Gale 2020), including the shallower sheath, the larger number of apicobasal ribs, which possess more strongly developed transverse ribs and the larger number of cavities set between folds on the interior of the parietes which are five to six in *C. bifida* and three in *C. diadema.* The larger specimens from North Carolina are typical *Coronula bifida*. These appear to be the first specimens from the Atlantic Coastal Plain of the USA.

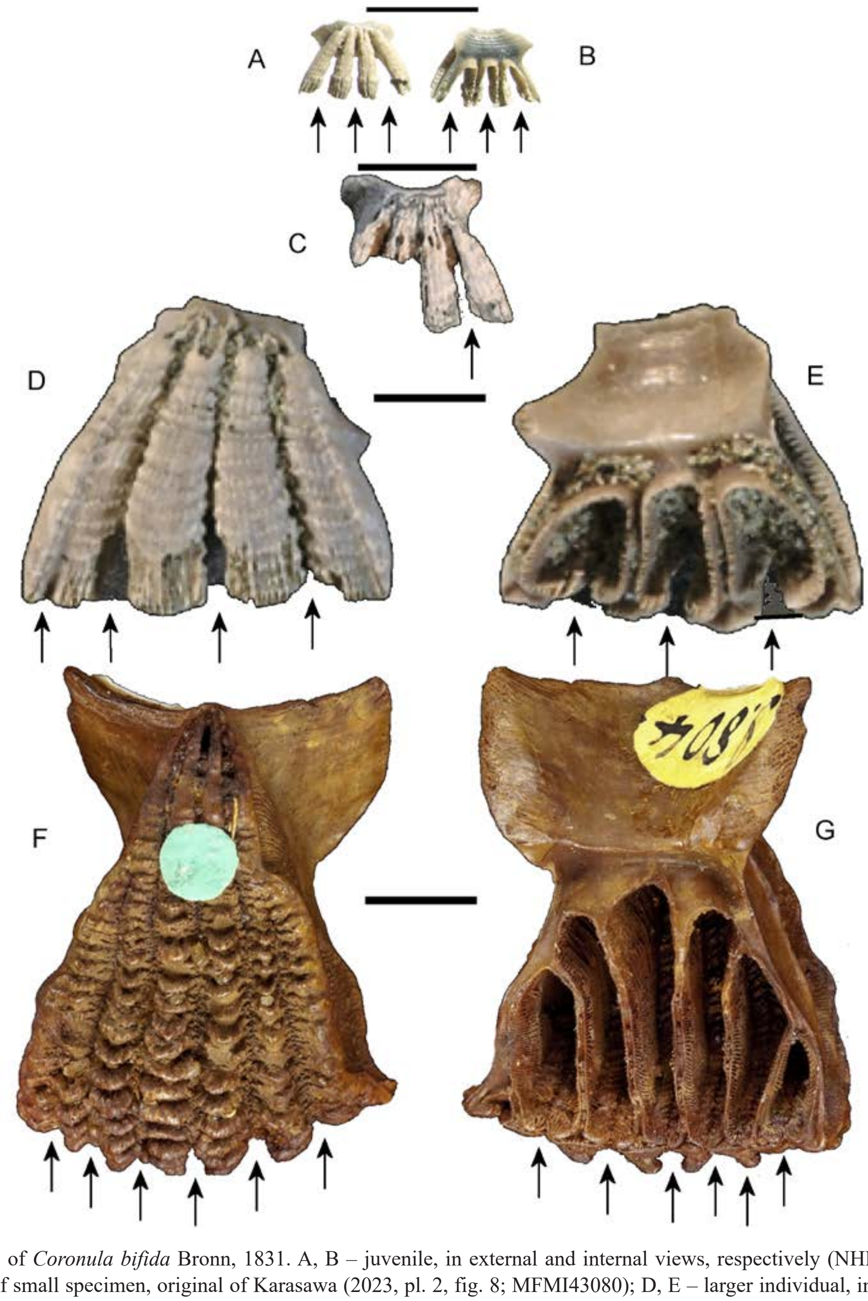
Family Balanidae Leach, 1817

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

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

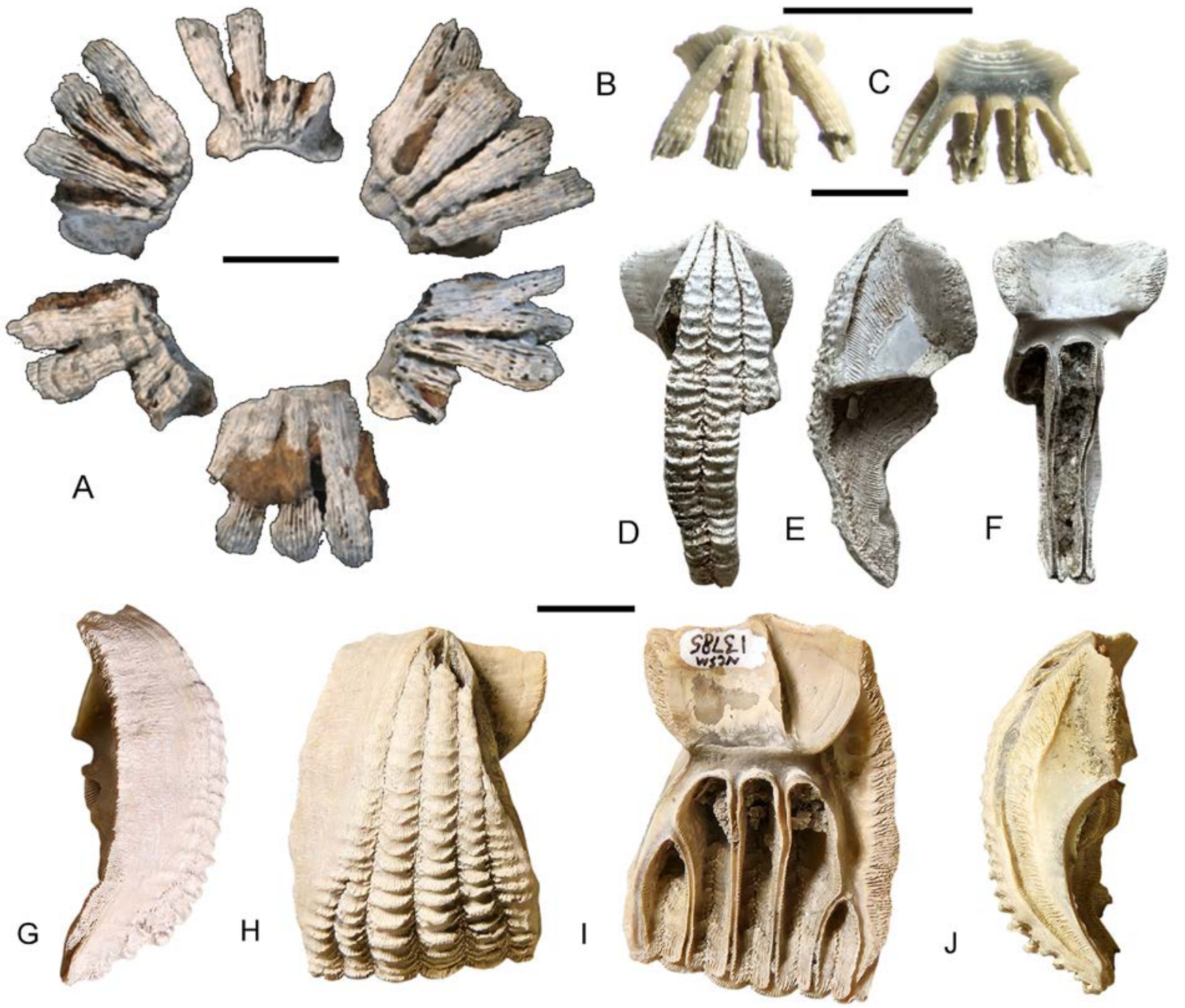
Subfamily Balaninae Leach, 1817

DIAGNOSIS: Wall of six plates generally relatively small, smooth or ribbed, tubiferous with one row of major tubes. Radii solid, transverse teeth on sutural edges smooth or with denticles on lower side and rarely on upper side; alae not cleft; lateral margin



