Bathyal Pliocene-Early Pleistocene cirripedes (Crustacea, Thoracica) from the Rodrigues Ridge, Mascarene Plateau, Indian Ocean. Part 1

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A large assemblage of thoracican cirripedes is described from the bathyal Upper Pliocene-Lower Pleistocene strata found adjacent to the Rodrigues Ridge, Mascarene Plateau (Indian Ocean), and a nearby site yielded a small number of living individuals. A total of 32 species is recorded, of which the following are new: *Catherinum busselli* sp. nov., *Costatolepas buckeridgei* gen. nov., sp. nov., *Neoeolasma rodriguesensis* gen. nov., sp. nov., *Altiverruca capsa* sp. nov., *A. fusione* sp. nov., *Gibbosaverruca youngi* sp. nov., *Cristallinaverruca ankylosa* sp. nov., *Newmaniverruca multitabulatum* sp. nov., *Costatoverruca baxteri* sp. nov. and *Rostratoverruca darwini* sp. nov. This fauna shows a high level of endemicity; six of the species recorded currently live in the southwest Pacific Ocean, in the region close to New Caledonia. The fauna provides evidence that significant extinction of benthonic cirripedes took place during the Pleistocene.

Key words: Cainozoic, present-day, Cirripedia, Indian Ocean, new taxa

Introduction

In 1987, a NERC (UK) funded expedition to the Indian Ocean, on board the RRS 'Charles Darwin', dredged the area around the Rodrigues Ridge, on the Mascarene Plateau, to the East and West of the Island of Rodrigues. Although the primary purpose of this research was to obtain igneous rock samples with which to date the ridge, a significant number of bathyal sediment samples was also recovered, using piston coring and pipe-dredges, and an Agassiz Trawl was used to obtain material of living deep-sea faunas. One pipe-dredge sample, RR9 (depth 1,800 m), consisted of carbonate sands containing basalt fragments and manganese-coated nodules. This yielded an abundant fauna of fossil gastropods, bivalves, corals, echinoderm ossicles, fish otoliths and cirripede plates. Another Agassiz Trawl (S2) yielded a few living cirripedes (Table 1). A total of over 1,000 barnacle valves, including some articulated specimens, was picked from the residues which are described in the present paper.

Extant deeper water cirripede faunas of the Indian Ocean have been described in an extensive series of papers. Gruvel (1907) described verrucids, while Nilsson-Cantell (1929, 1938) recorded verrucid material from off the Somalia coast and reviewed the overall cirripede faunas of the Indian Ocean, respectively. Stubbings (1936) described and illustrated material collected by the John Murray Expedition from the northwestern part of the Indian Ocean. Much later, Zevina (1978) described the Scalpellidae and some Verrucidae (Zevina, 1987), while Ren (1989) recorded cirripedes from Madagascar. Faunas collected from Réunion, relatively close to the site on Rodrigues (Fig. 1), were described by Foster & Buckeridge (1994). The faunas of the New Caledonia region in the South-West Pacific are relevant here, because it has been discovered that some of these were present in the fossil material from Rodrigues. These were monographed by Buckeridge (1994, 1997: verrucids) and Jones (2000: balanomorphs), while Jones (2007) provided a list of all species recorded.

Geological setting and material

The Rodrigues Ridge is an east-west trending volcanic structure which extends at 19° S from the Mascarene Plateau (59° 30'E) to 100 km east of Rodrigues Island (64° 30'E). It is neither parallel to seafloor spreading flowlines nor to the motion of Africa in the hotspot reference frame. ^{39}Ar-^{40}Ar dating of dredged samples has shown that the whole ridge formed between 8 and 10 million years ago, suggesting a rather rapid emplacement between the former position of the Réunion hotspot and the nearest segment of the Central Indian Ridge at 10-8 Ma (Mellor, 1998; Dyment *et al*., 2001).

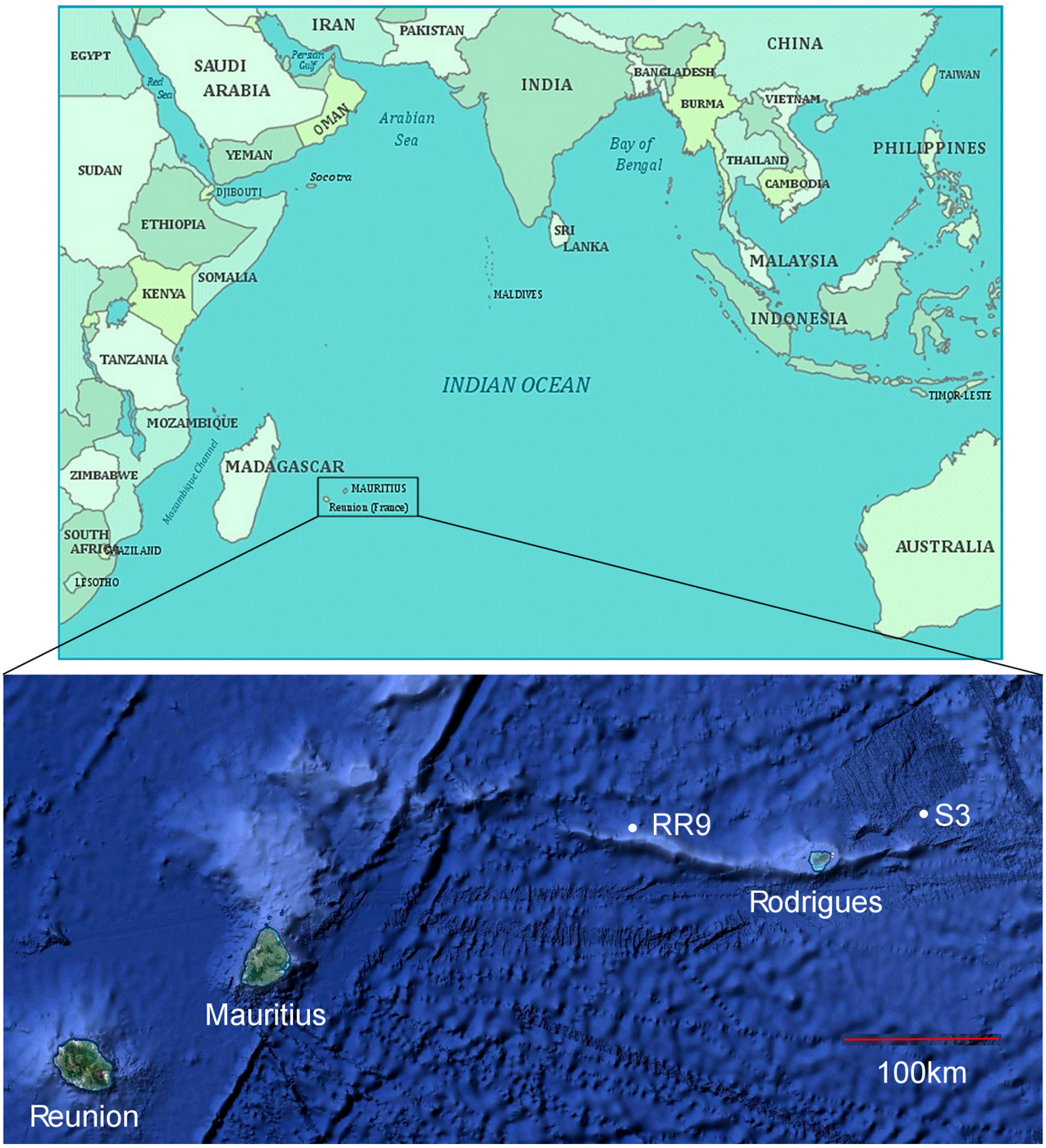


Figure 1. Map of the Indian Ocean to show the position of the Mascarene Islands (Réunion, Mauritius, Rodrigues), the Rodrigues Ridge and the sites of samples RR9 and S3.

Pipe-dredge sample RR9, situated approximately 5 kilometres north of the Rodrigues Ridge (Fig. 1) comprised carbonate sand, containing sparse fragments of manganese-coated limestone and basalt clasts, derived from the Rodrigues Ridge. The summit of the ridge close to this locality reaches 500 metres beneath sea level. RR9 yielded abundant fossil material, and dating is based on planktonic foraminifera, undertaken by Prof. Bridget Wade (University College [UCL], London). These indicated the presence of zones P3–P6 (2.3–4.3 Ma), and thus a Pliocene to Early Pleistocene age. Additional dating was provided by calcareous nannofossils (Prof. Paul Bown, UCL), which suggested a Pleistocene age younger than 1.99 Ma, but older than 0.44 Ma. The presence of teeth of the shark species *Otodus megalodon* (Agassiz, 1843) provides definite evidence of a Pliocene element (pre-3.7 Ma) in the fauna (D.J. Ward, pers. comm., Dec. 2019). Thus, the sample can be dated as Pliocene to early Pleistocene, although it is clear that material of mixed ages is present. The fauna in RR9 does not contain any

shallow-water elements, and probably largely represents an indigenous bathyal fauna.

Repository – All material from the Rodrigues Ridge is now contained in the collections of the Natural History Museum, London (abbreviation: NHMUK). Other repositories cited include:

AR University of Auckland, type collection, New Zealand
CPC Type collection Palaeontology Section, Bureau of Mineral Resources, Canberra, A.C.T., Australia
MNHN Muséum nationale d'Histoire naturelle, Paris, France
OU Collection of the University of Otago, New Zealand

Systematic palaeontology

Family Poecilasmatidae Annandale, 1909
Genus *Glyptelasma* Pilsbry, 1907

Type species – *Glyptelasma subcarinatum* Pilsbry, 1907, by original designation.

***Glyptelasma carinatum* (Hoek, 1883)**
Plate 1, figs 1-6

Material – 45 carinae, scuta and terga (NHMUK IC 1693-1698).

Discussion – This species is characterised by the presence of a short spur at the base of the scutum and by the highly distinctive carina. This was illustrated well by Hoek (1883, pl. 7, fig. 6) and Foster (1978, fig. 12d), showing basal flanges separated by a concavity (compare with Pl. 1, figs 3a, b). *Glyptelasma carinatum* is widely distributed in the deep oceans (Hoek, 1907; Foster, 1978)

Family Lepadidae Darwin, 1851
Genus *Lepas* Linnaeus, 1758

Type species – *Lepas anatifera* Linnaeus, 1758.

***Lepas pectinata* Spengler, 1793**
Plate 1, figs 7, 11

Material – A single scutum (NHMUK IC 1699).

Discussion – The distinctive sculpture on the scutum, comprising strong radial ribs, which form nodes where they intersect with growth increments are characteristic of this variable species, which is cosmopolitan in tropical to subtropical seas (Foster, 1978).

Family Scalpellidae Pilsbry, 1907

Diagnosis – Scalpellomorphs which possess a maximum of fourteen plates (carina, rostrum, paired scuta, terga, upper latera, carinolatera, rostrolatera and inferior median latera), rarely thirteen, by secondary loss of the rostrum.

Discussion – Scalpellids are not common in the Rodrigues material, and many forms are represented by small, single valves which are very difficult to assign to species. However, the fauna was clearly diverse.

Genus *Arcoscalpellum* Hoek, 1907

Type species – *Scalpellum michelottianum* Seguenza, 1876.

Diagnosis – Scalpellids in which a large upper latus surface is present on the carinolatus; umbo strongly incurved, carinal margin present; lateral surface of carinolatus inturned onto interior of plate, peduncular margin concave.

***Arcoscalpellum michelottianum* (Seguenza, 1876)**
Plate 3, figs 1-5.

Material – 15 large capitular plates (scuta, terga, carinae and a single upper latus).

Discussion – The material from Rodrigues Ridge compares well with figured examples of this species (e.g., Shalaeva & Boxshall, 2014, figs 15A-C); the scuta and terga are rather smooth, except for growth lines (Pl. 3, figs 1, 2a, 2b, 4) and the carina possesses a broad, slightly concave tectum and thin, striated parietes (Pl. 3, figs 3a, 3b).

***Arcoscalpellum* sp. 1**
Plate 3, figs 19a, 19b

Material – A single carina (NHMUK IC 1723).

Description – The carina has growth increments interrupted by regularly spaced constrictions; the tectum is flat and separated from the parietes by two broad ridges; intraparietes are deeply inset on the apical sides of the valve.

Discussion – The highly distinctive growth pattern of this species and presence of intraparietes distinguish it from *A. michelottianum* (see above).

***Arcoscalpellum* sp. 2**
Plate 3, fig. 8

Material – A single fragmentary carina (NHMUK IC 1710).

Discussion – This carina is comparable in shape to that of *A. michelottianum* (see above), but the tectum bears apicobasal striations which extend onto the tectum but weaken towards the mid-line.

Genus *Graviscalpellum* Foster, 1980

Type species – Scalpellum pedunculatum Hoek, 1883 by original designation.

***Graviscalpellum* cf. *pedunculatum* (Hoek, 1883)**
Plate 3, fig. 11

Material – A single scutum (NHMUK IC 1715).

Remarks – The scutum differs significantly from those of *A. michelottianum*, in that the upper latus and occludent margins are parallel, and the occludent margin is straight, rather than convex. In shape, this compares well with scuta of *G. pedunculatum* (see for example, Gale, 2015, fig. 2H), but, in the absence of other plates, this assignation must be tentative.

Genus *Amigdoscalpellum* Zevina, 1978

Diagnosis – Sculpture of strong, radially arranged, rounded, raised ridges on all plates except carina; carinolatera articulate across mid-line by means of zigzag, alternating ridges which diverge from umbones. Umbones of carinolatera central to subcentral, close to base of carina, not prominent. Inframedian latus narrow, triangular, more rarely elongate, rectangular; umbo apical, often not extending to top of carinolatus and rostrolatus. Rostrum small, less than half height of rostrolatus and narrow, rounded oval rhombic outline (after Gale, 2015).

Type species – Arcoscalpellum manum Zevina, 1973, by subsequent designation of Zevina (1978).

***Amigdoscalpellum mamillatum* (Aurivillius, 1898)**
Plate 2, figs 1-3; Plate 3, figs 9, 10; Plate 4, fig. 6

Material – A single scutum and tergum (NHMUK IC 1713, 1714).

Discussion – The delicately constructed valves, bearing finely striate sculpture on the tergal surface of the scutum and the scutal surface of the tergum, compare well with a specimen of this species figured by Young (2007, fig. 27) and with the living individual here figured in Plate 2, fig. 1; from sample S3. The species has a widespread distribution in the deep sea around the African continent (Young 2007, fig. 30), but, according to Young, is replaced by *A. truncatum* (Hoek, 1883) in the Indian and southwest Pacific oceans. *Amigdoscalpellum truncatum* is much more coarsely ribbed (see Shalaeva & Boxshall, 2014, fig. 18).

Genus *Catherinum* Zevina, 1978

Type species – Scalpellum recurvitergum Gruvel, 1900 (see redescription in Young, 1998).

Diagnosis – Inframedian latus waisted, hourglass shaped, umbo central to nearly basal**.** Well-defined margins contacting scutum and upper latus. Contact between carinolatera usually flat, symmetrical. Rostrum tiny, oval or, rarely, absent. Apex of scutum acuminate, incurved. Upper latus overlapping scutum, fitting into notch in scutum. Scutum trapezoidal, basal-occludent angle about 80°, tergal-upper latus angle 100-115°.

***Catherinum busselli* sp. nov.**
Plate 3, figs 14-18; Plate 4, fig. 5

Diagnosis – Catherinum with a sculpture of coarse apicobasal ridges, interrupted by regular growth increments.

Types – The scutum illustrated (Pl. 3, figs 14a, 14b) is the holotype (NHMNUK IC 1718); the other figured valves (carina, upper latus, tergum and carinolatus) are paratypes (NHMUK IC 1719-1722).

Etymology – Named after Dr Andy Bussell, one of the participants of the 1987 RRS 'Charles Darwin' cruise.

Material – 20 valves from sample RR9 (NHMUK collections).

Description – Scutum (Pl. 3, figs 14a, 14b) subrectangular, tall; apex rounded; occludent margin slightly convex; rostral and basitergal angles close to 90°. Internal surface bearing U-shaped notch for dwarf males. Tergum (Pl. 3, fig. 15) elongated, triangular, long carinal margin slightly sinuous, occludent margin shorter than scutal margin. Upper latus (Pl. 3, fig. 16) asymmetrically triangular. Carinolatus (Pl. 3, fig. 17) with tall, concave carinal margin, short upper latus margin. Carina (Pl. 3, fig. 18) with flat tectum, bordered by ridges; parietes striate; intraparietes short, apical. All valves share a distinctive sculpture of coarse apicobasal ridges interrupted by evenly spaced growth increments.

Discussion – This species differs from all congeners in its sculpture of short ridges that are interrupted by growth lines.

***Catherinum* sp. 1**
Plate 3, figs 12a, 12b

Material – A single carina (NHMUK IC 1716).

Discussion – This carina is similar in construction to that of *C. busselli* sp. nov. (see above), but differs in the smooth parietes and narrower tectum.

***Catherinum* sp. 2**
Plate 4, fig. 7

Material – A single carinolatus (NHMUK IC 1712).

Remarks – A single carinolatus has the shape typical of *Catherinum* (Gale, 2015) but has a very different sculpture to that of *C. busselli* sp. nov., with a thickened carinal margin, and weakly developed radial ribbing, strongest on the upper latus and inframedian latus margins.

Genus *Costatolepas* nov.

Type species – *Costatolepas buckeridgei* sp. nov.

Diagnosis – Scuta very robust, upright, triangular, bearing 4-5 coarse apicobasal ridges, separated by deep grooves; large tergal notch and concavity on tergal margin for articulation of tergum.

Etymology – Latin *costatus*, *-a*, meaning ribbed.

Remarks – The form of the available valves is so different from that of any described cirripede that it warrants separate generic status. They only resemble the Cretaceous Myolepadidae (Gale & Sørensen, 2015), which are also very robust, with scutal retractors but smooth valves. The assignation of *Costatolepas* gen. nov. to the Scalpellidae is provisional.

***Costatolepas buckeridgei* sp. nov.**
Plate 4, figs 1, 2, 4

Diagnosis – As for the genus.

Material – Three scuta (NHMUK IC 1724-1726).

Types – The valve here illustrated in Pl. 4, fig. 1 is the holotype (NHMUK IC 1724); the other two valves are paratypes (NHMUK IC 1725, 1726).

Etymology – For John S. Buckeridge, in honour of his work on fossil and living cirripedes.

Description – Scuta very robust, triangular; occludent margin straight to slightly convex, tergal margin straight. External surface bearing 4-5 coarse apicobasal ribs and intervening grooves with flat floors; conspicuous very fine growth lines present in grooves. On interior view, occludent margin formed by narrow, inflected slip of external valve surface; well-developed tergal notch present (Pl. 4, fig. 2b). A shallow groove along tergal margin articulated with tergum. Notches close to the apicobasal internal margin may have carried retractor muscle.

Scalpellid sp. 1
Plate 4, fig. 3

Material – A single carina (NHMUK IC 1727).

Remarks – This strongly incurved carina has a flat, broad tectum that is not separated from the parietes by ridges, as well as very narrow parietes and short intraparietes.

Scalpellid sp. 2
Plate 4, fig. 8

Material – A single carina (NHMUK IC 1731).

Remarks – This is a short, broad carina, externally convex, bearing strong apicobasal ridges. The parietes and tectum are not separate, but a short intraparietes is present close to the apex. This cannot be assigned to any described taxon.

Scalpellid sp. 3
Plate 3, figs 6, 7

Material – One scutum and one tergum (NHMUK IC 1711, 1712).

Description – Scutum subrectangular, convex occludent margin, broad apicobasal ridge, broad tergal surface. Tergum rhombic, with flat-topped apicobasal ridge and coarse, weak ridges on occludent margin.

Discussion – These two valves appear to belong to the same species, because both are rather robust, have weak, but coarse, radial ribbing, and a flat-topped apicobasal ridge.

Scalpellid sp. 4
Plate 3, fig. 13

Material – A single carina (NHMUK IC 1717).

Discussion – A short, apically tapering carina, with a V-shaped basal margin. Affinity unknown.

Order Balanomorpha Pilsbry, 1916

Discussion – In the present paper, I follow the nomenclature proposed by Gale & Sørensen (2014), who argued that the wall plates of balanomorphs were not homologous with lateral plates of scalpellomorphs, but evolved as *de novo* structures. Therefore, rostromarginal replaces rostrolateral, marginal replaces Cl1 and carinomarginal replaces Cl2.

Superfamily Chthamaloidea Darwin, 1854
Family Chionelasmatidae Buckeridge, 1983

Diagnosis – Shell six plated, with single rostrum, carina, paired carinomarginals (CM) and rostromarginals (RM), and several rows of imbricating plates at base; imbricating plates including two pairs of dedicated latera. Sheath formed by rostrum, carina and carinomarginals only, rostromarginals not entering sheath. Basis thin, calcareous.

***Chionelasmus darwini* (Pilsbry, 1907)**
Plate 6, figs 3, 5, 6

Material – A single tergum (NHMUK IC 1743) from the Pliocene-Lower Pleistocene of Rodrigues Ridge (sample RR9).

Discussion – Yamaguchi (1998) discussed the variation in *C. darwini* and erected two subspecies, namely *C. darwini darwini* (from Hawaii) and *C. darwini cantelli* Yamaguchi, 1998 (from the western Indian Ocean). These differ in the morphology of the scutum and tergum and the ontogeny of the imbricating plates. The basiscutal angle of the tergum is more angular in the Pacific form (Yamaguchi, 1998, fig. 2C, D); in its basiscutal development the specimen illustrated here (Pl. 6, fig. 3) is actually closer to the Pacific subspecies, and is closely similar to the tergum illustrated by Jones (2000, figs 2c, 2d; refigured here as Pl. 6, fig. 5) from the Norfolk Ridge, southwest Pacific. Without more material, further discussion is not possible.

