Bathyal Pliocene–Early Pleistocene cirripedes (Crustacea, Thoracica) from the Rodrigues Ridge, Mascarene Plateau, Indian Ocean. Part 2

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A second set of assemblages of thoracican cirripedes is described from bathyal Upper Pliocene-Lower Pleistocene strata adjacent to the Rodrigues Ridge, Mascarene Plateau (Indian Ocean). A total of 14 species is recorded, including a new species of calanticid, *Aurivillialepas mascarensis* sp. nov., two new verrucids, *Costatoverruca macropluteum* sp. nov. and *C. tredecima* sp. nov., as well as a pachylasmatid, *Pachylasma traceyi* sp. nov. New records for the region include the brachylepadid *Pycnolepas paronai* (De Alessandri, 1895), otherwise only known from the Miocene of the Mediterranean region, the poecilasmatid *Megalasma striatum* Hoek, 1883 and the coronulid (whale barnacle) *Coronula diadema* (Linnaeus, 1767). The total fossil bathyal cirripede fauna for Rodrigues is reviewed, and shown to include 43 taxa, dominated by verrucids (19 species), scalpellids (14 species), with smaller numbers of balanomorphs (7), poecilasmatids (3), brachylepadids (1) and calanticids (1). Eight of these species are living at the present day in the southwestern Pacific, whereas the assemblage has only three species in common with the living fauna of nearby Reunion, one with Madagascar, and two with the northeastern Indian Ocean and Arabian Sea living faunas. The Rodrigues Ridge Plio-Pleistocene fauna shows a high level of endemicity, with approximately 50% of taxa unknown from elsewhere, neither fossil nor living. During the Late Pliocene-Early Pleistocene bathyal cirripede faunas of the Mascarene Plateau were diverse and included a relic pre-Tethys-closure species (*Pycnolepas paronai*), and species which are nowadays restricted to the western Pacific. There has evidently been significant extinction in the bathyal faunas over the last million years. New records of the whale barnacle *Coronula diadema* provide the first evidence for ancient humpback whale migration routes in the Indian Ocean.

Key words: Cainozoic, Recent, Cirripedia, New Caledonia, 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 were also recovered, using piston coring and pipe-dredges, and an Agassiz Trawl was used to obtain material of living deep-sea faunas. A number of pipe-dredge samples that comprised carbonate sands containing basalt fragments and manganese-coated nodules, yielded an abundant fauna of fossil gastropods, bivalves, corals, echinoderm ossicles, fish otoliths and cirripedes. A total of over 1,500 barnacle valves, including some articulated specimens, were picked from the residues.

The first paper on the fossil bathyal cirripedes from this area (Gale, 2020) dealt entirely with material from a single sample (RR9). Subsequently, Steve Tracey supplied material from a number of further sites (RR9A, RR12a, RR13a and RR13b) which proved to contain additional taxa. The present paper deals with the taxonomy of the newly acquired material, and reviews the overall fauna in a palaeobiogeographical context.

Age and localities – The positions of the samples obtained are shown in Figure 1, and details of localities and lithology of the substrate are given in Table 1. The dating provided in Gale (2020) was based on planktonic foraminifera from one sample only, RR9, studied by Professors Paul Bown and Bridget Wade (University College, London), which 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 (Professor Paul Bown, UCL), suggesting a Pleistocene age younger than 1.99 Ma, but older than 0.44 Ma. Further samples (RR12a and RR13a) were sent to Professor Paul Pearson (University of Cardiff) and Professor Bown in March 2020, which yielded a Pleistocene age of 0.61

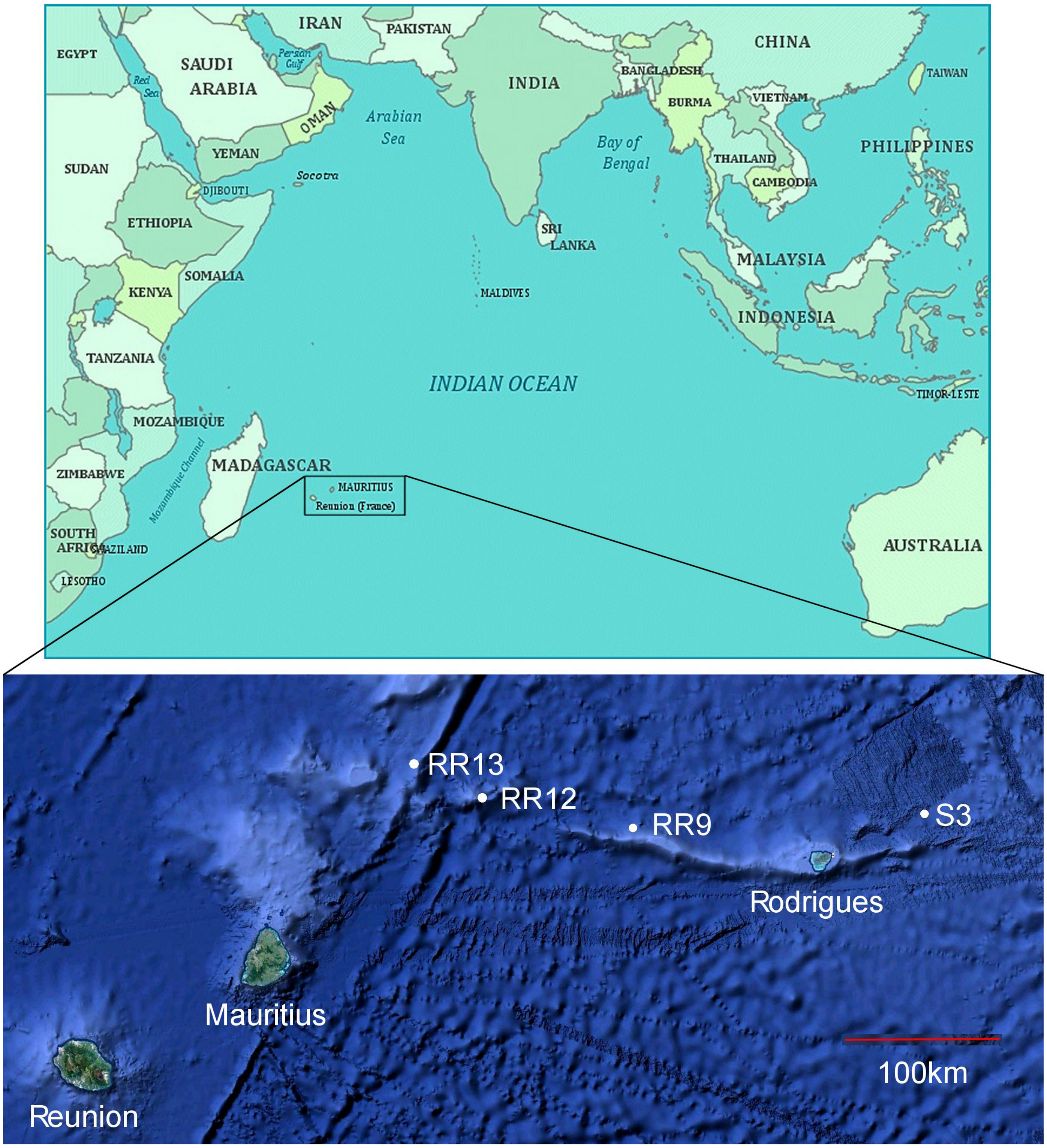

Figure 1. Map of Mascarene Plateau to show collecting sites.

Sample number	Position	Depth	Lithology
RR9	19°18’N 21°67’W	1,800 m	Carbonates, manganese nodules, basalt clasts
RR12a	18°54’N 59°57’W	1,200 m	Carbonates, basalt clasts
RR12b	18°54’N 59°57’W	1,540 m	Carbonates, corals
RR13a	18°28’ N 59°18’W	1,460 m	Carbonates, basalt clasts
RR13b	18°30’N 59°20’W	2,050 m	-

Table 1. Position, depth and lithology of Rodrigues samples.

to 1.88 Ma. A single reworked Miocene foraminifer was present in RR12a, and RR9 yielded a single tooth of the shark *Otodus megalodon* (Agassiz, 1843) which indicates that material older than 3.7 Ma is present (D.J. Ward, pers. comm., Jan. 2020). Thus the samples appear to represent mainly an Early to Middle Pleistocene fauna, possibly with some older material (Pliocene) present.

Repository – All specimens are deposited in the collections of the Natural History Museum, London (NHMUK) and the Natuurhistorisch Museum Maastricht, Netherlands (NMM). An extant specimen figured here is in the Zoological Museum, Florence University (MZUF).

Systematic palaeontology

Order Calanticomorpha Chan, Gale, Glenner, Dreyer, Ewers Saucedo, Pérez-Losada, Kolbasov, Crandall & Høeg, 2020
Family Calanticidae Zevina, 1978
Genus *Aurivillialepas* Newman, 1980

Type species – *Scalpellum calyculus* Aurivillius, 1898

Diagnosis – Sculptured calanticids which possess fourteen plates (paired scuta, terga, upper latera, carinolatera, rostrolatera, as well as single carina, rostrum, subcarina and subrostrum).

***Aurivillialepas mascarensis* sp. nov.**
Plate 1, figs 1-3, 7, 9, 10

Diagnosis– Tergum with basally broadening apicobasal ridge; carina with weak reticulate sculpture of evenly spaced, growth-parallel ridges and fine radial ridges.

Types – The tergum figured here (Pl. 1, fig. 2) is the holotype (NHMUK IC 1818), the other figured valves are paratypes (NHMUK IC 1817, 1819-1822). All are from sample RR12a from Pleistocene strata of Rodrigues Ridge, Indian Ocean.

Material – Three terga, 1 carina, 1 subcarina, 1 rostrum and 1 subrostrum, all from the same locality.

Description – Terga rhombic (Pl. 1, figs 2, 3), twice as tall as broad, scutal surface slightly broader than carinal surface; upper and lower carinal margins discrete in some specimens (Pl. 1, fig. 2), confluent in others (Pl. 1, fig. 3). Apicobasal ridge weakly inclined dorsally (Pl. 1, fig. 2) or ventrally (Pl. 1, fig. 3), flat topped, trifurcating basally (Pl. 1, fig. 3) or carrying fine striae. Valve surface bearing fine apicobasal ridges, interrupted where they intersect with growth increments. Smooth area present adjacent to scutal margin. Carina (Pl. 1, fig. 7) incurved ventrally, with central apicobasal ridge and fine, irregular, radial striae; tergal margins slightly thickened. Subcarina (Pl. 1, fig. 1) triangular, apex slightly incurved, external surface with strong growth ridges and irregular, discontinuous apicobasal ridges. Rostrum and subrostrum distinguished by the relative degree of dorsal incurvature, as shown by comparison with *A. calycula* (Pl. 1, fig. 6; see also Young, 2002, fig. 1). Rostrum (Pl. 1, fig. 10) equilaterally triangular, basal margin concave, external surface with narrow raised rims on convex lateral margins and weak central groove. Rostral margins straight in lateral aspect (Pl. 1, fig. 10a). Subrostrum (Pl. 1, fig. 9) with V-shaped basal margin, central groove and incurved lateral margins (Pl. 1, fig. 9b).