Text-fig. 6. Carinae of *Coronula bifida* Bronn, 1831. A, B – juvenile, in external and internal views, respectively (NHMUK PI In 66545); C – external view of small specimen, original of Karasawa (2023, pl. 2, fig. 8; MFMI43080); D, E – larger individual, in which the separate processes have fused, and new internal chambers have started to form, original of Karasawa (2023, pl. 2, fig 5; MFMI 143067); F, G – fully grown specimen, with complete complement of internal chambers, original of Collins *et al.* (2014, fig. 6O, P; NHMUK I.804). A, B is from the Rushmere Member, Pliocene (Piacenzian), Bells Bridge, North Carolina, USA; C is from locality C14, Shinzato Formation, Gelasian, Pleistocene, Toubaru, Uruma City, Japan; D, E is from locality CO5, Dainichi Formation, Gelasian, Pleistocene, Kakegawa City, Japan; F, G is from Red Crag Formation, Piacenzian, Suffolk or Essex, UK. Arrows indicate positions of spaces between processes on juvenile valves. Scale bars equal 5 mm.

of sheath not extending over the adjacent ala. Basis solid, irregular or uniformly tubiferous in a single layer. Scutum with weak adductor ridge. Tergum with spur having a gentle change in the direction of growth lines, and spur and furrow margins coincident; basicarinal angle with well-developed depressor muscle crests limited to border (Pitombo 2004, p. 263).



Text-fig. 7. *Coronula bifida* Bronn, 1831. A – disarticulated shell of juvenile, external view, original of Karasawa (2023, pl. 2, fig. 8; MFMI 43080); B, C – juvenile carina, in external and internal views, respectively (NHMUK PI In 66545); D–F – broken carina, in external, lateral and internal views, respectively (NHMUK PI In 66546); G–J – marginal plate, in dorsal, external, internal and ventral views, respectively (NHMUK PI In 66546). A is from locality C14, Shinzato Formation, Gelasian, Pleistocene, Toubaru, Uruma City, Japan; B, C is from Rushmere Member, Pliocene (Piacenzian), Bells Bridge, North Carolina, USA; D–F is from Rushmere Member, Pliocene (Piacenzian), Dixon, North Carolina, USA; G–J is from Rushmere Member, Pliocene (Piacenzian), Fountain, Pitt County, North Carolina, USA. Scale bars equal 5 mm (A–C) and 10 mm (D–J).

INCLUDED GENERA: *Balanus* Da Costa, 1778; *Fistulobalanus* Zullo, 1984; *Tamiosoma* Conrad, 1856; *Vectibalanus* Gale, 2021; *Zulloa* Newman and Ross, 1996.

REMARKS: Balanomorphs which possess tubiferous parietes but have solid radii are included in the subfamily Balaninae as used here. This group is almost certainly paraphyletic from molecular evidence (Pérez-Losada *et al*. 2014) but forms a useful grouping.

Genus *Fistulobalanus* Zullo, 1984

DIAGNOSIS: Shell wall of six, porous, compartmental plates; radii solid; basis calcareous, porous; parietal tubes in two or more rows; larger, primary parietal tubes arranged in a single row against inner lamina of shell wall; smaller, irregularly arranged, subsidiary rows of parietal tubes between primaries and outer lamina; sheath usually composed of irregular, thin-walled, calcareous vesicles; scutum usually with fine, external radial striae (after Zullo 1984, p. 1330).

TYPE SPECIES: *Balanus pallidus* Darwin, 1854.

Fistulobalanus multiseptatus (Ross, 1964)

(Text-fig. 5D–G)

1964. *Balanus* (*Megabalanus*) *multiseptatus* Ross, p. 485, pl. 71, figs 1–6.
1986. *Fistulobalanus multiseptatus* (Ross, 1964); Zullo, table 1.

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 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; Text-fig. 2 herein).

MATERIAL: 3 scuta from the Rushmere Member at Dixon, North Carolina, USA.

REMARKS: The scuta (Text-fig. 5E, F, H, I) are very similar in detail to that figured by Ross (1964, pl. 71, figs 2, 3, refigured here as Text-fig. 5F, G). The adductor ridge is short and passes upwards into a striated callus. The articular furrow is broad and deep, the articular ridge short and erect. The external face shows evenly spaced growth ridges and apicobasal striae on the tergal portion of the surface.

"Subfamily Archaeobalaninae
Newman and Ross, 1976"

DIAGNOSIS: Balanids in which the parietes lack pores; basis with or without pores.

INCLUDED GENERA: *Actinobalanus* Moroni, 1967; *Archaeobalanus* Menesini, 1971; *Armatobalanus* Hoek, 1913; *Bathybalanus* Hoek, 1913; *Chirona* Gray, 1835; *Conopea* Gray, 1825; *Hesperibalanus* Pilsbry, 1916, *Kathpalmeria* Ross, 1965a; *Membranobalanus* Hoek, 1913; *Notobalanus* Newman and Ross, 1976; *Palaeobalanus* Buckeridge, 1983; *Solidobalanus* Hoek, 1913; *Striatobalanus* Hoek, 1913; and *Zullobalanus* Buckeridge, 1989.

REMARKS: This is evidently a paraphyletic assemblage of genera, united by plesiomorphic characters.