Family Pachylasmatidae Utinomi, 1968

Diagnosis – Shell wall comprising eight distinct compartmental plates, including rostrum, paired rostromarginals, marginals and carinomarginals and carina. Shell with or without imbricating plates. Rostrum compound with RM but not entering sheath, solid parietes and radii absent. Base membranous, or solid and calcareous, not interdigitated with shell wall.

Subfamily Eolasminae Buckeridge, 1983

Diagnosis – Eight-plated pachylasmatids, in which the wall is formed of the carina C(1), RM (2), M(2), CM(2) and rostrum R(1). Rostromarginal large and triangular, not fused with rostrum.

Discussion – *Eolasma* Buckeridge, 1983 was originally based on 28 isolated plates from the upper Palaeocene and lower Eocene of South Island, New Zealand, described under the name of *E. maxwelli* Buckeridge, 1983. The material includes rostromarginals (Buckeridge, 1983, fig. 47c, reproduced here as Fig. 3/1-5) and the genus was therefore determined to be 8-plated. Subsequently, Buckeridge (1985) described another species, *E. rugosa*, from the lower Miocene of Victoria (Australia) on the basis of numerous isolated valves (his fig. 1, reproduced here as Fig. 3/6-12). Most recently, Buckeridge (*in* Buckeridge *et al*., 2014) erected a third species, *E. lepida*, from the upper Oligocene of Southland, New Zealand, also based on isolated valves (Fig. 3/13). Jones (2000) had earlier briefly discussed *Eolasma*, but was not convinced that all the valves of *E. maxwelli* came from the same taxon.
The discovery in the Rodrigues Ridge material of an eight-plated balanomorph that reveals certain similarities to *Eolasma* (represented by a living individual and fossil valves) is therefore interesting.

Genus *Neoeolasma* nov.

Diagnosis – Rostromarginal flat, triangular; scutum with convex occludent margin; tergum carrying broad, wing-like scutal auricle; alae large, triangular; delicate construction, external parietal sculpture of undulose growth lines with irregular, short, apicobasal folds and grooves; sheath very low, rostromarginal not entering sheath. Imbricating plates absent, basis membraneous.

Type species – *Neoeolasma rodriguesensis* sp. nov.

Etymology – After Rodrigues Ridge, Mascarene Plateau (Indian Ocean).

Discussion – The triangular rostromarginal plates, which internally bear articulation surfaces for both rostrum and marginal plates (Pl. 5, figs 1i, 1j) are similar in overall form to those of *Eolasma maxwelli* and *E. rugosa* (see Fig. 3/1, 9, 10). The scuta of *N. rodriguesensis* (Pl. 5, figs 1o, 1p) are also similar in outline to those of the three species of *Eolasma* known to date (compare Fig. 3/2, 6), but the occludent margin is convex in the new form, and the *Eolasma* material is insufficiently well preserved to see details of the scutal interior. The terga (Pl. 5, figs 1k, 1l) of the new genus and species, however, are quite different from those of *Eolasma*, or any described balanomorph, and possess a large, wing-like scutal auricle which forms a long, convex occludent margin. The overall plate construction is delicate, and the plates are rather thin. The external sculpture of the parietes, consisting of undulose growth lines interrupted by irregular, short, apicobasal folds and grooves, is also unique. The "indeterminate carina" figured by Young (1999, fig. 8) from the Atlantic, from the Vitoria-Trindade Seamounts off Brazil is very similar to the material of *Neoeloasma* figured here, and probably indicate that the genus exists (or existed) in the Atlantic Ocean.

***Neoeolasma rodriguesensis* sp. nov.**
Plate 5, figs 1, 2; Plate 6, figs 1, 2, 4

Diagnosis – As for the genus.

Types – The single living specimen, originally attached to a pebble, is the holotype (NHMUK IC 1738); it dried out and fell apart, but drawings of its original form had

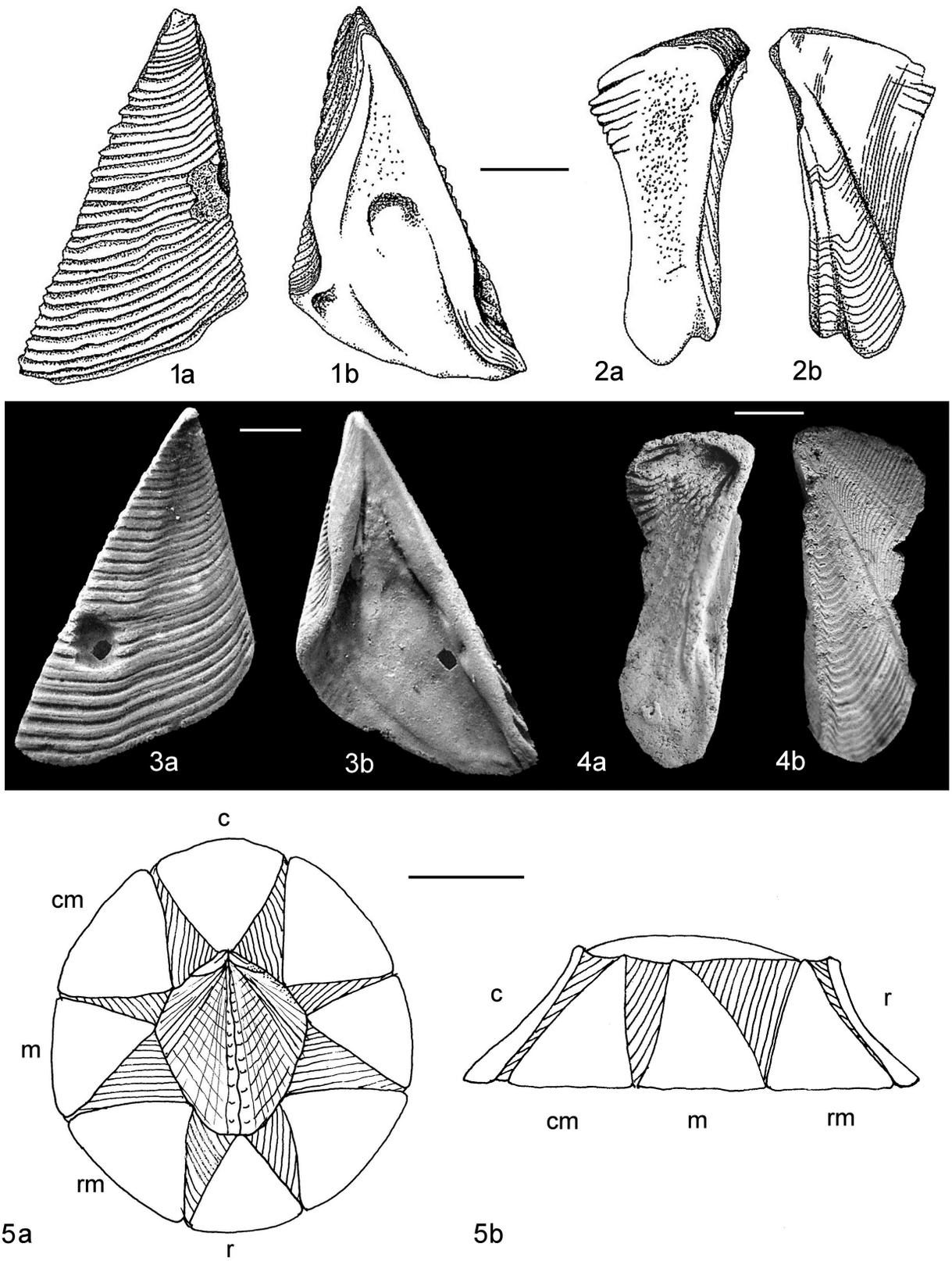
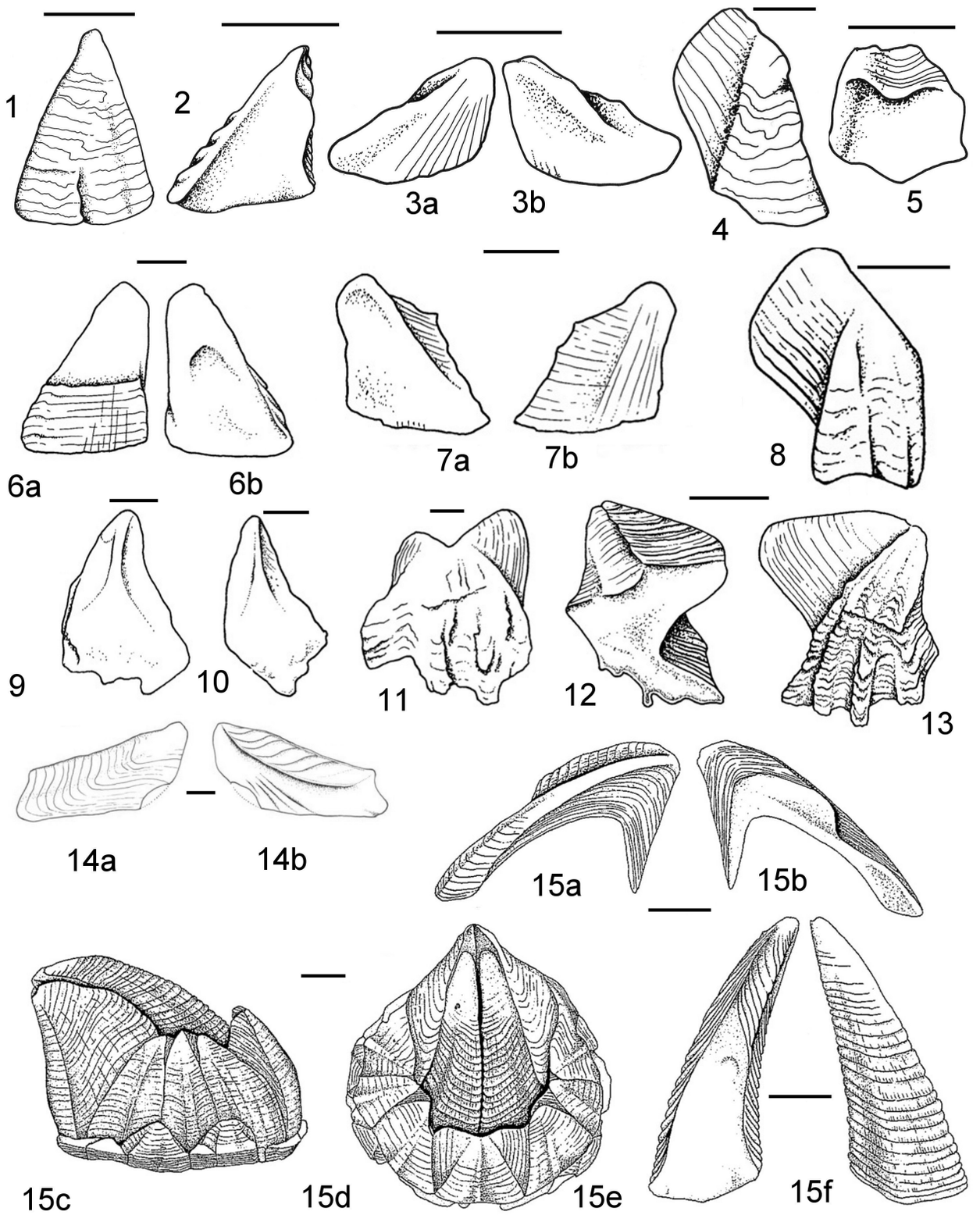


Figure 2. Opercular plates of *Hexelasma* (1-4) and reconstruction of *Neoeolasma rodriguesensis* gen. nov., sp. nov. (5a, b). 1a, 1b, 2a, 2b. Scutum and tergum of *Hexelasma foratum* Jones, 2000 (**paratype**, MNHN-Ci 2416), respectively; New Hebrides arc, present-day (from Jones, 2000, fig. 58). 3a, 3b, 4a, 4b. Scutum and tergum of *Hexelasma* aff. *foratum* respectively, NHMUK IC 1751, 1750), Pliocene-Lower Pleistocene, Rodrigues Ridge, sample RR9. 5a, b. Reconstruction of *Neoeolasma rodriguesensis* gen. nov., sp. nov., based on the holotype (NHMUK IC 1738); a, apical view, b, lateral view. Abbreviations: c, carina; cm, carinomarginal; m, marginal; rm, rostromarginal; r, rostrum. Scale bars equal 5 mm (5a, 5b), 1mm (1-4).

been made before (Fig. 2/5a, b). The soma is preserved for future study. The fossil valves illustrated here are paratypes (NHMUK IC 1739-1742).

Material – In addition to the holotype, the fossil specimens are paratypes, including carinae, a scutum, a marginal and a rostromarginal, all from Pliocene-Lower Pleistocene strata of Rodrigues Ridge (sample RR9).

Description – Capitulum oval in opercular view (Fig. 2/5a), low, truncated conical in lateral view (Fig. 2/5b). Orifice rhomboidal, approximately half of dorsal-ventral length. Carina (Pl. 5, figs 1a-c; Pl. 6, figs 1a-c) rectangular, bearing large, symmetrical, triangular alae; internally, sheath forms crescentic apical region. Carinomarginal (Pl. 5, figs 1m, 1n) rhomboidal, parietal wall triangular, single ventral ala; narrow sheath present along apical margin. Marginal



(Pl. 5, figs 1g, 1h) subrectangular, ala tall, triangular; sheath forms narrow triangular wing on inside of ala. Rostromarginal (Pl. 5, figs 1i, 1j) equilaterally triangular, external surface flat, interior bears articular surfaces for adjacent plates. Rostrum (Pl. 5, figs 1d-f) trapezoidal, alae large, symmetrical, sheath forms narrow internal apical rim. External sculpture of parietes comprising undulose growth lines interrupted by irregular, short, apicobasal folds and grooves; surface resembles crushed silk fabric. Alae bear evenly spaced, terraced growth increments, parallel with inferior margin, and weak radial ridges. Scuta (Pl. 5, figs 1o, 1p; Pl. 6, fig. 2a, 2b) triangular, basal margin straight, occludent margin gently convex. Tergal margin straight, short; articular ridge narrow, sharp, articular furrow narrow, deep. Tergal notch broad, triangular; marked scar for insertion of lateral scutal depressor. Exterior of scutum with slightly depressed area adjacent to tergal margin; surface with evenly spaced growth increments and fine apicobasal, radial ribs. Tergum (Pl. 5, figs 1k, 1l) subrectangular, bearing large scutal auricle and ridged apicobasal elevation; carinal surface flat. Sculpture of evenly spaced growth increments, locally forming raised ridges, and weak apicobasal ribbing. Interior with ridges for tergal depressor.

Discussion – The sculpture, form of the alae and shape of the tergum and scutum are all unique to this species. A rostrum (Pl. 4, fig. 9) appears to represent another species of this genus, differing in the coarser transverse sculpture, the lower sheath and move deeply concave interior.

Superfamily Tetraclitoidea Gruvel, 1907

Discussion – Chan *et al*. (2017) is followed in placing the family Bathylasmatidae in the Tetraclitoidea.

Family Bathylesmatidae Newman & Ross, 1971
Genus *Hexelasma* Hoek, 1913

***Hexelasma* aff. *foratum* Jones, 2000**
Fig. 2/3, 4; Plate 4, figs 10, 11, 14; Plate 7, figs 2-7

Material – Two scuta, three terga, one carina, two carinomarginals, two marginals and a single rostral plate (NHMUK collections).

Discussion – So far as I am aware, this is the only *Hexelasma* material known from the Indian Ocean. A fairly diverse assemblage (six species) is known from the western Pacific, and a single species from off Florida (Jones, 2000, fig. 51). The present material is comparable with *H. foratum*, from the New Hebrides Arc (Fig. 2/1, 2), but differs in the detailed morphology of the tergum in particular. In *H. foratum*, the tergal spur is bifid, whereas it is evenly rounded in the Rodrigues material. The scuta are similar, but the articular ridge is more apically positioned on the tergal margin than in *H. foratum* (Fig. 2/1, 2). The parietal plates (Pl. 7, figs 2-5) bear a very distinct sculpture (enlarged in Pl. 7, fig. 4c) comprising beaded ridges along the apical parts of the growth increments. The beads are probably associated with the "cuticular hairs" which Foster (1981, p. 356) stated to be typically developed in the genus.

Indeterminate balanomorph
Plate 6, fig. 7; Plate 7, fig. 1

Remarks – A single marginal wall plate bears a broad, triangular ala, but lacks the sculpture of *Hexelasma* (Pl. 7, fig. 1). A concavo-convex wall plate, bearing strong transverse ribbing is also present (Pl. 6, fig. 7).

Order Verrucomorpha Pilsbry, 1916
Family Verrucidae Darwin, 1854

Diagnosis – Verrucomorphs in which the carina and rostrum articulate and which lack peduncular plates.

Discussion – Extant verrucids were reclassified by Young (1998, 2002), who established a new generic classification based largely upon the angle of the opercular lid to the base and the presence/absence of secondary ridges on the rostrum and carina. Gale (2014) used the SEM to illustrate diverse fossil and living verrucids, and noted the significance of the morphology of the fixed scutum, the form of the scutal adductor scar and the articulation be-

Figure 3. Morphology of *Eolasma* spp. and *Waikalasma boucheti* Buckeridge, 1996. 1-5. *Eolasma maxwelli* Buckeridge, 1983 (from Buckeridge, 1983, fig. 47); 1. rostromarginal (original of Buckeridge, 1983, fig. 47c; AR872); 2. scutum (original of Buckeridge, 1983, fig. 47h; AR854); 3a, b. tergum (original of Buckeridge, 1983, fig. 47i, j; AR866); 4. marginal (original of Buckeridge, 1983, fig. 47b; AR877). 5, carina or rostrum (original of Buckeridge, 1983, fig. 47d; AR875). 6-12, *Eolasma rugosa* Buckeridge, 1985 (from Buckeridge, 1985, figs 2, 3): 6a, b. scutum (original of Buckeridge, 1985, fig. 1i, j; CPC 20221); 7a, b. tergum (original of Buckeridge, 1985, fig. 1g, h; CPC 20222); 8. marginal (original of Buckeridge, 1985, fig. 2f; CPC 20220); 9, 10. rostromarginals (originals of Buckeridge, 1985, fig. 1d, k; CPC 20219, CPC 20218); 11. carina (original of Buckeridge, 1985, fig. 1f; CPC 22590); 12a, b, marginal (**holotype**, original of Buckeridge, 1985, fig. 1a, b; CPC 20217); 13a, b. *Eolasma lepida* Buckeridge, *in* Buckeridge, Lee & Robinson, 2014, tergum (original of Buckeridge, *in* Buckeridge *et al*., 2014, fig. 6A, B; OU45266); 14a-f, *Waikalasma boucheti* Buckeridge, 1996 (**holotype**, original of Buckeridge, 1996, fig. 1; MNHN-Ci 2428): a, b. tergum; c, d. capitulum; e, f. scutum. Provenance: 1-5. uppermost Paleocene or Lower Eocene, South and Chatham Islands, New Zealand (all scale bars equal 2 mm). 6-12, Lower Miocene, Victoria, Australia (all scale bars equal 2 mm). 13, Oligocene, Southland, New Zealand (scale bar equals 1 mm). 14, Vanuatu, New Hebrides, present-day (all scale bars equal 5 mm).

tween fixed scutum and fixed tergum. However, he made significant errors in following the museum label identifications of some species, and his *Globosaverruca* is a *lapsus* for *Gibbosaverruca* Young, 2002. These errors are corrected under each genus. Subsequently, considerable time was spent examining the verrucid collections in the MNHN (Paris), the Smithsonian (USNM) and the Natural History Museum, London (NHMUK). These studies have permitted provisional identification of the abundant and diverse Rodrigues Ridge material. However, the fixed scutum has been used as a standard for identification and description. The hundreds of moveable scuta and terga cannot readily be assigned to taxa.

Extant verrucids fall into three more or less well-defined groups:

1. Genera and species in which the occludent margin and opercular lid are angled to the basal margin; these include *Altiverruca* Pilsbry, 1916, *Cristallinaverruca* Young, 2002, *Gibbosaverruca* and *Newmaniverruca* Young, 1998. In these, the scutal adductor scar on the fixed scutum consists of a variably well-defined depression, without a basal ridge.
2. Genera and species in which the opercular lid is parallel to sub-parallel to the basal margin, in which there is a ridge basal to the adductor on the fixed scutum; these include *Costatoverruca* Young, 1998 and *Rostratoverruca* Broch, 1922.
3. Genera and species in which the opercular lid is parallel to the basal margin, in which a curtain-like myophore on the fixed scutum extends from the tergal articular structure adjacent to the umbo, across towards the rostral margin; these include *Metaverruca* Pilsbry, 1916, *Priscoverruca* Gale, 2014and *Verruca* Schumacher, 1817.