Remarks – *Aurivillialepas mascarensis* sp. nov. differs from the only other species of the genus known from the Indian Ocean, *A. arnaudi* Newman, 1980 (Walters Shoal, south of Madagascar, 3,220 km distant), in its possession of a relatively broad, basally broadening apicobasal ridge on the tergum. In *A. arnaudi*, this is very narrow and corded (see Newman, 1980, figs 9A, D). The carina in *A. arnaudi* bears six strong apicobasal ridges, absent in *A. mascarensis* sp. nov., and the rostrum is equilaterally triangular in the latter species, whereas it is acuminate, narrowing apically in *A. arnaudi* (Newman, 1980, fig. 9B). The tergum is quite similar to that of *A. ornata* (Seguenza, 1876) from the Pleistocene of Sicily and northern Italy (Pl. 1, figs 4, 5), but in that species the carina is strongly ribbed and nodose (Pl. 1, fig. 8). It appears likely that the extant *A. calycula* (Aurivillius, 1898) from the northeastern Atlantic (e.g., Newman, 1980; Innocenti *et al*., 2016) is a junior synonym of *A. ornata* from the Pleistocene of Sicily (Gale *et al*., in prep.). *Aurivillialepas mascarensis* sp. nov. differs from *A. rhabdota* (see Young, 1999, 2002) from the Atlantic off Brazil in the stronger apicobasal ridging on the terga.

Order Scalpellomorpha Buckeridge & Newman, 2006
Family Scalpellidae Pilsbry, 1907
Genus *Arcoscalpellum* Hoek, 1907

Type species – *Scalpellum michelottianum* Seguenza, 1876.

***Arcoscalpellum michelottianum* (Seguenza, 1876)**
Plate 5, fig. 7

Material – Numerous terga, scuta and carinae from sample RR12a, fewer from RR9, RR13a and RR13b (Table 3), as well as a single carinolatus from RR12a.

Remarks – The carinolatus from RR12a is figured here (Pl. 5, fig. 7) for comparison with the same plate from a present-day specimen from the South China Sea (Pl. 5, fig 8). The plates are similar in overall construction, but the umbo of the present-day specimen is slightly more incurved, and the upper latus margin is less steeply inclined. The plates are of similar size, and it is not clear whether the differences are attributable to intraspecific or regional variations.

Order Lepadoidea Gale, Chan, Glenner, Dreyer, Ewers Saucedo, Pérez-Losada, Kolbasov, Crandall & Høeg, 2020
Family Poecilasmatidae Annandale, 1909
Genus *Megalasma* Hoek, 1883

Type species – Megalasma striatum Hoek, 1883

***Megalasma striatum* Hoek, 1883**
Plate 4, fig. 8.

Material – Two scuta from RR12a.

Remarks – The scuta have the typical morphology of this species, with an oblique ridge separating tergal and carinal surfaces, which have different sculptures. The tergal portion bears evenly spaced commarginal growth increments which are finely striate, whereas the carinal portion bears coarser striae which are subparallel with the carinal margin (compare with figures in Chan *et al*., 2009, fig. 26). This species is quite widely distributed in the western Pacific, with records extending from New Zealand and New Caledonia through the Philippines northwards to Japan. Nilsson-Cantell (1938) did not record this species from the Indian Ocean.

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

Type species – Lepas anatifera Linnaeus, 1758

***Lepas pectinata* Spengler, 1793**
Plate 4, fig. 9

Material – A single tergum from RR12a.

Remarks – The new record of a tergum is the second for the region (Gale, 2020). The species is epipelagic and cosmopolitan.

Order Brachylepadomorpha Withers, 1923
Family Brachylepadidae Woodward, 1901
Genus *Pycnolepas* Withers, 1914

Type species – Pollicipes rigidus Sowerby, 1836

***Pycnolepas paronai* (De Alessandri, 1895)**
Plate 2, figs 1-11

*1895 *Pollicipes paronai* De Alessandri, p. 260, pl. 3, fig. 8a-f.
1906 *Pollicipes paronai* De Alessandri – De Alessandri, p. 248, pl. 13, figs 1-9.
1914 *Pycnolepas paronai* (De Alessandri) – Withers, p. 184, pl. 7, figs 1-4.
1953 *Pycnolepas paronai* (De Alessandri) – Withers, p. 350, pl. 60, figs 7-10.
2007 *Pycnolepas paronai* (De Alessandri) – Jagt *et al*., p. 41.

Diagnosis – Large species; apex of scutum strongly incurved dorsally. Scuta flat, interior surface adjacent to occludent margin broad; intricate sculpture of regularly spaced, ridged growth increments intersecting with fine apicobasal ridges.

Type – The lectotype, designated by Withers (1914, p. 185), is an unregistered scutum, illustrated by De Alessandri (1895, pl. 3, fig. 8a, b), contained in the Luigi Di Rovasenda Collection (now at the Museo Regionale di Scienze Naturali, Torino), from Chieri, southeast of Torino, northern Italy and of Early Miocene (Aquitanian, *c*. 20-23 Ma) age.

Material – 73 valves, including scuta, terga, upper latera, carinae and rostra. Some of these valves are very large, with scuta reaching a height of 40 mm. All are from the Pleistocene, locality RR12a, west of Rodrigues, Indian Ocean.

Description – Scuta flat, apex incurved dorsally, occludent margin strongly convex, tergal margin concave (Pl. 2, figs 1-4). Curved apicobasal ridge, of variable width, generally broader in larger individuals (compare Pl. 2, fig. 2 and fig. 4b). Interior of scuta with flat, broad occludent surface and elongated tergal notch. Terga (Pl. 2, figs 6-8) rhomboidal, apicobasal ridge narrow, straight, scutal auricle variably marked. Region adjacent to scutal margin concave. Upper latus (Pl. 2, fig. 5) three times taller than broad, external surface flat, bearing transverse ridges. Carinae (Pl. 2, figs 9, 10) 2-3 times taller than broad, transverse section concavo-convex. Rostrum (Pl. 2, fig. 10) 1.5 times taller than broad, slightly incurved. External surfaces of carina and rostrum bear undulating transverse ridges and fine apicobasal ribbing.

Remarks – The material agrees with the Italian specimens figured by Withers (1953, pl. 60, figs 7-10) in the shape and sculpture of the rostrum, carina, scutum and tergum, but confirmation of conspecificity really requires re-examination of topotypical material. The species was known previously only from the Lower and Middle Miocene of the Torino area, northern Italy, but there is also material from the Lower Miocene of Carboneras, southeastern Spain (Pl. 2, figs 1, 7; J.W.M. Jagt, pers. comm., March 2020). It therefore appears that *P. paronai* had a distribution through the conjoined pre-Mediterranean and Indian oceans, which closed at 14 Ma (Hamon *et al*., 2013), and the species survived in the western Indian Ocean.

Order Verrucomorpha Pilsbry, 1916
Family Verrucidae Darwin, 1854
Genus *Costatoverruca* Young, 1998

Type species – Verruca nexa var. *alba* Pilsbry, 1907, by original 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 – There is a detailed discussion of this genus and its affinities in Gale (2020). The discovery of two new species in samples RR12a, RR13a and RR13b is of interest, because these, together with *C. baxteri* Gale, 2020, share a large number of characters with a Pleistocene to Recent Mediterranean species described as *Verruca crebricosta* by Seguenza (1873, p. 88, pl. 5, fig. 3), which is here referred to *Costatoverruca* and new material referred to this species is illustrated from Sicily (Pl. 3, figs 1, 2, 16).

***Costatoverruca macropluteum* sp. nov.**
Plate 3, figs 3, 10, 15

Diagnosis – Myophore very large, horizontal, positioned close to basal margin; occludent wing of fixed scutum, broad, occludent margin curved. Fixed scutum-tergum contact simplified. Fixed tergum broad and low.

Types – The associated valves figured (Pl. 3, fig. 3) are the holotype (NHMUK IC 1832), from Pleistocene strata (sample RR13B).

Material – Seven valves from RR13B, mostly plates of a single individual (fixed scutum and tergum, carina, rostrum) and a single fixed scutum from RR12a.

Origin of name – Latin *macro*, meaning large, and *pluteum*, meaning shelf, in allusion to the large, horizontal myophore.

Description – Fixed scutum (Pl. 3, fig. 3c, d) robust, trapezoidal, tapering towards tergal margin. Occludent wing large, with thickened margin, distal articular ridge simple, tergal notch flat, positioned on tergal margin, proximal articular ridge absent. Large scutal adductor scar, broad myophore extending horizontally from base of scar, positioned close to basal margin (Pl. 3, fig. 3d, f, g). Fixed tergum (Pl. 3, fig 3e) low, broad, with long occludent wing and well-developed scutal auricle. Rostrum (Pl. 3, fig. 3a) oval, convex, with two ridges for interpenetrant carinal contact, separated by groove. Carina (Pl. 3, fig. 3b) weakly convex, bearing three ridges for rostral contact, upright, with process for articulation with fixed tergum. Moveable tergum (Pl. 3, fig. 10) rhomboidal, with three ridges for articulation with moveable scutum. Moveable scutum (Pl. 3, fig. 15) triangular, occludent margin convex, with three ridges for contact with moveable tergum.

Remarks – The modified, secondarily simplified, fixed scutum-tergum articulation is unique in verrucids. The distal articular ridge is lost and the blunted proximal ridge separates the occludent margin from a flat tergal notch, with which the flattened margin of the fixed tergum articulates. This might be viewed as the continuation of a trend seen in *C. tridecima* sp. nov. (see below), but it is remarkable, because the overall evolution of the articulation in the family is towards greater complexity (Gale 2014, 2020). The development of the myophore is also remarkable (Pl. 3, fig. 3d, f, g) because it is essentially an expanded adductor ridge (compare with Pl. 3, figs 4, 7) which has enlarged and moved to a basal position. It is very different from the myophores developed in *Metaverruca* (Pl. 3, fig. 12) and *Verruca* (Pl. 3, fig 14), which are positioned on a sheet-like structure extending from the tergal margin to the rostral margin, on which the distal articular ridge is positioned. This condition was also present in the Late Cretaceous *Priscoverruca* (Gale, 2014).

***Costatoverruca tredecima* sp. nov.**
Plate 3, figs 7-9, 11, 13

Diagnosis – *Costatoverruca* in which the fixed scutum and tergum have elongated occludent wings with convex occludent margins; fixed scutum with large adductor scar and adductor ridge; fixed tergum low, triangular.

Type – The fixed scutum figured here (Pl. 3 fig. 7) is the holotype (NHMUK IC 1835). The other figured plates are paratypes (NHMUK IC 1836-1839), all from Pleistocene sediments (sample RR13a).

Material – 12 plates from RR13a.

Derivation of name – Latin, meaning thirteen, in reference to the locality, RR13a.

Description – Fixed scutum trapezoidal, basal margin convex, occludent wing large, triangular, making up one-third of valve; occludent margin convex, thickened, occludent wing bearing evenly spaced, straight growth increments; external sculpture of body of valve of coarse, imbricating growth increments, six poorly defined apicobasal ridges; interior of valve with large scutal adductor scar and prominent adductor ridge; proximal articular ridge long, forming tergal margin of valve, tergal notch deep, vertically orientated. Fixed tergum low, central ridge triangular, occludent wing broad, margin thickened, convex; scutal auricle triangular. Rostrum convex, bearing two large ridges for carinal articulation, separated by deep groove. Carina triangular, bearing two broad ridges and minor ridge, separated by two grooves.

Remarks – *Costatoverruca tredecima* sp. nov. differs from *C. baxteri* Gale, 2020 (Pl. 3, figs 4, 5 herein) in that the fixed scutum has a convex, rather than straight, basal margin, in the presence of six coarse apicobasal ridges (absent in *C. baxteri*) and the blunt apex, which is acuminate in *C. baxteri*. It differs from *C. macropluteum* sp. nov. (see above, Pl. 3, fig. 3c, d) in that the scutal adductor ridge does not bear a flange and is above the basal margin, in the taller fixed tergum and the presence of well-defined proximal and distal articular ridges on the fixed scutum.