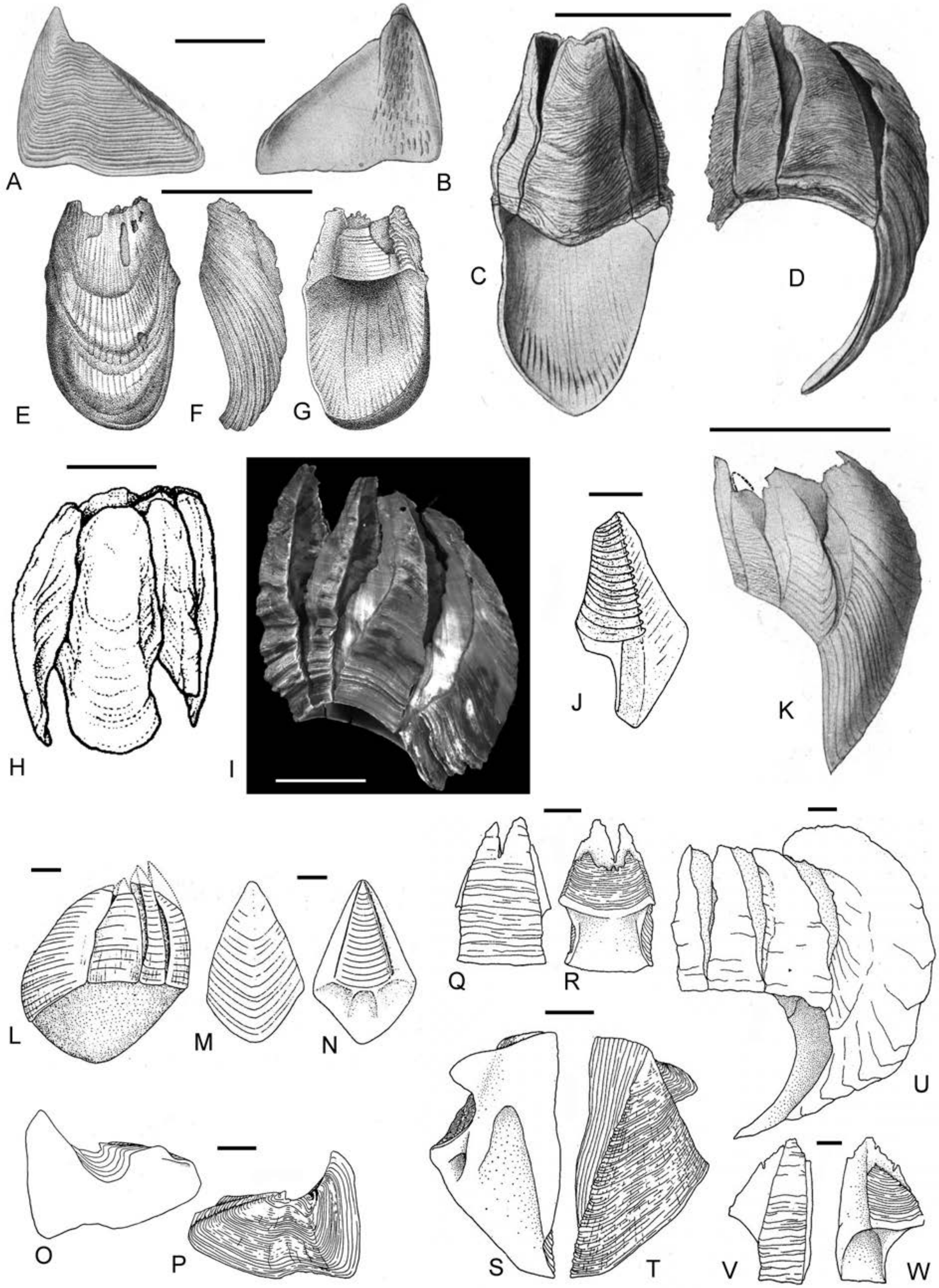
Membranobalanus Hoek, 1913

DIAGNOSIS: Parietes solid, unornamented, weakly articulated, basis membranous. Rostrum scoop or boat-shaped, often elongate relative to other parietes. Tergum with spur furrow open (after Hosie *et al.* 2019, p. 27).

TYPE SPECIES: *Balanus declivis* Darwin, 1854 (p. 275, pl. 7, fig. 4a–d); by subsequent designation of Pilsbry (1916, p. 229).

INCLUDED SPECIES: *Balanus brachialis* Rosell, 1972; *Balanus cuneiformis* Hiro, 1936; *Balanus* (*Membranobalanus*) *longirostrum* Hoek, 1913; *Balanus* (*Membranobalanus*) *nebrias* Zullo and Beach, 1973; *Balanus orcutti* Pilsbry, 1907; *Membranobalanus costatus* Zullo and Standing, 1983; *Membranobalanus koreanus* Kim and Kim, 1983; *Membranobalanus porphyrophilus* Hosie and Jones in Hosie *et al*., 2019, and *Membranobalanus robinae* Van Syoc, 1988.

REMARKS: The genus *Membranobalanus* includes 10 living species which are widely distributed at low to mid-latitudes, and are found in the Atlantic, Indian and Pacific Oceans, the Caribbean and the South China Sea. *Membranobalanus* species are all obligate symbionts of sponges, mostly of the family Clionaidae (Van Syoc 1988; Van Syoc *et al.* 2015; Hosie *et al.* 2019). The shell has solid parietes, loosely connected, a membranous basis, the rostral plate is concavo-convex (Text-fig. 8E–I, K) and in some species is prolonged basally (Text-fig. 5D, K, U). The growth lines on the parietes develop irregular flanges (Text-fig. 5D–I). The opercular plates are variable in form, but the tergum has a broad, flat spur furrow and lacks a spur (Text-fig. 8A, B, O, P). There is only a single fossil record of the genus, based on one rostral plate, from the Pliocene of California (Ross 1999; Text-fig. 5E–G). It was therefore surprising to find plates of *Membranobalanus* in picked material from the Rushmere Member, Dixon locality, including the distinctively beaked terga and all other plates except the scutum. It is here described as a new species.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← Text-fig. 8. Selected images of species of *Membranobalanus*. A–D – *Membranobalanus orcetti* Pilsbry, 1916; A, B – tergum, in external and internal views, respectively; C, D – shell in ventral and lateral views, respectively, figured after Pilsbry (1916, pl. 55, fig. 1). E–G – *Membranobalanus* sp., rostral plate, in ventral, lateral and internal views, respectively, figured after Ross (1999, fig. 1). H – *Membranobalanus robinae* Van Syoc, 1988, in lateral view, figured after Van Syoc (1988, fig. 1a). I – *Membranobalanus porphyrophilus* Hosie and Jones in Hosie *et al*., 2019, in lateral view, figured after Hosie *et al*. (2019, fig. 2B). J – *Acasta acutus* (Kolbasov, 1993), internal view of marginal plate, figured after Kolbasov (1993, fig. 5C). K – *Membranobalanus declivis* (Darwin, 1854), lateral view of shell, figured after Pilsbry (1916, pl. 55, fig. 1a). L–N – *Membranobalanus cuneiformis* (Hiro, 1936); L – lateral view of shell; M, N – rostral plate in external and internal views, respectively, original of Hiro (1936, fig. 5A, B, F). O–W – *Membranobalanus koreanus* Kim and Kim, 1983; O, P – tergum in internal and external views, respectively; Q, R – carina in external and internal views, respectively; S, T – scutum in internal and external views, respectively; U – shell in lateral view; V, W – marginal plate in external and internal views, respectively. Figured after Kim and Kim (1983, pl. 1, figs 1–9). A–D are from the present day of lower California, USA; E–G are from San Diego Formation, Pliocene, San Diego, California, USA; H is from present day of the Gulf of California; I is from present day of Western Australia; J is from present day of the Arctic Ocean, north of Greenland; K is from present day of Bermuda; L–N is from present day of Malaysia; O–W is from present day of Korea. Scale bars equal 10 mm (C–G, I), 5 mm (A, B, H, K), 1 mm (E, F, L–W) and 0.5 mm (J).

Membranobalanus distortus sp. nov.
(Text-fig. 9)

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DIAGNOSIS: Rostral plate of approximately the same height as the carina, tall, narrow, weakly convex. Carina kite-shaped, sheath tall and convex. Tergum broad, triangular, with large, shallow tergal spur furrow, beaked. Many individual plates strongly deformed, asymmetrical.

TYPES: The rostral plate illustrated in Text-fig. 9K, L is the holotype (NHMUK PI In 66552). The other figure plates (Text-fig. 9A–J, N–AA) are paratypes (NHMUK PI In 66547–66551, 66553–66558). All specimens are from the Rushmere Member, Pliocene (Piacenzian), Dixon, North Carolina, USA.