Phylogeny and morphology of verrucids

There is a morphological progression in verrucids, extending from the most basal living forms (*Altiverruca*), through *Gibbosaverruca* and *Newmaniverruca*, to *Rostratoverruca* and *Costatoverruca*, and thence to the derived *Metaverruca* and *Verruca* (Gale, 2014). The succession can be observed in a number of morphological features:

- The angle of the occludent margin to the base decreases from nearly 90° in *Altiverruca* (Pl. 12, fig. 3) to 40-50° in *Gibbosaverruca* (Pl. 17, fig. 1) and in all more derived genera, in which the opercular lid is parallel or subparallel to the base (e.g., Pl. 17, figs 3, 4; Pl. 10, figs 2, 3, 5, 6; compare Young, 1998).
- Concomitantly, the insertion site of the scutal adductor on the fixed tergum moves from an apical position in *Altiverruca* (Pl. 8, fig. 7) towards the base, through *Newmaniverruca* (Pl. 8, fig. 4; Pl. 11, fig. 1) and the size increases, with development of a basal scutal adductor ridge in *Costatoverruca* and *Rostratoverruca* (Pl. 11, figs 2-5); in *Metaverruca* and *Verruca*, a sheet-like myophore extends horizontally across part of the valve (Pl. 8, fig. 5).
- The nature of the fixed scutum/tergum articulation becomes more complex; plesiomorphically, this comprises a shallow, concave tergal notch on the fixed scutum, with a corresponding convex scutal auricle on the tergum (Pl. 8, figs 6, 7; *Altiverruca*, *Gibbosaverruca*). In *Newmaniverruca*, *Rostratoverruca* and *Costatoverruca* the tergal notch narrows and deepens, and articular ridges develop both distally and proximally (Pl. 8, figs 1, 3, 4); correspondingly, the scutal auricle on the fixed tergum extends laterally as a process and bears a narrow ridge which fits into the depression on the scutum and serves for articulation of proximal and distal ridges (Pl. 8, fig. 1b).
- The articulation between the rostrum and carina changes from a straight to undulose, simple contact in *Altiverruca* (e.g., Pl. 12, fig. 3) and develops deeply interpenetrant ridges in more derived taxa (e.g., Pl. 12, figs 2, 5; Pl. 10, figs 1a, 2a, 3a, 4a, 5a, 6a).
- In *Altiverruca*, *Gibbosaverruca* and *Newmaniverruca*, the upper margins of the rostrum and carina are straight and overlie the moveable scutum and tergum (e.g., Pl. 10, fig. 1a; Pl. 13, fig. 3a). In *Costatoverruca* and *Rostratoverruca*, secondary ridges on the upper margins of the rostrum and carina interpenetrate corresponding grooves on the moveable plates (e.g., Pl. 10, figs 2a, 3a, 6a).

Genus *Altiverruca* Pilsbry, 1916

Type species – Verruca hoeki Pilsbry, 1907, by original designation.

Diagnosis – Shell small and erect, wall plates delicate. Rostrum/carina suture straight or undulose. Opercular plates erect, at right angle to base, subparallel to fixed scuta and terga. Scutal adductor scar on fixed scutum apical, shallow. Articulation between fixed tergum and scutum simple (emended from Young, 2002). An extant species, *Altiverruca obliqua* (Hoek, 1883) is illustrated to show the form of the genus (Pl. 12, fig. 3).

Discussion – Altiverruca includes small, usually smooth verrucids in which the opercular lid and occludent margin are set approximately at 90° to the basal margin, illustrated here (Pl. 12, fig. 3) by *A. obliqua* (Hoek, 1883). Interpenetration between the carina and rostrum is poorly developed, and the scutal adductor on the fixed scutum occupies an apical position (Pl. 12, fig. 3e). The articulation between the fixed tergum and fixed scutum is simple; the scutal ridge on the tergum fits into a concave tergal notch on the scutum. This specimen was incorrectly identified by Gale (2014b) as '*Globosoverruca* [*sic*] *nitida*'.

***Altiverruca capsa* sp. nov.**

Plate 13, figs 1-8, 11, 12

Diagnosis – Small verrucid with a shiny external surface; scutum low, triangular to subrectangular, with large occludent wing. Basal margin of fixed scutum inflexed.

Type – The fixed scutum illustrated here (Pl. 13, fig. 1) is the holotype (NHMUK IC 1756); the other illustrated valves are paratypes (NHMUK IC 1757-1765).

Material – Several hundred valves from sample RR9.

Etymology – Latin *capsa*, meaning box-like, in allusion to the form of the fixed scutum.

Description – Valves small, maximum dimension of 2 mm; surface shiny, smooth, bearing regularly spaced growth increments. Fixed scuta (Pl. 13, figs 1, 2, 4, 7, 11) triangular to subrectangular, occludent margin straight, occludent surface broad, triangular. Base of valve inflexed; scutal adductor apical in position, set on ridge. Fixed tergum (Pl. 13, fig. 3) narrow, occludent wing broad, occludent margin convex, scutal auricle moderately large. Rostra (Pl. 13, figs 6, 8, 12) rectangular to rhombic, single concave ridge running from apex to upper rostral margin, immediately above concavity for carinal process. Carina (Pl. 13, fig. 5) rectangular, broadly rounded ridge extends into concavity in margin of rostrum.

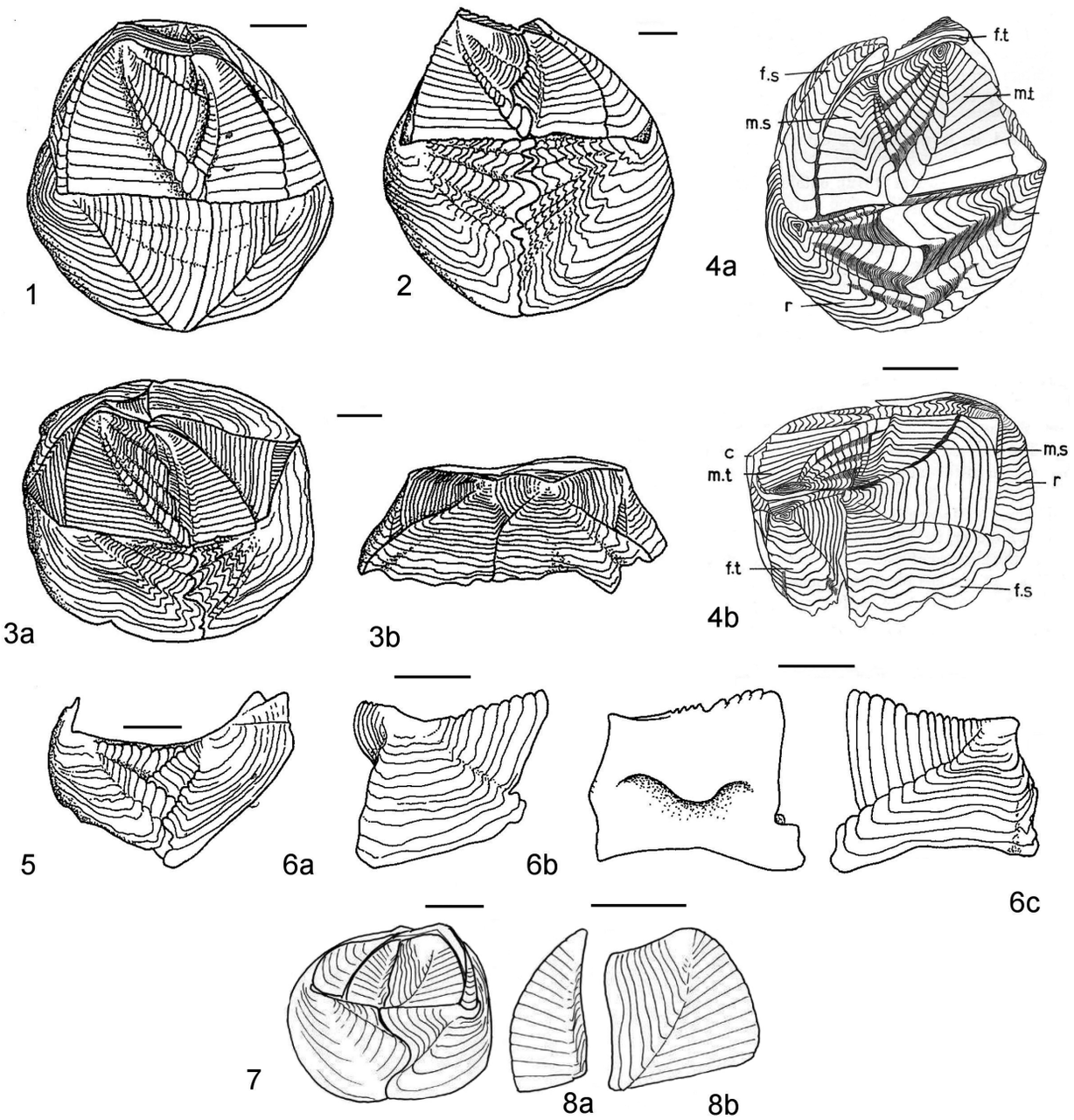


Figure 4. Present-day species of *Metaverruca*. 1, 2. *Metaverruca recta* (Aurivillius, 1898) (from Buckeridge, 1994, fig. 13a, b); 3. *Metaverruca defayae* Buckeridge, 1994 (from Buckeridge, 1994, fig. 9a, b); 4. *Metaverruca macani* (Stubbings, 1936) (from Stubbings, 1936, text-fig. 17); 5, 6a-c. *Metaverruca norfolkensis* Buckeridge, 1994 (from Buckeridge, 1994, fig. 10a, f-h); 7, 8. *Metaverruca reunioni* Foster & Buckeridge (from Foster & Buckeridge, 1994, fig. 12a-c). Provenance: 1-3, 5, 6. New Caledonia, southwestern Pacific; 4. near Zanzibar, Indian Ocean; 7, 8. near Réunion, Indian Ocean. Scale bars; Figs 2, 3, 4, 2 mm; Figs 1, 5-8, 1 mm.

Discussion – A small species (maximum dimension <3 mm), distinguished by the low, almost square fixed scutum, shiny external surface and inflexed basal margin of the fixed scutum. The species is assigned to *Altiverruca* on account of the steep occludent margin, the high scutal adductor scar on the fixed scutum, the nature of the fixed tergum/scutum articulation and the weakly interpenetrant contact between the carina and rostrum. It bears some comparison with *Verruca sinuosa* Foster & Buckeridge, 1994, in the shape of the rostrum, but the fixed tergum of that species is very large and broad and the occludent margin of the fixed scutum is convex. *Verruca sinuosa* was referred to *Costatoverruca* by Young (1998).

***Altiverruca fusione* sp. nov.**
Plate 13, fig. 10

Diagnosis – Tiny *Altiverruca*, in which the plates are fused and convex, and the contact between the rostrum and carina is straight.

Type – The specimen figured here (Pl. 13, fig. 10) is the holotype (NHMUK IC 1767).

Material – Three shells (NHMUK collections).

Etymology – Latin *fusione*, meaning fused, in reference to the fused plates of the shell.

Description – Shell small, maximum dimension (rostrum to apex of fixed tergum) 3 mm, plates fused. Growth lines undulating, irregular. Rostrum and carina convex, rectangular, umbones marginal, contact between the two plates straight. Fixed scutum convex, occludent wing convex. Fixed tergum rectangular, central ridge convex. Single ridge on scutum near base of tergal contact.

Discussion – Fusion of wall plates is a feature of full maturity, because further growth is impossible; the species is very small (maximum dimension 3 mm). This is not a typical *Altiverruca*, because the opercular lid is angled to the base at about 50°. However, the straight contact between the rostrum and carina and the absence of any ridges on these valves are characteristic features of this genus; this is the only species of the genus in which the wall plates are fused.

***Altiverruca* cf. *galapagosa* (Zevina, 1973)**
Plate 1, fig. 9

Material – A single fixed tergum (NHMUK IC 1701).

Discussion – The tergum agrees with the figured material of Zevina (1987, fig. 1) and Buckeridge (1994, fig. 3b) in its tall form, the presence of downward V-ing growth lines on the central ridge, and the large scutal auricle. The species is otherwise known from the Pacific (Young, 2002).

***Altiverruca* sp. 1**
Plate 1, figs 13, 14

Material – Two carinae (NHMUK IC 1703, 1704).

Discussion – These carinae are triangular and convex, and the apices are incurved. The margin with the rostrum is straight and vertical; there are no intersecting ridges. This is the only species of the genus in which there is no interpenetration between the margins of the rostrum and carina, and it is certainly new. The material currently available is insufficient to erect a new species for it.

Genus *Gibbosaverruca* Young, 2002

Diagnosis – Large, robust verrucids, in which rostrum and carina articulate by interpenetrant ridges, of which the uppermost on the rostrum is the largest. The opercular lid is inclined to the base at an angle <45° (emended from Young, 2002).

Type species – *Verrucagibbosa* Hoek, 1883

Discussion – *Gibbosaverruca* includes large, mostly sculptured, verrucids in which the occludent margin is significantly angled to the base, and in which the fixed scutal adductor scar is shallow and apical in position, and the articulation between fixed tergum and scutum is simple. The modern southwestern Pacific species *G. nitida* (Pl. 17, fig. 1) is common in the Rodrigues sample.

***Gibbosaverruca nitida* (Hoek, 1883)**
Plate 15, figs 1-11, 15, 16; Plate 17, fig. 1

Material – Several hundred valves (NHMUK collections).

Discussion – The material bears a close resemblance with *G. nitida* from the South-West Pacific in the MNHN (Paris) collections (Pl. 17, fig.1; compare with Rodrigues material in Pl. 15), particularly in the surface sculpture, which consists of loosely imbricating, undulose growth increments, and the form of the fixed terga and scuta. The broad occludent wing and subequal scutal auricle on the fixed tergum are closely similar in fossil and present-day material.

***Gibbosaverruca youngi* sp. nov.**
Plate 16, fig. 9

Diagnosis – Species of *Gibbosaverruca* in which the triangular fixed scutum carries a weakly defined narrow occludent wing; the convex occludent margin is set at 80° to the basal margin. Rostral margin short; sculpture comprises regularly spaced, flanged growth increments which bear short, flap-like nodes.

Type – The holotype, and sole specimen known to date, is a fixed scutum (NHMUK IC 1805).

Etymology – After the late Paulo Young, a verrucid expert *par excellence*.

Description – Fixed scutum triangular, slightly taller than broad, robust. Occludent margin long, gently convex, rostral margin very short, subparallel with basal margin. Occludent wing narrow, poorly differentiated from rest of valve. Tergal margin divided into lower, weakly concave part, and upper, concave region, which forms a short wing. Exterior of valve with regularly spaced, imbricate flanges which form short pustules on the tergal surface. Interior of valve with small, deep tergal notch, and large, oval scutal adductor scar, high on valve.

Discussion – The robust, large size of the valve, its complex sculpture and simple tergal articulation allow it to be placed in *Gibbosaverruca*. It differs from *G. nitida* and other species of the genus in the complex sculpture, the long occludent margin and the very short rostral margin.

***Gibbosaverruca* sp. 1**
Plate 15, fig. 12

Material – A single fixed tergum (NHMUK IC 1795).

Discussion – This tergum is very unusual in that the strongly convex occludent margin is joined to the basal margin by a flat occludent surface which possesses a convex carinal margin. In almost all other verrucids, the carinal margin extends approximately one half to two-thirds down the central ridge (compare with *G. nitida* in Pl. 15, fig. 3).

***Gibbosaverruca* sp. 2**
Plate 15, figs 13, 14; Plate 16, fig. 10.

Material – A fixed scutum (NHMUK IC 1795) and fixed tergum (NHMUK IC 1796).

Discussion – This species has a broad occludent wing, extending to the basal margin; the carinal margin is slightly concave and the growth increments on the wing are sinuous to concave. The scutal auricle is short, and the growth increments are acutely angled to the central ridge. The fixed scutum (Pl. 15, fig. 13) is low, equilaterally triangular, and has strongly marked growth increments.

Genus *Cristallinaverruca* Young, 2002

Type species – *Verruca cristallina* Gruvel, 1907, by original designation.

Diagnosis – Moderately sized verrucids, in which occludent margin is oblique to the base (>45°); the rostrum and carina articulate by means of numerous interpenetrating ridges of equal size.

Discussion – *Cristallinaverruca* is distinguished particularly by the numerous interlocking ridges and grooves, of nearly equal size, which form the suture between the rostrum and carina. The opercular lid and occludent margin are angled to the basal margin. The late Paulo Young was reluctant to include sculptured forms within the genus, but *C. jonesae*, which is strongly sculptured, fits here, as does an undescribed species from the South-West Pacific (Pl. 12, fig. 5). It is also noteworthy that a number of species has partly calcified bases, including *C. cristallina* (type material in NHMUK collections, London). Additionally, the type material shows the development of secondary ridges on the rostrum, not mentioned by Young (2002). An undescribed species of *Cristallinaverruca* from New Caledonia is illustrated (Pl. 12, fig. 5) to show the typical form of the genus.

***Cristallinaverruca jonesae* (Buckeridge, 1997)**
Plate 9, figs 1-7

*1997 *Altiverruca jonesae* - Buckeridge, p. 133, fig. 2.
2002 *Cristallinaverruca*? *jonesae* (Buckeridge) - Young, p. 32.

Material – 15 plates, including fixed scuta, terga, carinae and moveable terga.

Remarks – *Cristallinaverruca jonesae* was described on the basis of a single specimen from Vanuatu, South-West Pacific (Pl. 9, fig. 7), and is distinguished by the highly ornate shell surface, including apicobasal columns of spines and flanges, the long carina and the long, narrow, flanged median ridge on the fixed tergum. The material from Rodrigues is very similar, in the highly ornate valve surfaces with rows of short spines and flanges.

***Cristallinaverruca ankylosa* sp. nov.**
Plate 13, fig. 9; Plate 17, fig. 2

Diagnosis – A small *Cristallinaverruca*, in which the capitulum is low and valves of the wall are fused; the rostrum and carina are united by two interpenetrant ridges and corresponding grooves; there are a few secondary ridges on the rostrum.

Types – The specimen figured in Pl. 13, fig. 9a, b is the holotype (NHMUK IC 1766), from the Upper Pliocene-Lower Pleistocene (sample RR9) of Rodrigues Ridge, Indian Ocean. The paratype (Pl. 17, fig. 2), present-day, is from New Caledonia (MNHN 2016 10457).

Material – Two specimens (see above).

Etymology – Latin *ankylosa*, for fused, in reference to the fused wall plates.

Description – Small, maximum diameter 2-4 mm, along the fixed tergum-rostrum axis. Wall plates fused; rostrum and carina bearing two interpenetrate ridges, rostrum with two, short, secondary ridges on upper part. Fixed tergum tall, broad basal margin; fixed scutum triangular, convex; contact of fixed tergum and scutum with single interpenetrant ridge. Rostral margin of fixed scutum convex, occludent margin long, convex. Surface sculpture comprises irregular, undulating growth increments.

Discussion – The fused form of the shell indicates maturity (see above). The species is referred to *Cristallinaverruca* on the basis of an overall similarity of the specimens to the type series of *C. cristallina* (NHMUK collections, London), including the small secondary ridges on the rostrum. It differs in the smaller number of interpenetrant ridges on the rostrum and carina.

Genus *Newmaniverruca* Young, 1998

Type species – Verruca albatrossiana Pilsbry, 1912, by original designation.

Diagnosis – Form box like, opercular lid nearly parallel with base; umbones of rostrum and carina marginal, without secondary ridges.

Discussion – In many ways, *Newmaniverruca* (Fig. 6/1; Pl. 10, figs 1, 4) is morphologically intermediate between species of *Gibbosaverruca* (lack of secondary ridges on the rostrum and carina, occludent margin angled to the base, lack of myophore) and the more derived genera *Rostratoverruca* and *Costatoverruca*, in which the occludent margin is parallel with the base, but in which there are secondary ridges on the carina and rostrum (Pl. 10, figs 2, 3, 5). However, *Newmaniverruca* (Pl. 11, fig. 1) has a more complex fixed scutum/tergum articulation than *Gibbosaverruca* in the presence of proximal and distal articular ridges on either side of a deep tergal notch. The shallow, apically positioned scutal adductor scar on the fixed scutum is more like that of *Gibbosaverruca* and *Altiverruca* (e.g., Pl. 8, fig. 6). *Newmaniverruca albatrossiana* is illustrated here to show the form of the genus (Pl. 10, fig 1; Pl. 11, fig. 1).

***Newmaniverruca multitabulatus* sp. nov.**
Plate 16, figs 1-8

Diagnosis – Species of *Newmaniverruca* in which the sculpture of the robust valves comprises evenly spaced, irregularly flanged, imbricating growth increments; rostrum and carina united by four interpenetrant ridges and grooves.

Type – The fixed scutum figured (Pl. 16, fig. 2) is the holotype (NHMUK IC 1798); the other figured valves are paratypes (NHMUK IC 1797, 1799-1804).

Etymology – Latin *multi-*, meaning many; *tabulatum*, *-a*, meaning layers, in allusion to the sculpture of the valves.

Material – Fifteen valves, including fixed terga and scuta, rostra and carinae (NHMUK collections).

Description – Fixed scutum (Pl. 16, fig. 2) triangular, concavo-convex, length exceeding height, inclined towards tergum, occludent wing well differentiated, set beneath rest of surface; occludent margin straight; apex narrow, pointed. Interior shows deep, narrow tergal notch and weakly defined scutal adductor scar. Fixed tergum (Pl. 16, fig. 3) triangular, basal margin long, concave; occludent wing slightly convex, scutal auricle large. Rostrum (Pl. 16, figs 5, 7) oval, carinal surface well differentiated, bearing four ridges and three intervening grooves; scutal surface gently convex. Carinae (Pl. 16, figs 1, 4, 6) triangular to subrectangular, apex blunt, variably differentiated 3-4 apicobasal ridges on rostral side of valve. Surface sculpture comprises strongly imbricated, undulating growth increments, relatively consistent in width on fixed scutum and tergum, highly irregular and flanged on rostrum and carina.

