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Cirripedes (Crustacea, Thoracica) from the Plio-Pleistocene of Sicily (Italy) and a review of the history of Mediterranean Cainozoic cirripedes

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The extensive fauna of fossil cirripedes from Sicily originally described by Giuseppe Seguenza (1873, 1876) is reviewed, both by synoptic revision of the original material, destroyed in 1908, and from recently collected specimens. A total fauna of 41 taxa is identified from the upper Piacenzian to Calabrian of Sicily and many are revised taxonomically. The fauna includes three calanticids, two lepadids, five scalpellids, six verrucids and 25 balanomorphs. Two species are new, *Solidobalanus digeronimoi* Gale sp. nov. and *Gibbosaverruca milazzensis* Gale sp. nov. *Scillaelepas carinata* (Philippi, 1835) is shown to be the senior synonym of species of *Scillaelepas* Seguenza, 1876 recorded from the present-day Atlantic, and *Aurivillialepas ornata* (Seguenza, 1876) is a senior synonym of the extant *A. calycula* (Aurivillius, 1898). The names *Rostratoverruca romettensis* (Seguenza, 1873), *Metaverruca zanclea* (Seguenza, 1873) and *M. dilatata* (Seguenza, 1873) are demonstrated to be senior synonyms of living species generally referred to as *Metaverruca imbricata* (Gruvel, 1900), *M. recta* (Aurivillius, 1898) and *M. radiata* (Gruvel, 1901), respectively. The fossil Sicilian fauna largely represents benthic taxa which lived in the upper bathyal zone, with some taxa transported from shallower environments and minor epipelagic elements. The Cainozoic fossil cirripede fauna known from the Mediterranean Basin is reviewed, and the effects on the fauna of closure of the eastern Mediterranean, the Messinian Salinity Crisis, and middle Pleistocene events are evaluated. A major extinction around the end of the Calabrian (early Pleistocene) resulted in the loss of 50 per cent of the Mediterranean cirripede fauna.

Key words: bathyal, cirripedes, Plio-Pleistocene, Sicily

Introduction

In 1873 and 1876, Giuseppe Seguenza published two remarkable papers on fossil cirripedes he had collected in Pliocene-Pleistocene strata of northeast Sicily, describing and illustrating these in meticulous detail, following the style of Darwin's monographs (1851a, b, 1854a, b). Seguenza recorded a total of 33 species of fossil cirripedes and described 18 new species, a number of varieties as well as a new genus. He had a profound understanding of cirripede morphology and his illustrations are so detailed and accurate that they convey intricate detail. The Seguenza Collection was lost in the Messina earthquake of 1908, and his work has never received the widespread recognition which it undoubtedly deserves. He also had a detailed knowledge of cirripedes living in the Mediterranean (Seguenza, 1876, appendix 2) and was thus able to compare fossil and extant faunas.

Some of the species which Seguenza had discovered in the Pliocene of Sicily subsequently proved to be still living in the deep sea, and his work coincided with the first major dredging expedition, the Challenger Expedition (1872-1876). When Hoek (1883) described the cirripedes from the Challenger, he was unaware that a number of the species he named had been described previously as fossils by Seguenza. It was only in 1953 that the detailed research of T.H. Withers revealed that the common and widespread deep-sea species *Scalpellum velutinum* Hoek, 1883 should correctly be called *S. michelottianum* Seguenza, 1876. Similarly, *Calantica nudipes* Annandale, 1916, from the Java Sea, was originally described by Seguenza (1876) as *Scalpellum zancleanum* from the Pliocene of Sicily. Withers's (1953) synonymy was followed by zoologists, but neither he, nor anybody else, has investigated the Verrucidae, of which Seguenza described four species. Here, the validity of Seguenza's names is discussed. Claude Davadie (1953) described a collection of cirripedes from the Plio-Pleistocene of Sicily made by

M. Gignoux, and recorded and figured 10 species (three calanticids, one scalpellid and six balanomorphs).

We have made new collections of cirripedes from present-day exposures of deep-water Piacenzian-Gelasian deposits in northeast Sicily, and used these as a basis for taxonomic revision of Seguenza's taxa. The new collections are less extensive and less diverse, but do include a number of taxa which Seguenza did not find, including two new species. Continued collecting would undoubtedly extend this list.

Geological setting and localities

Located in the central-western Mediterranean, at the boundary between the African and the European plates, Sicily has a complex geology resulting from the Neogene collisional and post-collisional history of the Africa-Europe convergent system. The studied material has been collected mostly from northeast Sicily, close to the Messina Strait, and subordinately from the Sicilian southeastern sector (Fig. 1).

Northeast Sicily

This is a segment of the Neogene Apennine-Maghrebian orogenic belt, which includes the Kabilo-Calabride crystalline basement, made up of Palaeozoic rocks of various metamorphic grades. The sedimentary cover is represented by discontinuous upper Miocene strata unconformably covered by Plio-Pleistocene ones (Barrier, 1987; Lentini *et al*., 2000).

The Plio-Pleistocene marine deposits exposed along the coastal margins of northeast Sicily consist of discontinuous bodies, originally deposited on an irregular palaeotopography affected by active synsedimentary tectonics and swept by strong currents (Barrier *et al*., 1987). Barrier (1987), Barrier *et al*. (1987) and Vertino (2003) recognised a lower Pliocene succession consisting of whitish, deep-water, foraminifer-rich marls and marly limestones (regionally known as "Trubi") and more coarsely grained sediments including matrix-supported siliciclastic breccias. The overlying succession is more complex; middle Pliocene to middle Pleistocene deposits are exposed discontinuously and often as lateral heteropic bodies. These deposits have been grouped into a middle Pliocene to middle Pleistocene "Bathyal Facies Association" (PP) and a middle Pleistocene "Circalittoral-Infralittoral Facies Association" (mP) (Vertino 2003).

Of these, PP includes carbonate-dominated (Cd) facies and siliciclastic-dominated (Sd) facies. Cd facies mainly consist of coral-rich rudstones interfingering with calcarenites and carbonate sands. While the former are rich in fossils, mostly remains of frame-building deep-water scleractinians, such as *Madrepora oculata* Linnaeus, 1758, *Desmophyllum pertusum* (Linnaeus, 1758) and *D. dianthus* (Esper, 1794), the latter contain only locally scattered macrofossils such as rods of isidid octocorals and ossicles of echinoderms. These strata are locally truncated by erosional surfaces and are overlain or alternate with debris-flow deposits that are often rich in deep-sea coral fragments.

The Sd facies mostly consist of marly and silty clays, locally with embedded boulders of coral rudstones encrusted by deep-sea corals, bivalves, serpulids and bryozoans (Barrier, 1986, 1987; Vertino, 2003). The mP facies association consists of detrital gravelly to sandy sediments, interbedded with brecciated levels, including infralittoral to upper circalittoral fossils and scattered collapsed blocks covered by circumlittoral encrusters, as well as Gilbert-type delta deposits in places, known as the "Messina Formation" (Barrier, 1986, 1987; Vertino, 2003; Di Stefano & Longhitano, 2009). The succession is terminated by upper Pleistocene fluvio-marine terraces (Lentini *et al*., 2000).

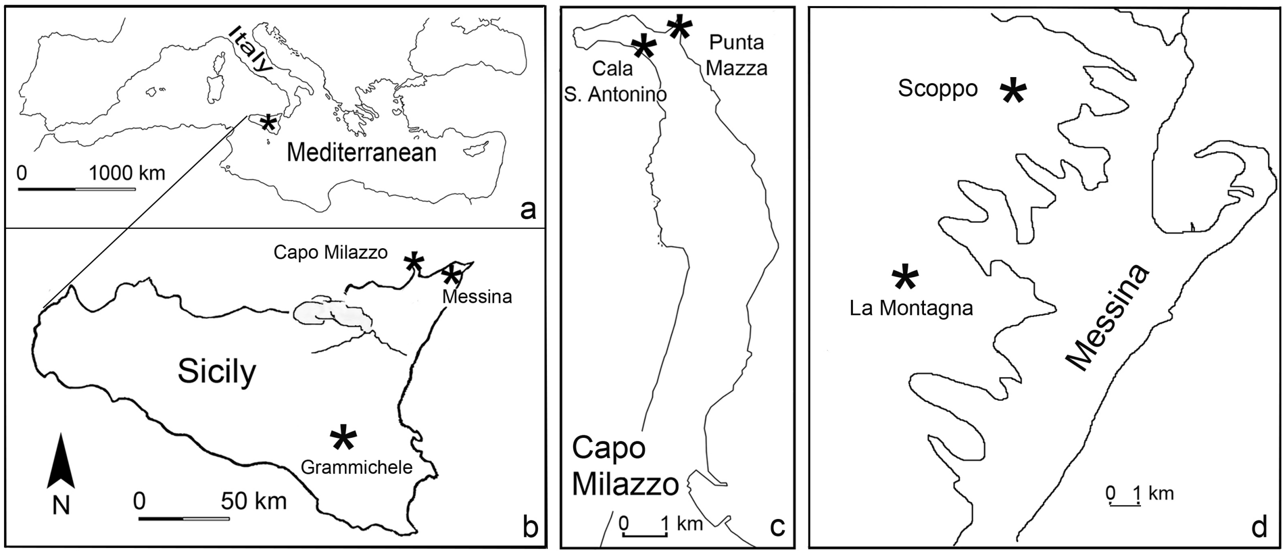


Figure 1. The Mediterranean Sea (a), with Sicily enlarged (b), with indication of the sampling localities of Grammichele, Capo Milazzo and Messina. Map (c) shows two sites at Capo Milazzo, namely the Cala Sant'Antonino and Punta Mazza sections, while map (d) shows the position of the two sites west of Messina: Scoppo and La Montagna.

Scoppo

Scoppo, located immediately west of Messina, has discontinuous outcrops of Pleistocene bathyal deposits (Barrier, 1984, 1987; Barrier *et al*., 1987; Vertino, 2003) on different substrata. Here, Messinian brecciated evaporitic limestone locally represents the substrate for the Cd facies association consisting of clinostratified rudstones (rich in fragments of the cold-water corals *M. oculata, D. pertusum* and *D. dianthus* and less common bryozoans), which alternate with poorly cemented sandy marls rich in cirripede plates and echinoderm ossicles. Both facies are locally truncated by heterogeneous and heterometric matrix-supported breccias, still belonging to the Cd association or already part of mP deposits. Fossils in the Cd facies (including brachiopods, bryozoans, molluscs, serpulids and ostracods) clearly point to deposition of both rudstones and marls in bathyal environments (Vertino, 2003; Vertino *et al*., 2013; Sciuto, 2016; Rosso *et al*., 2020) during the early Calabrian, correlating with the MNN19b-19c biozones (A. Baldanza, pers. comm., 2015).

La Montagna

A few kilometres south of Scoppo, the La Montagna (LM) hill offers one of the best exposures of the Cd facies in southern Italy. This WNW-ESE oriented, elongated hill, situated in the outskirts of the city of Messina, is composed mostly of bedded coral rudstone to floatstone deposits, occasionally interrupted by massive sedimentary rocks. These Cd facies unconformably overlie Serravallian-Messinian sands and marls, interpreted as terrigenous fluvio-deltaic strata (Lentini *et al*., 2000) and are truncated by a thin layer of mixed siliciclastic-carbonate deposits belonging to the mP succession. Several erosional boundaries, as well as mega cross-stratification, can be observed along the LM succession exposed (over a height of nearly 30 metres; see Vertino, 2003; Vertino *et al*., 2013). Similar to Scoppo, fossil assemblages are dominated by cold-water corals, but do include several other skeletal remains, such as cirripedes, brachiopods, bryozoans, decapod crustaceans and molluscs. In this succession, the following main facies groups can be recognised (in order of abundance): CWC rudstones rich in frame-building scleractinians (mostly *D. pertusum* or *M. oculata*); rudstones to floatstones mostly containing crustacean and echinoderm remains, isidid internodes, cirripede plates and only secondarily scleractinian fragments; CWC rudstones rich in fragments of the coral *Dendrophyllia cornigera* (Lamarck, 1816); brachiopod rudstones and *Pachylasma* rudstones. The predominance of frame-building coral rudstones suggests that the limestone outcrop of La Montagna can be seen as the remnant of a fossil coral buildup. Moreover, the great vertical and horizontal heterogeneity of facies, the layered and locally cross-stratified appearance of the coral rudstones, as well as the frequent erosional truncations and brecciated deposits imply a temporal and spatial discontinuous accretion under very strong bottom currents and within an unstable setting.

Capo Milazzo

In the Capo Milazzo peninsula, the sedimentary succession starts on top of an erosional surface on Palaeozoic metamorphic rocks. At the base, the small discontinuous bodies, including *Porites* bioconstructions, formed in shallow-water settings during the Tortonian-Messinian. In turn, these bodies witnessed an erosional phase and subsequent deepening, prior to the onset of Plio-Pleistocene sedimentation (Fois, 1990). Whereas lower Pliocene deposits are poorly represented and the occurrence of middle to upper Pliocene ones is essentially documented through reworked fossils, Gelasian and Calabrian strata are exposed extensively along the southwest and northeast coasts, including Cala Sant'Antonino and Punta Mazza, respectively. These strata, usually reported as yellow calcareous marls (YCM) although actually sandy silts, unconformably overlie erosive surfaces and form discontinuous bodies that filled small depressions. YCM deposition, previously dated as ate Pliocene (Fois, 1990), actually did not start until the MPl5 zone [now within the Gelasian, *i.e.*, earliest Pleistocene; see Gibbard *et al*., 2010; Violanti, 2012] and continued during the Calabrian and, locally, also into the Ionian, with greyish muddier sediments (Violanti, 1988; Sciuto, 2014a, b). The fossil content (brachiopods, bryozoans, corals, echinoids, serpulids, foraminifera, ostracods and, occasionally, molluscs) points to deposition of the YCM in epibathyal settings (e.g; Gaetani & Saccà, 1984; Violanti, 1988; Langer, 1989; Rosso, 2005; Borghi *et al*. 2014; Sciuto, 2014a, b; Rosso & Di Martino, 2015; Rosso & Sciuto, 2019; Rosso *et al*., 2020). The succession is topped by shallow-water sands and conglomerates of Tyrrhenian age and by volcanic ashes (Fois, 1990).

Catallarga Hill – northern side

The Catallarga Hill is located near the town of Grammichele, in southeast Sicily. In this area, the foreland is represented by the Hyblean Plateau which partly and temporarily emerged during the late Messinian and, more extensively, during the Plio-Pleistocene (*e.g.*, Grasso & Pedley, 1990) and was separated from the northerly, elevated Apennine-Maghrebian chain by the narrow, yet deep Gela-Catania Trough (*e.g.*, Di Grande & Giandinoto, 2002). During the Quaternary, linked with relative sea level changes, sediments were laid down along the coasts, either on volcanic rocks, or alternating with these. These deposits have been ascribed to several units, in particular, the Pleistocene "Poggio Spica Unit", which is exposed north of the Hyblean Plateau and is represented by basal packstones overlain by marly to clayey sediments topped by coarse sands and calcarenites (Pedley *et al*., 2001). The marly to clayey sediments have variable local thicknesses; these were deposited during the early Pleistocene in deep circalittoral to bathyal settings, often on volcanic submarine rocks. The fossiliferous content is represented mostly by scattered corals and molluscs, with subordinate bryozoans and other bathyal macrofauna (Di Geronimo, 1979; Di Geronimo *et al*., 2003).

Material and methods

The material analysed in the present paper was collected during several field trips aimed at studying Plio-Pleistocene deep-water sedimentary rocks that are exposed at different localities in northeast and southeast Sicily.

At Capo Milazzo (Fig. 1c) three samples each from the Cala Sant'Antonino (CA) outcrop and the Punta Mazza (PM) outcrop have yielded cirripede plates and entire specimens. Samples CA 4 (2002) and CA 8 (2002) were collected at about 3 m and 11 m from the base of the Cala Sant'Antonino main section, where the YCM reaches *c.*13 metres in thickness in the central part of a depression, of a width of *c.* 300 metres. Both samples were collected from fine-grained sediment almost devoid of macrofossils. CA 4 comes from yellow sandy silts, dated as MPl5 zone, whereas sample CA 8 was collected from muddy, darker-coloured levels close to the limit between zones MPl5 and MPl6. A further sample (CA picking) includes macrofossils handpicked from the entire outcrop surface and mostly from the northwestern end. Samples PM 6, PM 7 and PM 8 originate from the basal (Gelasian) part of the YCM cropping out at Punta Mazza. More specifically, PM 6 was collected from the very base of the outcrop from small depressions in the substrate. PM 7 and 8 come from the lower 3 metres of the section, where isidid internodes and cirripedes are apparent.