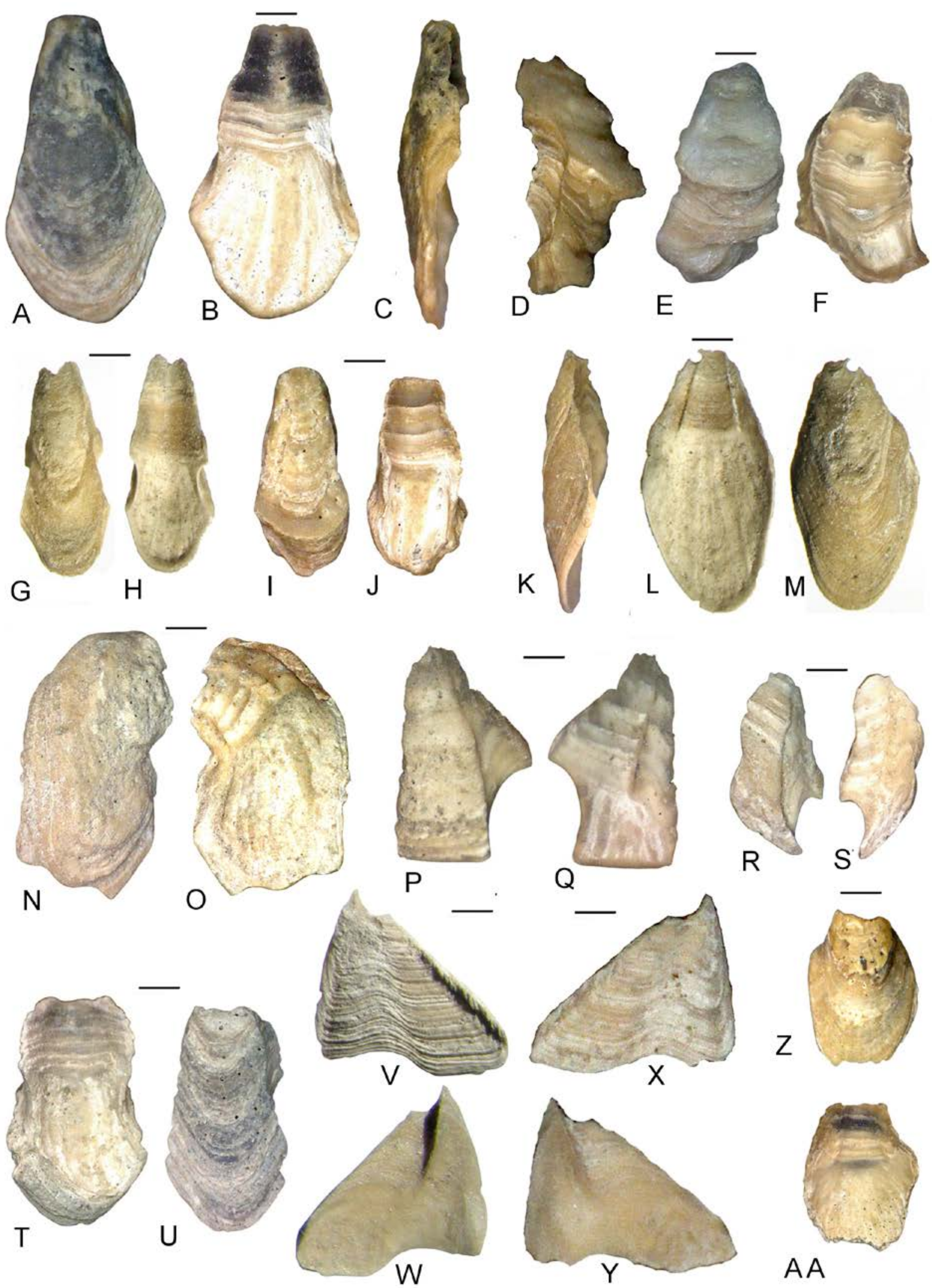
MATERIAL: 35 isolated valves including rostral plates, carinae, a marginal, a carinomarginal and 2 terga, all from the Rushmere Member, Pliocene (Piacenzian), Dixon, North Carolina, USA.

DERIVATION OF NAME: With reference to the asymmetrical, distorted form of many carinae and rostral plates.

DESCRIPTION: Material of the carinae and rostral plates include 2 intergrading types; bilaterally symmetrical plates which lack irregular and protuberant growth increments (e.g., Text-fig. 9A–C, G, H, K–M, Z, AA), which intergrade through to strongly asymmetrical plates with swollen external flanges (e.g., Text-fig. 9D–F, N, O). The holotype rostral plate (Text-fig. 9K–M) has an oval-rhombic outline, is gently concavo-convex, and the height is twice the breadth. The sheath is triangular, concave, a third of the height of the plate and the interior of the parietes is weakly ridged. The radii are narrow, smooth, and extend from the apex to the position of the maximum breadth. In lateral profile (Text-fig. 9K) the external margin is slightly convex. Externally, the plate is smooth with margin-parallel growth lines. A distorted rostral plate (Text-fig. 9N, O) has the sheath and radii angled to the axis of the plate at 40º, and the exterior is irregularly undulose. The symmetrical type of carina (Text-fig. 9A, B, G, H) is kite-shaped, with the maximum breadth at one third of the height above the base, and short alae. The concave sheath represents between one third and half the total height of the plate. In lateral profile, the carinae are very narrow (Text-fig. 9C). The irregularly shaped carinae (Text-fig. 9D–F) are asymmetrical, with very tall sheaths, and external flanges representing changes in the orientation of growth. Intermediate forms are present (Text-fig. 9I, J, T, U).

A marginal plate (Text-fig. 9P, Q) has a triangular, externally smooth parietes of which the height is twice the breadth, and a broad, triangular ala, the lower margin of which is strongly concave. The base of the tall sheath is angled to the basal margin of the plate. The radius is narrow and extends to the basal margin of the plate. The carinomarginal (Text-fig. 9R, S) has a convex dorsal margin and a concave ventral margin; the ala extends from the apex to the base and the basal margin of the ala is concave. The sheath is tall and narrow. There are two terga in the material (Text-fig. 9V–Y) which are broad and triangular. The scutal margin is straight and long, the occludent margin short and slightly convex, and the basal margin is weakly sigmoidal. A broad, shallow tergal spur furrow occupies half of the external face, and its base deflects the basal margin. On the interior of the tergum a broad, shallow articular furrow is present. A short, acute apical beak is present.

REMARKS: *Membranobalanus distortus* sp. nov. is closest to the living *M. orcutti*, from the present-day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← Text-fig. 9. *Membranobalanus distortus* sp. nov. A–C – large paratype carina in dorsal, internal and lateral views, respectively (NHMUK PI In 66547); D–F – paratype carina with irregular growth increments, in lateral, dorsal and internal views, respectively (NHMUK PI In 66548); G, H – paratype carina in dorsal and internal views, respectively (NHMUK PI In 66549); I, J – paratype carina in dorsal and internal views, respectively (NHMUK PI In 66550); K–M – holotype rostral plate in lateral, internal and ventral views, respectively (NHMUK PI In 66552); N, O – strongly deformed rostral plate, in external and internal views, respectively (NHMUK PI In 66553); P, Q – marginal plate, in external and internal views, respectively (NHMUK PI In 66555); R, S – carinomarginal plate, in external and internal views, respectively (NHMUK PI In 66556); T, U – paratype carina in internal and external views, respectively (NHMUK PI In 66551); V–Y – terga, in external (V, X) and internal (W, Y) views (NHMUK PI In 66557, 66558); Z, AA – broken rostral plate, in dorsal and internal views, respectively (NHMUK PI In 66554). All specimens are from the Rushmere Member, Pliocene (Piacenzian), Dixon, North Carolina, USA. Scale bars equal 1 mm.

southern California, in that the terga are very similar in shape (compare Text-fig. 9V–Y with Text-fig. 8A, B). In contrast, the rostral plates differ significantly, as in *M. orcutti* these are strongly convex and the basal extension represents half the height of the plate (compare Text-fig. 9K–M with Text-fig. 8C, D). In *M. distortus* sp. nov. the rostral plate is only slightly taller than the carina. Additionally, *M. orcutti* does not show the curious distortions of some carinae and rostral plates shown by *M. distortus* sp. nov.

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*.