Discussion – This species is referred to *Newmaniverruca* with some uncertainty. The closest species is the modern *Altiverruca sala* Young, 2002, from the North-East Pacific, which has a very similar sculpture, but in which the ridges on the rostrum and carina are poorly developed, and in which the fixed scutum is proportionately tall. The fixed tergum is similar in shape, but possesses a larger scutal auricle. I fail to see why Young (2002, fig. 8c) referred *A. sala* to *Altiverruca*, because the angle between the occludent margin and base is low.

Genus *Costatoverruca* Young, 1998

Type species – Verruca alba Pilsbry, 1907, subsequent designation of Young (1998)

Diagnosis – Robust, box-shaped verrucids, in which the fixed scutum is rectangular to trapezoidal in outline; variably developed secondary ridges on rostrum and carina.

Remarks – In his description, Young (1998, p. 79) cited the presence of secondary ridges on the rostrum as being the most characteristic feature of the genus. However, his illustration of the genus (Young, 1998, fig. 25b) does not indicate any significant differences between *Rostratoverruca* (his fig. 25c) and *Costatoverruca*, as both are shown as having secondary ridges on the rostrum. In the present study, it was found that a number of other genera and species also have secondary ridges on the rostrum, including the type material of *Cristallinaverruca cristallina* and *Rostratoverruca nexa* (see Pilsbry, 1916, pl. 3, fig. 1 and Darwin, 1854, pl. 21, fig. 1b, re-

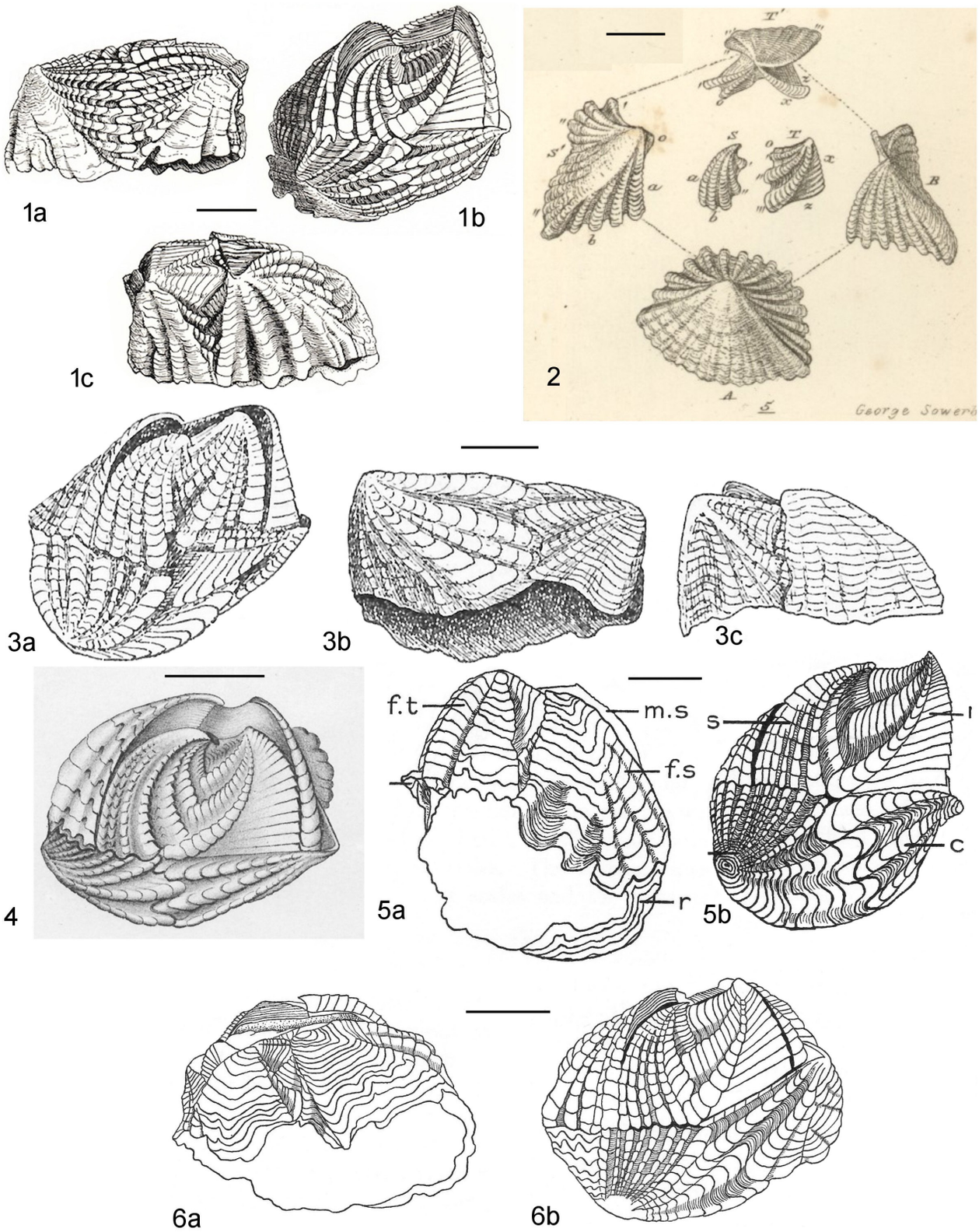


Figure 5. Present-day species of *Rostratoverruca*. 1a-c, 2. *Rostratoverruca nexa* (Darwin, 1854): 1a-c from Pilsbry (1916, pl. 3, fig. 1); 2 from Darwin (1854, pl. 21, fig. 1b); 3a-c. *Rostratoverruca krugeri* Broch, 1922 (from Broch, 1922, fig. 43a-c); 4. *Rostratoverruca koehleri* (Gruvel, 1907) (from Gruvel, 1907, pl. 1, fig. 7); 5a, b. *Rostratoverruca murrayi* Stubbings, 1936 (from Stubbings, 1936, text-fig. 14A, B); 6a, b.*Rostratoverruca sewelli* Stubbings, 1936 (from Stubbings, 1936, text-fig. 15A, B). Provenance: 1, 2. Caribbean; 4. Andaman Islands, Indian Ocean; 3. Tucuran, Indonesia; 5, 6. Zanzibar, western Indian Ocean. Scale bars 1 mm.

produced here as Figs 5/1a-c and 2), so this character cannot be used to define *Costatoverruca*. SEM imaging of isolated valves of various verrucids, particularly the fixed scutum (Gale, 2014) provides a number of characters which permit discrimination of *Costatoverruca*. These include:

- The shape of the fixed scutum, which is rectangular to slightly trapezoidal (Pl. 10, figs 5, 6; Pl. 11, figs 4, 5)
- The occludent margin is straight and long (Pl. 11, figs 4, 5)
- The boundary between the occludent wing and the body of the plate runs transversely across the plate, from the umbo to the lower rostral margin
- There is a process at the base of the carinal margin of the fixed scutum
- A myophore is not found, but a scutal adductor ridge is present

These features appear to be present in many of the species referred to the genus by Young (1998), including *C. alba* (Pilsbry, 1907) (Pl. 8, fig. 1; Pl. 10, fig. 5; Pl. 11, fig. 4), *C. pacifica* (Buckeridge, 1994) (Pl. 8, fig. 3; Pl. 10, fig. 6; Pl. 11, fig. 5), C. corrugata (Broch, 1931) (Pl. 10, fig. 7), *C. floridana* (Pilsbry, 1916), *C. xanthia* (Pilsbry, 1916) and, as thus defined, the genus will incorporate a number of species presently referred to *Metaverruca*.

***Costatoverruca baxteri* sp. nov.**
Plate 14, figs 1, 2, 5, 7-12

Diagnosis – Species of *Costatoverruca* in which the fixed scutum is rectangular and elongate, with an acuminate apex; complex sculpture of imbricating, undulating growth increments and blunt radial pustules.

Types – The fixed scutum illustrated here (Pl. 14, fig. 1) is the holotype (NHMUK IC 1768); the other figured valves are paratypes (NHMUK IC 1769-1776).

Material – 38 valves (NHMUK collections).

Etymology – For Dr Alistair Baxter, chief scientist on the 1987 RRS 'Charles Darwin' Indian Ocean expedition.

Description – Fixed scuta (Pl. 14, figs 1, 7, 11, 12) rectangular, 1.5 to 2 times longer than tall, narrow; acuminate apical process, projecting horizontally, bearing primordial valve at tip. Internally, scutal adductor scar dorsal in position with basal ridge, tergal notch narrow, deep. Occludent wing broad, triangular, occupying much of rostral margin. Fixed tergum (Pl. 14, fig. 2) with triangular central ridge, occludent wing large, scutal auricle smaller. Rostrum (Pl. 14, fig. 8) subrectangular, upper margin concave, bearing two strong apicobasal ridges. Carinae (Pl. 14, figs 5, 9, 10) elongated, upper margin convex, two to three ridges intersect with rostrum; sculpture very irregular.
A small fixed scutum (Pl. 14, fig. 3) is doubtfully referred to this species. Although the sculpture and form of the occludent wing is similar to other specimens, the outline is triangular, rather than rectangular. It is perhaps an aberrant specimen which attached to a differently shaped substrate.

Discussion – *Costatoverruca baxteri* sp. nov. differs from all congeners in the imbricate sculpture, and the elongated apical region of the fixed scutum.

Genus *Rostratoverruca* Broch, 1922

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

Diagnosis – Shell box-like, elongated along dorsal-ventral line; opercular lid parallel with base; fixed scutum triangular, occludent margin convex; short, blunt myophore present (emended from Young, 1998).

Discussion – It is necessary to modify Young's (1998, p. 80) diagnosis of the genus, because further investigation of *R. krugeri* Broch, 1922 and *R. koehleri* (Gruvel, 1907) have demonstrated some inconsistences (see also discussion of *Costatoverruca*, above). Firstly, the position of the rostral apex is variable, and not always displaced; in *R. koehleri* (Pl. 10, fig. 2) the apex of the rostrum is marginal. Secondly, a short myophore is present in *R. koehleri* and *R. krugeri* (Pl. 11, figs 2, 3). The main difference between *Rostratoverruca* and *Costatoverruca* appears to be in the shape of the fixed scutum and the nature of its occludent margin: in *Rostratoverruca*, the valve is triangular and the occludent margin is convex (Pl. 11, figs 2, 3). It has not been possible to examine material of the type species, *R. nexa*, but the illustrations available (see Figs 5/1-2) indicate similarity to *R. koehleri* and *R. krugeri* (Figs 5/3-4; Pl. 8, fig. 2). Other species in the genus have similar characteristics (Figs. 5/5-6; 6/2-4).

***Rostratoverruca darwini* sp. nov.**
Plate 14, figs 4, 6

Diagnosis – Species of *Rostratoverruca* in which the fixed scutum is triangular, has a narrow occludent wing and only a single apicobasal rib.

Types – The larger fixed scutum illustrated here (Pl. 14, fig. 4) is the holotype (NHMUK IC 1778), the smaller (Pl. 14, fig. 6) is the paratype (NHMUK IC 1779). Both are from Pliocene-Lower Pleistocene deposits (sample RR9) of the Rodrigues Ridge, Indian Ocean.

Material – Four valves, same locality and age (NHMUK collections).

Etymology – After the RRS 'Charles Darwin', the NERC UK research vessel.

Description – Fixed scutum equilaterally triangular, occludent margin gently convex; occludent wing narrow, basal margin concave, apex acuminate. Tergal surface of valve composed of sheet-like, imbricating growth layers, forming raised ridge adjacent to occludent wing. Interior of valve with large, oval, centrally placed adductor scar, bearing raised basal margin.

Remarks – Rostratoverruca darwini sp. nov. differs from the other four species of the genus described from the Indian and southwest Pacific oceans (see Fig. 5; *R. koehleri*, *R. krugeri*, *R. murrayi* and *R. sewelli*) in the shape and sculpture of the fixed scutum; specifically, the narrow occludent wing and the presence of a single ridge on the valve surface.

Genus *Metaverruca* Pilsbry, 1916

Type species – Verruca coraliophila Pilsbry, 1916, by original designation.

Diagnosis – Shell box-like, opercular lid parallel to base; myophore broad, curtain like, surface of valves not perforated by pores.

Discussion – In his generic revision of verrucids, Young (1998) removed a number of species from this genus, including *M. pacifica* Buckeridge, 1994. Present-day study of southwestern Pacific verrucids with the SEM indicates that external wall sculpture is a very useful guide to species; most importantly, they permit easy separation of *M. defayae* Buckeridge, 1994 (Fig. 4/3; Pl. 17, fig. 4) from *M. recta* (Aurivillius, 1898) (Fig. 4/1-2; Pl. 12, fig. 1; Pl. 17, fig. 3). In *M. defayae*, the fine, even growth increments are imbricate, whereas the external surface of *M. recta* is smooth. *Metaverruca plicata* Buckeridge, 1994 is illustrated on Pl. 12, fig. 4 and Pl. 17, fig. 5 and is distinguished by the coarsely corrugated shell and low, broad fixed tergum.
Metaverruca macani (Stubbings, 1936), Fig. 4/4, differs from *M. recta* in the smaller number of interdigitating ridges on the carina:rostrum articulation, and from *M. defayae* in the shape of the fixed scutum.

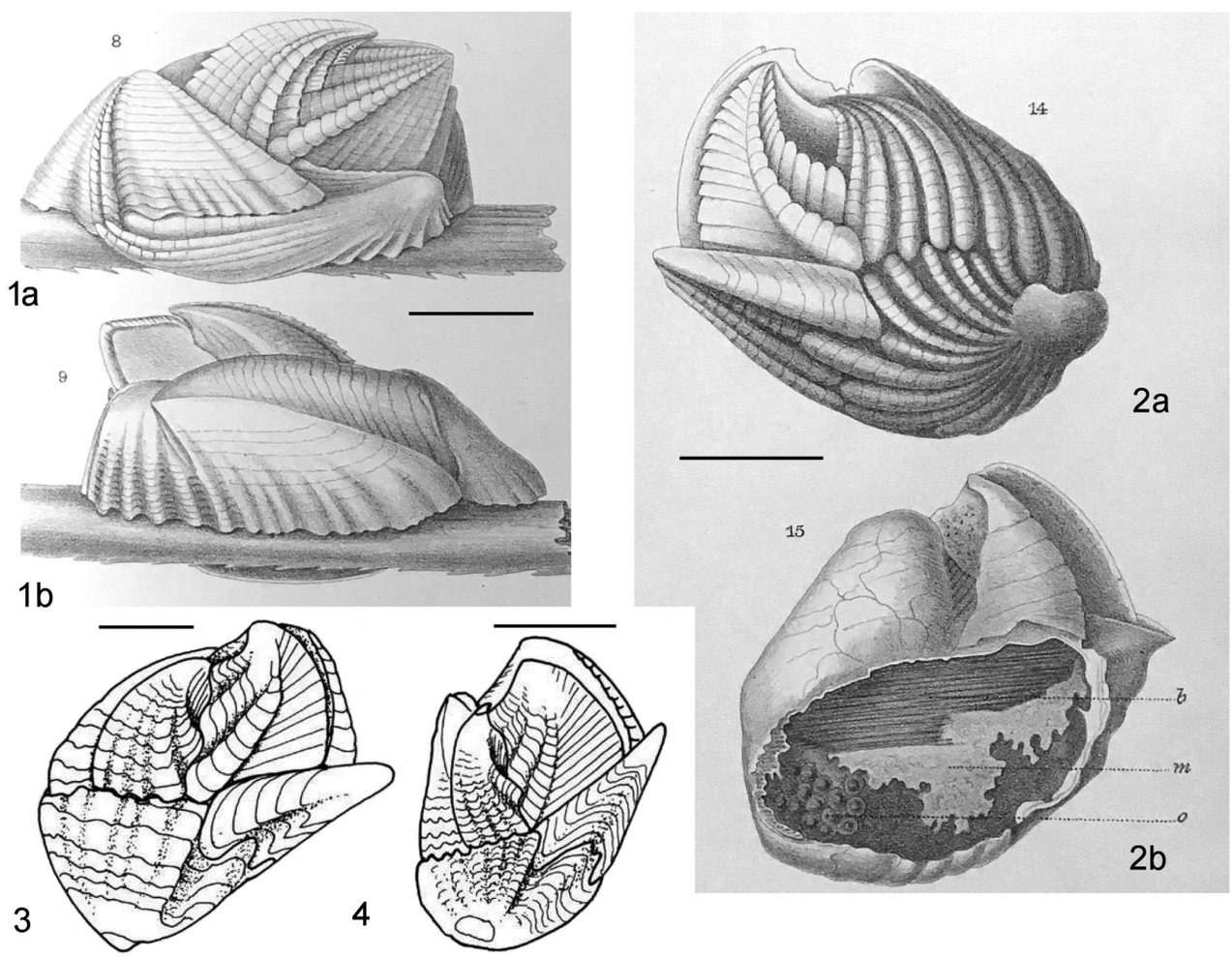


Figure 6. Present-day verrucids. 1a, b. *Newmaniverruca albatrossiana* (Pilsbry, 1912), original of Hoek (1913, pl. 31, figs 8, 9, holotype of *Verruca grex* Hoek, 1913); 2a, b. *Rostratoverruca conchula* (Hoek, 1913) (from Hoek, 1913, pl. 31, figs 14, 15); 3, 4. *Rostratoverruca conchula* (Hoek, 1913) (from Foster & Buckeridge, 1994, fig. 13A, D). Provenance: 1-3. southwestern Pacific; 4. close to Réunion Island, Indian Ocean. Scale bars 1 mm.

Metaverruca **cf. *recta*** (Aurivillius, 1898)
Plate 18, figs 2, 7

Material – Six valves, including rostra and carinae, and three corroded shells (NHMUK collections).

Remarks – The irregular, strongly undulating growth lines seen on this material show differences from those of *M. recta*, in which the growth lines are irregular but do not undulate so greatly (Pl. 18, figs 2, 7).

Metaverruca reunioni **Foster & Buckeridge, 1994**
Plate 18, figs 9-11

1994 *Metaverruca reunioni* Foster & Buckeridge, p. 369, fig. 12.

Material – 26 valves (NHMUK collections).

Discussion – These tiny valves, which are less than 1 mm in length, include fixed scuta (Pl. 18, fig. 9), fixed terga (Pl. 18, fig. 10) and rostra (Pl. 18, fig. 11). They belong to *Metaverruca*, because a myophore is present, and appear to be fully grown, because the bases of the valves are inflexed. The illustrations in Foster & Buckeridge (1994) unfortunately do not show the form of the fixed scuta and terga, but the carina (their fig. 12a, reproduced here as Fig. 4/7, 8) appears to be similar in shape to the new material. The species is locally abundant at Réunion, so its occurrence nearby (Fig. 1) would not be unexpected.

Metaverruca **cf. *norfolkensis*** **Buckeridge, 1994**
Plate 18, figs 1, 3-6, 8

*1994 *Metaverruca norfolkensis* Buckeridge, p. 110, fig. 10a-k.

Material – 45 valves (NHMUK collections).

Discussion – This species, based on two specimens from New Caledonia, was described and figured by Buckeridge (1994, fig. 10a-k), including dissociated fixed terga and scuta (refigured here, Fig. 4/5, 6a-c). Some of the scuta from Rodrigues (e.g., Pl. 18, fig. 6) are similar in shape and myophore development to his material, whilst others are of more diverse shapes, which perhaps is a consequence of intraspecific variation. The fixed tergum (Pl. 18, fig. 4) is of similar shape, but the scutal auricle is larger in the Rodrigues specimens. The rostrum (Pl. 18, fig. 5) is closely similar to that of *M. norfolkensis*. The evenly spaced growth lines, parallel to the basal margins of the Rodrigues specimens, also compare well with those of *M. norfolkensis*.

Unidentifiable specimens
A number of specimens could not be allocated to a specific genus. They are illustrated here without further description. Verrucids (Pl. 1, figs 8, 10, 12), a scalpellid (Pl. 4, fig. 13), a scalpellid or calanticid (Pl. 4, fig. 12) and balanomorphs (Pl. 6, fig. 7; Pl. 7, fig. 1).

Conclusions

The Plio-Pleistocene bathyal cirripede fauna from the Rodrigues Ridge (Indian Ocean) contains a number of discrete elements. Here, only taxa which can be positively identified to species level are included.

1. (3) Cosmopolitan taxa, including *Glyptelasma carinatum*, *Lepas pectinata*, *Arcoscalpellum michelottianum* and *Metaverruca* cf. *recta*.
2. (2) Taxa of which the present-day distribution is fairly widespread in the Pacific and Indian oceans: *Amigdoscalpellum mamillatum* and *Chionelasmus darwini.*
3. (5) Forms present-day known only from the South-West Pacific, including *Altiverruca* cf. *galapagosa*, *Cristallinaverruca jonesae*, *Gibbosaverruca nitida*, *Metaverruca* cf. *norfolkensis*, *Hexelasma* aff. *foratum* and *Cristallinaverruca ankylosa* sp. nov.
4. (5) Taxa which are endemic to the Réunion-Rodrigues region, and are still living there: *Neoeolasma rodriguesensis* gen. nov., sp. nov. and *Metaverruca reunioni.*
5. (8) Apparently extinct, endemic forms known only in this assemblage: *Catherinum busselli* sp. nov., *Costatolepas buckeridgei* gen. nov., sp. nov., *Altiverruca capsa* sp. nov., *Altiverruca fusione* sp. nov., *Costatoverruca baxteri* sp. nov., *Newmaniverruca multitubulatum* sp. nov. and *Rostratoverruca darwini* sp. nov.