The cirripedes from Scoppo (sample S1) were handpicked from the eastern side of the outcrop where a cirripede-rich, sandy marl lens, *c.* 2 m in thickness, is interbedded with deep-sea coral rudstones.

The samples from La Montagna were collected from a highly lithified *Pachylasma* rudstone lens (LM1) and from several rudstone to floatstone levels along the outcrop. At Catallarga Hill (Grammichele) material was collected from the basal part of the Pleistocene succession, a few decimetres above the volcanic succession (CH).

Samples were routinely washed and specimens belonging to all benthic taxonomic groups were handpicked from fractions larger than 0.5 mm. Additional present-day material was examined from individual samples, including the 2009 Hermione cruise MEDCOR of R/V Urania in the Mediterranean Sea (Sicily Straits and off Malta). Selected barnacle plates were cleaned in an ultrasonic tank; smaller specimens were imaged with a JEOL SEM at the University of Portsmouth, while larger specimens were coated with ammonium chloride and photographed with a USB camera. Specimens of extant species were treated with hypochlorite to remove soft tissues before imaging.

Repository of specimens

MSNC	Museo Civico di Storia Naturale di Comiso, Sicily, Italy.
NHMUK	The Natural History Museum, London, United Kingdom.
NOC	National Oceanography Centre collections, Southampton, United Kingdom.
PMC	Museum of Palaeontology of the University of Catania, Sicily, Italy.

Systematic palaeontology (ASG)

Order Calanticomorpha Chan, Gale, Glenner, Dreyer, Ewers Saucedo, Pérez-Losada, Kolbasov, Crandall & Høeg, 2021

Family Calanticidae Zevina, 1978

Diagnosis – Plate numbers highly variable, usually with three pairs of larger laterals (rostrolatus, upper latus, carinolatus), often with subrostrum and subcarina; inframedian latus commonly absent.

Remarks – The Calanticidae appears to be a monophyletic entity from molecular analysis (Lin *et al.*, 2015, fig. 3) and the genus *Scillaelepas* Seguenza, 1876 appears to be basal to the family. However, the two main genera, *Calantica* Gray, 1825 and *Smilium* Leach, 1825, appear to be polyphyletic from the molecular study; both genera are highly variable in morphology (*e.g.,* Jones & Hosie 2009). Innocenti *et al.* (2015) proposed a subfamily Scillaelepadinae to include *Scillaelepas, Aurivillialepas* Newman, 1980 and *Gruvelilepas* Newman, 1980. However, the morphology of the lateral plates and rostra (Figs 2, 3) is very different in *Scillaelepas* from that in *Aurivillialepas* and *Gruvelilepas*, and it appears that latter two are likely to be more closely related to *Calantica*. Therefore, the subfamily does not really seem justified.

Genus *Scillaelepas* Seguenza, 1876

Type species – *Pollicipes carinata* Philippi, 1835, original designation.

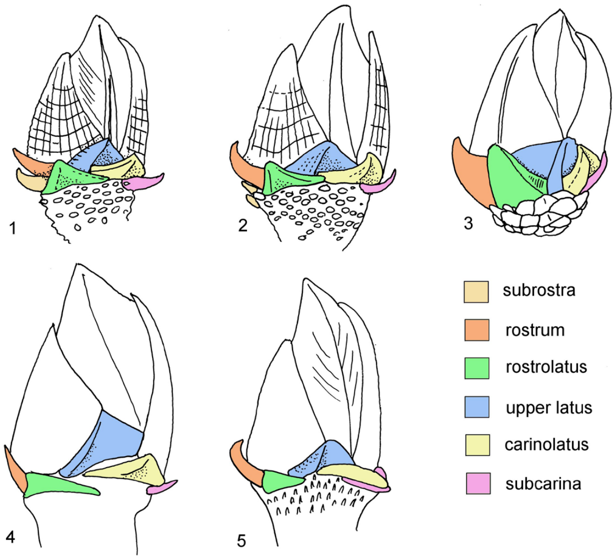


Figure 2. Construction of capitula in extant calanticomorph thoracicans. 1. *Aurivillialepas* sp., in lateral view, to show single subrostrum; 2. *Gruvelialepas* sp., in lateral view, to show two small subrostra; 3. *Scillaelepas* sp., in lateral view, to illustrate large rostrum and absence of subrostra; 4. *Calantica zancleana* (Seguenza, 1876), in lateral view (after Calman, 1918); 5. *Calantica* sp., in lateral view.

Diagnosis – Robust, weakly sculptured capitulum characterised by possession of large, imbricated, strongly incurved rostra, carinolatera, upper latera and rostrolatera; these significantly overlap scuta and carina; rostrum and upper latera with raised, flat-topped apicobasal ridge, upper latera with convex ventral process.

Referred species – In addition to the type species, *S. paronae* De Alessandri, 1895 and *S. fosteri* Newman, 1980.

Remarks – Newman (1980) ascribed a number of North Atlantic species to this genus (Fig. 4): *S. gemma* (Aurivillius, 1892) (Fig. 5.5), *S. superba* Pilsbry, 1907 and *S. grimaldi* (Aurivillius,1898). Young (1999) later added *S. brasiliensis* from the South Atlantic (Fig. 4). The validity of some of these species has been in doubt for a long time; Gruvel (1920) thought that *S. superba* was a synonym of *S. grimaldi* and Withers (1953) suspected in turn that *S. superba* was conspecific with *S. carinata*. New material of these species confirms these synonymies, and it appears that there is only a single Atlantic-Mediterranean species of *Scillaelepas*, *S. carinata*, described by Seguenza (1876). The other extant species of *Scillaelepas, S. fosteri* Newman, 1980, is known from localities around

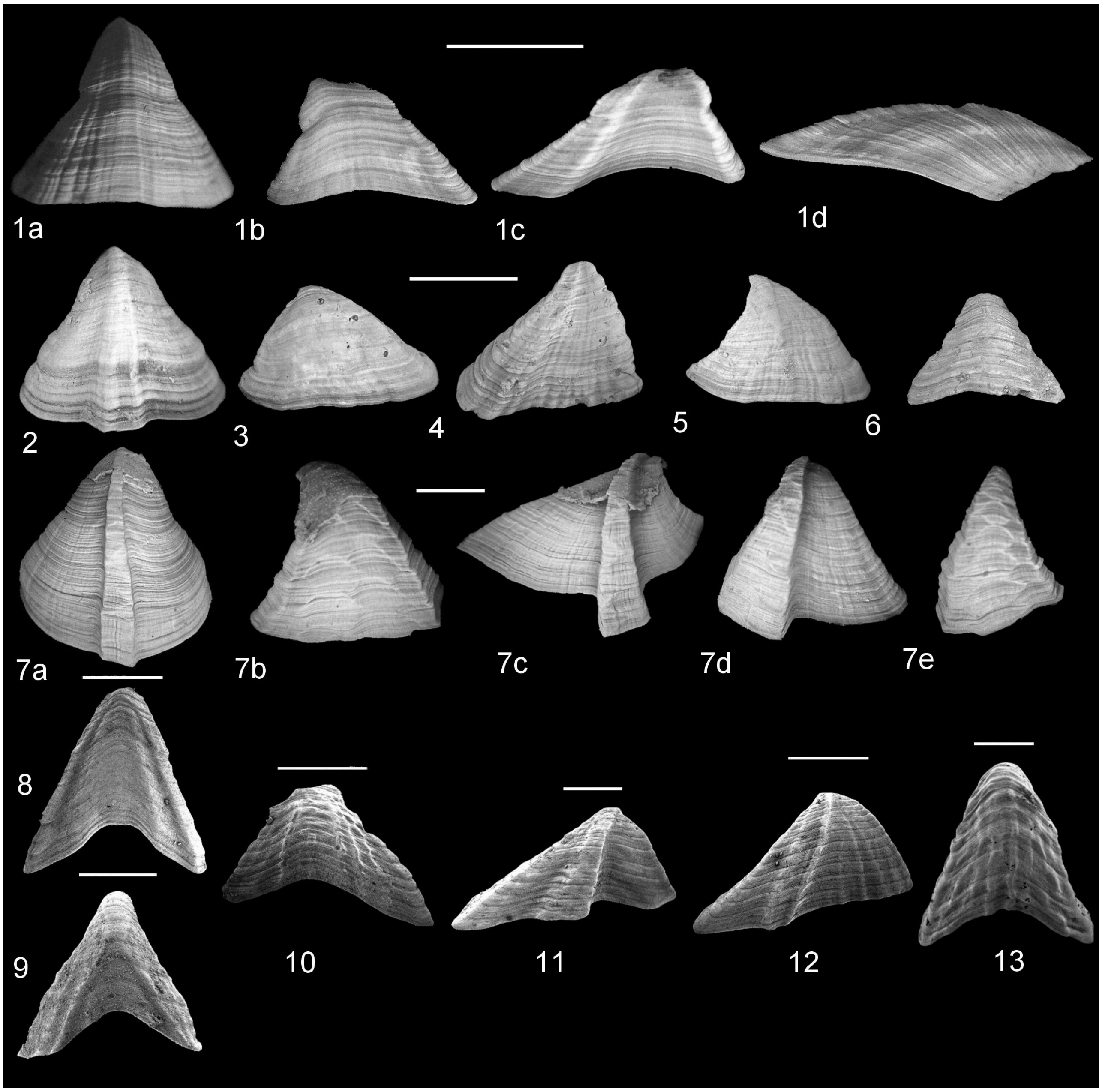


Figure 3. Rostra and lateral plates of calanticid cirripedes: 1a-d. *Calantica* sp.; 2-6, *Calantica dorsata* (Steenstrup, 1839); 7a-e. *Scillaelepas carinata* (Philippi, 1835); 8-13. *Aurivillialepas ornata* (Seguenza, 1876). Provenance: 1. Present-day, locality unknown; 2-6. Palaeocene, middle Danian, Faxe, eastern Denmark, Geomuseum Faxe, unregistered; 7. Recent, off Florida (see pl. 1); 8-13, Lower Pleistocene, Scoppo, Sicily. Rostra: 1a, 2, 7, 8. Subrostrum: 9. Rostrolatera: 1b, 3, 7b, 10. Upper latera: 1c, 4, 7c, 11. Carinolatera: 1d, 5, 7, 12. Subcarinae: 6, 7e, 13. Scale bars equal 5 mm (1-7) and 1 mm (8-13).

New Zealand (Foster 1978) and from south of Tasmania (Buckeridge 1999). In this form, the upper latus and rostrum appear to lack the narrow raised apicobasal ridge present in *S. carinata*, but otherwise the species are similar.

Numerous fossil species of Late Cretaceous and Cainozoic age were ascribed to *Calantica* (*Scillaelepas*) by Withers (1935, 1953); subsequently, Buckeridge (1983) and Collins (1983) added a few more. A number of the Cretaceous species were reviewed by Gale & Sørensen (2015) and placed in various genera and families, but this leaves over 20 fossil taxa with uncertain generic status. These species mostly share slightly asymmetrical rhombic terga with a flat-topped apicobasal ridge, scuta with convex occludent margins, angled basal margins and separation of tergal and occludent surfaces by a variably defined apicobasal ridge. The problem is that whilst some of these characters are shared with *Scillaelepas carinata,* they are also characteristic of various archaeolepadomorph taxa, such as *Loriololepas* Gale, 2015 and *Bosquetlepas* Gale, 2015 (in Gale & Sørensen, 2015, figs 3, 4). This means that the lateral plates provide the only secure criterion with which to determine affinity. Lateral plates are unknown in most of the taxa ascribed to *Calantica* (*Scillaelepas*), but they are found in the Paleocene *C.* (*S.*) *dorsata* (Steenstrup, 1839) (see Withers, 1935, pl. 5, figs 8-19) and the Miocene *C.* (*S.*) *paronae* De Alessandri, 1906 (see Withers, 1953, pl. 15, figs 5-9). Rostra and lateral plates of various fossil and living calanticids are illustrated here (Figs 2, 3). These show that *Aurivillialepas* (and *Gruvellialepas*) have very similar and distinctive lateral plates, which possess depressed surfaces which enable a considerable overlap of the carinolatus over the upper latus, and of the rostrolatus over

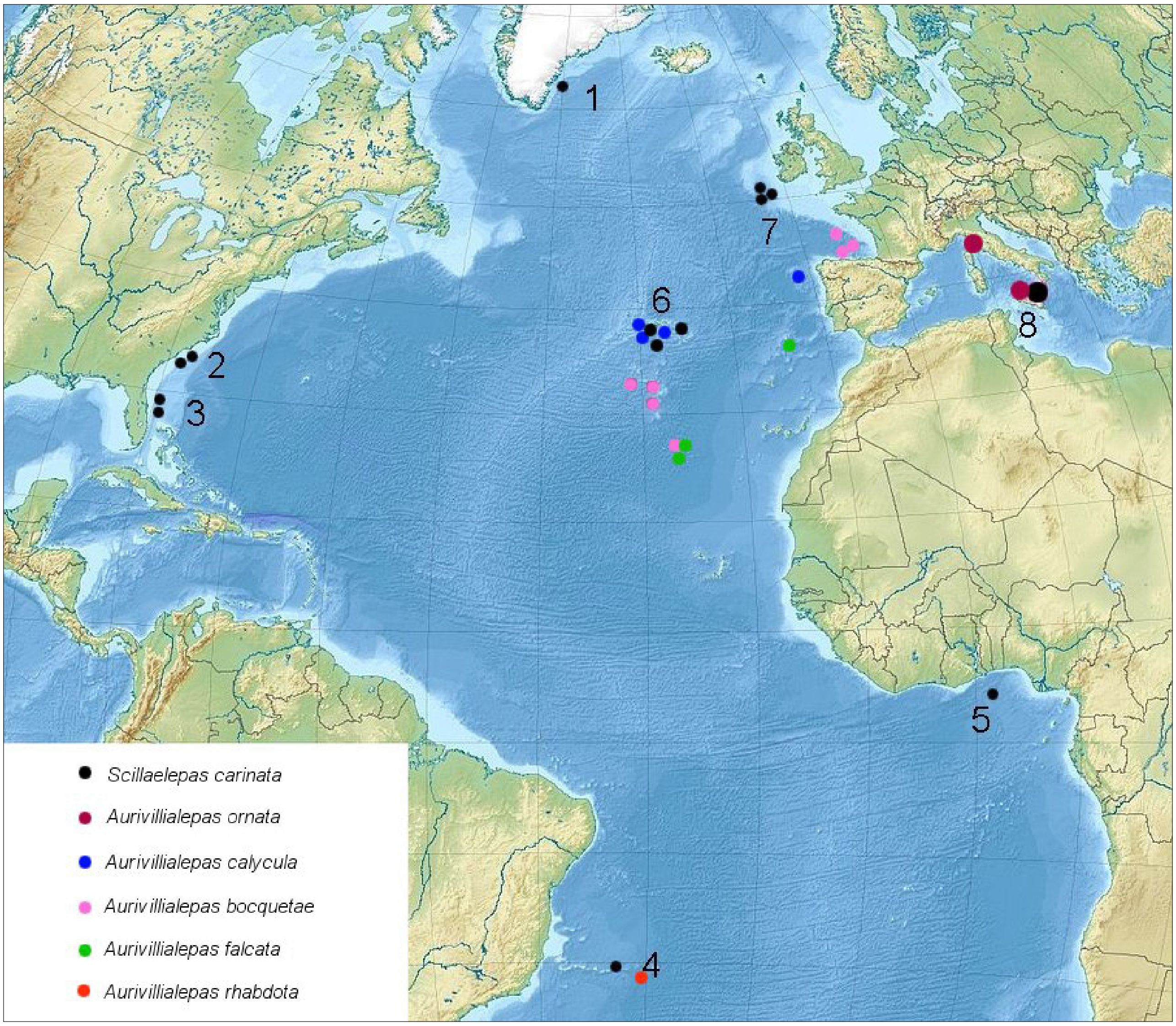


Figure 4. Map to show present and fossil distribution of calanticid species in the Mediterranean and Atlantic. Black dots represent individual populations of *Scillaelepas carinata*, referred to as: 1. "*S. gemma* (Aurivillius, 1892)"; 2, 3. "*S. superba* Pilsbry, 1907"; 4. "*S. brasiliensis* Young, 1999" and 5-7. "*S. grimaldi* (Aurivillius, 1898)". Further extant species of *Aurivillialepas* indicated with coloured dots are possibly conspecific with the Miocene to present-day *A. ornata* (Seguenza, 1876) originally described from Sicily.