Genus *Metaverruca* Pilsbry, 1907

Type species – *Verruca recta* Aurivillius, 1898

***Metaverruca recta* (Aurivillius, 1898)**
Plate 4, fig. 10

Material – A single well-preserved shell, lacking moveable valves, from RR12a.

Remarks – This individual is better preserved than those described from RR9 (Gale, 2020, pl. 17, figs 2, 7) and shows the characteristic form of the species (compare with Gale, 2020, pl. 17, fig. 3).

Order Balanomorpha Pilsbry, 1916
Superfamily Chthamaloidea Darwin, 1854
Family Pachylasmatidae Utinomi, 1968
Subfamily Pachylasmatinae Utinomi, 1968
Genus *Pachylasma* Darwin, 1854

Type species – *Balanus giganteus* Philippi, 1836

Diagnosis – Adult with fixed shell pattern of six parietal plates (carina, carinomarginal, marginal, rostral plate). Length of scutal basal margin half or more length of occludent margin; external growth lines undulating, apicobasal striae present. Tergum triangular, spur absent, basal margin straight, with large ridges for adductor attachment which protrude from the margin (modified after Jones, 2000, p. 185).

***Pachylasma traceyi* sp. nov.**
Plate 5, figs 1-6; Plate 6, figs 3-6

Diagnosis – Large *Pachylasma* in which the exterior of the scutum bears fine, straight commarginal ridges, without apicobasal ridges, and is separated into tergal and occludent surfaces by a deflection of the ridges; interior of scutum with adductor ridge and ridged lateral depressor pit.

Types – The scutum illustrated in Pl. 6, fig. 3a, b is the holotype (NHMUK IC 1857). The other scuta illustrated (Pl. 6, figs 4-6) are paratypes (NHMUK IC 1858-1860), as are the two terga (Pl. 5, figs 3, 6; NHMUK IC 1852, 1855).

Material – Several hundred loose valves from samples RR12a and RR13b, including 26 scuta and 10 terga.

Derivation of name – After Stephen Tracey, who rescued the Rodrigues Ridge samples from destruction and eventually sent them to the author.

Description – Scutum outline forms isosceles triangle, with basal and scutal margins of equal length; occludent and tergal margins straight, basal margin convex to slightly sinuous (Pl. 6, figs 3-6). External surface divided into slightly raised, triangular occludent surface and depressed tergal surface, boundary marked by deflection of ribbing. Commarginal ridges fine, evenly spaced, converging and weakening towards tergal margin. Ridges straight, but undulate weakly on very large valves (Pl. 5, fig. 5a), which display weak radial folds towards occludent margin. Interior of scuta with long, narrow adductor ridge, narrow articular ridge, not extending beyond tergal margin; lateral scutal depressor pit with 3-5 ridges and grooves, rostroscutal depressor pit present but poorly defined. Terga (Pl. 5, figs 3, 6) triangular, margins straight, occludent margin weakly convex in large specimens (Pl. 5, fig. 6). External surface separated into two triangular regions by weak apicobasal folds. Interior of tergum with ridges and grooves for tergal depressor; these extend over half of basal margin, and decrease in size towards the occludent margin. Adductor ridges prominent on external view of basal margin. Compartments tall, large (commonly with height of 40 mm), parietes smooth or with weak commarginal growth lines; thickened, inflected basal margin. Sheath extends over apical half of plates, region basal to sheath weakly ribbed. Carina (Pl. 5, fig. 5) triangular, basal margin broad. Carinomarginal (Pl. 5, fig. 1) with very narrow sheath, marginal with broad triangular sheath (Pl. 5, fig. 2). Rostral plate low, concavo-convex (Pl. 5, fig. 4).

Remarks – Assignation to *Pachylasma* was confirmed by tergal morphology; the distinctive *Pachylasma* terga (Jones, 2000, figs 20, 23, 26) lack a spur, have a broad zone of tergal depressor grooves and the intervening ridges form tooth-like projections on the basal margin, visible on the exterior face (compare Pl. 6, figs 1c, 1d with Pl. 5, figs 3, 4). This is important, because the associated scuta in RR12a bear a close resemblance to those of *Hexelasma aureolum* Jones, 2000 (her fig. 52a, b), in the external sculpture, internal apical rugosities and large lateral depressor pit.
The very large size of the compartments initially suggested comparison with the Mediterranean (Pleistocene and extant) *P. giganteum* (Philippi, 1836), the only equally large species of the genus known to date (Jones, 2000). However, the opercular plates differ very significantly in sculpture, shape and internal features from those of *P. giganteum* (Pl. 6, figs 1, 2); in particular, the scuta of that species are tall and narrow, bear up to five apicobasal ridges and strongly undulating, coarse growth increments. In *P. traceyi* sp. nov. (Pl. 6, figs 3-6), there is only a single, weak apicobasal ridge, the growth increments do not undulate and are narrow, and the rostrobasal angle is more acute, the basitergal angle more obtuse. The scutal interior of *P. giganteum* is smooth (Pl. 6, figs 1, 2), without an adductor ridge, and the pit for the lateral depressor muscle is poorly defined, but rather better so in large specimens (Pl. 6, fig. 2B). In *P. traceyi* sp. nov. an adductor ridge is present, the lateral depressor pit bears three to five coarse ridges

and the apical interior is rugose (Pl. 6, figs 5B, 6B, 7B, 8B). In *P. bacum* Jones, 2000, *P. ovatum* Jones, 2000, *P. laeviscutum* Jones, 2000 and *P. scutistriata* Broch, 1922 (Pl. 6, fig. 7), all from the southwestern Pacific, the sculpture of the external surface and interior of the scutum are closer to the condition seen in *P. giganteum*, and possess coarsely undulose growth ridges; only *P. ovatum* has a ridged lateral depressor pit. The terga in *P. giganteum* (Pl. 6, figs 1c, d) have a sharply defined ridge adjacent to the scutal margin, absent in *P. traceyi* sp. nov. (Pl. 5, figs 3, 6).

Family Chionelasmatidae Buckeridge, 1983
Genus *Chionelasmus* Pilsbry, 1911

Type species – *Catophragmus darwini* Pilsbry, 1907

***Chionelasmus darwini* (Pilsbry, 1907)**
Plate 4, figs 1-7, 11

Synonymy – See Jones (2000, p. 153).

Material – Over 50 isolated valves from RR12a, of Pleistocene age, Rodrigues Ridge.

Remarks – The material collected agrees closely with living specimens of the species; *C. darwini* (Pl. 4,fig. 1) is a wide-ranging modern species in the Pacific and Indian oceans, having been recorded from Hawaii to, Madagascar (Yamaguchi, 1998), and a living specimen has been collected from off Rodrigues (Nilsson-Cantell, 1928). Yamaguchi (1998) compared the morphology of populations across the range of the species, and named the Indian Ocean form *C. darwini cantelli*, based upon differences in the morphology of the opercular plates. The Rodrigues fossil material appears to be closer to the Indian Ocean subspecies in the form of the terga, which have a sharper, more acute basitergal termination, but also possess a very marked apicobasal groove on the external face on the basal side of the tergal ridge (Pl. 4, fig. 6). This is not apparent in either subspecies in Yamaguchi's illustrations (1998, fig. 2), or in those of Jones (2000, fig. 2C), but this may just be a problem of comparing drawings with photographs. It is also notable that the adductor ridge on the scutum is broad in both Jones' (2000, fig. 2B) material from New Caledonia, and the Rodrigues material (Pl. 4, fig. 3) described here, although for Yamaguchi (1998) this was a character of *C. darwini cantelli*. *Chionelasmus darwini* was recorded by Buckeridge (1983) from the Upper Eocene of Victoria, Australia, but the scutum he figured (fig. 46a, b) differs from the extant and Pliocene material in a number of features, most notably the very broad adductor ridge and the acute basiscutal angle.

Superfamily Coronuloidea, Leach, 1817
Family Coronulidae Leach, 1817
Genus *Coronula* Lamarck, 1802

Type species – *Lepas diadema* Linnaeus, 1767

***Coronula diadema* (Linnaeus, 1767)**
Plate 7, figs 1-3

Material – One group of associated compartments from RR12A which were reconstructed (rostrum, carina, marginals) and some isolated valves (RR12a, 13a), all of Pleistocene age, Rodrigues Ridge.

Remarks – Identification to species level is made by comparison with specimens of present-day *C. diadema* (Pl. 7, fig. 1), with which the Rodrigues material is closely similar in all details. *Coronula bifida* Bronn, 1831 differs in features such as the shallow sheath, bifurcating parietal ribs and stronger transverse ridging on the parietes (Collareta *et al*., 2018). *Coronula* spp. are commensal with the humpback whale, *Megaptera novaeangliae* (Borowski, 1781), 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*. The occurrences of *C. diadema* recorded here from the Rodrigues Ridge are plotted on fig. 3 of Bianucci *et al.* (2006) in Fig. 2, and provide the first evidence of fossil whale barnacles in the western Indian Ocean, confirming the known migration path northwards from Antarctica to the Madagascar region.

The oldest probable coronulid is *Emersonia* Ross, 1967 in Ross & Newman, 1967, from the Eocene of Florida.

Family Bathylasmatidae Newman & Ross, 1971
Subfamily Hexelasmatinae Newman & Ross, 1976
Genus *Hexelasma* Hoek, 1913

Type species – *Hexelasma velutinum* Hoek, 1913

***Hexelasma* aff. *foratum* Jones, 2000**

Material – Twelve terga, 10 from RR9a, one each from RR12a, RR13a, all from Plio-Pleistocene sediments, Rodrigues Ridge.

Remarks – The new specimens of terga are very similar to those figured by Gale (2020, fig. 2.4; pl. 4, figs 11, 14), and differ significantly from those of *H. foratum* Jones, 2000 in the broadly rounded spur, which is confluent with the base of the scutal margin. In *H. foratum*, these are separated by a notch.

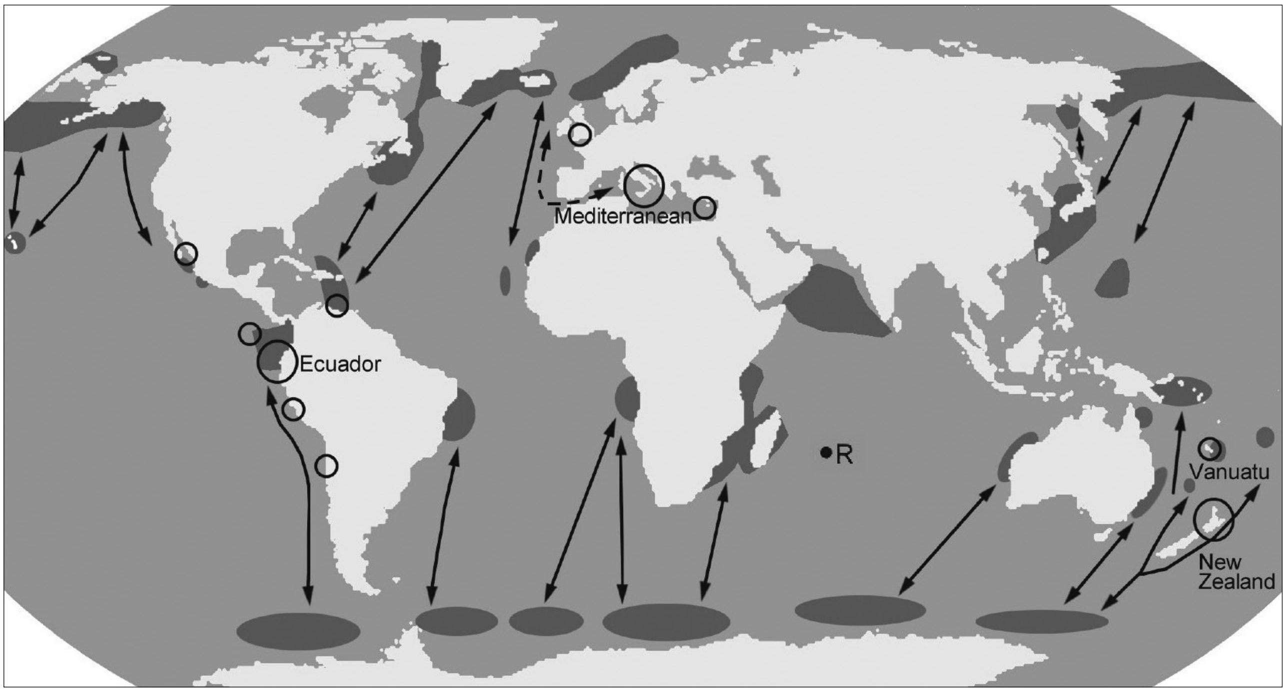

Figure 2. Map of the distribution of fossil *Coronula* (circled) in relation to the migratory pathways of (arrowed) and regions colonised by (grey) humpback whales. The new material from Rodrigues (red dot) provides evidence of early Pleistocene migration routes in the southwestern Indian Ocean. Modified after Bianucci *et al*., (2006, fig. 3).