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 glyptopoma (Pilsbry, 1916)

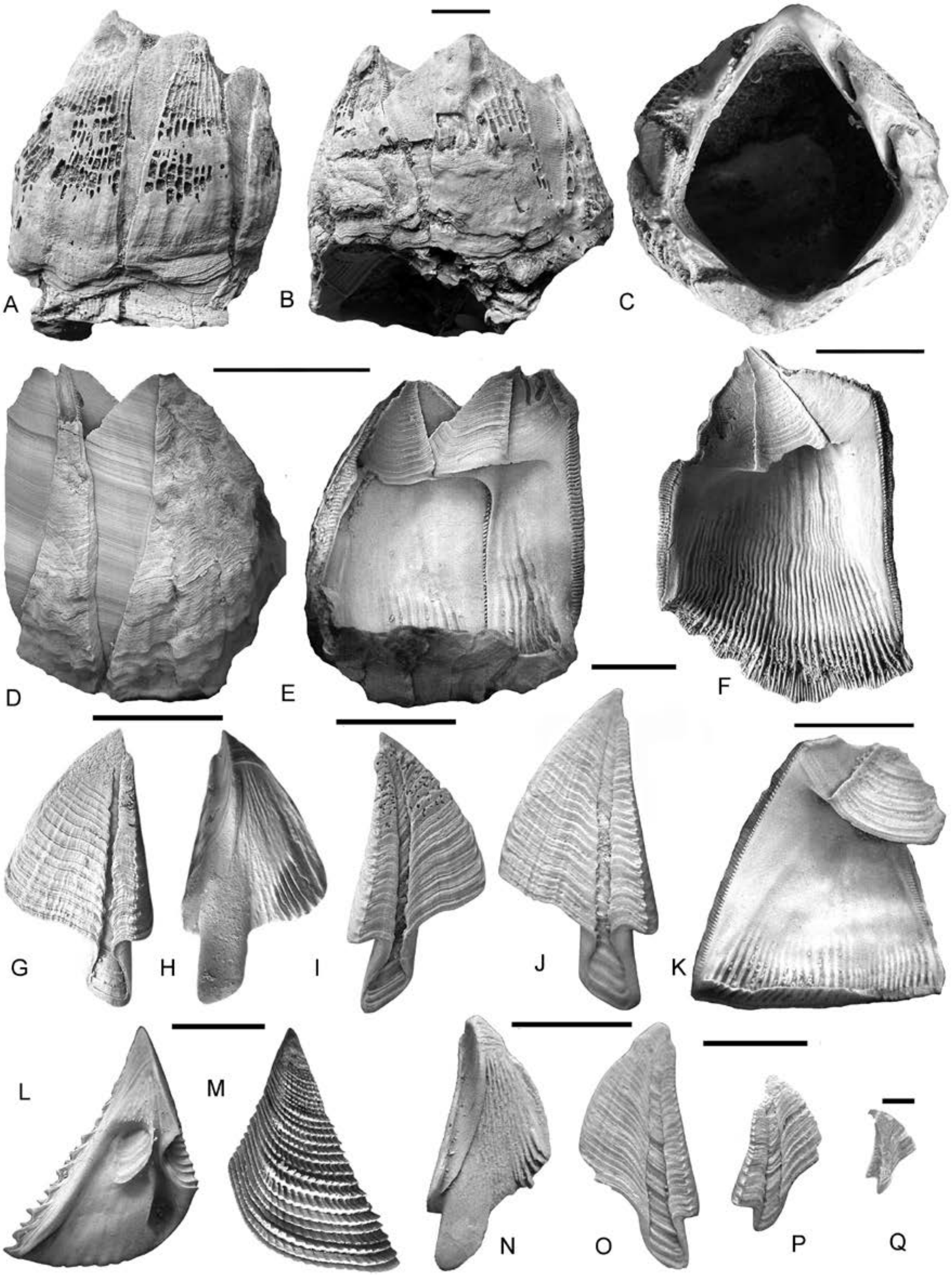
(Text-figs 5M–O, 10, 11G–K, M, N)

part 1916. *Balanus concavus glyptopoma* Pilsbry, p. 102, pl. 21, figs 2, 3, pl. 22, figs 2, 2a, 2c only.
1986. *Concavus glyptopoma* (Pilsbry); Zullo, p. 12, pl. 2, figs M–S.
1992. *Arossia glyptopoma* (Pilsbry); Zullo, p. 30, figs 17.10–17.20, 18.1–18.10.

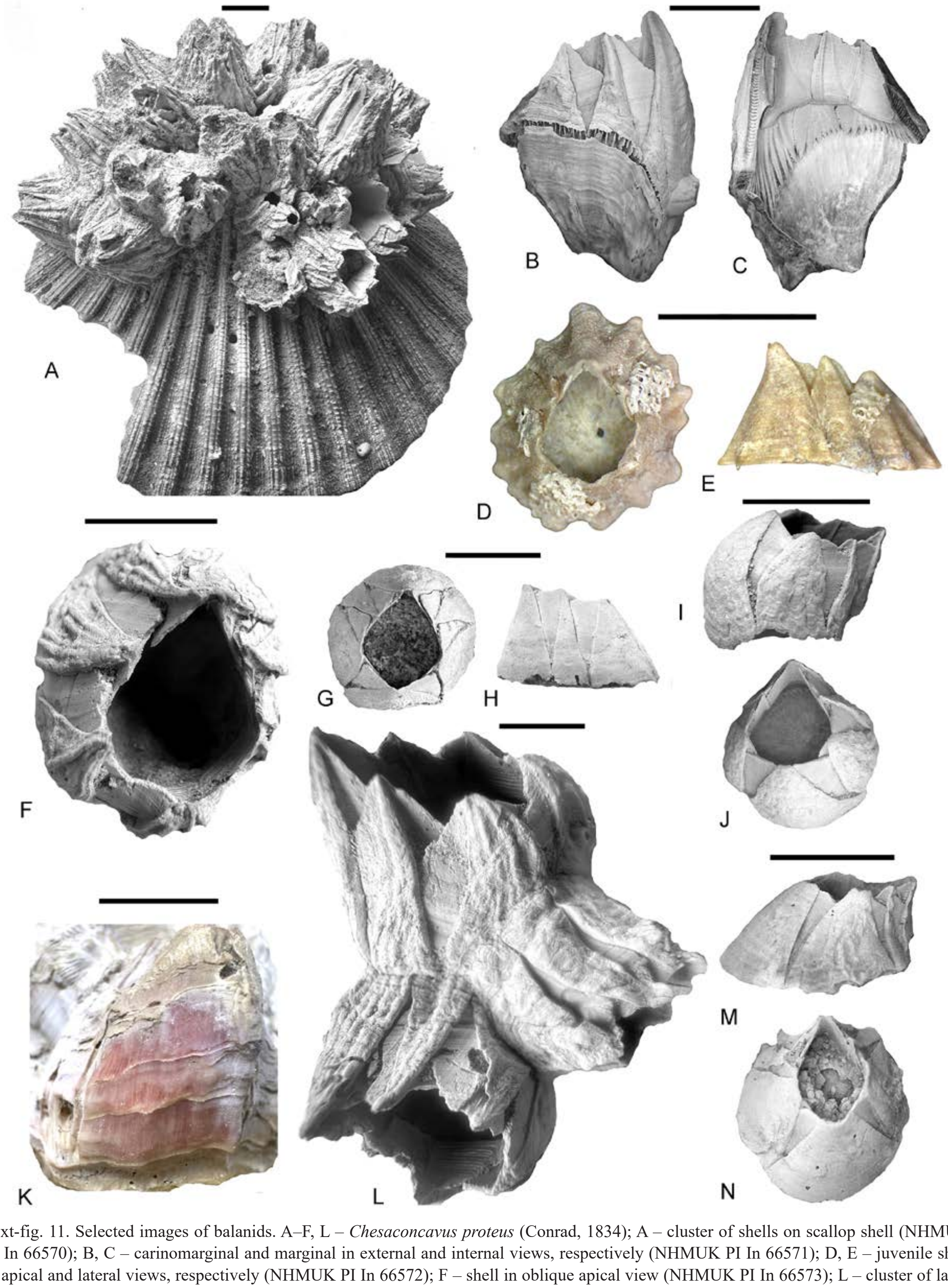
DIAGNOSIS: Radii broad, with oblique summits, angled at 45º, parietes with numerous transverse septa. Adductor ridge of scutum extending beyond upper end of adductor scar, separated from articular ridge by narrow groove or ridged callus. Scutum strongly noded. Tergum narrow, not arcuate, tergal spur furrow narrowly open, tergal spur truncate to subtruncate, variable in length (modified after Zullo 1992, p. 30).