It is problematic to compare a modern fauna, based upon dredges over the last 150 years, directly with an assemblage which may represent at least a million years of migration, colonisation and local extinction. However, a number of features are striking. Firstly, the sheer diversity of the cirripede assemblage, especially the verrucids, of which 17 species are present off the Rodrigues Ridge, precisely the same number known from the entire MUSORSTOM dredging expeditions in New Caledonia, the Futuna and Wallis Islands in an intensive survey going back over 30 years (Jones, 2007). Direct comparisons with other families are very difficult, as many taxa from New Caledonia (a total of 166 species) are from shallow and intermediate water depths. However, it is apparent that deep-water balanomorph, scalpellid and calanticid taxa during the Late Pliocene-Early Pleistocene off Rodrigues may never have achieved the great diversity seen in present-day New Caledonia.

1. The Upper Pliocene-Lower Pleistocene deposits of the Rodrigues Ridge area comprise a great diversity of verrucid species, most of which now appear to be extinct. Foster and Buckeridge (1994) recorded eight species of verrucids from nearby Réunion, of which only two are represented in the fossil faunas. This might be a reflection of high endemism, or alternatively, of the fact that the fossil species may originally have been far

more widespread, but underwent extinction over their entire range. Clearly, this can only be tested with further material.
2. The presence in the Upper Pliocene-Lower Pleistocene deposits of the eastern Indian Ocean of five taxa currently endemic to the New Caledonia region indicates that a significant range reduction of some deep-water benthos took place over the past 1-1.5 million years.
3. The complete absence in the Upper Pliocene-Lower Pleistocene of Rodrigues Ridge of the diverse pachylasmatid and bathylasmatid balanomorph taxa described from New Caledonia by Jones (2000) might be taken as evidence that they were always endemic to that region, or at least did not spread so far to the West.

It is difficult to draw broad conclusions from such a limited sample, but bathyal fossil faunas are so very rare. The Rodrigues Ridge sample at least shows that very large changes have taken place in deep-water benthonic faunas over the Pleistocene in the Indian Ocean, perhaps paralleling the studies of Hayward *et al.* (2012), who showed that major global extinctions (up to 25 percent of species) took place in deep benthonic foraminifera during the Pleistocene.

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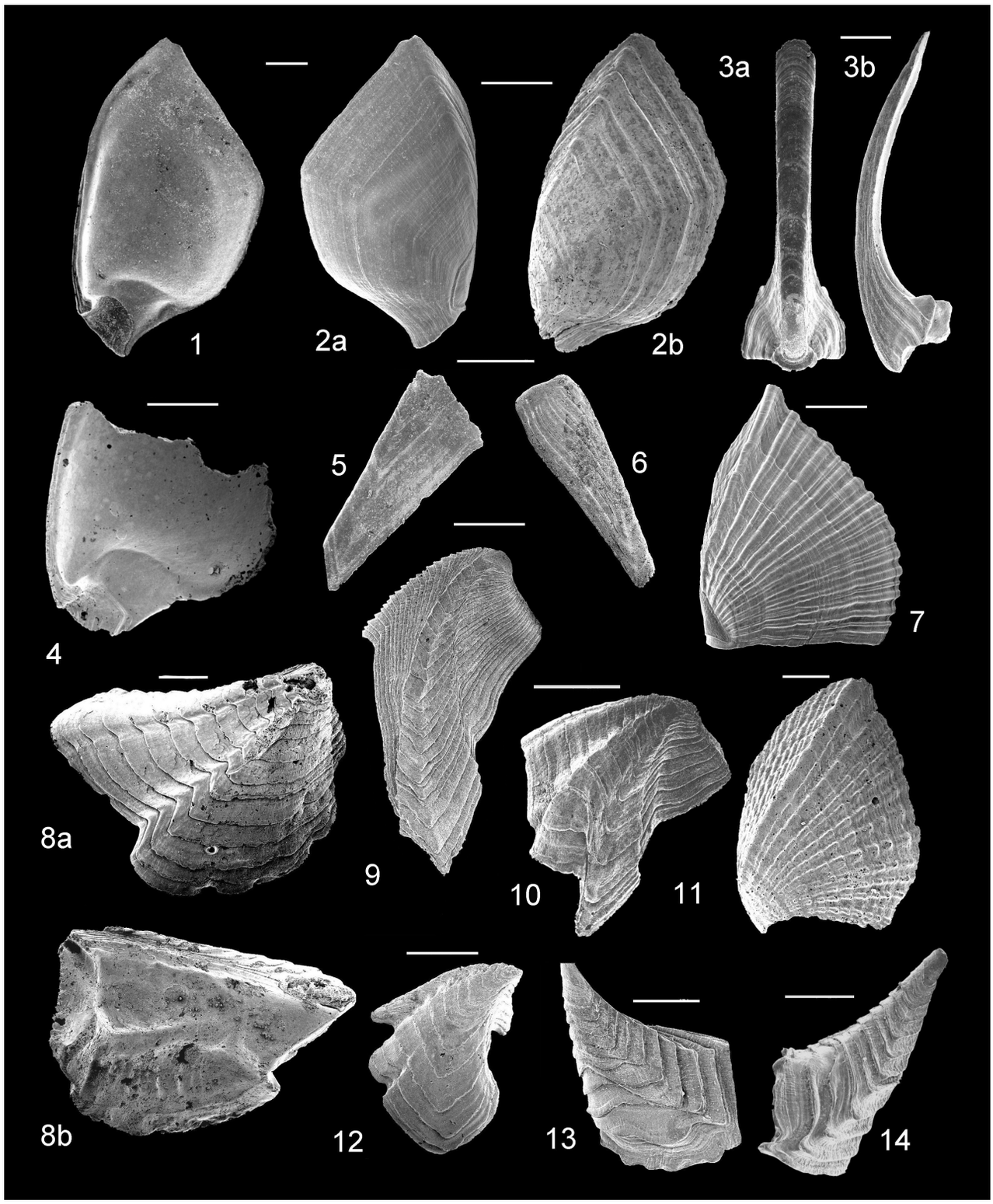

Plate 1. 1-6. *Glyptelasma carinatum* (Hoek, 1883). 1a, b. scutum in external and internal views (NHMUK IC 1693). 2, 4. scuta (NHMUK IC 1694, 1696). 3a, b. carina (NHMUK IC 1695). 5, 6. terga (NHMUK IC 1697, 1698). Figs 7, 11. *Lepas pectinata* Spengler, 1790 scuta (Fig. 11, NHMUK IC 1699). 8a, b, 10. undescribed verrucid, fixed scutum and fixed tergum, respectively (NHMUK IC 1700). 9. *Altiverruca* cf. *galapagosa* (Zevina, 1987), tergum (NHMUK IC 1701). 12. undescribed verrucid, rostrum (NHMUK IC 1702). 13, 14. *Altiverruca* sp. 1, carinae (NHMUK IC 1703, 1704). Scale bars equal 0.5 mm (3, 13, 14) and 1 mm (all others). Provenance: 7. Present-day, Paphos, Cyprus; all other specimens Late Pliocene-Early Pleistocene, Rodrigues Ridge, Indian Ocean, sample RR9.

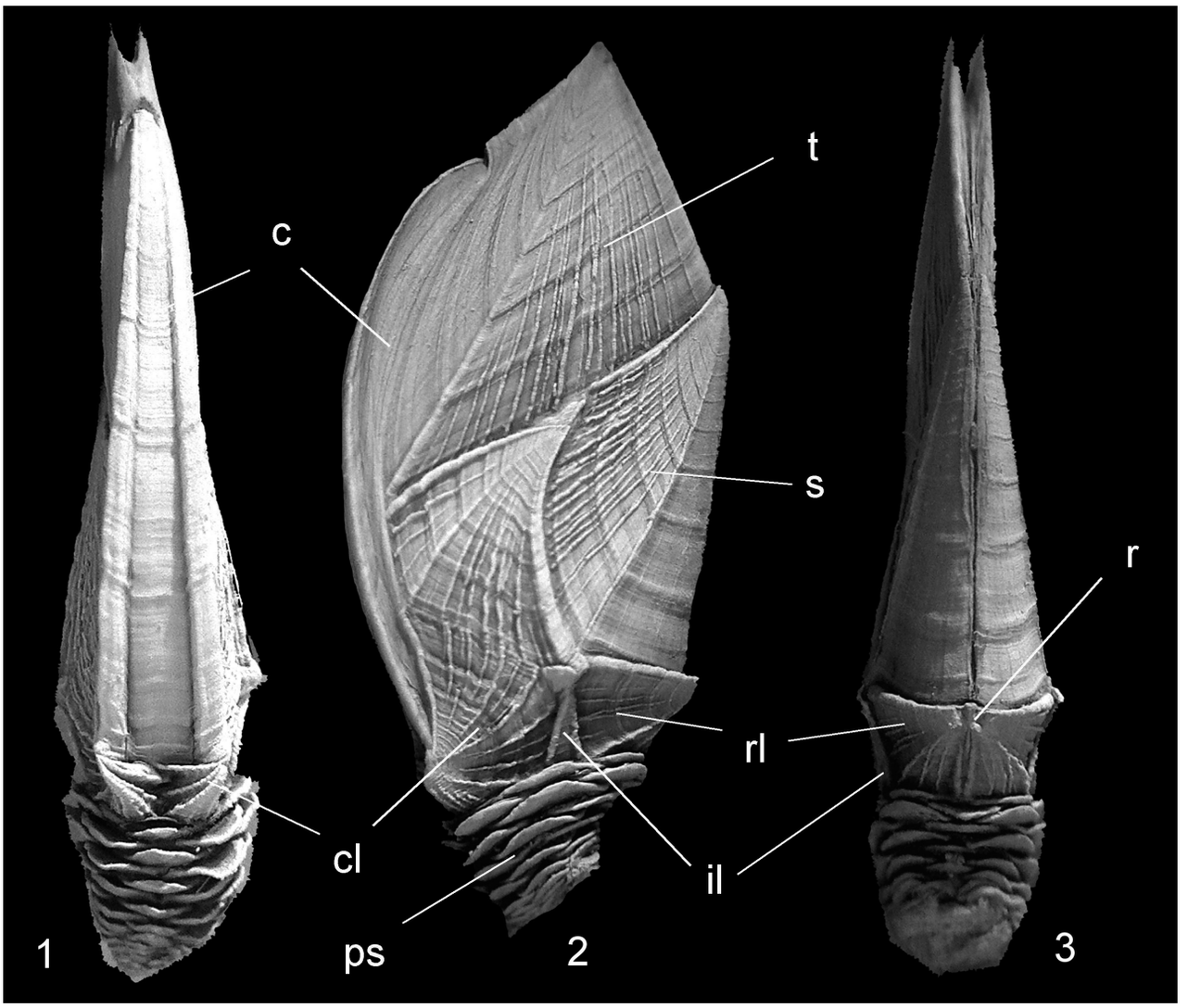

Plate 2. *Amigdoscalpellum mamillatum* (Aurivillius, 1898). Capitulum, to show plating structure. 1. dorsal view; 2. lateral view; 3. ventral view. *Abbreviations*: c, carina; cl, carinolatus; ps, peduncular scales; il, inframedian latus; rl, rostrolatus; s, scutum; t, tergum; r, rostrum. Present-day, Rodrigues Ridge, sample S2 (see Fig. 1).

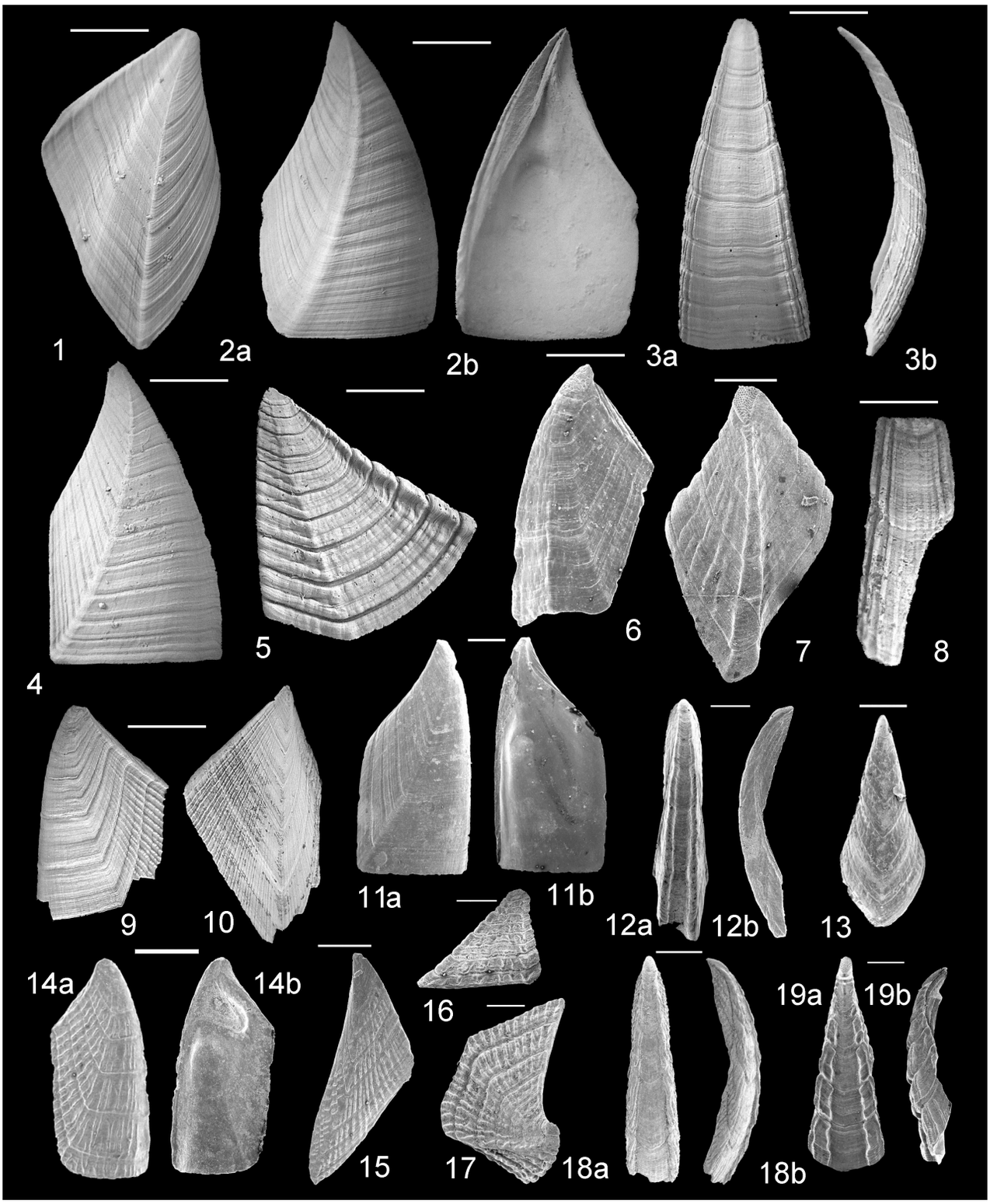

Plate 3. 1-5, *Arcoscalpellum michelottianum* (Seguenza, 1876). 1. tergum (NHMUK IC 1705); 2a, b, 4, scuta (NHMUK IC 1706, 1708); 3a, b. carina (NHMUK IC 1707); 5. upper latus (NHMUK IC 1709); 6, 7. Scalpellid sp. 3, scutum and tergum, respectively (NHMUK IC 1711, 1712); 8. *Arcoscalpellum* sp. 2, carina (NHMUK IC 1710); 9, 10. *Amigdoscalpellum mamillatum* (Aurivillius, 1898), scutum and tergum, respectively (NHMUK IC 1713, 1714); 11, *Graviscalpellum* cf. *pedunculatum* (Hoek, 1883), scutum (NHMUK IC 1715); 12a, b. *Catherinum* sp., carina (NHMUK IC 1716); 13. Scalpellid sp. 4, carina (NHMUK IC 1717); 14-18. *Catherinum busselli* sp. nov.; 14. scutum, **holotype** (NHMUK IC 1718); 15. tergum, **paratype** (NHMUK IC 1719); 16. upper latus, **paratype** (NHMUK IC 1720); 17. carinolatus, **paratype** (NHMUK IC 1721); 18a, b. carina, **paratype** (NHMUK IC 1722); 19a, b. *Arcoscalpellum* sp. 1, carina (NHMUK IC 1723). All specimens from Late Pliocene-Early Pleistocene, Rodrigues Ridge, Indian Ocean, sample RR9. Scale bars equal 10 mm (1-4), 5 mm (5), 1 mm (11-15, 18, 19) and 0.5 mm (6, 7, 16, 17).

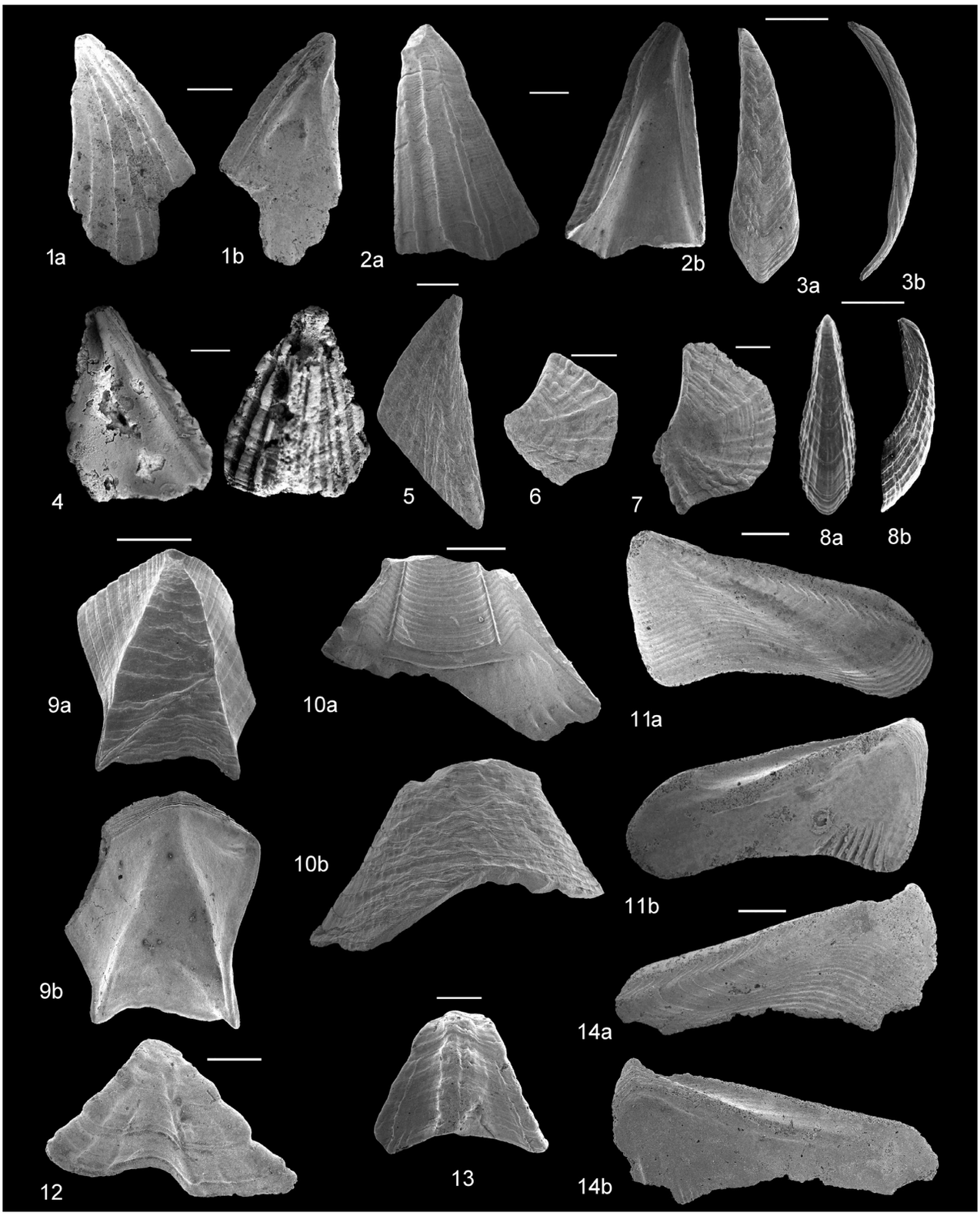

Plate 4. 1, 2, 4. *Costatolepas buckeridgei* gen. nov., sp. nov., scuta. 1a, b. **holotype** (NHMUK IC 1724); 2, 4. **paratypes** (NHMUK IC 1725, 1726); 3a, b. Scalpellid sp. 1, carina (NHMUK IC 1727); 5. *Catherinumbusselli* sp. nov., tergum (NHMUK IC 1728); 6. *Amigdoscalpellum mamillatum (*Aurivillius, 1898) carinolatus (NHMUK IC 1729); 7. *Catherinum* sp. 2, carinolatus (NHMUK IC 1730); 8a, b. Scalpellid sp. 2, carina (NHMUK IC1731); 9a, b. *Neoeolasma* sp., carina (NHMUK IC 1734); 12. scalpellid or calanticid inframedian latus (NHMUK IC 1732); 13. scalpellid rostrum (NHMUK IC 1733); 10a, b, 11a, b, 14a, b. *Hexelasma* aff. *foratum* Jones, 2000: 10. fused rostral plate (NHMUK IC 1735); 11, 14. terga (NHMUK IC 1736, 1737). All specimens from Pliocene-Lower Pleistocene strata of Rodrigues Ridge, Indian Ocean, sample RR9. Scale bars equal 0.5 mm (3, 6-8, 12) and 1 mm (all others).