Conclusions

The new fossil bathyal material from sites on the Rodrigues Ridge significantly augments material from RR9 described by Gale (2020), with the addition of seven new taxa from sites RR12a and RR13a, b (Table 2 gives an overview of all taxa found). These include four new species (*Pachylasma traceyi* sp. nov., *Costatoverruca tredecima* sp. nov., *Costatoverruca macropluteum* sp. nov., *Aurivillialepas mascarensis* sp. nov.), abundant large specimens of the brachylepadid *Pycnolepas paronai*, numerous valves of *Chionelasmus darwini*, and whale barnacles (*Coronula diadema*). The material of *Pycnolepas paronai* is of particular interest, because the species was previously known only from the bathyal Lower Miocene of the Mediterranean (Italy, Spain), and must therefore have had a wider distribution before the closure of Tethys at about 14 Ma (Hamon *et al*., 2013), and survived, for a while, in the Indian Ocean. This is also the youngest brachylepadid known, as the living *Neobrachylepas* has now been transferred to another group (Chan *et al*., 2020).

There are remarkable differences between the assemblages found at different sites along the Rodrigues Ridge (Table 3). The most diverse faunas were collected at RR9, where 36 taxa are present, whilst 13 taxa were found in the next most diverse assemblage, RR12a. There are only six taxa in common between the two assemblages, which are 120 km apart. Possible reasons for these differences could be differences in age, or more probably because the samples reflect different original biotopes.

Table 3 provides a summary of all the fossil cirripede material known from the Rodrigues Ridge, and includes 43 taxa in total, dominated by verrucids (19 species), scalpellids (14 species), with smaller numbers of balanomorphs (7), poecilasmatids (3), brachylepadids (1) and calanticids (1). Eight of these species are living at the present day in the southwestern Pacific (Jones, 2007), seven in the South China Sea (Jones *et al*., 2007), and four off Taiwan (Chan *et al*., 2009). The Rodrigues assemblage has only three species in common with the living fauna of nearby Reunion (Foster & Buckeridge, 1994), one with Madagascar (Ren, 1989), and two species in common with the northeastern Indian Ocean and Arabian Sea living faunas (Stubbings, 1936; Nilsson-Cantell, 1938). The Rodrigues Ridge Plio-Pleistocene fauna shows a high level of endemicity, with approximately 50% of taxa unknown from elsewhere.

It is apparent from the present study that there must have been major changes in the bathyal cirripede faunas of the Rodrigues region over the last two million years. Most notably, the extinction of ancient Tethyan species (*Pycnolepas*), the extinction of numerous endemic taxa, especially verrucids, and local extinction of species still found in the southwestern Pacific.

The records of the whale barnacle *Coronula diadema* provide evidence of migration pathways of the humpback whale in the Indian Ocean during the early Pleistocene (Fig. 2).

Order Scalpellomorpha Buckeridge & Newman, 2006
Family Scalpellidae Pilsbry, 1907 (**12**)
Arcoscalpellum michelottianum (Seguenza, 1876)
Arcoscalpellum sp. 1
Arcoscalpellum sp. 2
Amigdoscalpellum mamillatum (Aurivillius, 1898)
Catherinum busselli Gale, 2020
Catherinum sp.
Costatolepas buckeridgei Gale, 2020
Graviscalpellum pedunculatum (Hoek, 1883)
Unidentified scalpellid 1
Unidentified scalpellid2
Unidentified scalpellid3
Unidentified scalpellid4

Superfamily Lepadoidea Chan *et al*., 2020 (**3**)
Family Lepadidae Darwin, 1852
Lepas pectinata Spengler, 1793

Family Poecilismatidae Annandale, 1909
Megalasma striata Hoek, 1883
Glyptelasma carinata Hoek, 1883

Order Calanticomorpha Chan *et al*., 2020 (**1**)
Family Calanticidae Zevina, 1978
Aurivillialepas mascarensis sp. nov.

Order Brachylepadomorpha Withers, 1923 **(1)**
Family Brachylepadidae Woodward, 1901
Pycnolepas paronai (De Alessandri, 1895)

Order Verrucomorpha Pilsbry, 1916 (**19**)
Family Verrucidae Darwin, 1854
Altiverruca capsa Gale, 2020
Altiverruca fusione Gale, 2020
Altiverruca cf. *galapagosa* (Zevina, 1973)
Altiverruca sp. 1
Gibbosaverruca nitida (Hoek, 1883)
Gibbosaverruca youngi Gale, 2020
Gibbosaverruca sp. 1
Gibbosaverruca sp. 2
Cristallinaverruca jonesae (Buckeridge, 1997)
Cristallinaverruca ankylosa Gale, 2020
Newmaniverruca multitabulata Gale, 2020
Costatoverruca baxteri Gale, 2020
Costatoverruca macropluteum sp. nov.
Costatoverruca duodecima sp. nov.
Rostratoverruca darwini Gale, 2020
Metaverruca recta (Aurivillius, 1898)
Metaverruca cf. *recta* (Aurivillius, 1898)
Metaverruca reunioni Foster & Buckeridge, 1995
Metaverruca cf. *norfolkensis* Buckeridge, 1994

Order Balanomorpha Pilsbry, 1916 **(5)**
Superfamily Chthamaloidea Darwin, 1854
Family Pachylasmatidae Utinomi, 1968
Subfamily Eolasmatinae Buckeridge, 1983
Neoeolasma rodriguesensis Gale, 2020
Neoeolasma sp.
Subfamily Pachylasmatinae Utinomi, 1968
Pachylasma traceyi sp. nov.
Family Chionelasmatidae Buckeridge, 1983
Chionelasmus darwini Pilsbry, 1911

Superfamily Coronuloidea Leach, 1817
Family Coronulidae Leach, 1817
Coronula diadema (Linnaeus, 1767)
Family Bathylasmatidae Newman & Ross, 1971
Subfamily Hexelasmatinae Newman & Ross, 1976
Hexelasma aff. *foratum* Jones, 2000

Balanid undetermined

Table 2. List of taxa recorded from Plio-Pleistocene of Rodrigues sites.

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References

Agassiz, L.J.R. 1843. *Recherches sur les poissons fossiles.* Tome III (livr. 15-16). Neuchatel (Imprimerie de Petitpierre).

Annandale, N. 1909. An account of the Indian Cirripedia Pedunculata, Part 1. – Family Lepadidae (sensu stricto). *Memoirs of the Indian Museum* 2(2): 61–137, 7 pls.

Aurivillius, C.W.C. 1898. Cirrhipèdes nouveaux provenant des Campagnes scientifiques de S.A.S. le Prince de Monaco. *Bulletin de la Société zoologique de France*, 23: 189-198.

Bianucci G., Landini, W. & Buckeridge J.S. 2006. Whale barnacles and Neogene cetacean migration routes. *New Zealand Journal of Geology and Geophysics* **49**:115–120. doi: 10.1080/00288306.2006.9515152.

Borowski, G.H. 1781. *Gemeinnüzzige Naturschichte des Tier-*

Name	RR9	RR12a	RR9b	RR13a	RR13b	Occurrences
Lepas pectinata	1	1	-	-	-	Cosmopolitan
Glyptelasma carinata	30	-	-	-	-	Cosmopolitan
Megalasma striatum	-	2	-	-	-	Indo-West Pacific
Aurivillialepas mascarensis	-	8	-	-	-	-
Arcoscalpellum michelottianum	10+	30+	-	2	4	Cosmopolitan
Arcoscalpellum sp. 1	1	-	-	-	-	-
Arcoscalpellum sp. 2	1	-	-	-	-	-
Amigdaloscalpellum mamillatum	2	-	2	-	-	Eastern Atlantic and western Indian oceans
Catherinum busselli	20	-	-	-	-	-
Catherinum sp.	1	-	-	-	-	-
Graviscalpellum cf. *pedunculatum*	1	-	-	-	-	Pacific Ocean
Costatolepas buckeridgei	3	-	-	-	-	-
Unidentified scalpellid 1	1	-	-	-	-	-
Unidentified scalpellid 2	1	-	-	-	-	-
Unidentified scalpellid 3	2	-	-	-	-	-
Unidentified scalpellid 4	1	-	-	-	-	-
Pycnolepas paronai	-	72	-	-	-	Miocene, Mediterranean
Altiverruca capsa	150+	1	-	-	-	-
Altiverruca fusione	3	-	-	-	-	-
Altiverruca sp. 1	2	-	-	-	-	-
Altiverruca cf. *galapagosa*	1	-	-	-	-	Pacific Ocean
Gibbosaverruca nitida	200+	2	-	-	-	Tropical west Pacific
Gibbosaverruca youngi	1	-	-	-	-	-
Gibbosaverruca sp. 1	1	-	-	-	-	-
Gibbosaverruca sp. 2	1	-	-	-	-	-
Cristallinaverruca jonesae	15	-	-	-	-	New Caledonia
Cristallinaverruca ankylosa	2	-	-	-	-	New Caledonia
Newmaniverruca multitabulatum	15	-	-	-	-	-
Costatoverruca baxteri	38	-	-	-	-	-
Costatoverruca macropluteum	-	1	-	-	8	-
Costatoverruca tredecima	-	-	-	12	-	-
Rostratoverruca darwini	4	-	-	-	-	-
Metaverruca recta	-	1	-	-	-	Cosmopolitan
Metaverruca cf. *recta*	6	-	-	-	-	-
Metaverruca reunioni	26	-	-	-	-	Reunion Island
Metaverruca cf. *norfolkensis*	45	-	-	-	-	New Caledonia
Chionelasmus darwini	1	35	-	-	-	Indian and Pacific oceans
Neoeolasma rodriguesensis	4	-	-	-	-	possibly South Atlantic
Pachylasma traceyi	-	200+	-	-	32	-
Hexelasma aff. *foratum*	10	1	-	1	0	New Caledonia
Coronula diadema	-	4	-	-	4	Cosmopolitan
undetermined balanid	1	-	-	-	-	-

Table 3. Distribution of taxa recorded from Plio-Pleistocene of Rodrigues sites, and occurrences elsewhere.

reichs. Berlin and Stralsund (G.L. Lange). 2: 1-196.

Broch, H. 1922. Papers from Dr. Th. Mortensen's Pacific Expedition. 1914-16. No. X. Studies on Pacific Cirripeds. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 73: 215-358.

Bronn, H.G. 1831. Italiens Tertiär-Gebilde und deren organische Einschlüsse: vier Abhandlungen. Heidelberg (Groos): 176 pp.