TYPES: Shell with opercular plates, ANSDU no. 1140, from the Tamiami Formation, Pliocene, Caloosahatchee River, Florida, USA.

MATERIAL: Over 50 complete shells, some with opercular valves, numerous isolated compartments and opercular plates from the Rushmere Member at



Text-fig. 10. Selected images of *Arossia glyptopoma* (Pilsbry, 2016). A–C – shell in lateral, ventral and apical views, respectively (NHMUK PI In 66559); D, E – isolated marginal and carinomarginal in external and internal views, respectively (NHMUK PI In 66560); F – rostral plate in internal view (NHMUK PI In 66561); G–J, N–Q – terga, H is in internal view, all others external (NHMUK PI In 66563–66565, 66567–66569); K – marginal plate in internal view (NHMUK PI In 66562); L, M – scutum in internal and external view, respectively (NHMUK PI In 66566). All specimens are from the Rushmere Member, Pliocene (Piacenzian), Dixon, North Carolina, USA. Scale bars equal 10 mm (A–C), 5 mm (D–P), and 0.5 mm (Q).



Text-fig. 11. Selected images of balanids. A–F, L – *Chesaconcavus proteus* (Conrad, 1834); A – cluster of shells on scallop shell (NHMUK PI In 66570); B, C – carinomarginal and marginal in external and internal views, respectively (NHMUK PI In 66571); D, E – juvenile shell in apical and lateral views, respectively (NHMUK PI In 66572); F – shell in oblique apical view (NHMUK PI In 66573); L – cluster of large shells (NHMUK PI In 66574). G–J, K, M, N – *Arossia glyptopoma* (Pilsbry, 2016); G–J, M, N – juvenile shells in apical (G, J, N) and lateral (H, I, M) views (NHMUK PI In 66575, 66576, 66578); K – basal shell in external view to show original colouration (NHMUK PI In 66577). A is from Rushmere Member, Bells Bridge, Edgecombe County, North Carolina, USA; B–N are from Rushmere Member, Dixon, Edgecombe County, North Carolina, USA. Scale bars equal 10 mm (A, D–F, L) and 5 mm (B, C, G–K, M, N).

both Dixon and Bells Bridge localities, Edgecombe County, North Carolina, USA.

REMARKS: Zullo (1992, p. 30) provided an extended diagnosis of this species, concentrating on features of the opercular valves. The new, extensive material, including early growth stages, permits us to add further details on shell structure and development.

The smallest individuals found have a carinal-rostral length of 1 mm (Text-fig. 5M) are smooth externally and have a low conical lateral profile. At a carinal-rostral length of about 5 mm (Text-figs 5O, 11M, N) the radii are broadened, the upper margins are horizontal and the tip of the carina is curved dorsally. In shape and sculpture they resemble smooth forms of *Balanus crenatus* Bruguière, 1789 (e.g., Southward 2008, fig. 81B). However, in *B. crenatus* the upper margins of the radii are rounded and expose the upper parts of the alae. At dimensions of 10–15 mm (Text-fig. 11G–J), the shell is proportionately taller, more cylindrical, the radii are broader, and the orifice is larger. The external surface of the shell develops irregularly undulating fine growth lines in some specimens. The development is diametric, with progressive broadening of the orifice with growth (Anderson 1992). The basis is thin and perforated by widely spaced pores. The terga (Text-fig. 10G–J, N–Q) display some variation in the curvature of the spur furrow (compare Text-fig. 10G with 10I). The smallest terga (Text-fig. 10Q), with a height of 1.2 mm, are similar in shape to fully grown specimens, but the spur furrow is shallow, lacking folded margins.

In fully grown individuals, the shell is cylindrical, the orifice large and kite-shaped (Text-fig. 10A–C) and the upper margins of the radii are oblique (40–60º). The sheath on the marginals and carinomarginals is very broad (Text-fig. 10E, K) and bears evenly spaced ridges, marking successive attachment sites of the arthrodial membrane. The denticulate inner margin of the radii on the marginals and rostral plate has a central groove. The exterior of the parietes shows irregular, undulose growth lines and very weak, indistinct ribbing. The interior of the rostral plate (Text-fig. 10F) bears fine ribbing which extends up to the sheath; on the other valves, ribbing is restricted to the basal parts. The external sculpture of the parietes comprises convoluted, irregular growth lines. Worn valves (Text-fig. 10A, B) show the presence of numerous transverse septa. A purplish reddish-pink colouration is retained on parts of some specimens (Text-fig. 11K).

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

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, 1965a; *Concavus belgradensis* Zullo, 1984; *Chesaconcavus myosulcatus* Zullo, 1992; *Chesaconcavus rossi* Zullo, 1992; *Chesaconcavus santamaria* Zullo, 1992.

Chesaconcavus proteus (Conrad, 1834)

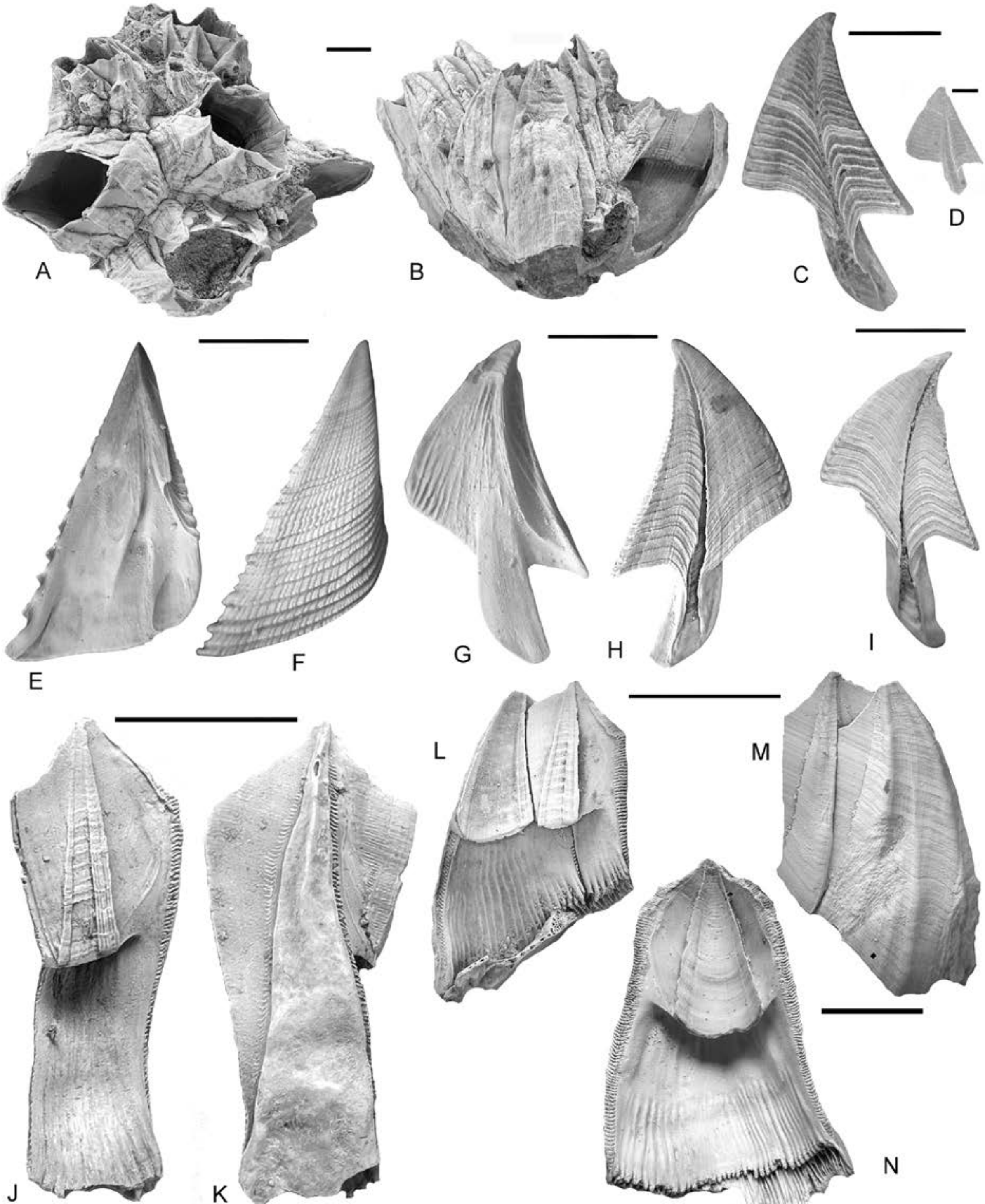
(Text-figs 5H–K, 11A–F, L, 12A–M)