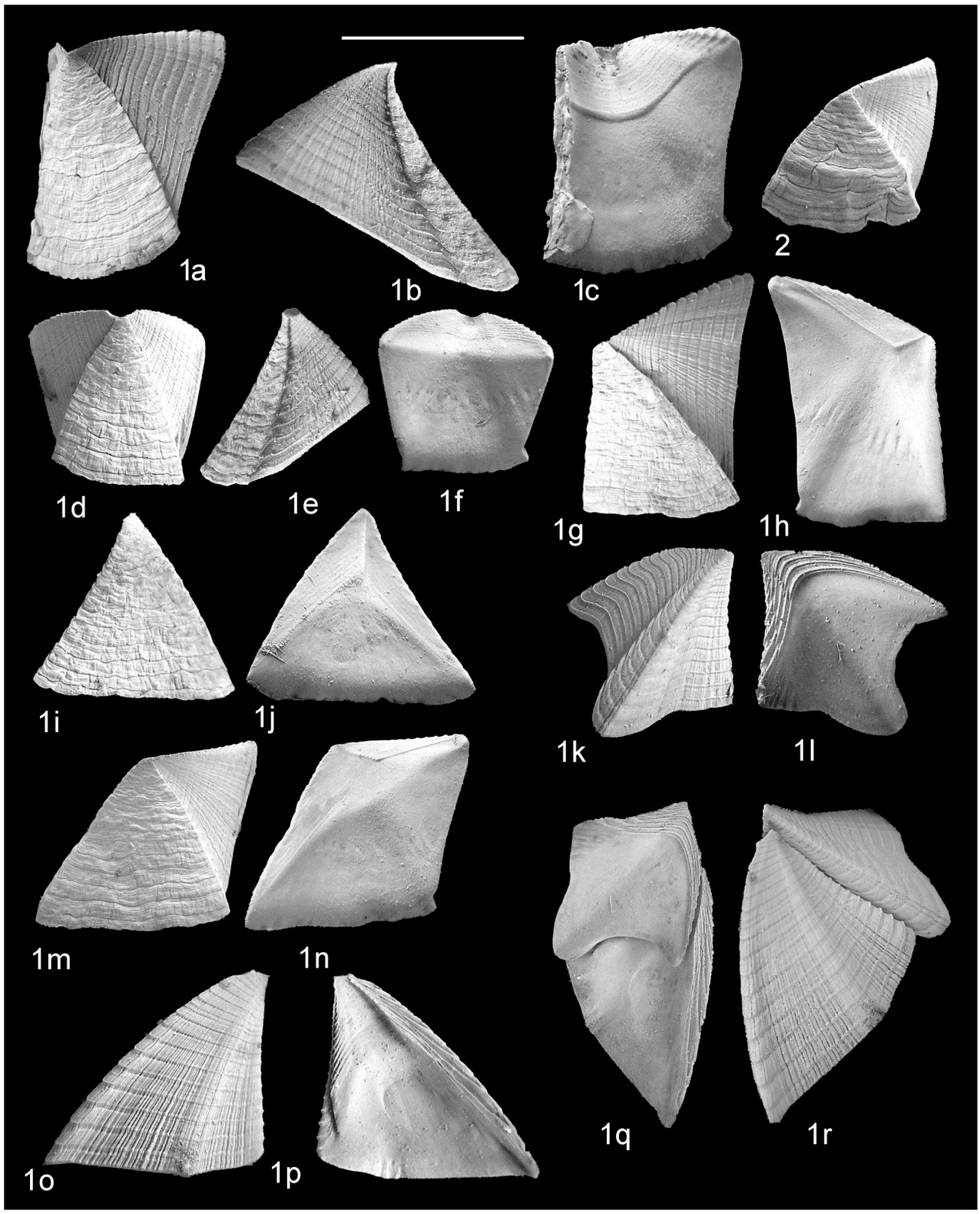

Plate 5. *Neoeolasma rodriguesensis* gen. nov., sp. nov. 1, **holotype** (NHMUK IC 1738): 1a-c. Carina; 1d-f. Rostrum; 1g, 1h. Marginal; 1i, 1j. Rostromarginal; 1k, 1l. Tergum; 1m, 1n. Carinomarginal; 1o, 1p. Scutum; 1q, 1r. Paired scutum and tergum; 2. **paratype**, carinomarginal (NHMUK IC 1739). Provenance: 1. Present-day, Rodrigues Ridge, Indian Ocean; 2. Upper Pliocene-Lower Pleistocene, sample RR9, Rodrigues Ridge, Indian Ocean. Scale bar equals 5 mm.

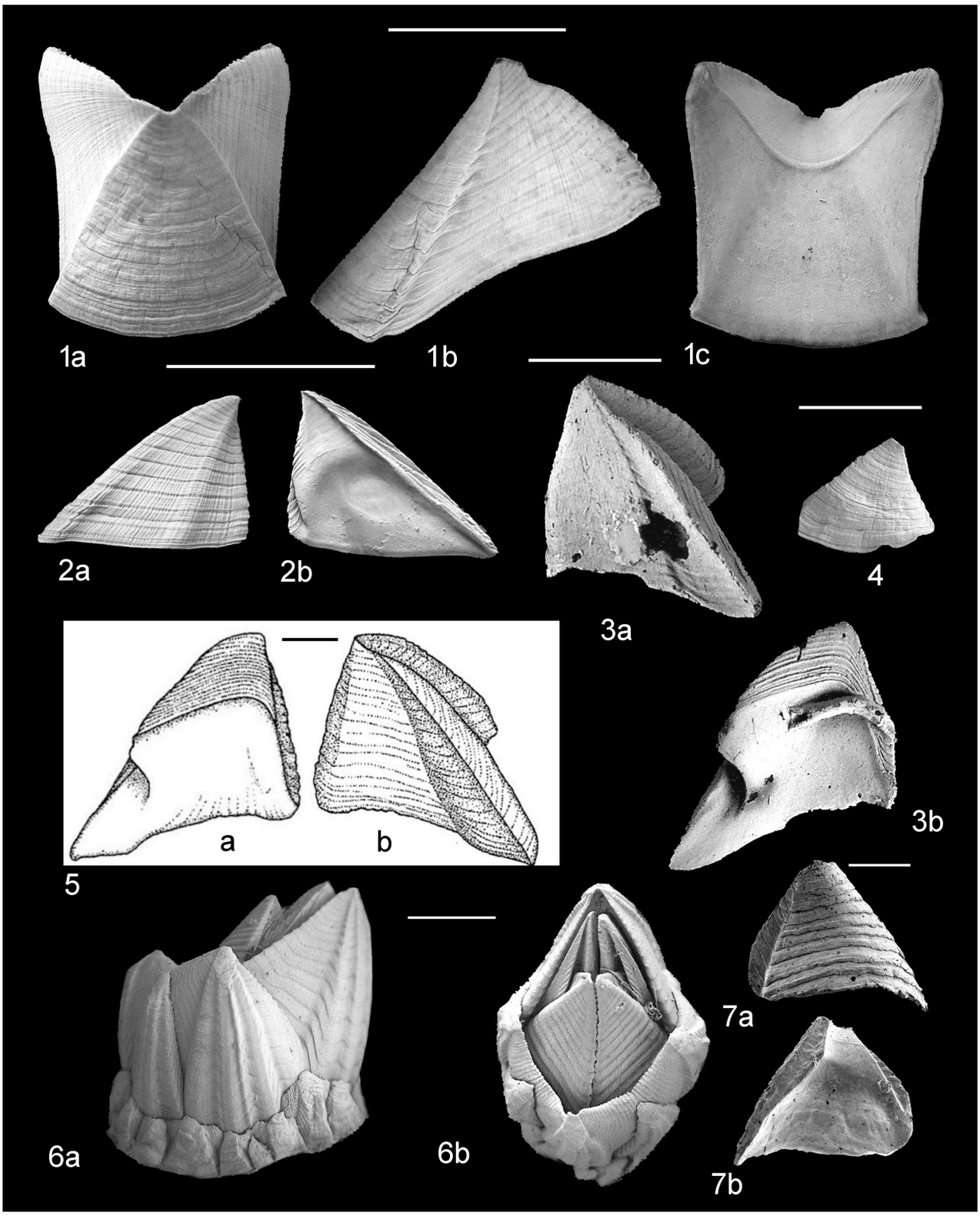

Plate 6. 1, 2, 4. *Neoeolasma rodriguesensis* gen. nov., sp. nov., **paratypes**. 1a-c. large carina, in external, lateral and internal views, respectively (NHMUK IC 1740); 2. scutum, in external and internal views, respectively (NHMUK IC 1741); 4. rostromarginal, external view (NHMUK IC 1742); 3, 5, 6. *Chionelasmus darwini* (Pilsbry, 1907): 3a, b. tergum, in external and internal views, respectively (NHMUK IC 1743); 5a, b. tergum (after Jones, 2000, fig. 2c, d); 6a, b. capitulum, in lateral and opercular views, respectively; 7a, b. unidentified balanomorph plate (NHMUK IC 1924). Provenance: 1-4, 7. Pliocene-Lower Pleistocene, Rodrigues Ridge, Indian Ocean; 5, 6. Present-day, New Caledonia. Scale bars equal 5 mm (1, 2, 3, 6), 3 mm (4), 1mm (5, 7).

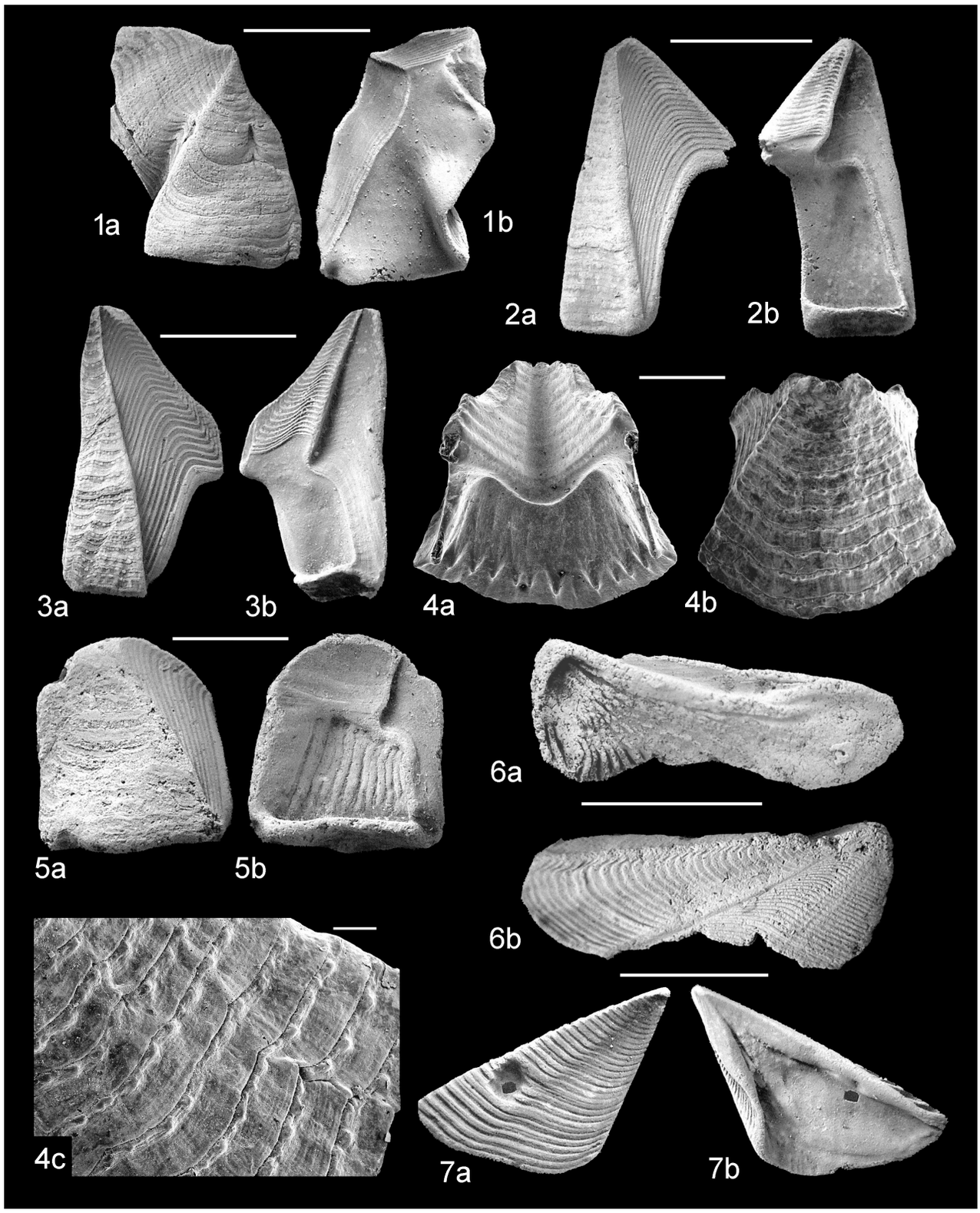

Plate 7. 1a, b. unidentified balanomorph marginal plate (NHMUK IC 1745); 2-7. *Hexelasma* aff. *foratum* Jones, 2000: 2, 3. carinomarginals, in external and internal aspects, respectively (NHMUK IC 1746, 1747); 4a-c. carina, in internal and external views and enlargement of external surface, respectively (NHMUK IC 1748); 5. worn marginal plate, in external and internal views, respectively (NHMUK IC 1749); 6. tergum, in internal and external views, respectively (NHMUK IC 1750); 7. scutum, in external and internal views, respectively (NHMUK IC 1751). All specimens are from Pliocene-Lower Pleistocene deposits (sample RR9) of the Rodrigues Ridge, Indian Ocean. Scale bars equal 5 mm (1-3, 5-7), 1 mm (4a, b) and 0.2 mm (4c).

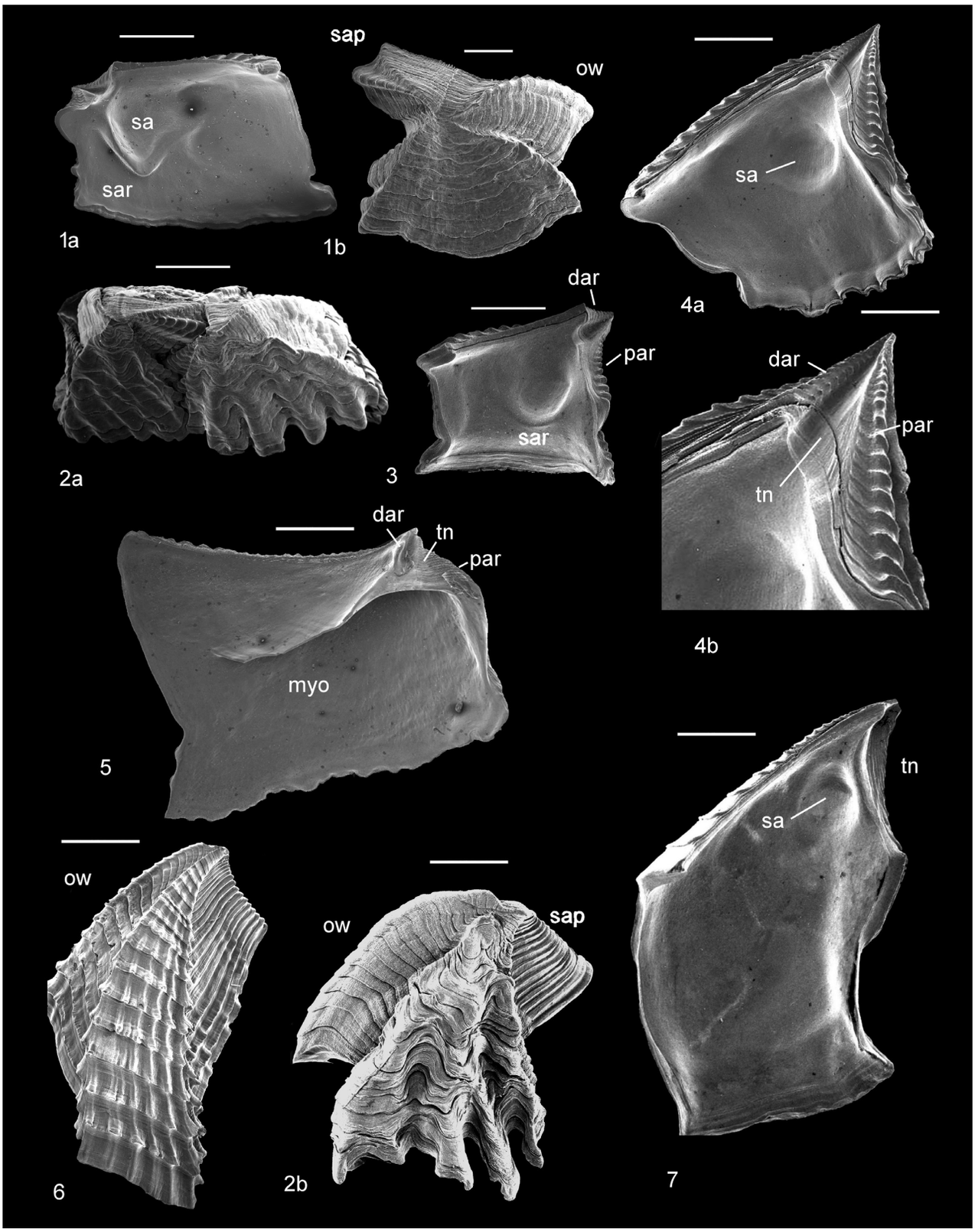

Plate 8. Structure of present-day verrucid valves. 1a, b. *Costatoverruca alba* (Pilsbry, 1916); interior of fixed scutum (1a) and exterior of fixed tergum (1b); 2a, b. *Rostratoverruca krugeri* Broch, 1922; fixed scutal-tergal view (2a) and fixed tergum (2b); 3. *Costatoverruca pacifica* (Buckeridge, 1994), interior of fixed scutum; 4a, b. *Newmaniverruca albatrossiana* (Pilsbry, 1912), interior of fixed scutum; 5. *Metaverruca recta* (Aurivillius, 1898), interior of fixed scutum; 6. *Gibbosaverruca* sp., exterior of fixed tergum; 7. *Altiverruca obliqua* (Hoek, 1883), interior of fixed scutum. *Abbreviations*: dar, distal articular ridge; myo, myophore; ow, occludent wing; par, proximal articular ridge; sa, scutal adductor; sap, scutal articular process; sar, scutal adductor ridge; tn, tergal notch. Scale bars equal 0.5 mm (1, 2a, 4b, 7) and 1 mm (all others).

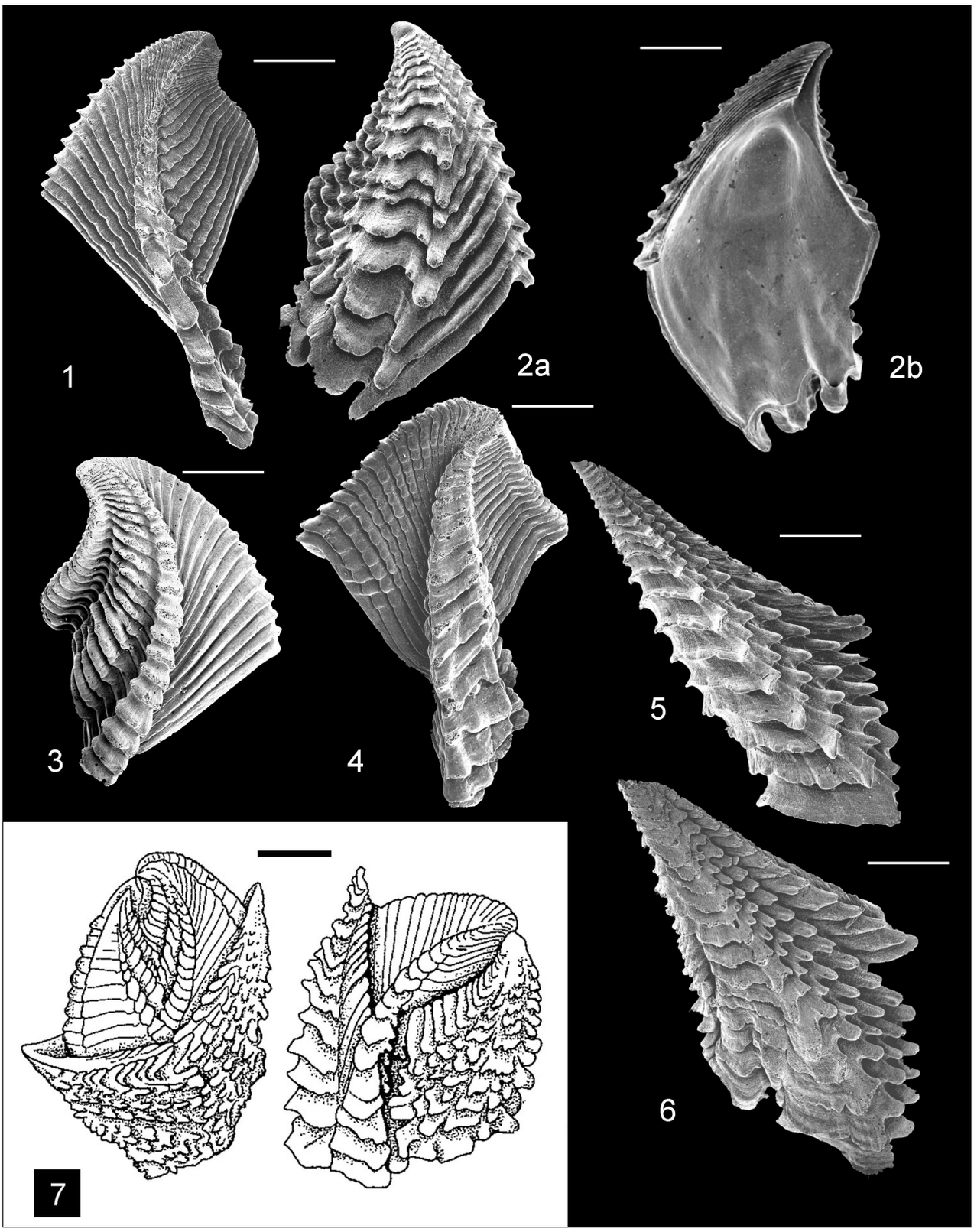

Plate 9. 1-7. *Cristallinaverruca jonesae* (Buckeridge, 1994); 1, fixed tergum, original of Gale 2019 fig. 11C (NHMUK IC 1400). 4, fixed tergum (NHMUK IC 1754); 2a, b. fixed scutum, in external and internal views, respectively (NHMUK IC 1753); 3. moveable tergum, original of Gale 2019 fig. 11D (NHMUK IC 1399); 5, 6. carinae (NHMUK IC 1755, 1833); 7. **holotype**, after Buckeridge (1997, fig. 2a, d). Provenance: 1-6. Pliocene-Lower Pleistocene deposits, Rodrigues Ridge, Indian Ocean (sample RR9); 7. Present-day, southwestern Pacific. All scale bars equal 1 mm.