Buckeridge, J.S. 1983. Fossil barnacles (Cirripedia: Thoracica) of New Zealand and Australia. *New Zealand Geological Survey Paleontological Bulletin* 50: 1-151, 13 pls.

Buckeridge, J.S., Chan, B.K.K. & Lee, S.W. 2018. Accumulations of fossils of the whale barnacle *Coronula bifida* Bronn, 1831 (Thoracica: Coronulidae) provides evidence of a late Pliocene cetacean migration route through the Straits of Taiwan. *Zoological Studies* 57: 54. doi:10.6620/ZS.2018.57-54.

Buckeridge, J.S., Chan, B.K.K. & Lin, J.P. 2019. Paleontological studies of whale barnacles in Taiwan reveal new cetacean migration routes in the western Pacific since the Miocene. *Zoological Studies* 58: 39. doi:10.6620/ZS.2019.58-39.

Buckeridge, J.S. & Newman, W.A. 2006. A revision of the Iblidae and the stalked barnacles (Crustacea: Cirripedia: Thoracica) including new ordinal, familial and generic taxa, and two new species from New Zealand and Tasmanian waters. *Zootaxa* 1136: 1-38.

Chan, B.K.K., Gale, A.S., Glenner, H., Dreyer, N., Ewers Saucedo, C., Pérez-Losada, M., Kolbasov, G.A., Crandall, K.A. & Høeg, J.T. in press, 2020. The evolutionary diversity of the barnacles with an updated classification. *Zoological Journal of the Linnean Society* xx, xx-xx.

Chan, B.K.K., Prabowo, R.E. & Kwen-Shen, L. 2009. *Crustacean fauna of Taiwan: Barnacles, volume 1 – Cirripedia: Thoracica, excluding Pyrgomatidae and Acastinae.* National Taiwan Ocean University, Taipei, 297 pp.

Collareta, A., Insacco, G., Reitano, A., Catanzariti, R., Bosselaers, M. & Biannuci, G. 2018. Fossil whale barnacles from the lower Pleistocene of Sicily shed light on the coeval Mediterranean cetacean fauna. *Carnets de Géologie/ Notebooks on Geology* 18(2): 9-22.

Darwin, C.R. 1851. *A monograph on the sub-class Cirripedia, with figures of all the species. The Lepadidae, or pedunculated crripedes*. London (The Ray Society): xii + 400 pp., 10 pls.

Darwin, C.R. 1854. *A monograph on the sub-class Cirripedia, with figures of all the species, The Balanidae (or sessile cirripedes); the Verrucidae etc., etc., etc.* London (The Ray Society): 684 pp., 30 pls.

De Alessandri, G. 1895. Contribuzione allo studio dei Cirripedi fossili d' Italia. *Bolletino della Società Geologica d'Italia* 13: 234-314.

De Alessandri, G. 1906. Studi monografici sui Cirripedi fossili d'Italia. *Palaeontographica Italia* 12: 207–324, pls 13–18.

Foster, B.A. & Buckeridge, J.S. 1994. Barnacles (Cirripedia, Thoracica) of seas off Réunion Island and the East Indies. *Bulletin du Muséum national d'Histoire naturelle Paris* 16: 345-382.

Gale, A.S. 2014. Origin and phylogeny of the verrucomorph barnacles (Crustacea, Cirripedia, Thoracica). *Journal of Systematic Palaeontology*, http://dx.doi.org/10.1080/14772019.2014.954409

Gale, A.S. 2020. Bathyal Pliocene-Early Pleistocene cirripedes (Crustacea, Thoracica) from the Rodrigues Ridge, Mascarene Plateau, Indian Ocean – Part 1. *Cainozoic Research* 20(2): 151-188.

Hamon, N., Sepulchre, P., Lefebvre, V. & Ramstein, G. 2013. The role of eastern Tethys seaway closure in the Middle Miocene Climatic Transition (ca. 14 Ma). *Climates of the Past* 9: 2687-2702.

Hoek, P.P.C. 1883. Report on the Cirripedia. *Report on scientific results from the exploratory voyages of the Challenger*, *Zoology* 8(25), 1-169.

Hoek, P.P.C. 1907. The Cirripedia of the Siboga Expedition. A. Cirripedia Pedunculata. *Siboga-Expedition Monograph* 31a: 127 pp., 10 pls.

Hoek, P.P.C. 1913. The Cirripedia of the Siboga Expedition. B. Cirripedia Sessilia. *Siboga-Expedition Monograph* 31b: 129-275.

Innocenti, G., Di Geronimo, R. & Newman, W.A. 2015. A range extension of a deep-sea barnacle of the genus *Aurivillialepas* (Scalpellomorpha), a Macaronesian and amphitropical refugial genus having Mesozoic affinities. *Zootaxa* 3974(2): 257-266.

Jagt, J.W.M., Zonova, T.D. & Jagt-Yazykova, E.A. 2007. A review of the Brachylepadomorph cirripede genus *Pycnolepas*, including the first record of an Early Cretaceous species from the Russian Far East. *Zootaxa* 1545: 33-47.

Jones, D.S. 2000. Crustacea Cirripedia Thoracica: Chionelasmatoidea and Pachylasmatoidea (Balanomorpha) of New Caledonia, Vanuatu and Wallis and Futuna Islands, with a review of all currently assigned taxa. *In:* Crosnier, A. (ed.). Résultats des Campagnes MUSORSTOM, volume 21. *Mémoires du Muséum national d'Histoire naturelle* 184: 141–283.

Jones, D.S. 2007. *The Cirripedia of New Caledonia. In:* Payri, C.E. & Richer de Forges, B. (eds). *Compendium of marine species from New Caledonia.* Noumea (Institut de Recherche pour le Developpement): 289-294.

Jones, D.S., Hewitt, M.A. & Sampey, A. 2007. A checklist of the Cirripedia of the South China Sea. *The Raffles Bulletin of Zoology*, *Supplement* 8: 233-307.

Lamarck, J.B. de. 1802. Mémoire sur la Tubicinelle. *Annales du Muséum national d'Histoire naturelle Paris* 1: 461-464.

Leach, W.E. 1817. Distribution systématique de la classe des Cirripèdes. *Journal de Physique* 85: 67-69.

Linnaeus, C. 1758. *Systema Naturae*, edition 12, I, part 2. Holmiae (Laurentius Salvius): 533-1372.

Linnaeus, C. 1767. *Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis.* Ed. 12. 1., *Regnum Animale. 1 & 2*. Holmiae [Stockholm] (Laurentii Salvii): 1-532 [1766], 533-1327 [1767].

Müller, O.F. 1776. *Zoologicae Danicae Prodromus, seu Animaliae Daniae et Norvegiae, Indigenarum characteres, nomina, et synonima imprimis popularium.* Havniae (Hallageriis): 282 pp.

Newman, W.A. 1980. A review of extant *Scillaelepas* (Cirripedia: Scalpellidae) including recognition of new species from the North Atlantic, western Indian Ocean and New Zealand. *Tethys* 9(4): 379-398.

Newman, W.A. & Ross, A. 1971. Antarctic Cirripedia. *Antarctic Research Series* 14: 1-257.

Newman, W.A. & Ross, A. 1976. Revision of the balanomorph barnacles; including a catalog of the species. *Memoirs of the San Diego Natural History Society* 9: 1-108.

Nilsson-Cantell, C.A. 1928. The cirripede *Chionelasmus* (Pilsbry) and a discussion of its phylogeny. *The Annals and Magazine of Natural History* (10)2(1): 445-455.

Nilsson-Cantell, C.A. 1938. Cirripedes from the Indian Ocean in the collection of the Indian Museum, Calcutta. *Memoirs of the Indian Museum*, *Calcutta* 13: 1-81.

Philippi, R.A. 1836. *Enumeratio Molluscorum Siciliae, cum viventium tum in tellure tertiaria fossilium quae in itinere suo observavit*. Halis Saxonicum (Berolini).

Pilsbry, H.A. 1907. The barnacles (Cirripedia) contained in the collections of the U.S. National Museum. *Bulletin of the United States National Museum* 60: 1-122, 11 pls.

Pilsbry, H.A. 1911. Barnacles of Japan and Bering Sea. *Bulletin of the Bureau of Fisheries* 29: 59–84.

Pilsbry, H.A. 1916. The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum; including a monograph of the American species. *Bulletin of the United*

States National Museum 93: 1-366.

Ren, X. 1989. On a collection of Cirripedia Thoracica from Madagascar and adjacent waters. *Bulletin du Muséum national d'Histoire naturelle Paris* 11: 431-468.

Ross, A. & Newman, W.A. 1967. Eocene Balanidae of Florida, including a new genus and species with a unique plan of "turtle barnacle" organisation. *American Museum Novitates* 2288: 1-21.

Seguenza, G. 1873. Ricerche palaeontologiche intorno al Cirripedi Terziarii della provincia di Messina. Parte I. Balanidi e Verrucidi. *Atti dell'Accademica Pontoniana* 6: 1-102, 5 pls.

Seguenza, G. 1876. Ricerche palaeontologiche intorno al Cirripedi Terziarii della provincia di Messina. Parte II. Terza famiglia Lepadi Darwin. *Atti dell'Accademica Pontoniana* 10: 1-101.

Sowerby, J. De C. 1836. Descriptive notes respecting shells figured in plates 11-22 (pp. 335–348). Appendix A to Fitton, W.H. Observations on some of the strata between the Chalk and the Oxford Oolite in the south-east of England. *Transactions of the Geological Society of London* (2)4: 103–389, pls 11–23.

Spengler, L. 1793. Beskrivelse over tvende nye arter af *Lepas*. *Skrifter af Naturhistoriske Selskabet* 2: 103-110.

Stubbings, H.G. 1936. Cirripedia. Scientific report of the John Murray Expedition, 70 pp.

Utinomi, H. 1968. A revision of the deep-sea barnacles *Pachylasma* and *Hexelasma* from Japan, with a proposal of new classification of the Chthamalidae (Cirripedia, Thoracica). *Publications of the Seto Marine Biological Laboratory* 16: 21-39.

Withers, T.H. 1914. Some Cretaceous and Tertiary Cirripedes referred to *Pollicipes*. *The Annals and Magazine of Natural History* 8(14): 167-206, pls 7, 8.

Withers, T.H., 1923. Die Cirripidien der Kreide Rügens. *Abhandlungen der geologische-paläontologische Institut Greifswald* 3: 54 pp., 3 pls.

Withers, T.H. 1953. *British Museum (Natural History). Catalogue of the fossil Cirripedia in the Department of Geology Vol. III. Tertiary*. Dorking (Bartholomew Press): 396 pp., 64 pls.

Woodward, H. 1901.On "*Pyrgoma cretacea*", a cirripede from the Upper Chalk of Norwich and Margate. *Geological Magazine* (4)8: 145-152, pl. 8.

Yamaguchi, T. 1998. Review of *Chionelasmus darwini* (Pilsbry, 1907) (Cirripedia, Balanomorpha): a comparison between the Pacific and Indian Ocean populations. *Species Diversity* 3: 117-131.

Young, P.S. 1998. Cirripedia (Crustacea) from the "Campaign Biacores" in the Azores, including a generic revision of the Verrucidae. *Zoosystema* 20: 31-92.

Young, P.S. 1999. The Cirripedia (Crustacea) collected by the R.V. Marion Drufesne along the Vitoria-Trinidade seamounts. *Zoosystema* 23: 607-624.

Young, P.S. 2002. A reassignment of *Scillaelepas rhabdota* Young, 1999 to *Aurivillialepas rhabdota* (Cirripedia: Thoracica). *Arquivos do Museu Nacional*, *Rio de Janeiro* 60(2): 95-101.