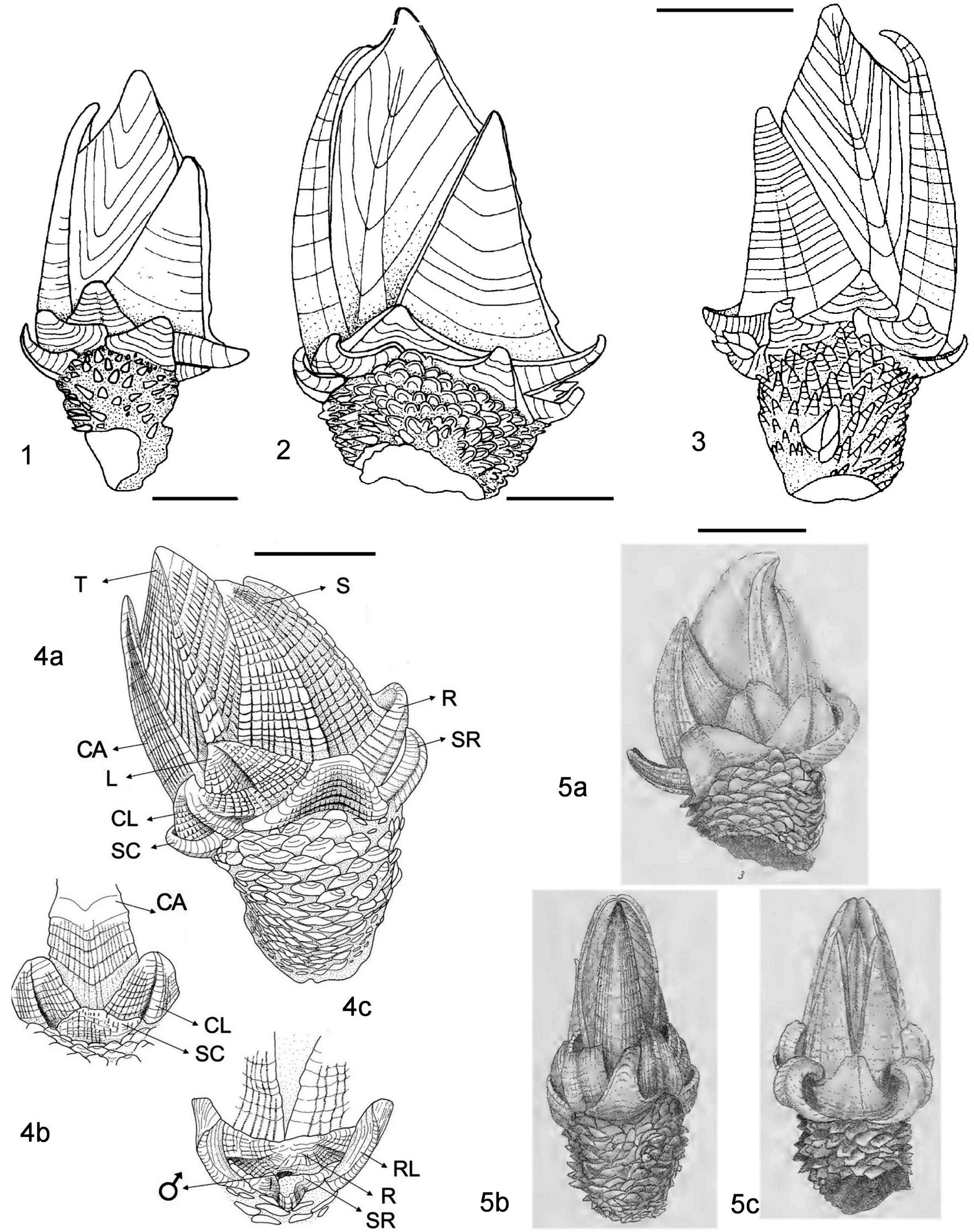


Figure 5. Species of *Aurivillialepas* (1-4) and *Scillaelepas* (5): 1, 2. *A. bocquetae* (Newman, 1980), capitula in lateral view (after Young, 1998); 3. *A. falcata* (Aurivillius, 1894), capitulum in lateral view (after Young, 1998, fig. 4d, e); 4. *A. rhabdota* Young, 2001, capitulum in various views (after Young, 2002, fig. 1); 5. *Scillaelepas carinata* (Philippi, 1835), capitulum in various views; the original of *Scalpellum gemma* Aurivillius, 1894 (p. 9, fig. 7). Scale bars 5 mm.

both the upper latus and the ventral part of the carinolatus (Fig. 2/1, 3). *Scillaelepas* also has distinctive arrangement and morphology of the lateral plates, notably the strong, flat-topped ridges on the upper latus, carinolatus and rostrum. "*Calantica* (*Scillaelepas*)*" dorsata* (Fig. 3/2-6) does not share many characters of lateral plates with *Scillaelepas*, except that it has a weakly developed apicobasal ridge on the rostrum. The lateral plate development in *Calantica* is highly variable (Withers, 1953; Jones & Hosie, 2009), but the lateral plates in the *Calantica* sp. figured here (Fig. 3/1a-d) are not very different from those of the early Palaeocene (Danian) species, which is therefore referred to here as *Calantica dorsata*. This is the oldest undisputed *Calantica*; the oldest *Scillaelepas* is probably Miocene in age. Thus, the argument that *Scillaelepas, Aurivillialepas* and *Gruvelialepas* are Mesozoic relics which survived in the deep sea into the Cainozoic (Newman, 1980; Innocenti *et al*., 2015) is highly improbable.

***Scillaelepas carinata* (Philippi, 1835)**
Plate 1, figs 1-3; Plate 2, figs 1-15

1670	Rostra (ut puto) animalis polypo similis – Scilla, pl. 14.
*1835	*Pollicipes carinatum* Philippi, p. 512, pl. 4, figs 3-9.
1876	*Scillaelepas carinatum* Philippi – Seguenza, p. 396, pl. 8, figs 1-14.
1906	*Scillaelepas ornata* Seguenza – De Alessandri, p. 243, fig. 8.
1892	*Scillaelepas gemma* Aurivillius, p. 248.
1894	*Scillaelepas gemma* Aurivillius, p. 41, pl. 3, figs 3-5; pl. 5, fig. 7.
1898	*Scillaelepas grimaldi* Aurivillius, p. 192.
1920	*Scillaelepas grimaldi* (Aurivillius) – Gruvel, p. 15, pl. 5, figs 7-9.
1907	*Scillaelepas superba* Pilsbry, p. 11, fig. 3.
1953	*Scillaelepas carinata* (Philippi) – Withers, p. 157, pl. 16, figs 1-8; pl. 17, figs 1-6.
1953	*Scillaelepas paronae* De Alessandri – Davadie, p. 86, pl. 2, figs 2-4.
1953	*Scillaelepas carinata* Seguenza – Davadie, p. 88, pl. 1, figs 1-3.
1980	*Scillaelepas gemma* (Aurivillius) – Newman, p. 380.
1980	*Scillaelepas grimaldi* (Aurivillius) – Newman, p. 381.
1980	*Scillaelepas superba* Pilsbry – Newman, p. 381, fig. 1.
1999	*Scillaelepas brasiliensis* Young, p. 615, fig. 4A-G.
2001	*Scillaelepas grimaldi* (Aurivillius) – Young, p. 727.
2003	*Scillaelepas carinatum* (Philippi) – Young, p. 182, table 1.

Diagnosis – *Scillaelepas* in which the rostrum and upper latus bear a narrow, raised, flat-topped ridge which forms a projection on the basal margin.

Types – Withers (1953, p. 158) designated a scutum from Sicily, figured by Philippi (1835, pl. 4, fig. 4) lectotype. Its current whereabouts are unknown.

Material – The NHMUK collection comprises 37 valves from Messina, Sicily (Withers, 1953); present-day specimens from off Florida were provided by Dr Charles Messing and material from the Porcupine Sea Bight was received from Dr Tammy Horton (NOC, Southampton). A large collection (PMC. R. 1. Cal. CIR-1c-5c, 7c-10c, 6l, m) of valves, including all lateral plates, from the Calabrian of Scoppo (Sicily) has also been used for the present study and also valves from La Montagna, Messina, Cala Sant'Antonino (samples CA4, CA8) and Punta Mazza (sample PM8) (Table 1).

Description – Capitulum oval, laterally flattened, broadest at summit of rostral apex (Pl. 1, figs 1a, 1b, 2a, b, 3a, f). Lateral plates large, forming basal third of capitulum, overlapping scuta, terga and carina. Rostrum and upper latus overlapped by rostrolatus; carinolatus overlaps upper latus and, in turn, is overlapped by subcarina. Rostrum (Pl. 1, fig. 1e-g; Pl. 2, fig. 1a, b) very large, strongly incurved at tip, triangular in ventral view with convex basal margin and flat-topped apicobasal ridge broadening to base, occasionally forming short spur at base of plate (Pl. 2, fig. 11). Scuta thick, triangular, incurved dorsally, with convex occludent margin and narrow, curved apicobasal ridge, broader in large specimens (Pl. 2, fig. 4). Terga (Pl. 2, figs 5-7) rhombic, height 2-2.5 times greater than breadth, lower carinal and scutal margins longer than upper carinal and occludent margins. Terga with sharp, straight or slightly curved apicobasal ridge. Carinae (Pl. 1, fig. 1c, d; Pl. 2, fig. 3a, b) triangular, incurved ventrally, height 2.5 to 3 times greater than breadth, basal margin angled at base of fine, sharp apicobasal ridge. Rostrolatus (Pl. 1, figs 1k, 3d; Pl. 2, fig. 12) equilaterally triangular, apex strongly incurved over rostrum and upper latus. Upper latera (Pl. 1, figs 1j, 3b; Pl. 2, figs 8, 9, 13) convex, with asymmetrically triangular outline; curved, flat-topped ridge separating shorter dorsal portion from elongated ventral region and protruding on basal margin. Ventral margin of upper latus terminating acutely in smaller individuals (Pl. 1, figs 1j, 3b), bluntly in larger ones (Pl. 2, fig. 8). Carinolatus (Pl. 1, figs 1l, 3c; Pl. 2, figs 14, 15) not incurved, triangular, dorsal portion of valve inset, variably elongated (compare Pl. 2, figs 14, 15). Subcarina (Pl. 1, fig. 3e, f; Pl. 2, fig. 10) triangular, symmetrical when complete, usually apical region is broken. Scuta, terga, carinae, rostra and upper latera bear sculpture of finely spaced commarginal growth lines, and some fine radial ribs especially on large plates (e.g., Pl. 2, fig. 4). Rostrolatera, subcarinae and raised parts of carinolatera bear sculpture of irregularly undulating growth lines (e.g., Pl. 1, figs 1k, 1l, 3e). Peduncle short, robust, covered with 15-20 alternating columns of basally imbricating scales; scales oval, apical margin subacute to rounded, larger scales bear 1 or 2 low ridges.

There is significant variation in the shape of the capitular plates in the Sicilian material, most notably in the proportionate elongation of the terga (Pl. 2, figs 5-7) and the size

Cala Sant'Antonio (CA4) MP15

Solidobalanus milensis	6
Solidobalanus digeronimoi	24
Metaverruca zanclea	5
Metaverruca dilatata	1
Gibbosaverruca milazzensis	7
Pyrgomina sp.	2

Cala Sant'Antonio (CA8) MP15/16

Scillaelepas carinata	2
Aurivillialepas ornata	3
Rostratoverruca romettensis	8

Punte Mezzo (PM8) Gelasian

Solidobalanus digeronimoi	1
Scillaelepas carinata	8
Rostratoverruca romettensis	1

Capo Milazzo (Gelasian-Calabrian?)

Acasta sp.	1
Pyrgomina costata	2
Pyrgomina elargatum	2

Capo Milazzo-Punta Massa Camp 7 (PM7) Gelasian

Aurivillialepas ornata	9
Rostratoverruca romettensis	85
Scillaelepas carinata	2
Metaverruca zanclea	3
Solidobalanus milensis	2

Capo Milazzo-Punta Massa Camp 6 (PM6), Gelasian

Solidobalanus digeronimoi	22
Scillaelepas carinata	4
Metaverruca zanclea	1
Solidobalanus milensis	9
Aurivillialepas ornata	2
Gibbosaverruca milazzensis	21

Scoppo (SC), Calabrian, biozones MNN19b-c

Aurivillialepas ornata	100+
Rostratoverruca romettensis	1,000+
Scillaelepas carinata	200+
Scalpellum sp.	3
Balanus sp.	1
Acasta sp.	1

Catallarga Hill, Grammichele, lower Pleistocene

Metaverruca dilatata	15
M. zanclea	100+

La Montagna (LM), lower Pleistocene

Pachylasma giganteum	100+
Aurivillialepas ornata	2
Scillaelepas carinata	6

Table 1. Records of cirripedes collected from lower Pleistocene strata in Sicily.

and shape of the ventral portions of the upper latera (Pl. 2, figs 8, 9, 13) and carinolatera (Pl. 2, figs 13, 14).

Remarks – For the present study, I have examined two specimens of *Scillaelepas* from off Florida (Pl. 1, figs 2, 3) and two specimens from the Porcupine Sea Bight (east-central Atlantic; NOC collections, Southampton; Pl. 1, fig. 1), as well as numerous valves of Pleistocene *S. carinata* from Scoppo (Sicily). I am unable to find any consistent or significant differences between these taxa, and therefore provisionally place the living species *S. superba* and *S. grimaldi* in synonymy with the fossil *S. carinata*. The illustrations of *S. gemma* (Aurivillius, 1894) are poor (see Fig. 5/5 here), but there do not appear to be significant differences from *S. carinata*, and the isolated valves (carina, rostrum, scutum, tergum) on which *S. brasiliensis* is based (Young, 1999, fig. 4A-G) are essentially identical with those from Sicily and the North Atlantic. *Scillaelepas carinata* at the present day is thus interpreted as a single, rare, circum-Atlantic species (Fig. 4), symbiotically associated with scleractinian corals, notably of the genus *Lophelia* Milne-Edwards & Haime, 1849 (Newman *et al*., 2002). During the early Pleistocene, the range of *S. carinata* extended into the central Mediterranean, where it was extraordinarily abundant and found in association with corals.

The only other species of *Scillaelepas* recognised here is *S. fosteri* Newman, 1980 which occurs around New Zealand and in the Tasman Sea. It differs from *S. carinata* in the narrower, less strongly incurved rostrum and in the absence of sharply defined raised ridges on the rostrum and upper latus (see Foster 1978, pl. 6B, C). *Scillaelepas carinata* differs from the Miocene species, *S. paronae* De Alessandri, 1895, in its taller scuta, and the presence of sharply defined ridges on the rostrum and upper latus.

Genus *Aurivillialepas* Newman, 1980

Type species – *Scillaelepas calyculus* Aurivillius, 1898 (= *Scillaelepas ornata* Seguenza, 1876) by original designation.

Diagnosis – Sculptured calanticids which possess fourteen plates (paired scuta, terga, upper latera, carinolatera, rostrolatera, single carina, rostrum, subcarina, subrostrum); lateral plates low, elongated, imbricate.

***Aurivillialepas ornata* (Seguenza, 1876)**
Plate 3, figs 1-14; Plate 4, figs 1-14

*1876	*Scillaelepas ornata* Seguenza, p. 36, pl. 8, figs 16-27.
1898	*Scillaelepas calyculus* Aurivillius, p. 193.
1920	*Scillaelepas calycula* Aurivillius – Gruvel, p. 13, pl. 5, figs 16-18.
1953	*Scillaelepas ornata* Seguenza – Withers, p. 161, pl. 17, figs 7-15.
1980	*Scillaelepas* (*Aurivillialepas*) *calycula* – Newman, p. 385, fig. 5A-E.
2015	*Aurivillialepas calycula* (Aurivillius) – Innocenti *et al*., p. 259, figs 1-4.

Diagnosis – Species of *Aurivillialepas* which bears variably fine apicobasal ribs, transected by regularly spaced growth increments to form a cancellate sculpture.

Types – Withers (1953) designated a scutum (NHMUK In.33675), labelled "Messina, Sicily" neotype.