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.
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.

DIAGNOSIS: Shell sharply and regularly ribbed, orifice moderately toothed, upper margins of radii oblique, scutum narrow. Adductor ridge long, Tergal spur 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: Over 50 complete shells, some with opercular valves and numerous compartments and opercular plates from the Rushmere Member at both Dixon and Bells Bridge, Edgecombe County, North Carolina, USA.



Text-fig. 12. *Chesaconcavus proteus* (Conrad, 1834). A, B – cluster of large shells in apical and lateral views, respectively (NHMUK PI In 66579); D, E – scutum, in internal and external views, respectively (NHMUK PI In 66581); C, F–H – terga, in external (C, G, H) and internal (F) views (NHMUK PI In 66580, 66582, 66583); I, J – carinomarginal, in internal and external views, respectively (NHMUK PI In 66584); K, L – articulated marginal and carinomarginal, in internal and external views (NHMUK PI In 66585); M – rostral plate in internal view (NHMUK PI In 66586); N – Internal view of rostral plate (NHMUK PI In 66587). A, B, E–M are from Rushmere Member, Dixon, Edgecombe County, North Carolina, USA; C, D, N are from Rushmere Member, Bells Bridge, Edgecombe County, North Carolina, USA. Scale bars equal 10 mm (A, B, N), 5 mm (C, E–M) and 0.5 mm (D).

REMARKS: The species is particularly characterised by the ribbing on the parietes. The opercular valves (Text-fig. 12C–H) conform closely with those figured by Zullo (1992, fig. 13.1–13.7). The terga have similar shapes, the tergal spur furrow is narrowly open and the tergal spur is elongated. In particular, the long adductor ridge, and presence of a ridge bordering the lateral depressor muscle scar on the interior of the scutum are very similar. The elongated shape of the scutum, with a sculpture of fine apicobasal ridges forming nodes where these intersect with the growth increments are also diagnostic.

The extensive new material provides additional information about the species to the description of Zullo (1992), particularly concerning the shell structure and ontogeny. The smallest shells have rostrocarinal dimension of 1.5 mm (Text-fig. 5H) and have a low conical profile and an oval orifice representing 25–35% of the r-c length. The outline is oval and becomes irregularly lobate with increased size (up to 10 mm; Text-fig. 5A–K) and each plate has 1–3 rounded ridges which form projections on the margin. The radii are very narrow and strongly oblique. The external surface is weakly rugose, bears regularly spaced growth lines and the alae bear transverse grooves to accommodate the ridges on the radii (Text-fig. 5L). With increased size (11 mm; Text-fig. 11D, E) the orifice enlarges to represent 50% of the r-c length, and the ribs weaken. At larger sizes (15 mm; Text-fig. 11B, C) the radii broaden and their upper margins become more steeply inclined (50–60º); concomitantly, the shell becomes more cylindrical and the orifice larger. As in *Arossia glyptopoma*, the growth pattern is classically diametric. The terga (Text-fig. 12C, D, G, I) display little ontogenetic change in morphology. The smallest (Text-fig. 12D), with a height of 1.5 mm, has a similar outline to those of larger specimens, but the tergal spur furrow is open and the tergal spur proportionately short.

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 (Text-fig. 12I, K, M). In the carinomarginal, the ventral part of the sheath bears raised transverse bars, like the rungs of a ladder (Text-fig. 12I, K) representing positions of the attachment of the arthrodial membrane. Apicobasal ribs are present on the basal interior of the parietes, but do not extend up to the sheath. These ribs are coarser and less numerous in smaller specimens (Text-fig. 11C) and finer and more numerous in larger ones (Text-fig. 12I, K, M). The exterior of the parietes is strongly and irregularly ribbed (Text-figs 11A, B, 12A, B), or have few, sharply defined apicobasal ribs (Text-figs 11B, 12L). The basis is thin and perforated by widely spaced pores, but patches of an underlying vesicular material are visible on some specimens (Text-fig. 12L).

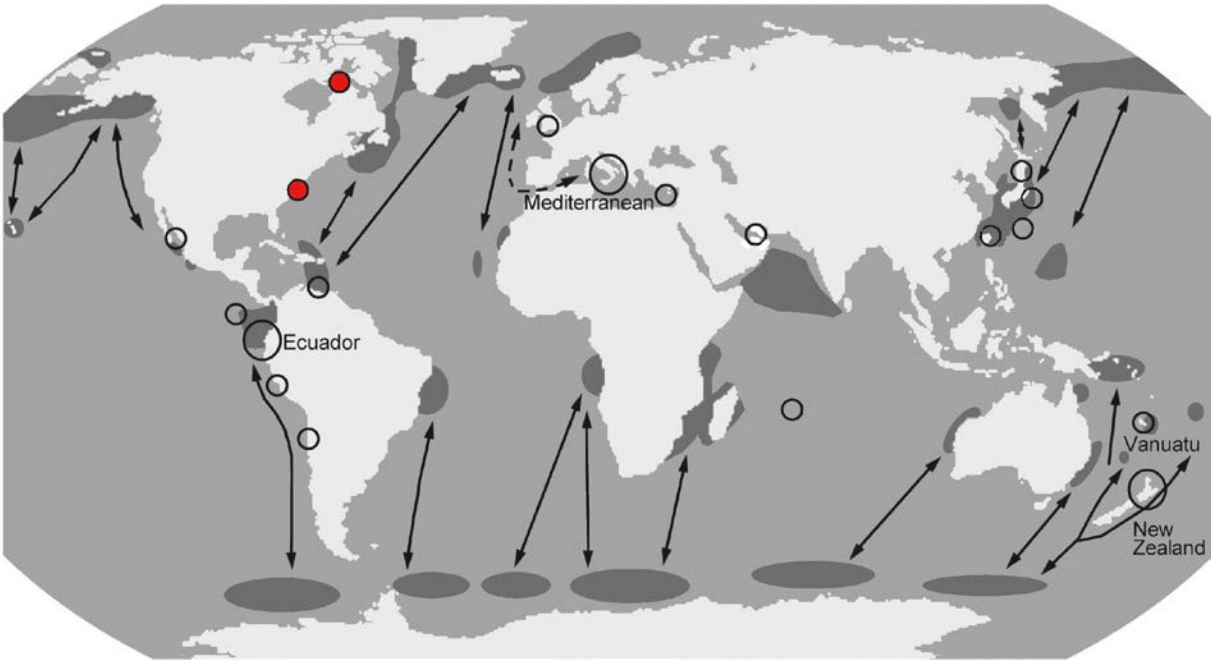
OCCURRENCE: Pliocene (Piacenzian) of North Carolina and Virginia, USA.