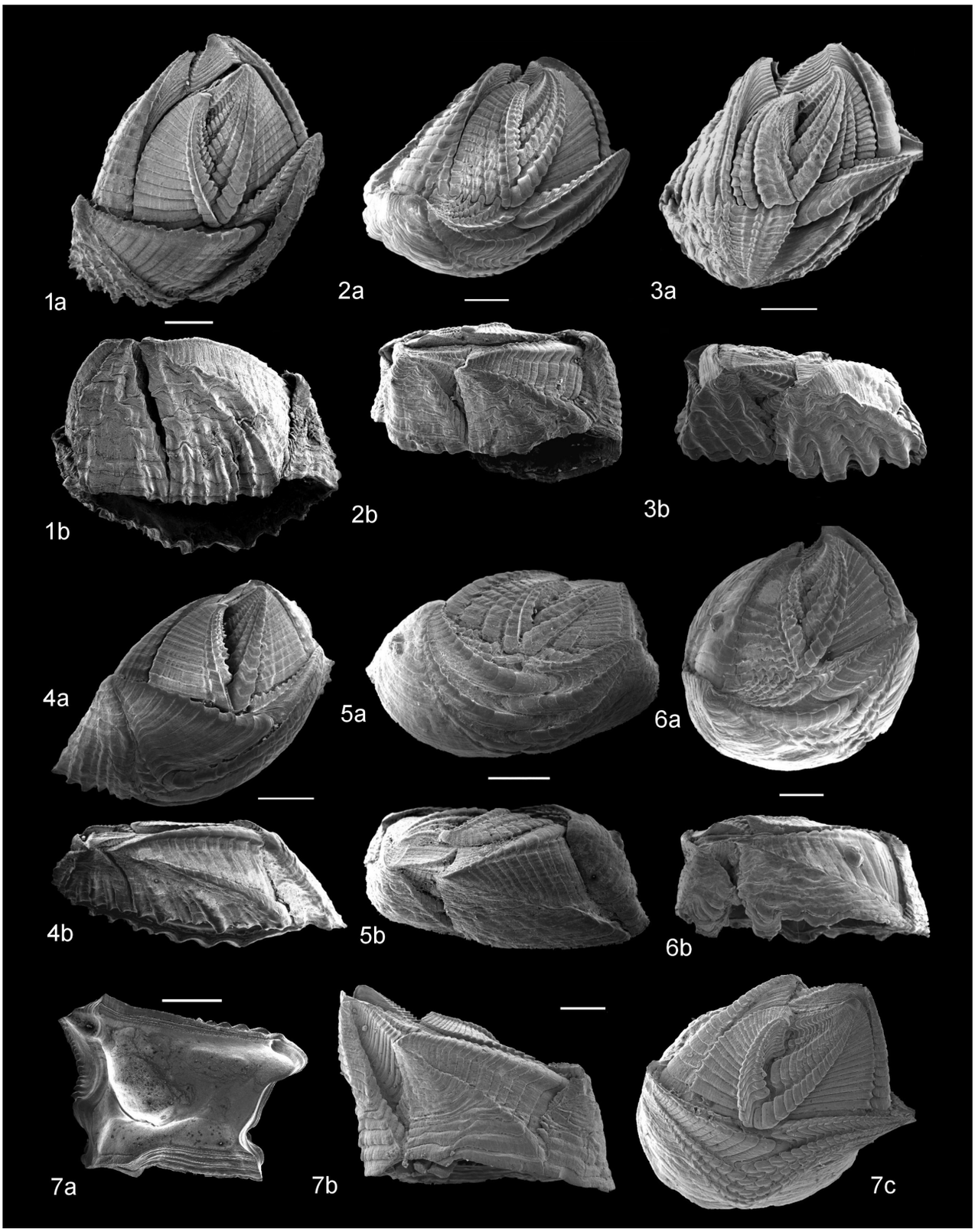

Plate 10. 1a, b, 4a, b. *Newmaniverruca albatrossiana* (Pilsbry, 1912), apical (1a, 4a) and lateral (1b, 4b) views of shell; 2a, b. *Rostratoverruca koehleri* (Gruvel, 1907), apical and lateral views of shell, respectively; 3a, b. *Rostratoverruca krugeri* Broch, 1922, apical and lateral views of shell, respectively; 5a, b. *Costatoverruca alba* (Pilsbry, 1907), apical and lateral views, respectively; 6a, b. *Costatoverruca pacifica* (Buckeridge, 1994), apical and lateral views, respectively; 7a-c.*Costatoverruca corrugata* (Broch, 1931), apical (7c) and lateral (7b) views of shell, and interior of fixed scutum (7a). All are present-day specimens. Provenance: 1. Kei Islands, Indonesia (collections Zoological Museum, Copenhagen); 2-4, 6, 7. southwestern Pacific, New Caledonia (collections MNHN, Paris); 5. Florida. All scale bars equal 1 mm.

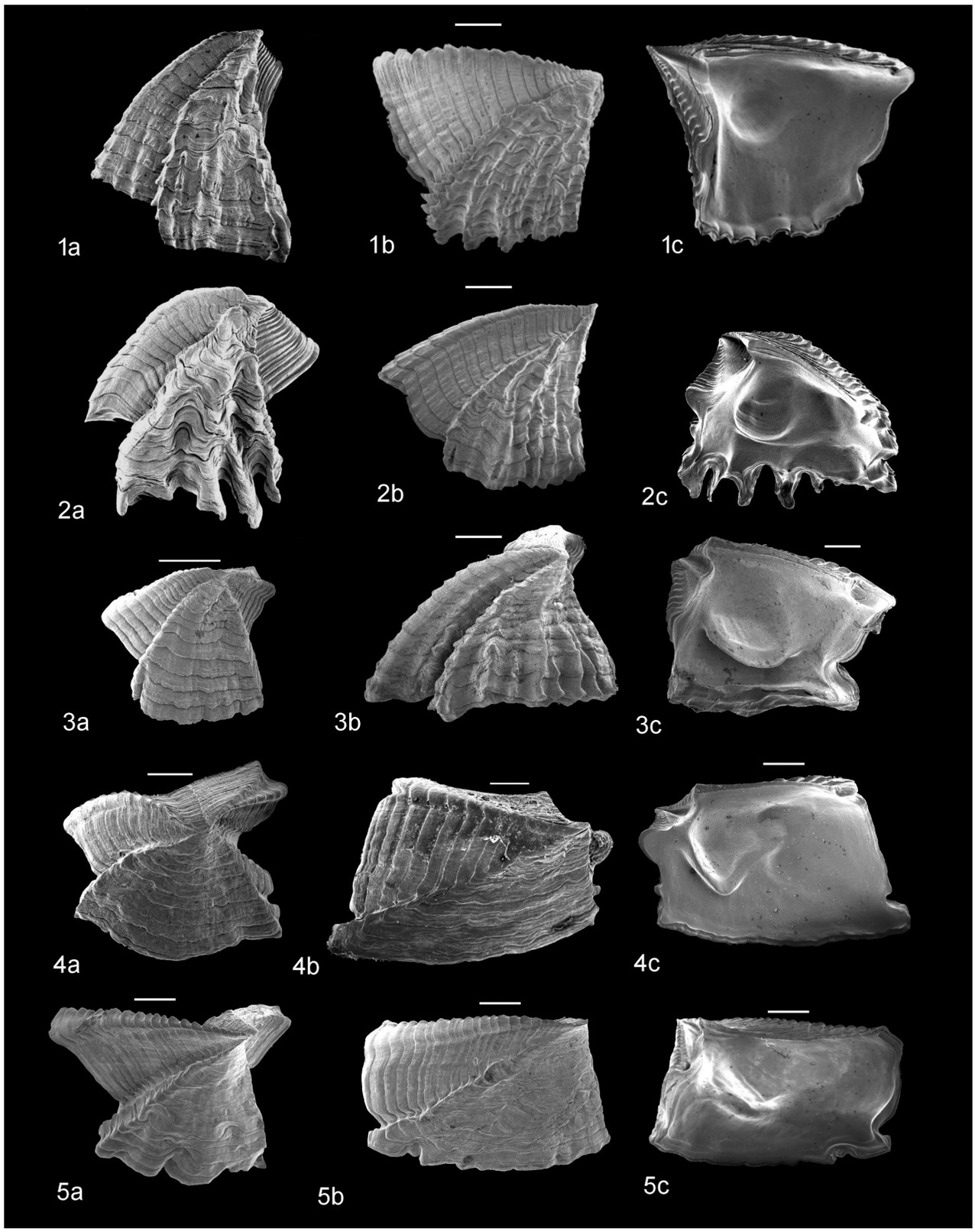

Plate 11. Comparative morphology of fixed terga and scuta of present-day verrucids. 1a-c. *Newmaniverruca albatrossiana* (Pilsbry, 1912); 2a-c. *Rostratoverruca krugeri* Broch, 1922; 3a-c. *Rostratoverruca koehleri* (Gruvel, 1907); 4a-c. *Costatoverruca alba* (Pilsbry, 1916); 5a-c.*Costatoverruca pacifica* (Buckeridge, 1994). Left-hand column (a): external views of fixed terga; middle column (b): external views of fixed scuta; right-hand column (c): interior views of fixed scuta. All are present-day specimens. Provenance: 1. Kei Islands, Indonesia (collections Zoological Museum, Copenhagen); 2, 3, 5, southwestern Pacific, New Caledonia (collections MNHN, Paris); 4. Florida. Scale bars equal 1 mm (1-3) and 0.5 mm (4, 5).

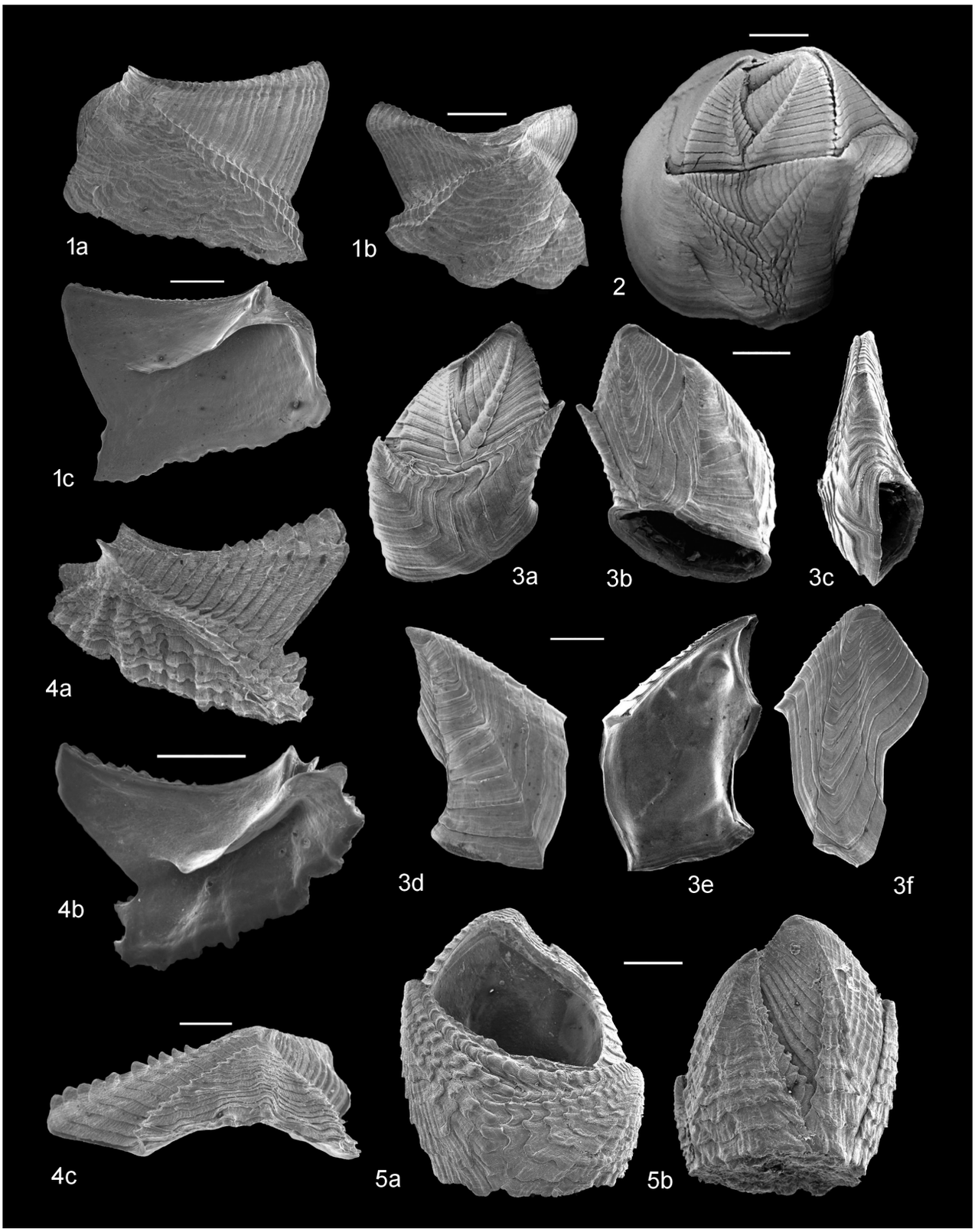

Plate 12. Morphology of present-day verrucids. 1a-c, 2. *Metaverruca recta* (Aurivillius, 1898), fixed scutum (1a), fixed tergum (1b) and shell in apical view (2); 3a-c. *Altiverruca obliqua* (Hoek, 1883), shell in rostral-carinal, fixed scutal-tergal and ventral views, respectively; 3d, e, fixed scutum and fixed tergum, respectively; 4a-c. *Metaverruca plicata* Buckeridge, 1994, fixed scutum (4a, b) and fixed tergum (4c); 5a, b. *Cristallinaverruca* sp. nov. (undescribed), shell (MNHN 2016 10457) in rostral-carinal and fixed tergal-scutal views, respectively. Provenance: 2. sample S2, Rodrigues Ridge, Indian Ocean; 3. Arctic; all others from New Caledonia, southwestern Pacific. Scale bars equal 0.5 mm (3) and 1 mm (all others).

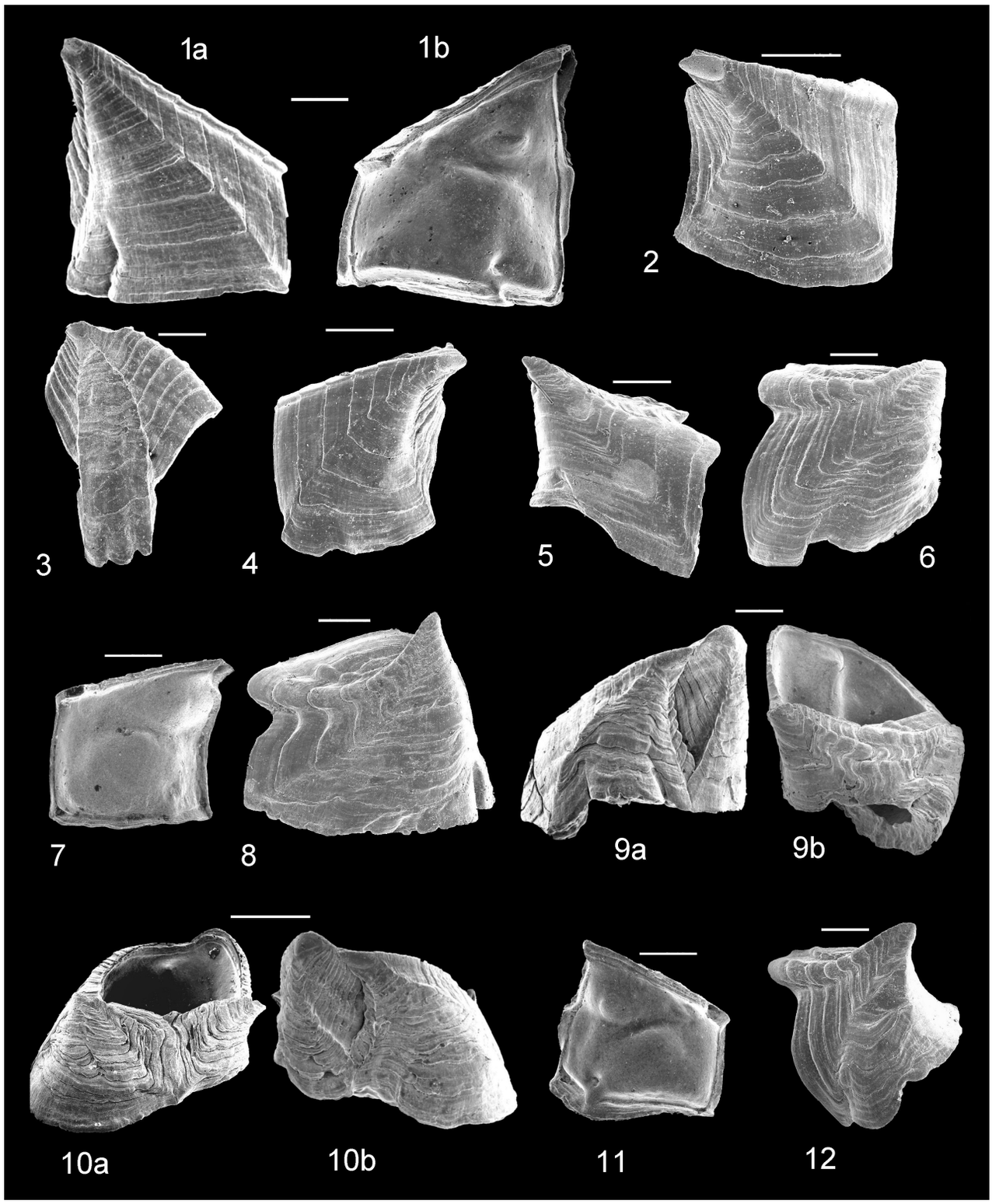

Plate 13. 1-8, 11, 12. *Altiverruca capsa* sp. nov.; 1a, b. **holotype** fixed scutum, in external and internal views, respectively (NHMUK IC 1756); 2, 4, 7, 11. **paratype** fixed scuta (NHMUK IC 1757, 1759, 1762, 1764); 3. **paratype** fixed tergum (NHMUK IC 1758); 5. **paratype** carina (NHMUK IC 1760); 6, 8, 12. **paratype** rostra (NHMUK IC 1761, 1763, 1765); 9a, b. *Cristallinaverruca ankylosa* sp. nov., **holotype** capitulum, in fixed scutal-tergal and rostral-carinal views, respectively (NHMUK IC 1766); 10. *Altiverruca fusione* sp. nov., **holotype** capitulum (NHMUK IC 1767). All are from Pliocene-Lower Pleistocene strata, Rodrigues Ridge, Indian Ocean (sample RR9). Scale bars equal 1 mm (10) and 0.5 mm (all others).