Material – NHMUK collections include five valves of this species (NHMUK In.33674-33678), all labelled Messina, Sicily (Withers, 1953). The locality at Scoppo, Sicily (Calabrian; see Table 1), has provided abundant plates of this species (200+), inclusive of numerous lateral plates as well as rostra and subrostra (PMC. R. 1. Cal. CIR-15c-38c), which permit a full description of the species. It is here also recorded from La Montagna and Cala Sant'Antonino (sample CA8) (Table 1).

Description – Capitulum oval (Pl. 3, fig. 3), laterally flattened; triangular, broad lateral plates forming low tier (one-third height of capitulum) at base of capitulum; apices of subcarina, rostrum and subrostrum protruding from dorsal and ventral margins; carinolatus, upper latus and rostrolatus incurved apically. Strong imbrication of rostrolatus over rostrum and upper latus; carinolatus over upper latus; subcarina over carinolatus. Scuta variable in outline, from nearly equilaterally triangular (Pl. 3, fig. 1a, b) to taller (height twice breadth) isosceles triangle (Pl. 3, figs 2, 9, 10a, b, 13, 14a, b); apex slightly inclined ventrally, occludent margin gently convex, tergal margin gently concave. Basal margin obtusely angled at intersection with apicobasal ridge. Occludent surface slightly narrower than tergal surface, bearing fewer, coarser apicobasal ribs. Number of apicobasal ribs variable, from forms with relatively few irregularly sized and spaced (Pl. 4, figs 2, 3, 9) to dense, more evenly sized (Pl. 4, figs 10, 14). Ribs interrupted by stepped growth increments, producing cancellate sculpture. Scutal adductor scar large, rounded, positioned at mid-height of valve. Terga (Pl. 3, figs 4-6, 8) rhombic to triangular, height twice breadth; upper carinal and occludent margins shorter than lower carinal and scutal margins. Carinal margins confluent, weakly separated; raised, flat topped apicobasal ridge present, sometimes with 2 or 3 separate ridges (Pl. 4, figs 5, 6, 8). Terga with sculpture of fine apicobasal striiae. Carinae (Pl. 3, fig. 3; Pl. 4, figs 4, 7, 14a, b) 2-3 times taller than broad, concavo-convex in transverse section, gently curved ventrally; sculpture of apicobasal ribs, more (Pl. 4, fig. 7) to less (Pl. 4, fig. 14) dense, cut by transverse, commarginal growth increments, occasionally evenly and widely spaced (Pl. 4, fig. 14) or more irregular (Pl. 4, fig. 7). Rostra (Pl. 3, fig. 11; Pl. 4, fig. 5), nearly equilaterally triangular, flattened, with basal margin notched; external surface bearing marginal groove to accommodate subrostrum. In lateral view (Pl. 4, fig. 5b), rostrum gently concavo-convex (compare with articulated specimen, Pl. 3, fig. 3). Subrostrum (Pl. 4, fig. 3) equilaterally triangular, basal margin deeply notched, V-shaped depression on external face; in lateral aspect, sharp apex strongly incurved (compare Pl. 3, fig. 3). Subcarina (Pl. 4, figs 1, 2) triangular, slightly taller than broad, basal margin concave, strongly incurved, talon-like; external sculpture of irregular, coarse, apicobasal ridges. Upper latus (Pl. 4, figs 8, 11-13) asymmetrically triangular, breadth twice height, depressed dorsal surface separated by step-like ridge from elevated ventral portion. Rostrolatus (Pl. 4, fig. 9) asymmetrically triangular, shorter upper margin on ventral side, depressed centrally, basal margin concave. Carinolatus (Pl. 4, fig. 10) elongated triangular, short, upright dorsal margin, tapering to acute ventral margin; oblique ridge running from apex to ventral part of basal margin.

Remarks – The discovery of lateral plates of *A. ornata* (rostra, subrostra, subcarinae, carinolatera, inframedian latera and rostrolatera) at Scoppo show that *S. ornata* possessed a single subrostrum and is therefore a member of the genus *Aurivillialepas* (see also Gale, 2020b). The valve shapes and sculpture of some specimens of *A. ornata* are remarkably similar to those of *A. calycula* (see figures in Innocenti *et al*., 2015, reproduced here as Pl. 3, fig. 3). In particular, the shape and sculpture of the neotype scutum (broad, flat tergal surface, more strongly ribbed occludent surface), the carinae (strong radial ribs, regularly spaced commarginal increments) and the terga. Therefore, *A. calycula* is here placed in synonymy with Seguenza's species *S. ornata*.

There is considerable variation in the valve morphology of *A. ornata* from Scoppo and other localities in Sicily, including scuta and carinae (Pl. 3, fig. 10; Pl. 4, fig. 7) which are strongly ribbed, and interrupted by numerous, fine growth increments, creating a rugose sculpture. This is highly reminiscent of *A. rhabdota* (Young, 1999) (see Young, 2002b) from offshore Brazil (Figs 4, 5/4a-c). Other forms have valves which are only sparsely ribbed, or almost smooth (Pl. 3, figs 2, 9, 12, 13) and the broad-based scuta are comparable with those of the living eastern Atlantic *A. falcata* (Aurivillius, 1898) (Figs 4, 5/3) and *A. bocquetae* (Newman, 1980) (Figs 4, 5/1, 2). In reality, there are so few present-day specimens known of *Aurivillialepas* that it is impossible to gauge the variation within, and between, populations (Fig. 4). The new Sicilian material could be taken to demonstrate that there is only one, highly variable species of *Aurivillialepas* in the Atlantic Ocean, paralleling the situation which exists with *Scillaelepas carinata*. The alternative, of course, is that there are regionally distinct populations of separate species. Without new material, and molecular analysis, it is impossible to know the correct answer.

Genus *Calantica* Gray, 1825

Type species – *Pollicipes villosa* Leach, 1824, by original designation.

Remarks – There are considerable difficulties in the definition of both *Calantica* and *Smilium* and the assignation of species to each genus has long been controversial. Foster (1978, p. 49) provided criteria for the diagnosis of those species of *Smilium* which have a subcarina, including the presence of a carinal margin on the upper latus, which is therefore quadrangular, and the presence of a 90° bend in the basal margin of the scutum, such that rostral and upper latus margins are present on either side of the apicobasal ridge. However, there are species with intermediate morphologies, and the type species, *Smilium peronii* Gray, 1825 has an elongated upper latus, set high on the capitulum, which articulates with the elongated carinolatus, the carina, the tergum and the scutum. This condition is also present in all other species referred to *Smilium* by Withers (1953, figs 69-73). In contrast, the type species of *Calantica, C. villosa*, has small, triangular lateral plates set in a single, low whorl at the base of the capitulum. This condition is closer to that in *C. zancleana*, although the individual laterals are larger and much broader. Here, I follow Withers (1953) in the assignation of *zancleana* to *Calantica*.

Calantica zancleana (Seguenza, 1876)
Fig. 2/4

1670	Rostra (ut puto) animalo polypo similis – Scilla, pl. 14, fig. 9.
*1876	*Scalpellum zancleanum* Seguenza, p. 386, pl. 7, figs 1-13.
1916	*Scalpellum* (*Smilium*) *nudipes* Annandale, p. 287, pl. 4, fig. 1; pl. 5, figs 1-6; pl. 6, figs 1, 2.
1953	*Calantica zancleana* (Seguenza) – Withers, p. 143, pl. 12, figs 5, 6; pl. 13, figs 1-7; pl. 54, fig. 1.
1953	*Scalpellum* cf. *zancleanum* Seguenza – Davadie, p. 83, pl. 1, fig. 6.
1978	*Smilium zancleanum* (Seguenza) – Foster, p. 49, fig. 29, pl. 6D, E.

Diagnosis – A species of *Calantica* with moderately narrow carina, subcarinated; tectum moderately to strongly arched transversely, with a variably raised border on each side; parietes narrow and sharply inturned; basal margin rounded or obtusely angular. Upper latus much wider than high (after Withers, 1953, p. 143).

Types – Withers (1953, p. 144, pl. 12, fig. 6) designated a scutum (NHMUK In. 33607) from Messina (Sicily) neotype.

Material – NHMUK collections include 63 registered valves of this species (In.18546-33646, In.33697) (Withers, 1953 p. 144). No further material has been recovered for the present study.

Remarks – This very large (individual terga and carinae measuring up to 50-60 mm in height), distinctive species was, for Seguenza, one of the most abundant Messinian cirripedes, and he recorded it from numerous localities (Seguenza, 1876, p. 22). Withers (1953) provided a detailed redescription of the species based on both material in the NHMUK collections and Seguenza's illustrations of lateral plates. Withers noted that the species was still living in the Java Sea (Calman, 1918; Withers, 1953, pl. 64, fig. 1), where it had been recorded as *C. nudipes* Annandale, 1916. It is also present in the Tasman Sea and at numerous stations around New Zealand (Foster, 1978). These records provide important, and unusual, evidence of relic species distributions which must have preceded the closure of the eastern Mediterranean at about 16-20 Ma (Hamon *et al*., 2013).

Order Scalpellomorpha Buckeridge and Newman, 1996
Superfamily Lepadoidea Chan, Gale, Glenner, Dreyer, Ewers Saucedo, Pérez-Losada, Kolbasov, Crandall & Høeg, 2021
Family Lepadidae Darwin, 1851
Genus *Lepas* Linnaeus, 1758

Type species – *Lepas anatifera* Linnaeus, 1758, by monotypy.

Lepas mallandriniana Seguenza, 1876

*1876	*Lepas mallandriniana* Seguenza, p. 369, pl. 6, fig. 1.
1953	*Lepas mallandriniana* Seguenza – Withers, p. 334, pl. 49, fig. 7.

Type – The unique scutum (now lost) figured by Seguenza is here selected lectotype.

Remarks – Withers (1953, p. 334) discussed this species at some length and concluded that it was probably a separate species which compared with *Lepas rovasendai* De Alessandri, 1895 (Miocene, northern Italy), in its thinness, smoothness and the presence of a reflexed basal margin.

However, it differs in that the umbonal-apical ridge is placed near the occludent margin, the carinal margin is flattened and the basal margin is comparatively longer.

Lepas hilli **(Leach, 1818)**

1876 *Lepas hilli* Leach – Seguenza, p. 371, pl. 6, fig. 2.
1953 *Lepas hilli* Leach – Withers, p. 353.

Material – A single tergum (now lost) figured by Seguenza was from Scoppo (Sicily).

Remarks – Withers (1953, p. 353) referred this specimen to *L. hilli* with some doubt, considering the possibility that it might belong to *L. rovasendai*.

Superfamily Scalpelloidea Chan, Gale, Glenner, Dreyer, Ewers Saucedo, Pérez-Losada, Kolbasov, Crandall & Høeg, 2021
Family Scalpellidae Pilsbry, 1907
Genus *Scalpellum* Leach, 1817

Type species – Lepas scalpellum Linnaeus 1767 designated by Leach, 1824.

Scalpellum molinianum **Seguenza, 1876**

*1876 *Scalpellum molinianum* Seguenza, p. 378, pl. 6, figs 9-13.
1876 *Scalpellum magnum* Darwin – Seguenza, p. 376, pl. 6, fig. 8.
1953 *Scalpellum molinianum* Seguenza – Withers, p. 281, pl. 47, figs 1-9.

Diagnosis – A species of *Scalpellum* in which the carina has an umbo situated less than one third the length of the valve from the apex, tectum flat to flatly rounded, bordered on each side by a low, unusually strong ridge. Tergum with a comparatively wide outward extension of the valve along the occludent margin. Scutum with the upper extension of the valve curved outwards. Upper latus with the umbo situated about one third of the distance from the apex (after Withers, 1953, p. 281).

Type – The scutum (now lost) figured by Seguenza (1876, pl. 6, fig. 10) is here selected as lectotype.

Material – Seguenza's material came from Trovasi nel Modense (Sicily) and also included two carinae and one fragmentary scutum from Capo Milazzo; material now lost.

Scalpellum sigmoideum **Withers, 1953**

1876 *Scalpellum vulgare* Leach, var. – Seguenza, p. 372, pl. 6, figs 3-7.
*1953 *Scalpellum sigmoideum* Withers, p. 395, pl. 55, figs 1-5.

Diagnosis – A species of *Scalpellum* with the umbo of the scutum removed from the apex to about one fifth the length of the valve. Tergum with the apical part curved towards the carinal side, and the basal part curved towards the scutal side, the outward growth along the occludent margin moderately wide. Upper latus short and broad, with the umbo almost central. Carinal latus low and wide, incurved, the angle formed by the carinal and inframedian lateral margins well removed from the middle of the valve (after Withers, 1953, p. 395).

Type – The lectotype, designated by Withers (1953), was the tergum figured by Seguenza (1876, pl. 6, figs 3, 3a), as *Scalpellum vulgare.*

Remarks – No further material of the species has been obtained.

Scalpellum **sp.**

Plate 5, figs 1-3

Material – Two carinae (one fragmentary) and the apical part of a scutum from the Calabrian of Scoppo (PMC. R. 1. Cal. CIR-39c-41c) (Table 1).

Remarks – The fragmentary apical portion of a scutum (Pl. 5, fig. 1) has an acuminate apex above umbo; the original valve was approximately 6 mm in length. It lacks the transverse rib which extends dorsally from the umbo in *S. molinianum* (see Seguenza, 1876, pl. 6, figs 9, 10; Withers, 1953, pl. 48, fig. 7). The small carina (Pl. 5, fig. 2a, b) is complete and has a slightly subapical umbo, broad intraparietes and a convex tectum; the larger fragment (Pl. 5, fig. 3) has broad intraparietes and probably had a significant extension apical to the umbo. Withers (1953, figs 13-18) illustrated the ontogeny of *Scalpellum* and showed that the umbones on the scutum and carina moved progressively to a subapical position with growth, and the apical process on the scutum enlarged gradually. The specimens illustrated here are probably too immature to show specifically diagnostic features. Seguenza (1876, p. 76, pl. 12, fig. 14) named an incomplete carina as *S. fragmentarium*, which Withers (1953) suspected to be indeterminate.

Genus *Arcoscalpellum* Hoek, 1907

Type species – Scalpellum michelottianum Seguenza, 1876, by original designation.

Arcoscalpellum michelottianum **(Seguenza, 1876)**

Plate 5, fig. 4a, b

*1876 *Scalpellum michelottianum* Seguenza, p. 381, pl. 6, figs 15-25.

1907 *Scalpellum* (*Arcoscalpellum*) *michelottianum* Seguenza – Hoek, p. 59.
1953 *Scalpellum* (*Arcoscalpellum*) *michelottianum* Seguenza – Withers, p. 225, pl. 37, figs 1-10; pl. 54, fig. 4.
1953 *Scalpellum michelottianum* Seguenza – Davadie, p. 83, pl. 1, fig. 4.
1971 *Arcoscalpellum michelottianum* (Seguenza) – Newman & Ross, p. 71, text-fig. 34; pl. 9b.
2015 *Arcoscalpellum michelottianum* (Seguenza) – Gale, p. 5, fig. 2C.

Synonyms – *Scalpellum velutinum* Hoek, 1883; *Scalpellum eximum* Hoek, 1883; *Scalpellum erectum* Aurivillius, 1898; *Scalpellum alatum* Gruvel, 1900. Reference is made to Withers (1953, p. 225) and Newman & Ross (1971) for fuller synonymies.

Type – As the original material was lost, Withers (1953, p. 226, pl. 37, fig. 1) designated a carina from Messina, Sicily (NHMUK In. 33680) neotype.

Material – NHMUK collections include 21 registered valves of this species from Messina (Sicily) (In.33679-33700). We have collected a single carina (Pl. 5, fig. 4a, b) from the Calabrian of Scoppo (PMC. R. 1. Cal. CIR-42c).

Remarks – This large, distinctive species occurs globally in the deep sea, and the names proposed by various authors for specimens discovered by the late-19th century dredging expeditions were synonymised with Seguenza's original name by Hoek (1907, see above). Seguenza's Sicilian material came from the "upper Zanclean" of Scoppo, Trapani and Gravitelli, and he had over 1,000 valves of the species available. Only a single carina has been collected during the present study. The species is first recorded from the 'Helvetian' (middle Miocene) of the Turin Hills, northern Italy, as *A. michelottianum* var. *nanum* Withers, 1953.