Zevina, G.B. 1978. [A new classification of the Scalpellidae (Cirripedia, Thoracica). 1. Subfamilies Lithotryinae, Calanticinae, Pollicipinae, Scalpellinae, Brochiinae and Scalpellopsinae]. *Zoologicheskii Zhurnal* 7: 998-1005 (in Russian).

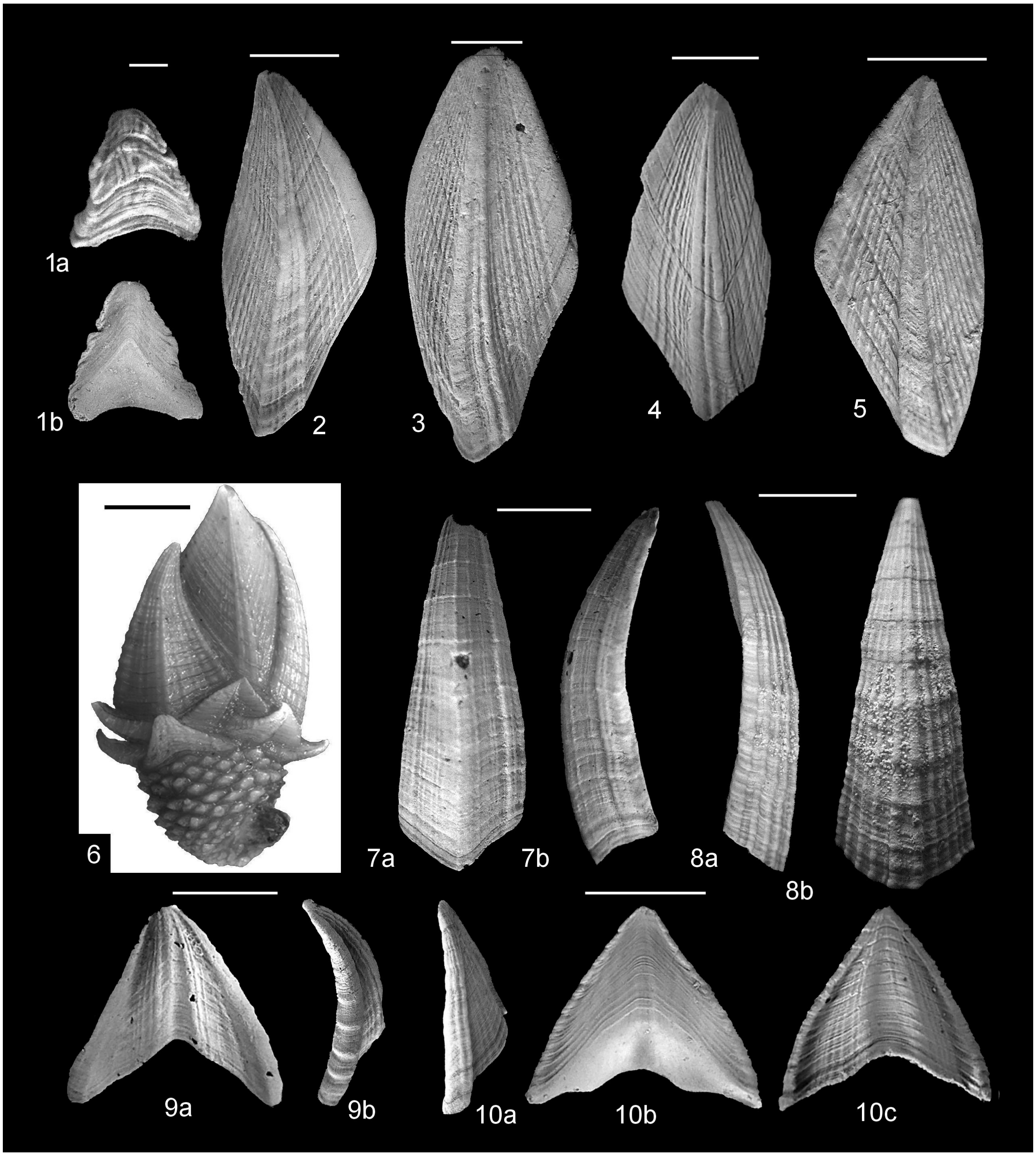

Plate 1. 1-3, 7, 9, 10**.** *Aurivillialepas mascarensis* sp. nov.; 1**.** subcarina (**paratype**, NHMUK IC 1817). 2, 3. terga, 2 is **holotype** (NHMUK IC 1818), 3 is **paratype** (NHMUK IC 1819**); 7.** carina (**paratype**, NHMUK IC 1820); 9. subrostrum (**paratype**, NHMUK IC 1821); 10. rostrum (**paratype**, NHMUK IC 1822). 4, 5, 8. *Aurivillialepas ornata* (Seguenza, 1876). 4. tergum (A. S. Gale Collection); 5. tergum, the original of Withers (1953, pl. 17, fig. 9; NHMUK In. 33678); 8. carina, the original of Withers (1953, pl. 17, fig. 7; NHMUK IC 33674). 6. *Aurivillilepas calycula* (Aurivillius, 1898), lateral view of individual, after Innocenti *et al.* (2015, fig. 4; MZUF 335116). Provenance: 1-3, 7, 9, 10 are from the Plio-Pleistocene of sample RR12a, Rodrigues Ridge, Indian Ocean; 5, 8 are from Pleistocene, Messina, Sicily, Italy; 4 from Lower Pleistocene, Scoppo, near Messina, Italy; 6 is a present-day specimen, Banco de Galicia, 200 km from northwest corner of Iberia, Atlantic Ocean. Scale bars equal 10 mm (6), 5 mm (2-5, 7-10) and 1 mm (1).

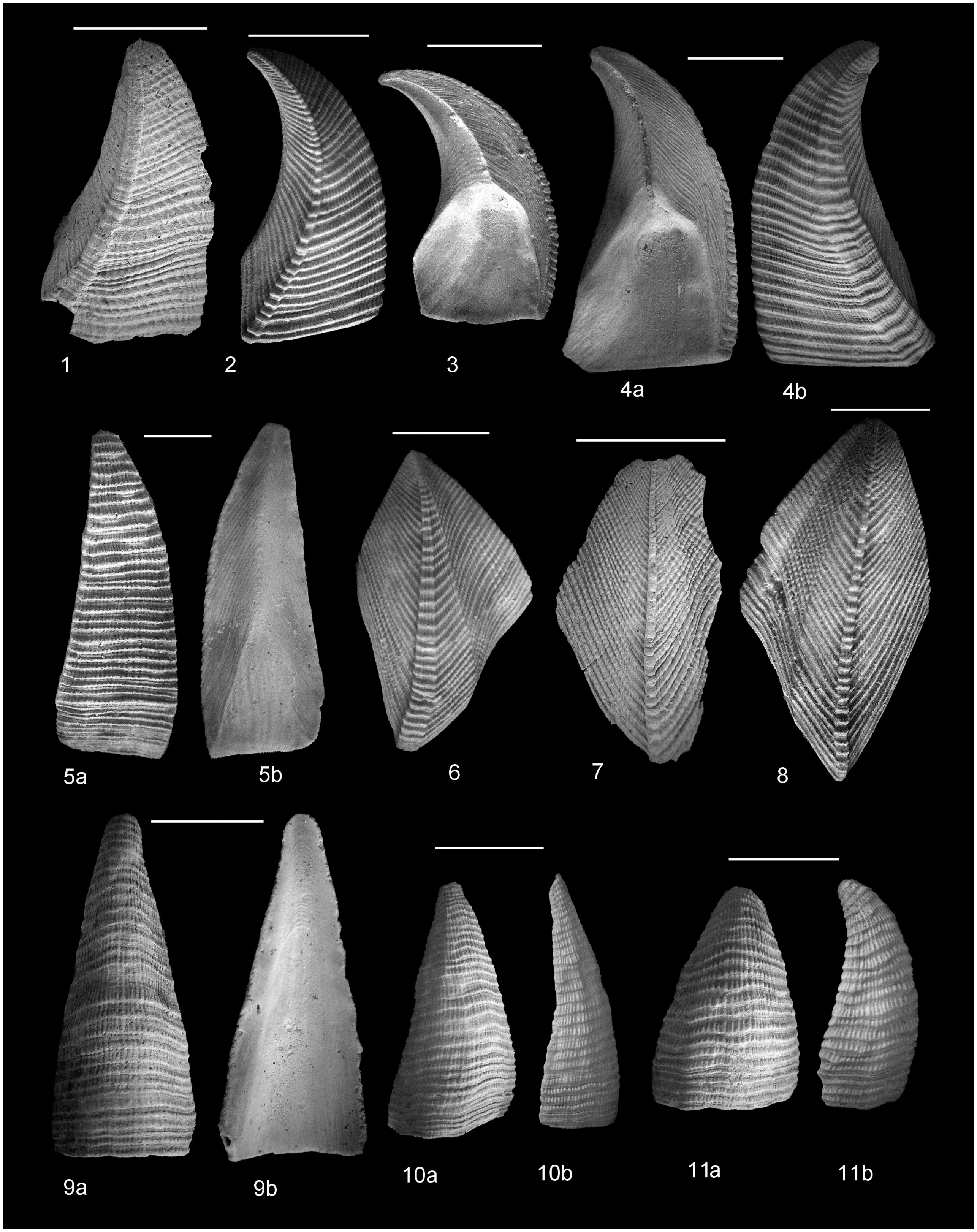

Plate 2. 1-11. *Pycnolepas paronai* (De Alessandri, 1895). 1-4. scuta (1, NHMM 2020 001; 2-4, NHMUK IC 1823-1825); 5. upper latus (NHMUK IC 1826); 6-8. terga (7, NHMM 2020 002; 6, 8, NHMUK IC 1827, 1828); 9, 10. Carinae (NHMUK IC 1829, 1830); 11. rostrum (NHMUK IC 1831). Provenance: 2-6, 8-11 are from sample RR12a, west of Rodrigues, Indian Ocean; Upper Pliocene-Lower Pleistocene. 1, 7 are from the Lower Miocene, Carboneras, Almeria Province, Spain (*ex* J.W.M. Jagt Collection, don. E. Wille). Scale bars equal 10 mm (1-4, 6-11) and 5 mm (5).