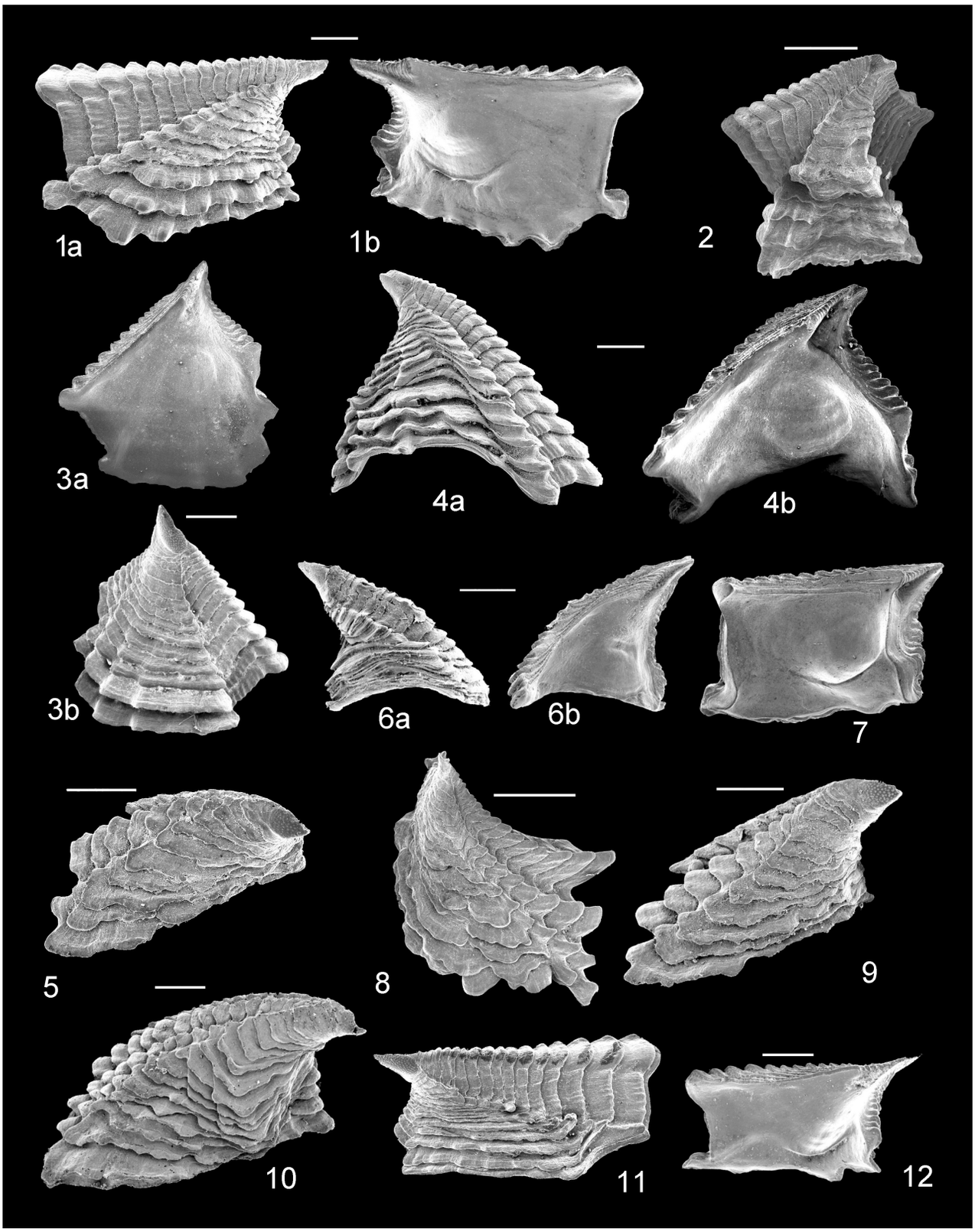

Plate 14. 1, 2, 5, 7-12. *Costatoverruca baxteri* sp. nov. 1a, b. **holotype** fixed scutum (NHMUK IC 1768); 7, 11, 12. **paratype** fixed scuta (NHMUK IC 1771, 1775, 1776); 5, 9, 10. **paratype** carinae (NHMUK IC 1770, 1773, 1774); 8. **paratype** rostrum (NHMUK IC 1772); 3. fixed scutum possibly belonging to *Costatoverruca baxteri* sp. nov. (NHMUK IC 1777); 4, 6. *Rostratoverruca darwini* sp. nov. 4. **holotype** fixed scutum (NHMUK IC 1778); 6. **paratype** fixed scutum (NHMUK IC 1779). All from Pliocene-Lower Pleistocene strata, Rodrigues Ridge, Indian Ocean (sample RR9). Scale bars equal 1 mm (2, 7) and 0.5 mm (all others).

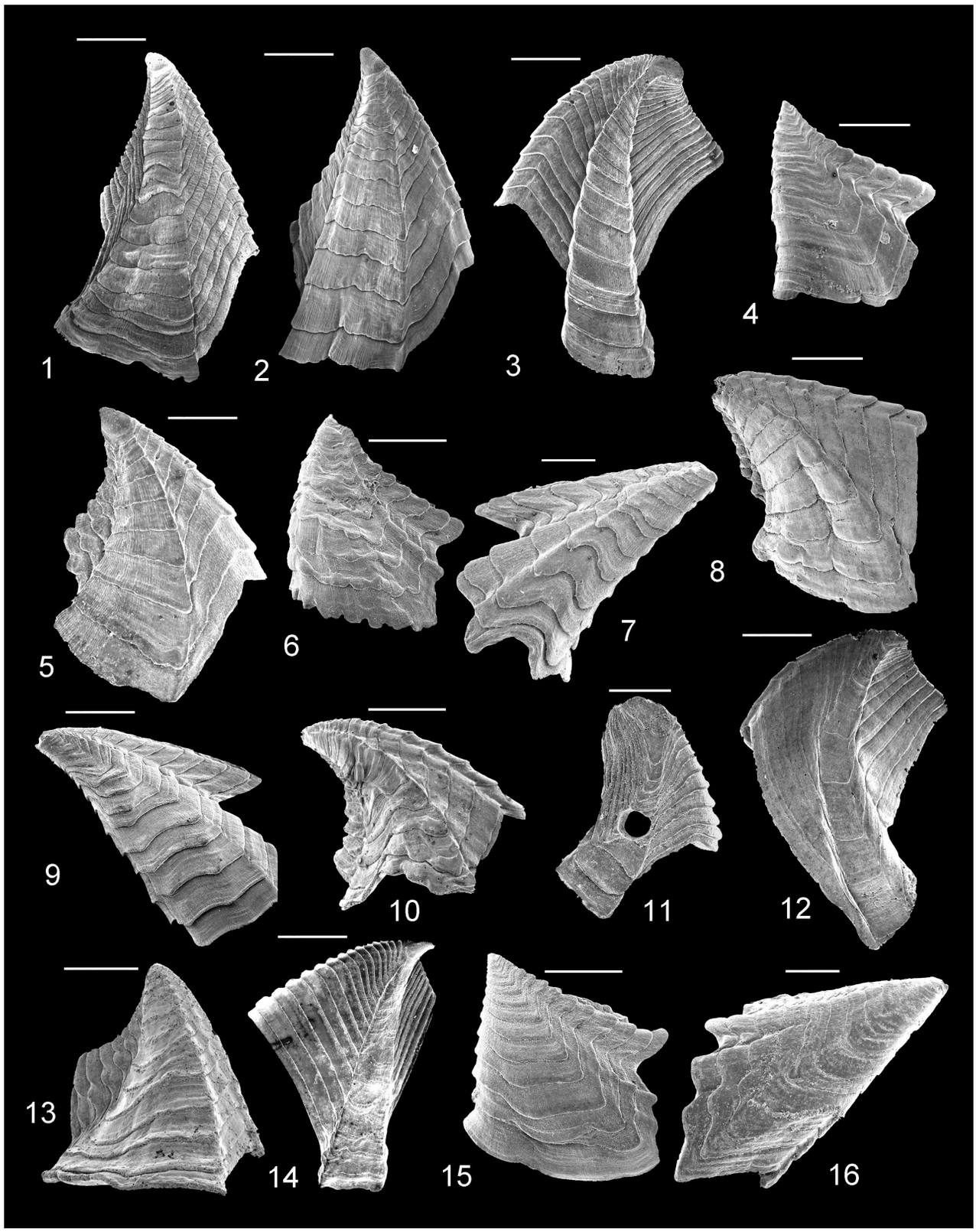

Plate 15. 1-11, 15, 16. *Gibbosaverruca nitida* (Hoek, 1883); 1, 2, 5, 8, 10. fixed scuta (NHMUK IC 1780, 1781, 1784, 1787, 1790); 3, 11. fixed terga (NHMUK IC 1782, 1791); 4, 6, 15. rostra (NHMUK IC 1783, 1785, 1792); 7, 9, 16. carinae (NHMUK IC 1786, 1789, 1793); 12. *Gibbosaverruca* sp. 1, fixed tergum (NHMUK IC1794); 13, 14.*Gibbosaverruca* sp. 2, fixed scutum and fixed tergum, respectively (NHMUK IC 1795, 1796). All are from Pliocene-Lower Pleistocene deposits of Rodrigues Ridge, Indian Ocean (sample RR9). All scale bars equal 0.5 mm.

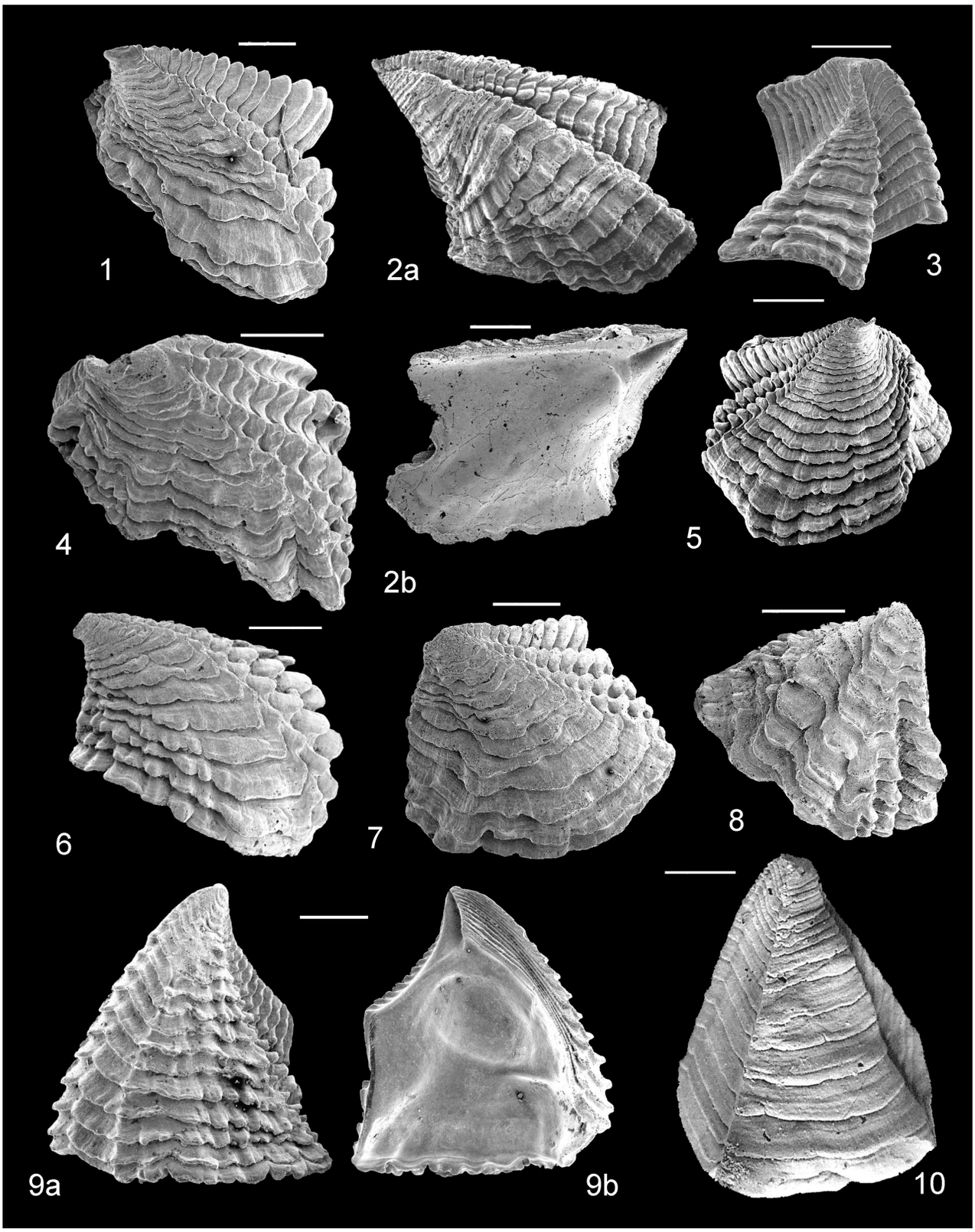

Plate 16. 1-8. *Newmaniverruca multitabulata* sp. nov.; 1, 4, 6, carinae (NHMUK IC 1797, 1800, 1785, 1802); 2a, b. **holotype** fixed scutum, in external and internal views, respectively (NHMUK IC 1798); 3. **paratype** fixed tergum (NHMUK IC1799); 5, 7, 8, rostra (NHMUK IC 1801, 1803, 1804); 9a, b. *Gibbosaverruca youngi* sp. nov., **holotype** fixed scutum, in external and internal views, respectively (NHMUK IC 1805); 10.*Gibbosaverruca* sp., fixed scutum (NHMUK IC 1806). All are from Pliocene-Lower Pleistocene strata, Rodrigues Ridge, Indian Ocean (sample RR9). Scale bars equal 0.5 mm (1) and 1 mm (all others).

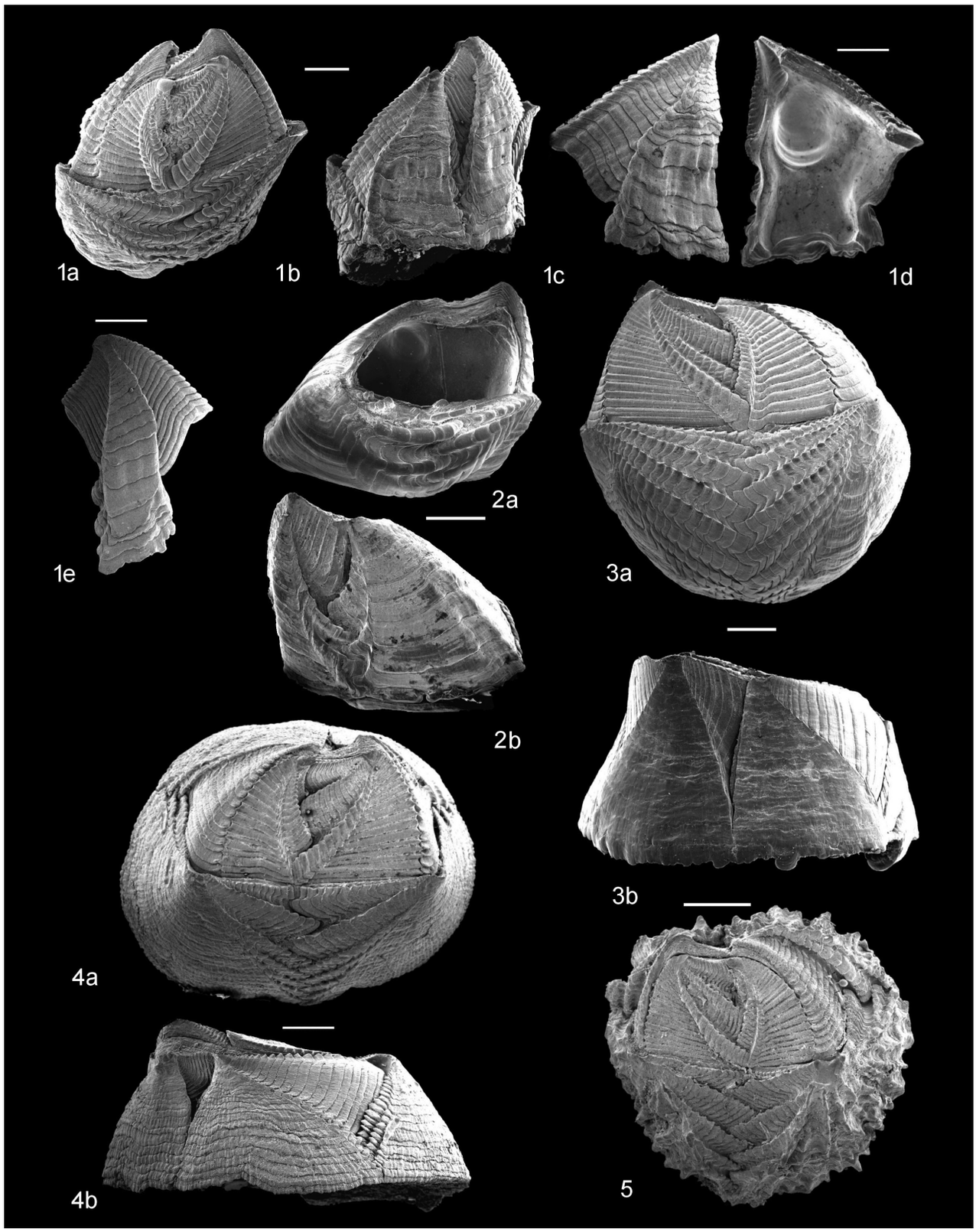

Plate 17. 1a-c. *Gibbosaverruca nitida* (Hoek, 1883), apical and lateral views of shell (1a, b), internal and external views of fixed scutum (1c, d) and fixed tergum (1e); 2a, b. *Cristallinaverruca ankylosa* sp. nov., **paratype**, in apical and lateral views, respectively (MNHN 2016 10457); 3a, b. *Metaverruca recta* (Aurivillius, 1898), apical and lateral views of shell, respectively; 4a, b. *Metaverruca defayae* Buckeridge, 1994, apical and lateral views of shell, respectively; 5. *Metaverruca plicata* Buckeridge, 1994, apical view of shell. All are present-day specimens from New Caledonia, southwestern Pacific. Scale bars equal 1 mm (1a, b, 2-5) and 0.5 mm (1c-e).

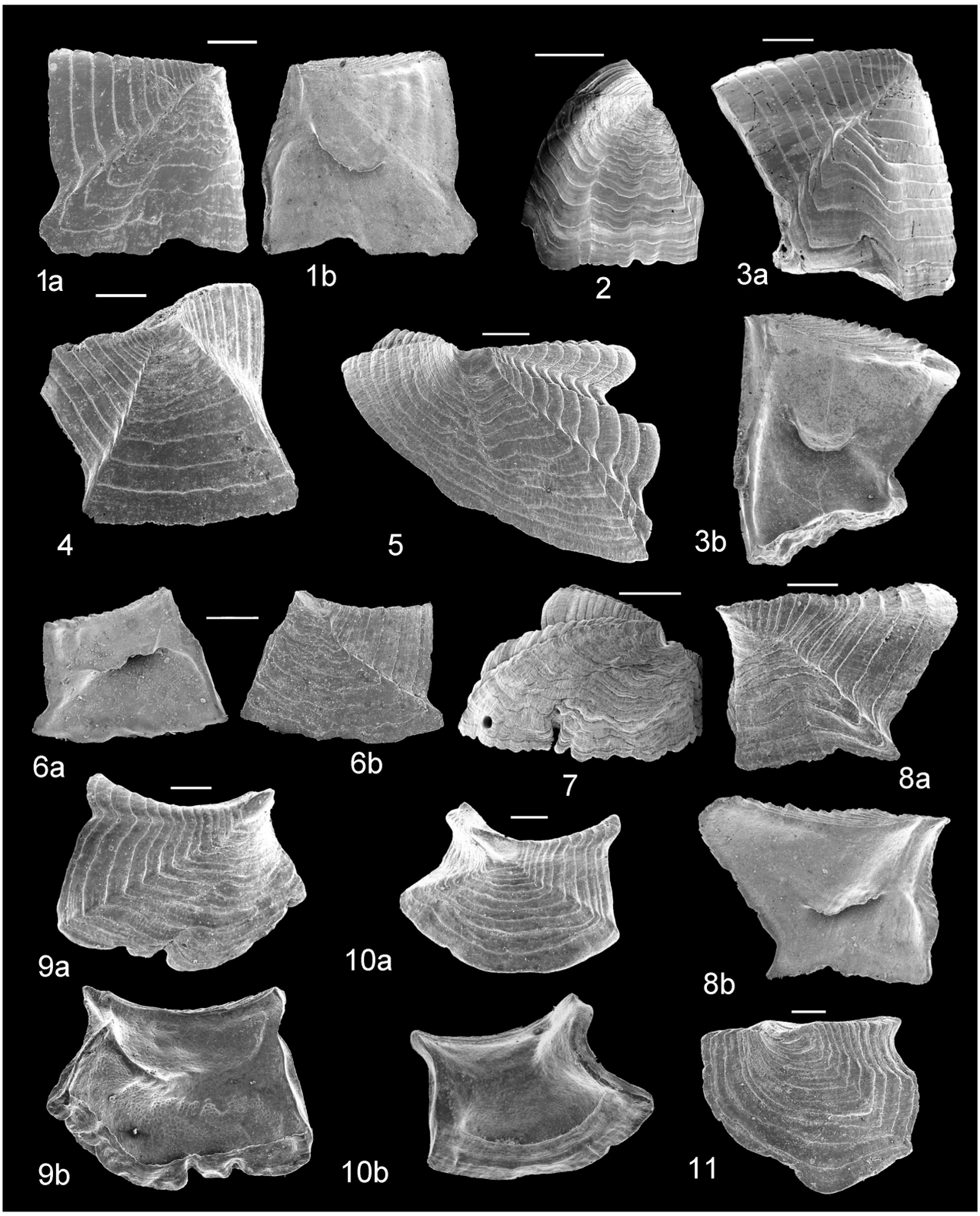

Plate 18. 1, 3-6, 8. *Metaverruca* cf. *norfolkensis* Buckeridge, 1994; 1, 3, 6, 8. scuta (NHMUK IC 1807, 1808, 1834, 1811); 4. tergum (NHMUK IC 1809); 5. carina or rostrum (NHMUK IC 1810); 2, 7. *Metaverruca* cf. *recta* (Aurivillius, 1898), carinae or rostra (NHMUK IC 1812, 1813); 9-11. *Metaverruca reunioni* Foster & Buckeridge, 1994; 9. Fixed scutum (NHMUK IC 1814); 10. Fixed tergum (NHMUK IC 1815); 11. rostrum (NHMUK IC 1816). All are from Pliocene-Lower Pleistocene strata, Rodrigues Ridge, Indian Ocean (sample RR9). Scale bars equal 0.2 mm (9-11) and 0.5 mm (all others).