Order Verrucomorpha Pilsbry, 1916
Family Verrucidae Darwin, 1854b

Remarks – Seguenza's (1873) work on verrucids, whilst detailed and figuring five species, has not been widely referred to in either palaeontological or zoological papers on the family. He recorded five species of Verruca, including *V. stroemia* (Müller, 1776) and four new ones, *V. crebricosta, V. dilatata, V. romettensis* and *V. zanclea*. So far as I am aware, only Di Geronimo (2010) and Gale (2020b) have used any of Seguenza's species names for figured material since the original publication, although Withers (1953, p. 62) did list three of his species (*V. dilatata, V. romettensis* and *V. zanclea*). This is in contrast to his work on scalpellids and calanticids which has been widely cited. However, various authors, notably Gruvel (1900), described possibly conspecific living taxa from the east-central Atlantic. Gruvel's (1900) taxa were redescribed and illustrated by Young (1998a, 2002a) and synonymies are here discussed under individual species. This creates a dilemma, because three of Seguenza's verrucid species have subsequently been described under different names by zoologists. His names from 1873 (*Verruca romettensis, V. dilatata* and *V. zanclea*) have been used since 1899, by De Alessandri (1906), Withers (1953) and Di Geronimo (2010) and thus appear to qualify as justified senior synonyms.

Another problem is that Seguenza's (1873) illustrations of his species are quite stylised; in particular, the external surfaces of many plates are shown to be completely smooth, sometimes lacking even growth lines; verrucid valves are never really like this. Additionally, there is no certainty that all the figured isolated valves really belong to the named species. This is particularly true of rostra and carinae which can be very difficult to assign to taxa.

Verrucids have a long history in the Mediterranean region; Carriol & Dieni (2005) described three new species, *Costatoverruca? seguenzai*, *Metaverruca eugenea* and *Verruca veneta*, from the upper Eocene (Priabonian) of northern Italy, and De Alessandri (1906) recorded *Verruca stroemia*, and described *V. miocrebricosta* and *V. gruveli* from the Miocene of the Colli di Torino (Turin, northern Italy).

The species *C. seguenzai* is particularly interesting, because it is a member of the genus *Rostratoverruca*. The ribbing on the moveable terga and scuta indicates a close relationship, if not conspecifity, with the living Indo-Pacific *R. kreugeri* (Broch, 1922) (see Gale, 2020a, pl. 10 fig. 3a; compare Carriol & Dieni, 2005, figs 5, 7, 8). In parallel, *R. crebricosta*, in which the moveable scutum has short radial ribs which do not extend far above the contact with the rostrum, and which lacks ribs on the dorsal portion of the moveable tergum, comes close to the arrangement in *R. koehleri* (Gruvel, 1907) and *C. pacifica* (Buckeridge, 1994) (see Gale, 2020a, pl. 10, figs 2a, 6a). It therefore appears likely that relatives of the extant species of *Rostratoverruca* lived in the Mediterranean region, perhaps recolonising from the Atlantic, and at least two survived into the Pleistocene.

Genus *Gibbosaverruca* Young, 2002b

Type species – *Verruca gibbosa* Hoek, 1883, by original designation.

Diagnosis – Robust, usually large 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 of <45° (emended from Young, 2002b).

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 Sicilian material includes one new species of the genus.

Gibbosaverruca milazzoensis **sp. nov.**

Plate 7, figs 1-10, 12, 13, 16

Diagnosis – Small *Gibbosaverruca* in which the apicobasal ridge on the fixed tergum is narrow and dorsally convex and broadens towards the base.

Type – The fixed tergum figured here is the holotype (Pl. 7, fig. 2; PMC.CIR.18.1.2021.a); other illustrated valves are paratypes (Pl. 7, figs 1, 3-10, 12, 13, 16; PMC.CIR.18.1.2021.b1-b11). All are from the Gelasian of Capo Milazzo, Punta Massa, Sicily (sample PM6).

Derivation of name – After Capo Milazzo, Sicily.

Material – 21 dissociated valves from the Gelasian of Capo Milazzo, Punta Massa (sample PM6) and 7 from Cala Sant'Antonino (sample CA4) (Table 1).

Description – Shell tall, total height 3-4 mm, fixed tergum (Pl. 7, figs 1-4) with elongated, narrow central apicobasal ridge, convex on dorsal margin, broadening basally. Scutal auricle and occludent wing subequal, occupying apical half of valve. Occludent margin gently convex. Fixed scutum (Pl. 7, figs 5, 10) rhombic, occludent wing broad, central ridge narrow, single broad ridge articulating with fixed tergum; interior of valve (Pl. 7, fig. 10) with high, shallow scutal adductor scar. Carina (Pl. 7, figs 13, 16) elongated, triangular, curved dorsally, bearing three strong apicobasal ridges which articulate with rostrum. Rostrum (Pl. 7, fig. 12) short, slightly inclined ventrally. Moveable tergum (Pl. 7, figs 6, 9) with convex occludent margin, strong apicobasal ridge forming short prominence at basiscutal angle; second rib broad, low, separated from third (apical) rib by concavity. Moveable scutum (Pl. 7, figs 7, 8) with strongly convex occludent margin, and two apicobasal ribs, ventral one being narrow, dorsal one broader.

Remarks – *Gibbosaverruca milazzoensis* sp. nov. is a small, tall species, 3-4 mm in height, and thus smaller than most congeners, which are commonly up to 10 mm in height. It is assigned to the genus because it has a rather elongated, dorsally curved carina, which bears three strong ridges (Pl. 7, figs 13, 16) and a short rostrum (Pl. 7, fig. 12), similar in development to *G. nitida* (Hoek, 1883; see Fig. 6/3, Pl. 7, figs 14, 15). The fixed scutum (Pl. 7, figs 5, 10) has a single articular ridge with the fixed tergum, but the occludent surface is broader than that in *G. nitida* (Pl. 7, fig. 17).
The fixed terga (Pl. 7, figs 1-4) are also similar in shape to those of *G. nitida* (Pl. 7, fig. 18), but the apicobasal ridge is consistently narrower and more strongly curved. The moveable terga (Pl. 7, figs 6, 9) and scuta (Pl. 7, figs 7, 8) possess three articulating ribs, of which the central one is broad and low, and very similar to those of *G. nitida* (Fig. 6/3; Pl. 7, fig. 11a, b). The only *Gibbosaverruca* known from the central Atlantic (Young, 2001, fig. 15) are *G. costata* (Aurivillius, 1898), which has four articulating ribs on the moveable valves (see Gruvel, 1920, pl. 6, fig. 4), *G. darwini* (Pilsbry, 1907, pl. 10, figs 4-8) and *G. rathbuniana* (Pilsbry, 1916, pl. 7, fig. 2). *Gibbosaverruca milazzoensis* sp. nov. differs from *G. darwini* in its narrower fixed tergum and stronger articular ridges on the moveable valves, plus the narrower carina. It differs from *G. rathbuniana* in the narrower ridges on the fixed tergum and scutum.

Genus *Rostratoverruca* Broch, 1922

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

Diagnosis – Shell box-like, elongated along dorsal-ventral line; opercular lid parallel with base; fixed scutum trapezoidal to triangular, occludent margin convex.

Remarks – The generic separation of *Rostratoverruca* and *Costatoverruca* Young, 1998a was not clear from Young's original description (p. 79), as he diagnosed *Costatoverruca* by the presence of secondary ridges on the rostrum. In his fig. 25c, both genera are shown as having these ridges, and they are also present on some *Cristallinaverruca* Young, 2002, and on the type species of *Rostratoverruca, R. nexa*. Gale (2020a) attempted to separate *Costatoverruca* from *Rostratoverruca* using differences in the shape of the fixed scutum (*i.e.*, triangular in *Rostratoverruca* and rectangular to trapezoidal in *Costatoverruca*) and the curvature of the occludent margin. However, although the fixed scutum is triangular in *R. kruegeri*, it is rectangular in other species such as *R. koehleri* (Gruvel, 1907) and the type species, *R. nexa*. In the absence of other distinguishing characters, it is therefore recommended to place *Costatoverruca* in synonymy with *Rostratoverruca*, which action is followed here.

Rostratoverruca romettensis **(Seguenza, 1873)**

Fig. 6/1; Plate 5, figs 5-19; Plate 6, figs 1-10

*1873	*Verruca romettensis* Seguenza, p. 85, pl. 5, figs 1, 1a-m.
?1873	*Verruca romettensis squamulosa* Seguenza, p. 87.
1900	*Verruca imbricata* Gruvel, p. 244.
1902	*Verruca imbricata* Gruvel, p. 105, pl. 5, figs 13, 14.
1905	*Verruca imbricata* Gruvel, p. 188, fig. 187.
1998a	*Newmaniverruca imbricata* (Gruvel) – Young, p. 77.
2003b	*Metaverruca imbricata* (Gruvel) – Young, p. 780, figs 8, 9.
2020b	*Costatoverruca crebricosta* (Seguenza) – Gale, p. 193, pl. 3, figs 1, 2, 16.

Diagnosis – Surface sculpture of closely spaced, undulose, imbricate growth increments; fixed scutum quadrangular, broad tergal surface, occludent wing sharply demarcated; moveable tergum and scutum bear 4-5 interpenetrant articular ribs; rostrum and carina with three strong, interpenetrant ridges.

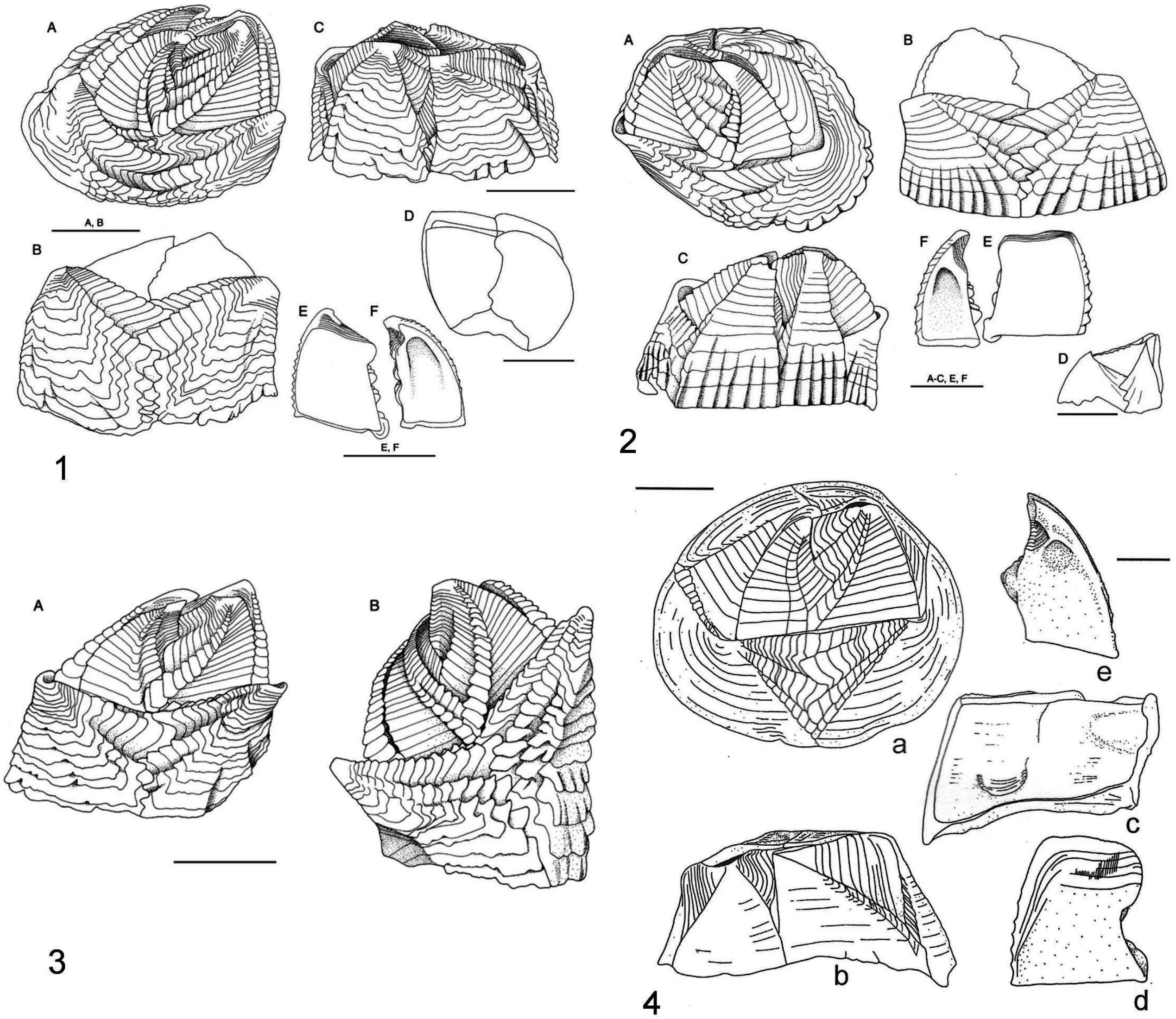


Figure 6. Extant verrucid species: 1. *Rostratoverruca romettensis* (Seguenza, 1873), the original of Young (2003, fig. 8a-f, as *Metaverruca imbricata* (Gruvel, 1900)); 2. *Metaverruca dilatata* (Seguenza, 1873), the original of Young (2003, fig. 12a-f, as *Metaverruca radiata* (Gruvel, 1901)); 3. *Gibbosaverruca nitida* (Hoek, 1883), the original of Young (2003, fig. 18A, B); 4. *Metaverruca zanclea* (Seguenza, 1873), the original of Young (1998b, fig. 23a-e, as *Metaverruca recta* (Aurivillius, 1898)). Scale bars equal 2 mm.

Type – The specimen figured by Seguenza (1873, pl. 5, fig. 1n) is here designated lectotype.

Material – Over 1,000 isolated valves from the Calabrian of Scoppo, Sicily (SC); two articulated individuals and several articulated carinae/rostra (PMC. R. 1. Cal. CIR-43-57c, 59-67c). The species is also present at Cala Sant'Antonio (sample CA8) and Punta Mazza (sample PM8) (Table 1).

Variation in form – The new, abundant (> 1,000 loose valves and some articulated individuals) material of *Rostratoverruca romettensis* from Scoppo provides an unparalled opportunity to study the variation in a single assemblage of a verrucid species. The invariant morphology of the moveable valves (Pl. 6, figs 2-5) indicates that only a single species is present, but the variation in other valves is very considerable. The angle between the fixed and moveable scuta varies from approximately 45° in tall specimens (Pl. 5, fig. 13) to 90° in low ones (Pl. 5, fig. 7) and the relative height is reflected particularly in the development of the fixed tergum (Pl. 5, figs 5, 8, 11, 14, 16). In high specimens, the central ridge is tall and narrow (Pl. 5, figs 5, 8), in low specimens (Pl. 5, figs 14-16) it is low, basally broad and triangular. The fixed scuta display a parallel variation in form, from tall valves in which the adductor scar is weakly impressed and positioned high on the valve (Pl. 5, fig. 6), through to low, broad valves in which the adductor scar has a basal ridge and is positioned close to the lower margin of the plate (Pl. 5, fig. 17).

Thus, a single large sample of a verrucid species includes individuals which would, on their own features, be referred to *Altiverruca* Pilsbry, 1916 others to *Newmaniver-*

ruca Young, 1998 or *Rostratoverruca*. It is perhaps time to reassess the generic classification of the family.

Remarks – This species is common in the east-central Atlantic; it was described in detail by Young (2003b, p. 780; see Fig. 6/1 here) under the name of *Metaverruca imbricata*. It still lives in the Mediterranean (Medcor 25) and also Seguenza (1876, appendix 2) noted present-day occurrences. I am unable to find any differences between the material described as *V. romettensis* by Seguenza (1873) and *R. imbricata*. The most important similarities are:

- Identical shape of moveable terga and scuta, and arrangement and number of ridges on these plates;
- Arrangement and size of ridges on rostrum and carina, comprising (apically) 2-3 large, deeply interpenetrant ridges and grooves, and basally 3-4 small ridges and grooves.

As the name *V. romettensis* Seguenza, 1873 predates its synonym, *V. imbricata* Gruvel, 1900, the former is here taken as the correct name for this species.

***Rostratoverruca crebricosta* (Seguenza, 1873)**

Fig. 7/1

*1873 *Verruca crebricosta* Seguenza, p. 88, pl. 5, figs 3, 3a-l.