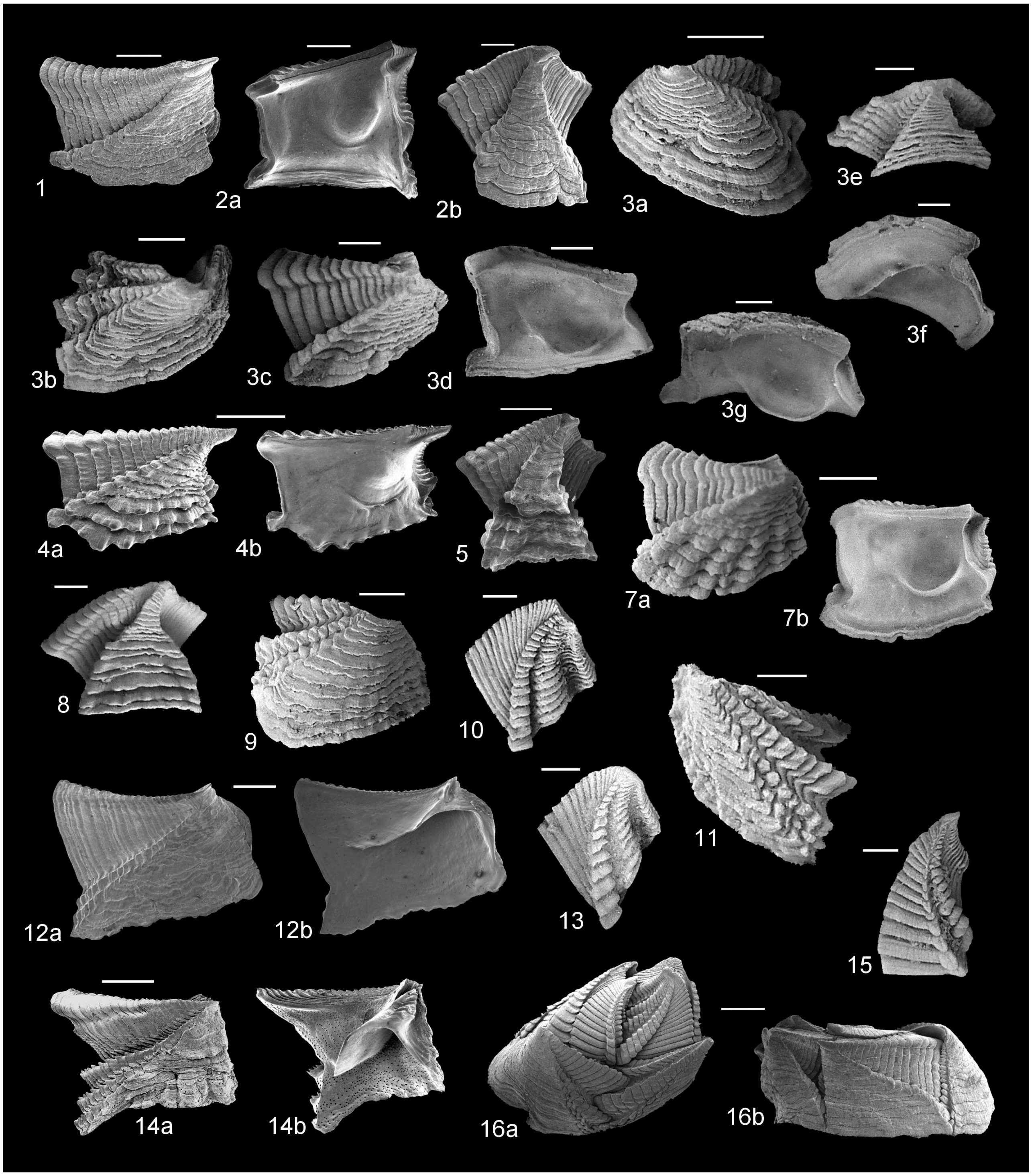

Plate 3. 1, 2, 16. *Costatoverruca crebricosta* (Seguenza, 1873); 1. external aspect of fixed scutum; 2a. internal view of fixed scutum; 2b. external view fixed tergum; 16. entire individual, in scutal-tergal (a) and apical (b) views. 4, 5. *Costatoverruca baxteri* Gale, 2020; 4a, b. external and internal views of fixed scutum, respectively (**holotype**, the original of Gale, 2020, pl. 14, fig. 1; NHMUK IC 1768); 5. fixed tergum, the original of Gale (2020, pl. 14, fig. 2; NHMUK IC 1863). 3, 10, 15. *Costatoverruca macropluteum* sp. nov.; 3. associated plates from an individual (**holotype**, NHMUK IC 1832); 3c, 3d, 3f, 3g. fixed scutum in various aspec(ts (internal, basal, apical to show large myophore); 3e. Fixed tergum; 3a. Rostrum; 3b. carina; 10. moveable tergum; 15. moveable scutum. 7-9, 11, 13**.** *Costatoverruca tredecima* sp. nov.; 7. **holotype,** fixed scutum (NHMUK IC 1835); 8. fixed tergum (NHMUK IC 1836); 9. rostrum (NHMUK IC 1837); 11. carina (NHMUK IC 1838); 13. moveable tergum (NHMUK IC 1839). 12. *Metaverruca recta* (Aurivillius, 1898), fixed scutum. 14. *Verruca stroemia* (O.F. Müller, 1776), fixed scutum. Provenance: 1. Lower Pleistocene, Scoppo, Messina, Sicily; 2, 1 are present-day speciemens from the Mediterranean Sea, off Sicily; 7-9, 11, 13 are from sample RR13a; 3, 10, 15 from sample RR13b, both west of Rodrigues Ridge, Indian Ocean, Upper Pliocene-Lower Pleistocene; 12 is a present-day specimen from New Caledonia; 14 present-day, from Murvah, Donegal, Ireland. All scale bars equal 0.5 mm.

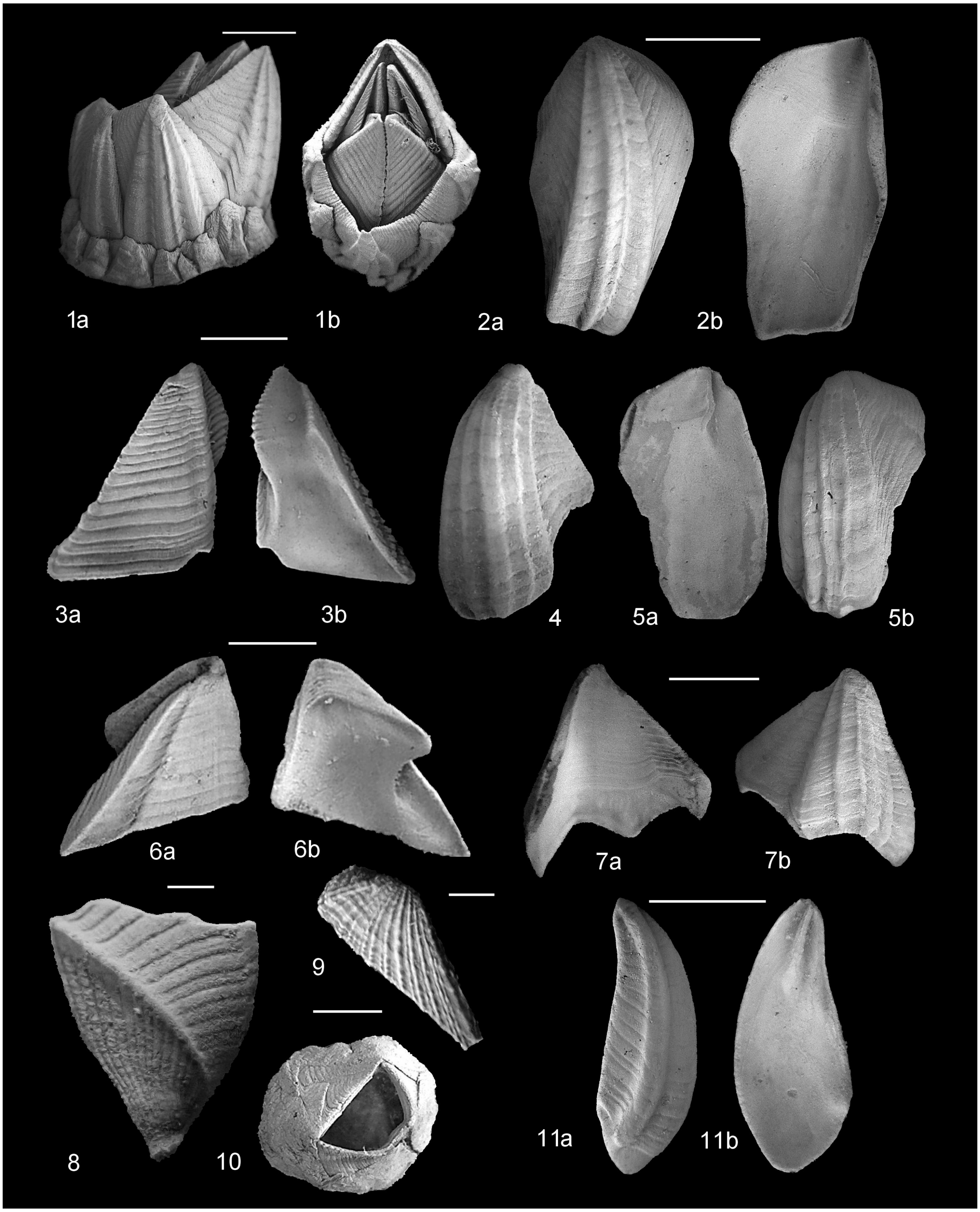

Plate 4. 1-7, 11. *Chionelasmus darwini* (Pilsbry, 1907); 1a, b. individual in lateral and apical views, respectively (A.S. Gale Collection); 2a, b. rostrum, in external and internal views, respectively (NHMUK IC 1840); 3a, b. scutum, in external and internal views, respectively (NHMUK IC 1841); 5a, b. marginal plate, in internal and external views, respectively (NHMUK IC 1843); 4, 7. carinae (NHMUK IC 1842, 1845); 6a, b. tergum, in external and internal views, respectively (NHMUK IC 1844); 11a, b. rostromarginal, in external and internal views, respectively (NHMUK IC 1846. 8. *Megalasma striatum* Hoek, 1883, scutum (NHMUK IC 1847). 9. *Lepas pectinata* Spengler, 1793, tergum (NHMUK IC 1848). 10. *Metaverruca recta* (Aurivillius, 1898), shell, lacking moveable plates (NHMUK IC 1849). Provenance: 1. Recent, Indian Ocean; all other specimens (2-11) from sample RR12a, Plio-Pleistocene, Rodrigues Ridge, Indian Ocean. Scale bars equal 5 mm (1-7, 10, 11) and 1 mm (8, 9).