DISCUSSION

We record a total of 7 cirripede species from the Rushmere Member of the Dixon and Bells Bridge localities (Table 1) in North Carolina, USA. The concavine balanomorphs *Chesaconcavus proteus* and *Arossia glyptotoma* are the most abundant, and the largest taxa, with over 500 isolated valves and 40 articulated shells recorded. The next most common taxon is the scalpellid *Scalpellum multangulatum*, represented by over 200 isolated valves. *Verruca stroemia* and *Membranobalanus distortus* sp. nov. are known from less than 50 valves, and *Coronula bifida* and *Balanus multiseptatus* from respectively 2 and 3 valves each.

Taxon	Family	Rushmere Member, North Carolina, USA	Morgarts Beach Member, Rice's Pit, Virginia, USA	Pliocene, NW Europe
Scalpellum multangulatum	Scalpellidae	common	absent	absent
Verruca stroemia	Verrucidae	common	absent	present
Coronula bifida	Coronulidae	rare	absent	present
Membranobalanus distortus	Archaeobalanidae	common	absent	absent
Fistulobalanus multiseptatus	Archaeobalanidae	rare	present	absent
Chesaconcavus proteus	Concavinae	common	present	absent
Arossia glyptopoma	Concavinae	common	absent	absent
Notomegabalanus obliquus	Concavinae	absent	present	absent
Paraconcavus prebrevicalcar	Concavinae	absent	present	absent
Chesaconcavus tamiamiensis	Concavinae	absent	present	absent

Table 1. Distribution of cirripede species in the Pliocene of North Carolina, Virginia, and NW Europe.



Text-fig. 13. World map showing present day migration paths of humpback whales (arrowed) and occurrences of fossil *Coronula* (circles). The new records from North Carolina can be taken to indicate that whale migration in the Piacenzian was close to the palaeocoastline. Modified after Biannuci *et al*. (2006, fig. 3), with the addition of data from Buckeridge *et al.* (2018, 2019), Gale (2020) and Stewart *et al*. (2010). New records of *Coronula bifida* from the Pliocene of North Carolina and *Coronula diadema* from the Late Pleistocene of Montreal, Canada, are marked in red.

There are rather few regional barnacle assemblages with which to compare this fauna. The material described by Ross (1964) from the Morgarts Beach Member of the Yorktown Formation of Rice's Pit, Hampton, Virginia, USA, is stratigraphically higher than the Rushmere and approximately 100 kyr younger (Text-fig. 2). Ross (1964) recorded 6 species of balanomorphs from this locality (Table 1). The species described by him as *Balanus oppidieboraci* (Ross 1964, pl. 72, figs 16–30) and *Balanus pacificus prebrevicalcar* (Ross 1964, pl. 72, figs 2–15) were both placed in *Paraconcavus prebrevicalcar* by Zullo (1992, p. 38). Some of the material referred to *Balanus concavus proteus* Conrad by Ross (1964) was provisionally placed in *Chesaconcavus tamiamiensis* (Ross, 1965) by Zullo (1992, p. 24), the remainder in *Chesaconcavus proteus*. Of Ross' other species, *Balanus multiseptatus* was referred to *Fistulobalanus* by Zullo (1986) and *Balanus obliquus* (Ross 1964, pl. 71, figs 7–19, provisionally referred to *Notomegabalanus* by Zullo 1986, table 1), although the opercular valves are unknown. In conclusion, the Rice's Pit Morgarts Beach Member assemblage shares two species with that found in the Rushmere of North Carolina, i.e., *Fistulobalanus multiseptatus* and *Chesaconcavus proteus*. There therefore appears to be considerable stratigraphical (and geographical) variation within the cirripede faunas of the Yorktown Formation. The absence of smaller species from Rice's Pit is possibly attributed to the fact that finer residues were not studied.

Only a single species (9%) of the Piacenzian barnacle fauna from North Carolina and Virginia is living at the present day, albeit not in North America (*Verruca stroemia*). In contrast, the Zanclean–Piacenzian Crag formations of eastern England yield 15 species of barnacle (Gale 2025b), of which seven are still extant (46%). Concavine balanomorphs of the genera *Chesaconcavus*, *Paraconcavus* and *Arossia* make up 45% of the cirripede fauna of North Carolina and Virginia. These were dominantly warm water taxa, which probably invaded the region during the basal Rushmere Member transgression, coincident with the M1 oxygen isotope warm event (Dowsett *et al*. 2021).

Concavines were the dominant shallow marine balanomorphs in the Miocene and Pliocene of the warmer regions of the Northern Hemisphere, and locally were rock forming (e.g., Radwańska and Radwański 2008; Gale 2025b). A major extinction event in the Lower Pleistocene reduced the subfamily to scattered occurrences of a few species in the eastern Pacific Ocean (Zullo 1992). The precise dating of the extinction is not certain, but probably occurred in the late Calabrian, possibly contemporaneous with major extinctions which also affected deep-sea Mediterranean and Indian Ocean cirripedes (Gale *et al.* 2021). The causes of these extinctions are uncertain although they are associated with the Mid Pleistocene Transition (0.8–1.2 Ma). Preferential extinction of shallow marine, warm water cirripedes such as the concavines explains the difference between the low survival rate of Atlantic Plain Pliocene taxa and the higher survival of cooler water northwest European taxa such as those from the Pliocene (Zanclean–Piacenzian) Crags in England.

The records of the whale barnacle *Coronula bifida* from the Rushmere Member appear to be the first records from the eastern USA of any whale barnacle species. *Coronula* spp. are parasites on the humpback whale, and Bianucci *et al.* (2006) demonstrated the coincidence of the known fossil occurrences of *Coronula* spp. with present-day migration paths and regions of occurrence of this whale. Buckeridge *et al.* (2018, 2019) added further data from Taiwan and Japan for *Coronula bifida*, and Gale (2020) recorded *C. diadema* from the Plio-Pleistocene off the Rodrigues Ridge in the Indian Ocean. The new records are plotted in Text-fig. 13 (modified from fig. 3 of Bianucci *et al.* 2006) and indicate that the likely migration route for Pliocene humpbacks ran close to the palaeoshoreline in North Carolina. Additionally, we provide a new record of *Coronula diadema* from post-glacial deposits of Montreal, Canada (c. 12,000 year BP) based on specimens in the NHMUK.

The occurrences of *Verruca stroemia* are only the second and third records of this species from North America, and we recorded the species as common in the Rushmere Member at Fountain, Pitt County, North Carolina (Gale and Sadorf 2025). It appears that the Rushmere transgression, and the Mid Piacenzian Warm Period, coincided with significant migrations of cirripedes in the Atlantic Coastal Plain region.

Perhaps the most unexpected find in the Rushmere Member assemblage is *Membranobalanus*, which has only one other known fossil occurrence (Ross 1999). This genus, obligately associated with clionaid sponges, is known from a scatter of present-day occurrences, summarised by Hosie *et al.* (2019). The valves of this genus are small and fragile, and easily broken post-mortem, or overlooked in washed residues.

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