Diagnosis – *Rostratoverruca* with subquadrate outline, rostrum and carina united by numerous (6-7) narrow, evenly sized ribs; moveable scutum carrying radial ribs on basal part, forming crenulations where these intersect with growth lines.

Type – The articulated shell (now lost) figured by Seguenza (1873, pl. 5, fig. 3) is here designated lectotype.

Material – No further specimens have been collected. Seguenza (1873, p. 94) recorded this species from Gravitelli, Scoppo, Trapani and Rometta (Sicily).

Description (based on illustrations in Seguenza, 1873, pl. 5, figs 3, 3a-l; refigured here as Fig. 7/1) – Shell compact, subquadrangular, rostrum and carina bearing numerous (6-7) fine ribs which interdigitate at suture. Apex of rostrum marginal, close to junction of fixed and moveable scuta. Rostrum bearing secondary ridges which articulate with those on moveable scutum (clear in Seguenza's fig. 3i, but not shown on entire shell, fig. 3). Fixed tergum rectangular, with three coarse, rounded ribs on scutal surface. Moveable tergum with four ridges, moveable scutum bearing six apicobasal ridges which weaken apically.

Remarks – This species is distinguished by the numerous (6-7) interdigitating ribs, of equal size, on the carina and rostrum, and the ribs on the lower rostral margin of the moveable scutum which articulate with secondary ribs on the rostrum. The species shows affinities with the living *R. nexa* from the Caribbean, with which it shares the numerous ribs on the carina/rostrum, but differs from that in the sculpture of the moveable plates. In *R. nexa*, there are five robust ribs on the moveable scutum, which extend to the apex, but in *R. crebricosta* six weak ribs are present, which do not extend to the apex of the valve, similar to the arrangement in *R. pacifica* (Buckeridge, 1994) (see Gale, 2020a, pl. 10, fig. 6a, as *Costatoverruca pacifica*). *Rostratoverruca pacifica* also has undulations in the growth lines on the lower part of the moveable scutum, as are shown in Seguenza's illustrations of *V. crebricosta*.

***Metaverruca zanclea* (Seguenza, 1873)**

Fig. 6/4; Plate 8, figs 1-10

*1873 *Verruca zanclea* Seguenza, p. 74, pl. 4, figs 1, 1a-1o.
1898 *Verruca recta* Aurivillius, p. 195.
1898 *Verruca sculpta* Aurivillius, p. 197.
1900 *Verruca linearis* Gruvel, p. 243.
1901 *Verruca magna* Gruvel, p. 261.
1902 *Verruca magna* Gruvel, p. 109, pl. 5, figs 1, 2.
1902 *Verruca linearis* Gruvel, p. 107, pl. 5, figs 11, 12.
1905 *Verruca linearis* Gruvel, p. 182, fig. 201.
1905 *Verruca magna* Gruvel, p. 184, figs 204, 205.
1905 *Verruca recta* Aurivillius – Gruvel, p. 181.
1905 *Verruca sculpta* Aurivillius – Gruvel, p. 175.
1906 *Verruca gruveli* De Alessandri, p. 278, pl. 15, figs 1-6.
1907 *Verruca linearis* Gruvel – Hoek, p. 9.
1907 *Verruca magna* Gruvel – Hoek, p. 9.
1907 *Verruca recta* Aurivillius – Hoek, p. 9.
1907 *Verruca sculpta* Aurivillius – Hoek, p. 9.
1912 *Verruca recta* Aurivillius – Gruvel, p. 6.
1913 *Verruca capsula* Hoek, p. 130, pl. 12, figs 1-3; pl. 13, figs 1-4.
1916 *Verruca coraliophila* Pilsbry, p. 130, pl. 1, figs 1-5.
1916 *Verruca halotheca* Pilsbry, p. 46, pl. 8, figs 1, 1a.
1920 *Verruca magna* Gruvel, p. 50.
1920 *Verruca recta* Aurivillius – Gruvel, p. 46, pl. 2, fig. 18; pl. 3, figs 3, 4.
1920 *Verruca sculpta* Aurivillius – Gruvel, p. 41, pl. 5, figs 26, 27.
1929 *Verruca sculpta* Aurivillius – Nilsson-Cantell, p. 461, fig. 1.
1931 *Verruca* (*Metaverruca*) *sculpta* Aurivillius – Broch, p. 41.
1936 *Verruca capsula* Hoek – Stubbings, p. 38.
1938 *Verruca sculpta* Aurivillius – Nilsson-Cantell, p. 12.
1940 *Verruca sculpta* Aurivillius – Krüger, p. 463.
1943 *Verruca halotheca* Pilsbry – Kolosváry, p. 73.
1953 *Verruca zanclea* Seguenza – Withers, p. 62.
1958 *Verruca recta* Aurivillius – Southward and Southward, p. 637, fig. 4.
1968 *Verruca halotheca* Pilsbry – Zullo, p. 219.

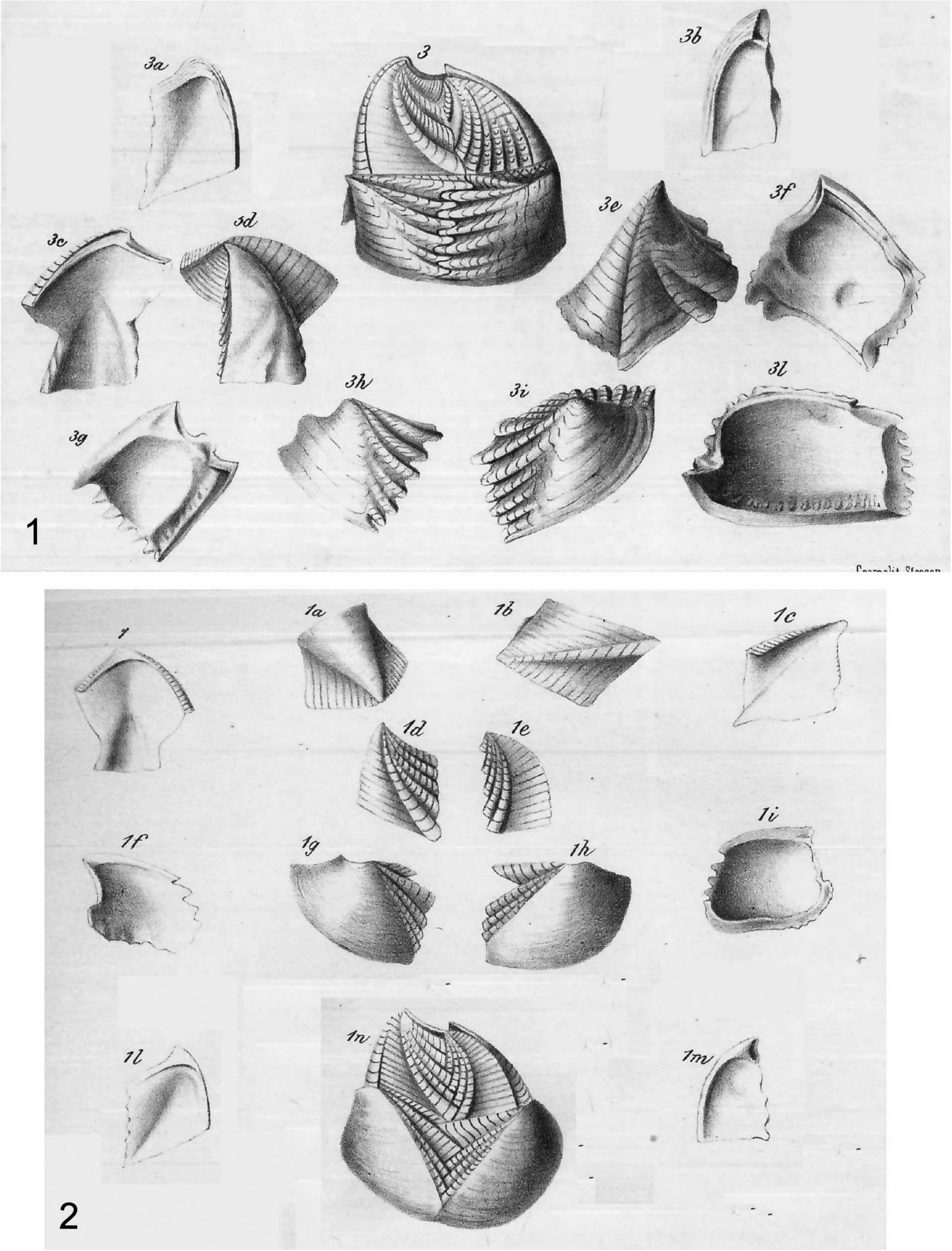


Figure 7. Reproduction of part of Plate 5 in Seguenza (1873): 1 – *Rostratoverruca crebricosta* (Seguenza, 1873): 3. shell, with articulated moveable valves; 3a. interior of moveable tergum; 3b. interior of moveable scutum; 3c, d. fixed tergum, interior and exterior; 3e, f. fixed scutum, exterior and interior; 3g, h. rostrum, interior and exterior; 3i, j. exterior and interior of carina. Original specimens lost; 2 – *Rostratoverruca romettensis* (Seguenza, 1873). 1, 1a. fixed tergum, internal and external view; 1b, 1c. fixed scutum, exterior and interior; 1d. moveable tergum, exterior; 1e. moveable scutum, exterior; 1f, 1g. carina, interior and exterior; 1h, 1i. rostrum, exterior and interior; 1., interior of moveable scutum; 1m. interior of moveable scutum; 1n, shell, with articulated moveable valves.

1968 *Verruca halotheca* Pilsbry – Zullo, p. 219.
1969 *Verruca sculpta* Aurivillius – Zevina, p. 68.
1970 *Verruca coraliophila* Pilsbry – Bayer et al., p. A43.
1975 *Verruca halotheca* Pilsbry – Buckeridge, p. 129.
1978 *Verruca halotheca* Pilsbry – Foster, p. 69, pl. 8F, fig. 42.
1979 *Verruca magna* Gruvel – Weisbord, p. 98.
1979 *Verruca sculpta* Aurivillius – Weisbord, p. 97.
1979 *Verruca holotheca* Pilsbry – Weisbord, p. 98.
1979 *Verruca coraliophila* Pilsbry – Weisbord, p. 98.
1979 *Verruca capsula* Hoek – Weisbord, p. 98.
1980 *Verruca recta* Aurivillius – Anderson, p. 349, figs 1-4.
1981 *Verruca* (*Metaverruca*) *cookei* Rosell, p. 299, pl. 11, figs r, s, u, v.
1981 *Verruca sculpta* Aurivillius – Foster, p. 352.
1983 *Verruca* (*Metaverruca*) *sculpta* Aurivillius – Buckeridge, p. 59 fig. 45.
1984 *Verruca sculpta* Aurivillius – Ren, p. 166, fig. 1; pl. 1, figs 1-6.
1989 *Verruca sculpta* Aurivillius – Ren, p. 420, fig. 10.
1994 *Metaverruca recta* (Aurivillius) – Buckeridge, p. 116, fig. 13a-f.
1995a *Metaverruca recta* (Aurivillius) – Foster and Buckeridge, p. 368, fig. 9C-E.
1995b *Metaverruca recta* (Aurivillius) – Foster and Buckeridge, p. 182 fig. 15.
1997 *Metaverruca recta* (Aurivillius) – Buckeridge, p. 143, fig. 7b.
1998a *Metaverruca recta* (Aurivillius) – Young, p. 52.
1998b *Metaverruca recta* (Aurivillius) – Young, p. 35 figs 23, 24.
2001 *Metaverruca recta* (Aurivillius) – Young, p. 745.
2002a *Metaverruca recta* (Aurivillius) – Young, p. 795, figs 21, 22.
2010 *Metaverruca zanclea* (Seguenza) – Di Geronimo, p. 490, fig. 1L-T.
2020a *Metaverruca* cf. *recta* (Aurivillius) – Gale, p. 168, pl. 18, figs 9-11.
2020b *Metaverruca recta* (Aurivillius), Gale, p. 194, pl. 4, fig. 10.

Diagnosis – Shell smooth, robust, domed, rounded in apical outline; rostrum and carina low, umbones marginal, united by 4-8 interpenetrant ridges; occludent wings on fixed scutum and tergum broad, triangular, bearing evenly spaced growth lines; aperture D-shaped, with straight rostral/carinal margin; moveable valves united by three articular ridges.

Synonymy – The full synonymy of the species is provided above. Important synonyms are *Verruca recta* Aurivillius, 1898, *V. sculpta* Aurivillius, 1898, *V. capsula* Hoek, 1907, *V. halotheca* Pilsbry, 1916 and *V. coraliophila* Pilsbry, 1916.

Type – The complete shell with articulated moveable plates from Trapani, near Messina, figured by Seguenza (1873, pl. 4, fig. 1o) is here designated lectotype.

Material – 50+ valves from the lower Pleistocene, Catallarga Hill (near Grammichele, Sicily) (PMC. R. 1. Cal. CIR-69ch-76ch). A single complete shell from the Gelasian-Calabrian at Capo Milazzo (PMC. R. 1. Cal. CIR-68cm) (Table 1).

Remarks – Seguenza's (1873, pl. 4, fig. 1) material of *V. zanclea* is clearly illustrated and all features indicate conspecifity with the species subsequently described as *V. recta* by Aurivillius (1898), which has since then been found widely in the world's oceans (Buckeridge, 1994; Young, 2002a). In particular, the complete individual figured by Seguenza (his pl. 4, fig. 1o; in part reproduced here as Fig. 8/1) shows the typically quadrate moveable tergum, bearing three broad ridges; the moveable scutum is identical with that of *V. recta*, as is the nature of the interpentrant carina/rostrum margin and the D-shaped outline of articulated moveable valves and orifice (compare with Fig. 6/4). In addition, the straight, evenly separated growth lines on the occludent wings of the fixed scutum and tergum (Seguenza, 1873, pl. 4, fig. 1a, b) are like those on *M. recta* and different to those found in *M. dilatata* (see below).
Seguenza's (1873) name predates that of Aurivillius (1898), *i.e.*, *Verruca* (subsequently *Metaverruca*) *recta,* which has been widely used over the past decade for a species common in the world's ocean basins (*e.g.*, Buckeridge, 1994; Young, 2002a). However, Seguenza's name is valid under Article 29.1 of the ICZN Code.

***Metaverruca dilatata* (Seguenza, 1873)**

Fig. 6/2; Plate 9, figs 1-12

*1873 *Verruca dilatata* Seguenza, p. 80, pl. 4 figs 2, 2a-m.
?1873 *Verruca dilatata minor* Seguenza, p. 83.
1901 *Verruca radiata* Gruvel, p. 262.
1902 *Verruca radiata* Gruvel, p. 94, pl. 2, figs 19, 20.
1905 *Verruca radiata* Gruvel, p. 180, fig. 198.
1953 *Verruca dilatata* Seguenza – Withers, p. 62.
1994 *Cameraverruca radiata* (Gruvel) – Buckeridge, p. 93.
1998a *Newmaniverruca radiata* (Gruvel) – Young, p. 77.
2003 *Metaverruca radiata* (Gruvel) – Young, p. 784, figs 12, 13.

Diagnosis – Shell with crenulated growth lines and apicobasal ridges; rostrum and carina articulate by means of 3–5 interpenetrant ridges. Moveable tergum and scutum each bearing four articular ridges.

Types – The articulated individual (now lost) from Sant'Nicandro, near Messina, figured by Seguenza (1873, pl. 4, fig. 2) is here designated lectotype.

Material – 22 valves from probable Gelasian strata, Catallarga Hill (near Grammichele, Sicily) (PMC.R.1.Cal. CIR-77ch-88ch) (Table 1).