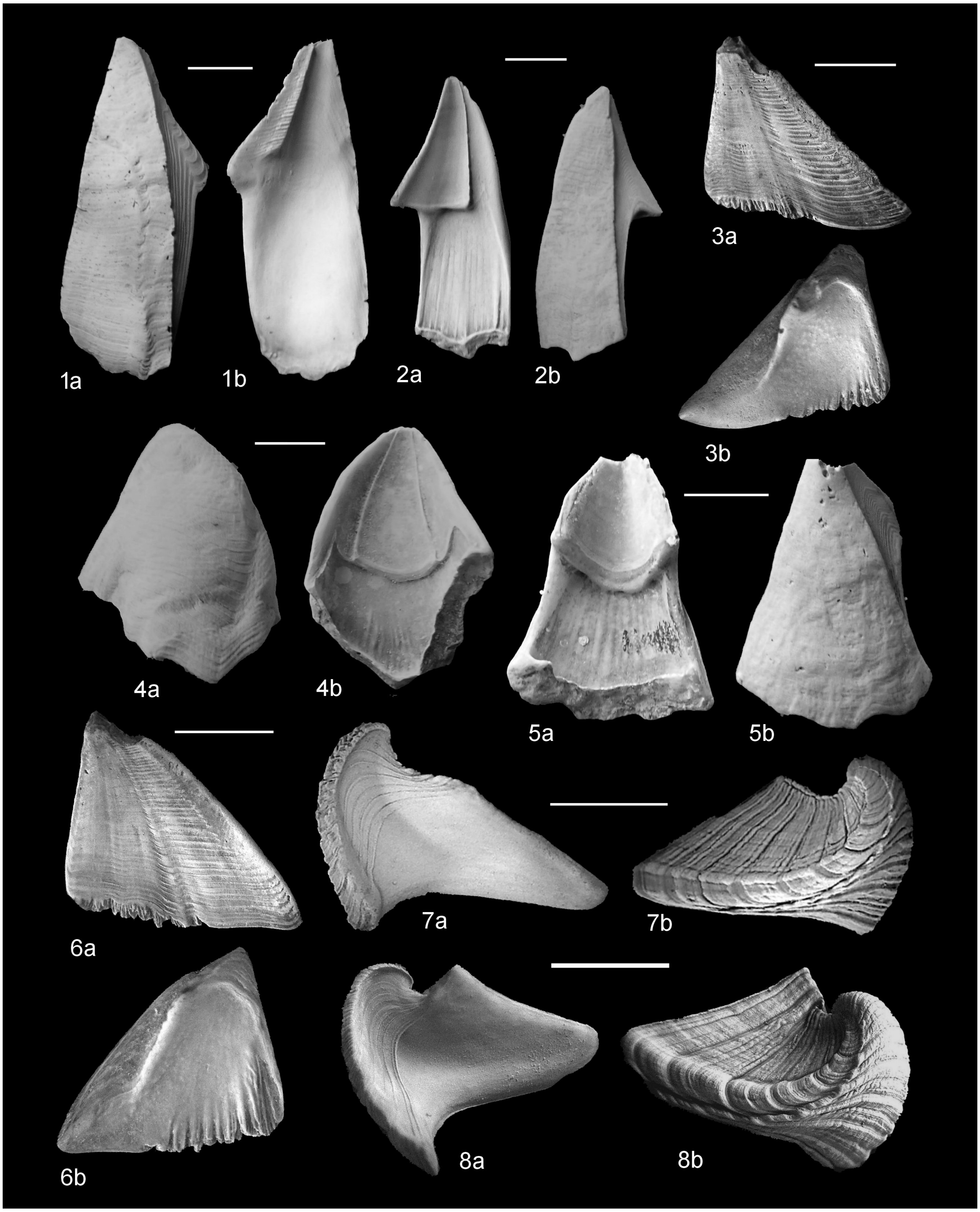

Plate 5. 1-6. *Pachylasma traceyi* sp. nov.; 1a, b. marginal plate, in external and internal views, respectively (NHMUK IC 1850); 2a, b. carinomarginal plate, in external and internal views, respectively (NHMUK IC 1851); 4a, b. rostral plate, in external and internal views, respectively (NHMUK IC 1853); 5a, b. carina, in external and internal views, respectively (NHMUK IC 1854); 3, 6. terga, in external (3a, 6a) and internal (3b, 6b) views (NHMUK IC 1852, 1855). 7, 8. *Arcoscalpellum michelottianum* (Seguenza, 1876), carinolatera, in external (7b, 8b) and internal (7a, 8a) views (7, NHMUK IC 1856; 8, A.S.Gale Collection). Provenance: 1-7 are from sample RR12a, Plio-Pleistocene, Rodrigues Ridge, Indian Ocean; 8 is a present-day specimen from the South China Sea. Scale bars equal 10 mm (1-6) and 5 mm (7, 8).

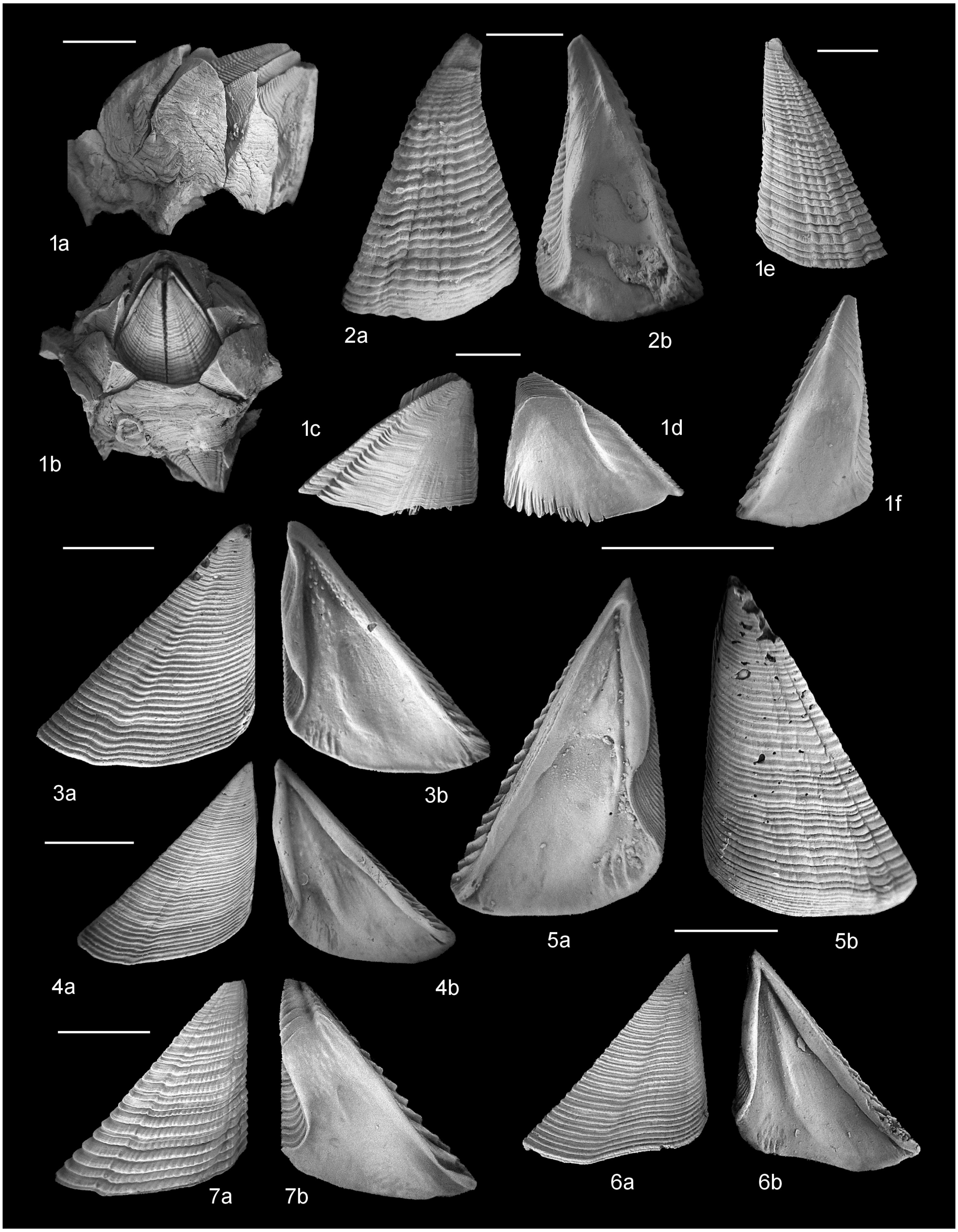

Plate 6. 1, 2. *Pachylasma giganteum* (Phillipi, 1836); 1a, b. capitulum of present-day individual, offshore from Sicily (A.S. Gale Collection), in lateral and apical views, respectively; 1c, d. tergum; 1e, f. scutum; 2. large scutum (A.S. Gale Collection). 3-6. *Pachylasma traceyi* sp. nov., 3 is **holotype** (NHMUK IC 1857), Figs 3, 4, are **paratypes** (NHMUK IC 1859-1860). 7. *Pachylasma scutistriata* Broch, 1922, topotypical scutum, Zoological Museum, Copenhagen (unregistered), China Sea, Recent. Provenance: 2 is from the Lower Pleistocene, Messina, Sicily; 3-6 are from sample RR12a, Plio-Pleistocene, Rodrigues Ridge, Indian Ocean. Scale bars equal 10 mm (1a, b, 2, 5) and 5 mm (1c-f, 3, 4, 6, 7).

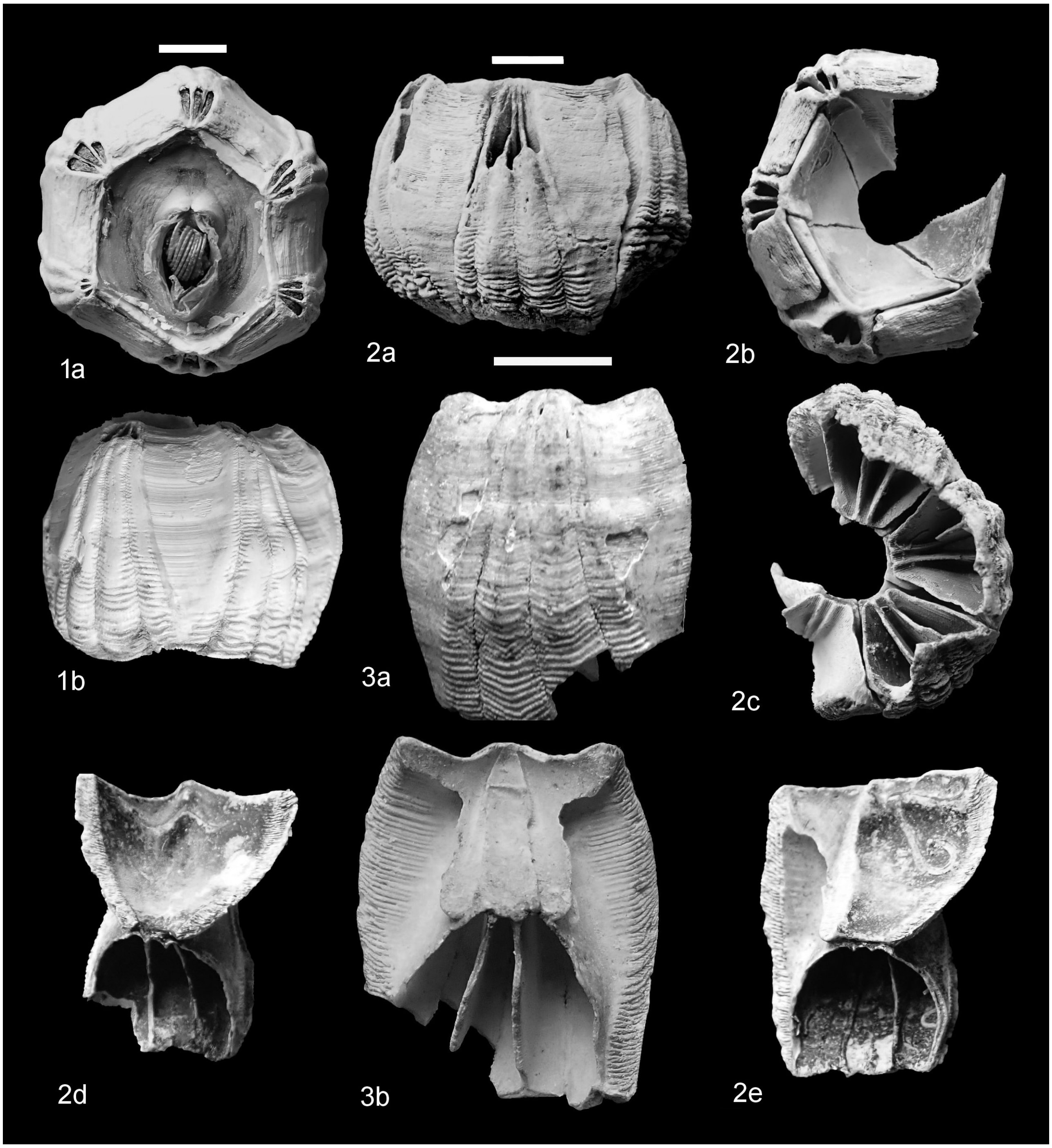

Plate 7. 1-3. *Coronula diadema* (Linnaeus, 1767); 1a, b. present-day specimen, in apical and lateral views, respectively (A.S. Gale Collection), North Sea; 2a-e. associated plates from an individual, reconstructed in lateral, apical and basal views, respectively, and separate internal views of carina and marginal, respectively (NHMUK IC 1861); 3a, b. isolated rostral plate, in external and internal views, respectively (NHMUK IC 1862). Provenance: 1, present-day, North Sea. 2, 3. sample RR13a, Plio-Pleistocene, Rodrigues Ridge, Indian Ocean. Scale bars equal 10 mm.