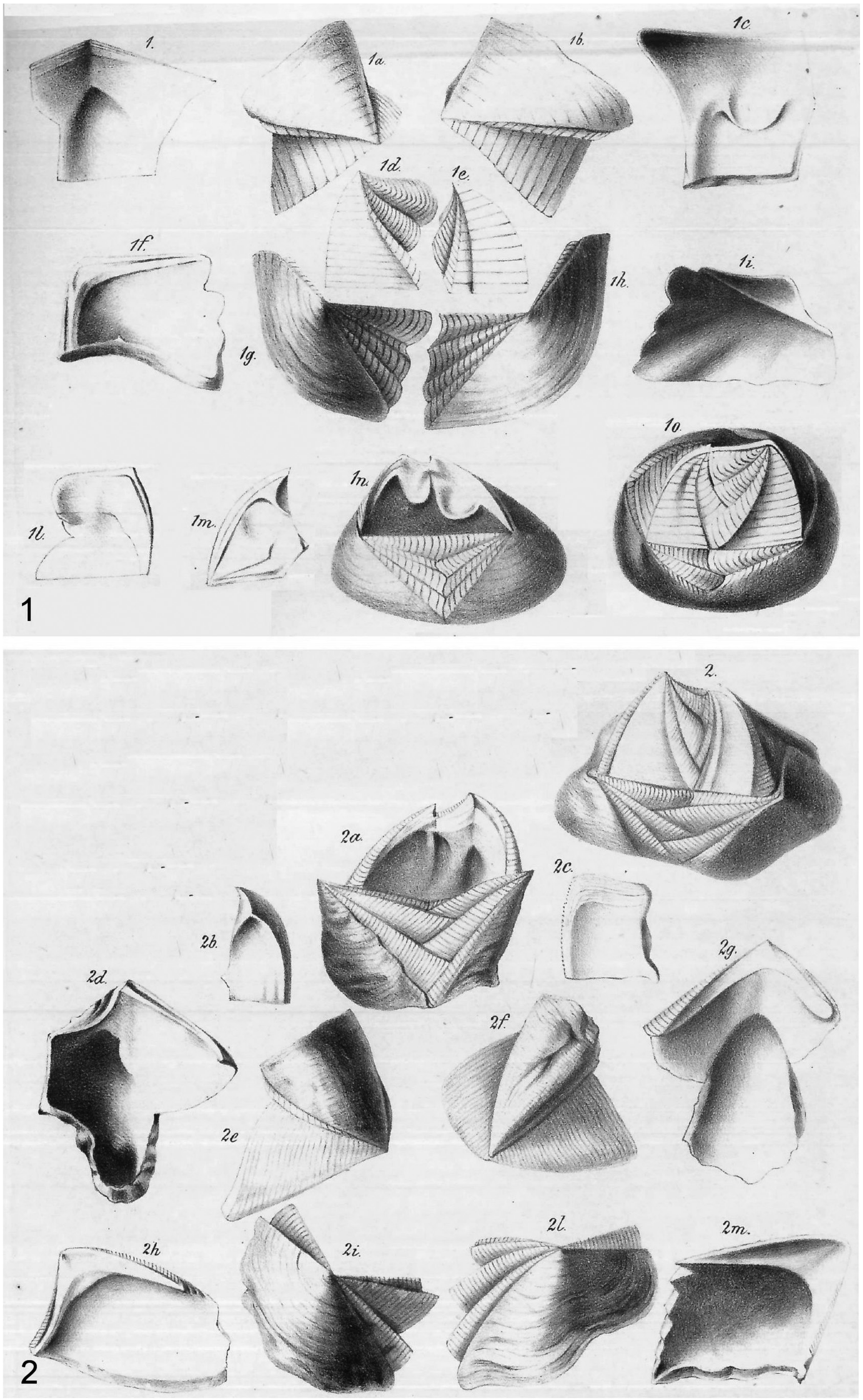


Figure 8. Reproduction of part of Plate 4 of Seguenza (1873), rearranged: 1 – *Metaverruca zanclea* (Seguenza, 1873). 1, 1a. fixed tergum, interior and exterior; 1b, 1c. fixed scutum, exterior and interior; 1d. moveable tergum; 1e. moveable scutum, exterior views; 1f, 1g. rostrum, interior and exterior; 1h, 1i. carina, external and internal views; 1l, 1m. internal view of moveable valves; 1m. shell lacking moveable valves; 1o. complete shell. 2 – *Metaverruca dilatata* (Seguenza, 1873). 2. complete shell; 2a. shell lacking moveable valves; 2b, 2c. interior view of moveable valves; 2d, 2e. fixed scutum, interior and exterior views; 2f, 2g., fixed tergum, exterior and interior views; 2h. 2i. interior and exterior of carina; 2l, 2m. rostrum, exterior and interior views.

Remarks – This is a senior synonym of *M. radiata* (Gruvel, 1901) from the northeast Atlantic. The distinctive features are the ribbing of the lower wall plates, the crenulated growth lines on the wall plates (Pl. 9, figs 1-9), plus the presence of four articular ribs on the moveable scutum and tergum (compare Fig. 6/2 with Pl. 9, figs 11, 12) (Young, 2003). The very broad occludent wings on the fixed scuta and terga, which bear fine, slightly sigmoidal growth lines (Pl. 9, figs 7-9) are also characteristic. Seguenza's material of *M. dilatata* (1873, pl. 4, figs 2, 2a-m) compares well in the ribbing of the moveable plates and the broad, finely ribbed occludent wings on the fixed scuta and terga, but only one of his figured valves shows the characteristic apicobasal ribbing (his pl. 4, fig. 2f). However, most of the external surfaces of the valves illustrated by Seguenza appear rather smooth, a feature also shown in his illustrations of *M. romettensis* (Seguenza, 1873, pl. 5, fig. 1a, g, h, n). At the present day, *M. dilatata* occurs in the eastern Atlantic off Spain and northern Morocco (Young, 2003, fig. 11). As such, its presence in the Pleistocene of the Mediterranean Basin is not surprising.

***Verruca* sp.**

1873 *Verruca stroemia* (O.F. Müller, 1776) – Seguenza, p. 69, pl. 5, figs 2, 2a-h.

Material – Seguenza (1873) had material from San Filippo and Rometta (Sicily.)

Remarks – The illustrations of Seguenza show a form with a radially plicate shell, strongly interpenetrant ridges on the rostrum and carina, and a tall, narrow moveable scutum. The apparent absence of an adductor ridge on the interior of the moveable scutum suggests reference to *V. stroemia* (compare Young, 1998), but further material is needed in order to confirm this. The specific identification of *Verruca* occurring in the present-day Mediterranean region presents some difficulties. Although some authors have recorded, exclusively, *V. stroemia* (Müller, 1776) (see *e.g.* Koukouras & Matsa (1998), whereas Ruggieri (1977) believed that all citations of *Verruca* from the Mediterranean referred to *V. spengleri* Darwin, 1854b, which was also recorded from the Black Sea (Tarasov & Zevina, 1957). Young (1998) and Young *et al*. (2003) discussed the records of verrucids from the Mediterranean species and determined that all specimens identified with certainty belonged to *V. spengleri*. However, Young *et al*. (2003) considered it likely that *V. stroemia* did inhabit the Mediterranean during the Pleistocene.

Order Balanomorpha Pilsbry, 1916

Seguenza (1873, 1876) recorded 20 balanomorph species from the Pleistocene of Sicily, of which 10 were new. Of these, very few have been studied subsequently. De Alessandri (1906) and Moroni (1967) redescribed *Balanus milensis* Seguenza, 1873, on the basis of new material, which was later reassigned to *Solidobalanus* (Newman & Ross, 1976). Moroni (1967) also discussed and figured material of Seguenza's coral barnacle species *Pyrgoma costata*, which was subsequently placed in the genus *Pyrgomina* by Bałuk & Radwański (1967). Ross & Pitombo (2002) revived the name *Pyrgoma elargatum* Seguenza, and placed it in the genus *Pyrgomina*. Gale (2020b, pl. 6, fig, 2) illustrated material of *Pachylasma giganteum* from the lower Pleistocene of Messina.
During recent collecting, relatively few balanomorphs have been found, with the exception of abundant *Pachylasma giganteum* at La Montagna (Messina) and *Solidobalanus* spp. and pyrgomatids from Capo Milazzo.

Superfamily Chthamaloidea Darwin, 1854b
Family Pachylasmatidae Utinomi, 1968

***Pachylasma giganteum* (Philippi, 1836)**
Plate 10, figs 1-10

*1836 *Chthamalus giganteus* Philippi, p. 250.
1854 *Pachylasma giganteum* Philippi – Darwin, p. 477, pl. 19, fig. 5a-d.
1873 *Pachylasma giganteum* Philippi – Seguenza, p. 63, pl. 3, figs 2, 2a-p.
1953 *Pachylasma giganteum* (Philippi) – Withers, 1953, pp. 60, 61.
1953 *Pachylasma giganteum* (Philippi) – Davadie, p. 92 pl. 3, figs 1, 2; pl. 4, figs 1-3.
1998 *Pachylasma giganteum* (Philippi) – Young, p. 44.
2000 *Pachylasma giganteum* (Philippi) – Jones, p. 192.
2020b *Pachylasma giganteum* (Philippi) – Gale, p. 206, pl. 6, figs 1, 2.

Diagnosis – Rostral plate sutures obscure. Marginal and carinomarginal plates of equal size. Scutum with prominent, sinuous growth ridges cut by 4-6 longitudinal striae. Tergum with growth ridges prominent, spur short, half width of basal margin; 8-10 muscle attachment ridges projecting well beyond basal (modified after Jones, 2000, p. 192).

Material – Numerous shells, loose compartmental plates, scuta and terga (PMC. R. 1. Cal. CIR-90lm-98lm) from La Montagna (Messina, Sicily) (sample LM1; see Table 1).

Remarks – *Pachylasma giganteum* is a very large species which is distinguished from congeners particularly by its coarsely sculptured scuta, which bear longitudinal striae and raised growth-parallel ridges (Pl. 10, figs 1e, f, 3a, b). The compartmental plates have irregularly swollen exteriors, bear fine, convoluted growth lines and the basal interior is coarsely rugose (Pl. 10, figs 4b, 6). The species has been recorded from Burdigalian to lower Pleistocene deposits in northern Italy and Sicily (Withers, 1953), and is living in deep water around southern Italy, at depths between 150-250 m (Young, 1998) and at shallower depths (*c*. 80-150 m) in the Messina Straits (Di Geronimo & Fredj, 1987). It also inhabits the Straits of Gibraltar (Foster & Buckeridge, 1995b) and is found around the Azores and off the coast of southwest Spain (Young, 1998b). The species was recorded as encrusting mineralised hardgrounds formed of corals from 460-480 m depths south of Malta (Angeletti *et al*., 2011).

Superfamily Coronuloidea Leach, 1817
Family Chelonibiidae Pilsbry, 1916
Genus *Chelonibia* Leach, 1817

Type species – *Lepas testudinaria* Linnaeus, 1757

Chelonibia depressa **Seguenza, 1876**

*1876 *Chelonibia depressa* Seguenza, p. 43.

Remarks – A single fragmentary rostral plate, rostro-lateral part, from San Filippo, not figured. Seguenza stated that the species was distinguished by “Radial laminae much more numerous than in *C. testudinaria* and thinner. Conical, depressed form, not convex.“ Without illustration, or futher material, little can be said about this species.

Genus *Platylepas* Gray, 1825

Type species – *Lepas hexastylos* Fabricius, 1886.

Platylepas mediterranea **Collareta, Reitano, Rosso, Sanfilippo, Bosselaers, Bianucci & Insacco, 2019**

*2019 *Platylepas mediterranea* Collareta, Reitano, Rosso, Sanfilippo, Bosselaers, Bianucci & Insacco, p. 4, figs 1-3.

Type – Holotype, and sole specimen known to date, is MSNC 4562, from the Gelasian at Capo Milazzo.

Remarks – Collareta *et al*. (2019) illustrated a unique “carinolateral” (*i.e*., marginal) as holotype of this species from the Gelasian of Cala Sant’Antonino at Capo Milazzo. This differs in a number of significant features from congeners, and is the oldest known species of *Platylepas*.

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

Type species – *Lepas diadema* Linnaeus, 1767

Coronula bifida **Bronn, 1831**

1873 *Coronula bifida* Bronn – Seguenza, p. 60, pl. 3, figs 1, 1a-1d.
1876 *Coronula bifida* Bronn – Seguenza, p. 90, pl. 10, fig. 24.
1953 *Coronula ficararrensis* De Gregorio – Davadie, p. 104, pl. 7, figs 1-3.
2018 *Coronula bifida* Bronn – Collareta *et al*., p. 15, fig. 5a-h.

Remarks – This species is distinguished from its congeners in features such as the shallow sheath, bifurcating parietal ribs and stronger transverse ridging on the parietes (Collareta *et al*., 2018). There are numerous other records from Sicily, summarised by Collareta *et al*. (2018), from uppermost Piacenzian to lower Calabrian (1.93-1.71 Ma) levels. Seguenza’s material was recorded as coming from Rometta.

Superfamily Balanoidea Leach, 1817

Remarks – Newman & Ross (1976) divided the Balanoidea into two families; a more basal Archaeobalanidae, usually with solid parietes, radii and bases, and a more derived Balanidae, characterised by tubiferous parietes and, commonly, tubiferous radii and bases. Molecular phylogeny of balanomorphs (Pérez-Losada *et al*., 2014) strongly supported a monophyletic Balanoidea, sister-group to the Pyrgomatidae, but failed to recover a monophyletic Balanidae or Archaeobalanidae; this was reflected in the classification provided recently by Chan *et al*. (2021). However, using morphological data, Gale (2020c, text-fig. 9) recovered a well-supported monophyletic Balanidae, and a paraphyletic Archaeobalanidae. This classification is applied here.

Clade Archaeobalanidae Newman & Ross, 1976

Diagnosis – A paraphyletic assemblage of basal balanoids in which the bases, radii and parietes are usually solid.

Subfamily Acastinae Kolbasov, 1993

Remarks – Acastines are balanomorphs which have specialised to live within sponges, and typically possess a deep, cup-shaped basis, broad radii and thin parietes. Many acastines have spines on the external parietes, which penetrate as anchors into the surrounding sponge tissue (Kolbasov, 1993). There are perhaps 100 living species in the subfamily, apportioned to the genera *Acasta, Neoacasta* Kolbasov, 1993, *Archiacasta* Kolbasov, 1993, *Euacasta* Kolbasov, 1993 and *Pectinoacaster* Kolbasov, 1993 (Chan *et al*., 2021). The various genera are distinguished by features which include the shape and construction of the basis, the presence or absence of internal ribs on the internal surfaces of the parietes, the breadth of the parietes and features of the opercular plates (Kolbasov, 1993). A number of fossil species have been assigned to the subfamily under the name of *Acasta*, including *A. undulata* Darwin, 1854a (Pliocene of southeast England), *A. muricata* Seguenza, 1876, *A. sarda* De Alessandri, 1895 and *A. formae* De Alessandri, 1897 (Oligocene and Miocene of Italy), *A. fischeri* Locard, 1877, *A. vesiculosa* Carriol, 2008, *A. martillacensis* Carriol, *in* Carriol, Cahuzac & Lesport, 2011 (Miocene of France) and examples of the extant species, *A. spongites*, from the Pliocene of Italy (De Alessandri, 1906; Moroni Ruggieri, 1952).When these are represented by well-preserved shells that retain the basis, assignation to living genera may be possible, but others, including *A. muricata*, are based on isolated parietal plates and are difficult to place. The status of all of these species requires reassessment.

"*Acasta*" sp.
Plate 12, figs 8, 10

1873	*Acasta muricata* Seguenza, p. 48, pl. 2, figs 3, 3a-g.
2008	*Acasta muricata* Seguenza – Carriol, p. 44.

Types – The specimen (now lost) figured by Seguenza (1873, pl. 2, fig. 3d, e) is here designated lectotype of *A. muricata*.

Material – Seguenza (1873) illustrated four wall plates, from Scoppo and Capo Milazzo (refigured here as Fig. 9). I have seen one compartmental plate from Scoppo (PMC. R. 1. CIR-102s) and one Capo Milazzo (PMC. R. 1. CIR-104cm) (Table 1).

Description – Seguenza's four specimens (1873, pl. 2) are a rostral plate (fig. 3b, c), a carina (fig. 3, 3a), a carinomarginal (fig. 3f, g) and a marginal (fig. 3d, e). The carina and rostrum have relatively broad, triangular parietes and sparse, irregularly placed short spines. The carinomarginal has narrow, tall parietes and broad radii and variably elongated spines and the marginal bears irregularly sized, elongated spines. The smaller of the two new specimens (Pl. 12, fig. 8a, b) is a strongly convex, rhombic marginal, the external surface of which bears numerous, irregularly arranged, weakly recurved, rounded spines. In its spine development, this specimen resembles the carinal plate of *A. spongites* (Poli, 1795) figured by Southward (2008, fig. 76g). The larger specimen (Pl. 12, fig. 10a, b) is a robust, large carina which carries rather sparse, irregularly arranged short spines that are concentrated on the apical part of the plate.

Remarks – There are a number of problems with the identification of isolated acastine parietal compartments. Firstly, there is currently little understanding of the variability within individual species; secondly, the morphology of the basis is important in characterising species and genera (Kolbasov, 1993). Moroni (1952) assigned material of *Acasta* from the Pliocene of northern Italy to the living species *A. spongites*. Carriol (2008, p. 45) briefly discussed *A. muricata* and stated that it differed from his species *A. vesiculosa* "in the absence of striiae [*sic*] on the internal surface of the parietes". In view of the long, recurved spines present in two of the specimens, *A. muri-*

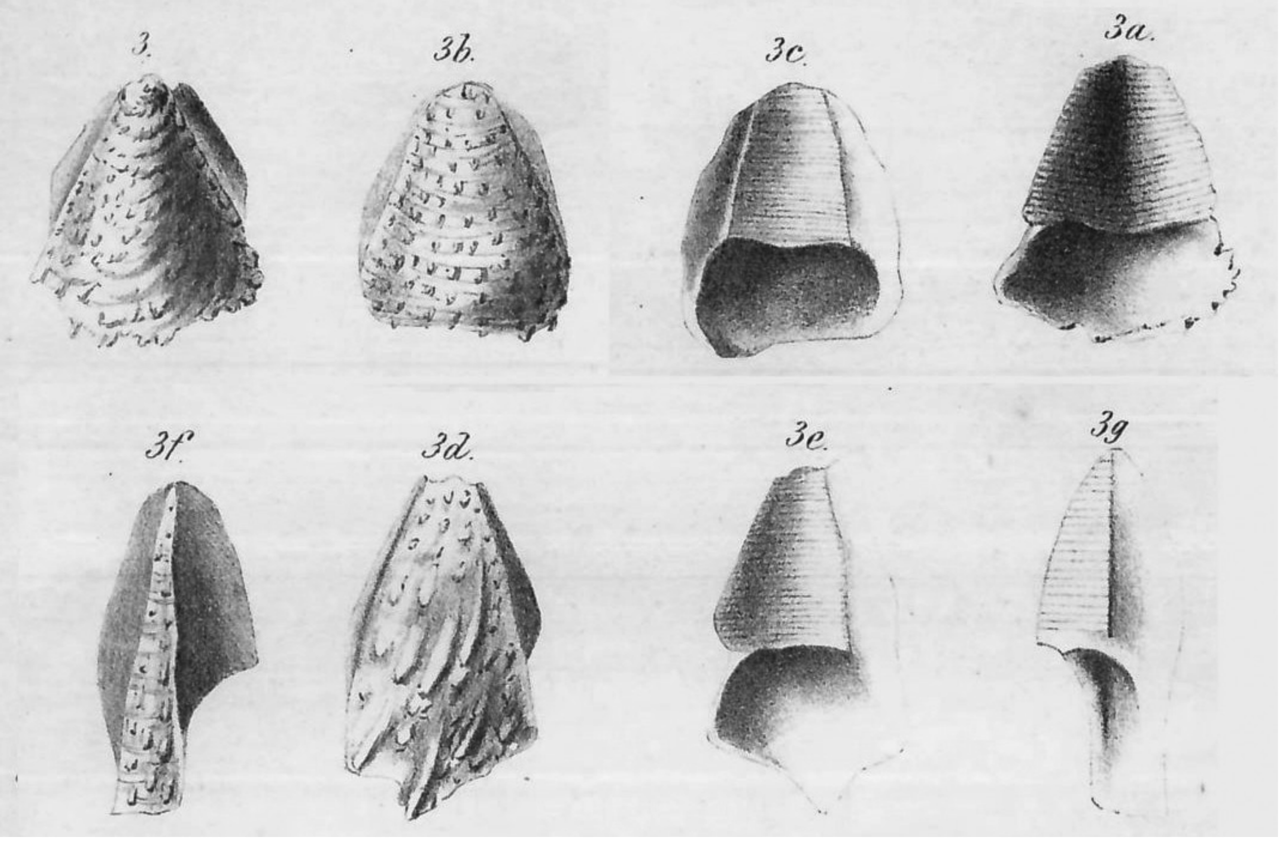


Figure 9. "*Acasta*" sp., the originals of Seguenza (1873, pl. 2, fig. 3, as *Acasta muricata* Seguenza, 1873).

cata may be synonymous to *A. spongites*, but the material is inadequate for certain identification. Dr G. Kolbasov (pers. comm., December 2020) was unable to place the specimens within a genus and recommended caution.

Balanus stellaris **Brocchi, 1814**

1873 *Balanus stellaris* Brocchi – Seguenza, p. 41.
1976 *Actinobalanus stellaris* (Brocchi) – Newman & Ross, p. 49.
1989 *Balanus stellaris* Brocchi – Zullo & Perreault, p. 1.

Remarks – Seguenza did not illustrate this species, but recorded it from Masse near Messina. The species is recorded by De Alessandri (1906, p. 97) as occurring widely in the Miocene and Pliocene of Italy. Menesini (1984) noted that *B. stellaris* first occurred in the middle Eocene of Hérault (France), after which it is found widely in the upper Eocene, Oligocene, Miocene and Pliocene and lower Pleistocene of the Mediterranean region. Extra-Mediterranean occurrences are more uncertain (Menesini, 1984).

Genus *Solidobalanus* Hoek, 1913

Type species – *Balanus auricoma* Hoek, 1913, by original designation

Diagnosis – Parietes, basis and radii solid; opercular plates lack scutal adductor ridge, internal rugosities and calluses (Zullo & Kite, 1985, p. 15).

Remarks – The concept of the genus used here follows Zullo & Kite (1985), for a group of solid-walled species in which the interior of the scutum lacks adductor ridges, rugosities and calluses. Zullo & Kite (1985) separated *Solidobalanus* from *Hesperibalanus* Pilsbry, 1916, within which it had previously been included.

Solidobalanus milensis **(Seguenza, 1873)**

Plate 12, figs 5-7, 9

*1873 *Balanus milensis* Seguenza, p. 43, pl. 2, figs 1, 1a-1c.
1876 *Balanus mylensis* Seguenza, pp. 48, 53.
1906 *Balanus mylensis* Seguenza – De Alessandri, p. 308, pl. 17, figs 22-25.
1967 *Balanus mylensis* Seguenza – Moroni, p. 25, pls 1-9.
1976 *Solidobalanus* (*S.*) *mylensis* (Seguenza) – Newman & Ross, p. 51.

Diagnosis – Shell cylindrical to tulip shaped, orifice broad, toothed; parietes with transverse, pink-white banding. Radii broad, tergum elongated with short, pointed tergal spur.

Type – The specimen (now lost) figured by Seguenza (1873, pl. 2, fig. 1, 1a) is here designated lectotype. It was from Capo Milazzo (Sicily) and of Gelasian-Calabrian age.

Spelling of name – Seguenza (1873, 1876) spelt the name in two ways, *i.e.*, *mylensis* and *milensis*, and both have been used by later authors. The extensive first usage (1873: 6 references; 1876: 1 reference) of the name, *Balanus milensis*, is here taken as the correct spelling.

Material – This species was described from the Gelasian-Calabrian of Capo Milazzo (Table 1) and was figured in detail by Moroni (1967). The new material includes six plates from Cala Sant'Antonio (sample CA4), two from Punta Mazza (sample PM7) and nine from Punta Mazza (sample PM6).

Remarks – This species was identified by De Alessandri (1906), who figured numerous shells, as well as the tergum and scutum (his pl. 17, figs 24, 25). The strongly convex carinal margin of the tergum, the deep V-shaped notch between the tergal spur and tergal margin, and the concave scutal margin, are distinctive and separate this species from extant congeners. De Alessandri (1906) recorded it from diverse localities exposing Miocene and Pliocene strata in Italy, at Cagliari and places in Umbria and Genoa. Moroni (1967) described and illustrated numerous well-preserved specimens of this species, including opercular plates, from Capo di Milazzo, and figured specimens with a distinctive pink-white horizontal banding on the parietes. The species is probably closely related to *Solidobalanus fallax* (Broch, 1927), but differs in the cylindrical rather than conical form of the shell, the very smooth, thickened parietes, the elongated tergum and the coloured banding on the parietes. The species occurs in Sicily and widely in northern Italy, in both Miocene and Pliocene strata (De Alessandri, 1906) and has also been recorded from the Miocene (Langhian) of the Central Paratethys, *i.e.*, the Holy Cross Mountains in Poland (Świerczewska-Gładysz, 1994). Seguenza (1876, Appendix 2) recorded *B. milensis* as occurring alive in Sardinia, but this probably refers to specimens of *S. fallax*, a species which occurs commonly in the Mediterranean (Koukouras & Matsa, 1998).

Solidobalanus digeronimoi **sp. nov.**

Plate 11, figs 1-7; Plate 12, figs 1-4

Diagnosis – Six-plated; parietes, radii and basis solid, radii broad. Interior of parietes with weak ribs; exterior of parietes bearing numerous fine, solid short spines arranged in closely spaced, undulating commarginal rows. Basis perforated by concentrically arranged pores.

Types – The marginal plate illustrated (Pl. 11, fig. 1a, b) is the holotype (PMC.CIR.18.1.2021a), the other figured plates (Pl. 11, figs 2-7; Pl. 12, figs 1-4) are paratypes (PMC.CIR.18.1.2021b1-b10). All are from the Gelasian-Calabrian at Capo Milazzo, Sicily.

Derivation of name – After Professor Italo Di Geronimo, in recognition of his work on the Pleistocene of Italy.

Material – 24 compartmental plates, two scuta and one tergum from Cala Sant'Antonino (sample CA4), one plate from Punta Mazzo (sample PM8), 22 from Capo Milazzo (sample PM6); all from the Capo Milazzo Peninsula, Sicily.

Description – Parietes solid, rather thin, bearing sculpture of numerous fine, solid short spines which are arranged in closely spaced, undulating commarginal rows (Pl. 11, Figs 1a, 2a, 3a, 4, 5a, 6, 7a). In detail (Pl. 11, fig. 1c) these consist of apically directed, rounded processes. Basal interior of parietes (Pl. 11, figs 2b, 5b, 7b) bearing short, irregular ribs, which on rostral plate have inverted U-shaped apical terminations. Rostral plate (Pl. 11, figs 2a, b, 4; Pl. 12, fig. 4) approximating to isosceles triangle in outline, gently convex, bearing broad, striated radii where preserved (Pl. 11, fig. 2a). Marginal plate (Pl. 11, figs 1a, 1b, 6, 7a, b) taller than broad, externally flat to slightly convex, bearing symmetrically triangular radius (Pl. 11, fig. 7a). Parietes of carinomarginal (Pl. 11, figs 5, 6) tall, narrow, becoming narrower with size, bearing narrow radius. Carina (Pl. 11, fig. 3) triangular, externally convex, height twice breadth. Basis (Pl. 11, fig. 7c) thick, undulose, containing irregularly sized, concentrically arranged pores.

Opercular plates: scutum (Pl. 12, figs 1, 2) triangular, occludent margin straight, external surface bearing closely spaced commarginal flanges which protrude on occludent margin. Narrow apicobasal ridge close to occludent margin, tergal surface weakly concave. Internal surface smooth, lacking adductor ridge, scutal adductor scar indistinct; few, impersistent ridges beneath apex. Lateral scutal depressor scar deep, elongated, articular ridge short. Tergum (Pl. 12, fig. 3a, b) externally smooth, tergal spur very short, broad, gently convex margin. Narrow depression running parallel to scutal margin. Interior, with tergal depressor scars short, a few short ridges present close to apex.

Remarks – This species is referred to *Solidobalanus* on the evidence of the solid parietes and, in particular, because of the very smooth interior of the scutum (Zullo & Kite, 1985), which lacks a callus and adductor ridge. However, the assignation is provisional, because the definition of the genus is based largely upon plesiomorphic characters, as are most genera within the Archaeobalanidae. The external sculpture is unusual in the presence of short commarginal spines and it is possible that this species lived inside sponges, paralleling developments in the Acastinae (see above). This type of sculpture is quite widespread in balanomorphs, and was found, for example, on *Megabalanus tintinnabulum peninsularis* Pilsbry, 1916 (pl. 15, fig. 2). The present species differs from *S. milensis* in which the parietes are robust and smooth and in its spiny external sculpture and thinner parietes.

Family Balanidae Leach, 1817

Diagnosis – Balanoids in which the parietes, and often the radii and bases, are permeated by pores; intralaminate figures complex.

Genus *Amphibalanus* Pitombo, 2004

Type species – *Balanus amphitrite* Darwin, 1854b

Amphibalanus amphitrite (Darwin, 1854b)

1873 *Balanus amphitrite* Darwin – Seguenza, p. 36, pl. 1, figs 6, 6a-6f; pl. 2, figs 2, 2a.

Remarks – The scuta and terga figured by Seguenza (1876, pl. 1, fig. 6a-f) compare well with the ranges of morphology of this species illustrated by Pilsbry (1916, pls 19, 20), Davadie (1963, pls 21-23) and Shadadi *et al.* (2014, fig. 10a-l) in overall shape, plus the broad articular ridge on the scutum, the short, round-tipped tergal spur and the deep, flat-based tergal fasciole. Menesini (1984) recorded this species as first occurring in the Oligocene of the Paris Basin (France) and subsequently (early Miocene) extending its range eastwards into the into Mediterranean Basin and Paratethys, extending up into the Pleistocene. However, Zullo (1992a) expressed doubts that the Oligocene-Miocene specimens were correctly referred to *A. amphitrite*. These were subsequently allayed by the illustration of material of this species from the Miocene (Langhian) in the Central Paratethys, namely the Holy Cross Mountains in Poland (Świerczewska-Gładysz, 1994). The species is widespread in the present-day Mediterranean (Koukouros & Matsa, 1998), and is cosmopolitan in warm and temperate seas (Newman & Ross, 1976).

Genus *Balanus* Da Costa, 1778

Type species – *Lepas balanus* Linnaeus, 1758

Balanus crenatus Bruguière, 1789

1953 *Balanus crenatus* Bruguière – Davadie, p. 100, pl. 6, figs 2, 3.

Remarks – Davadie (1953) identified a single shell in the M. Gignoux Collection from the "Astian" of Torre Colona, Sicily, as belonging to this species. The low, conical form, with coarse, irregular, rounded apicobasal ribs and narrow radii tend to confirm this identification (compare with Pilsbry, 1916, pls 40, 41). Although this is the only record from Sicily, the species was recorded as present, but usually rare, in the Mediterranean from the Oligocene to the early Pleistocene (Menesini, 1984).

Balanus darwinii Seguenza, 1876

*1876	*Balanus darwinii* Seguenza, p. 85, pl. 10, figs 11-13.
?1906	*Balanus darwinii* Seguenza – De Alessandri, p. 161, pl. 17, fig. 21.
1953	*Balanus darwinii* Seguenza – Davadie, p. 90, pl. 6, fig. 4.
1976	*Balanus darwinii* Seguenza – Newman & Ross, p. 65.

Type – The well-preserved shell (now lost) figured by Seguenza (1876, pl. 10, fig. 13) is here designated lectotype.

Remarks – Seguenza (1876) did not provide a description of this species; I have not seen any material. The illustrated specimens comprise a shell, figured in lateral view (pl. 10, fig. 13), internal and external views of a tergum (pl. 10, fig. 12, 12a) and a scutum (pl. 10, fig. 11, 11a). The shell is low and conical, with a broad aperture, broad radii; compartments carry 3-4 strong, basally diverging apicobasal ribs. De Alessandri (1906) considered the species to be related to *Balanus trigonus* Darwin, 1854b, presumably on the basis of similarities to the shell of that species, and Newman & Ross (1976, p. 65) and Pitombo (2004) referred the species to the “Group of *B. trigonus*”. However, the scuta and terga do not resemble those of *B. trigonus* or any other known species; in particular, the exterior of the scutum (Seguenza, 1876, pl. 10, fig. 11a) has a ridge running subparallel with the tergal margin and a concave occludent surface. The species is known from Altavilla in Sicily and from Calabria; De Alessandri (1906, pl. 17, fig. 21) illustrated a poorly preserved shell which he assigned to this species. *Balanus trigonus* itself was recorded from the Pliocene of Andoria (Liguria, northern Italy) by Davadie (1963) and Menesini (1984), and from the Miocene of Hungary (Kolosváry, 1949). Zullo (1992b), in a review of the biogeography of this species, rejected these records and suggested that the species was absent from the Atlantic and adjacent regions prior to the 1850s. However, the illustration of material from the middle Miocene (Langhian) of the Central Paratethys, the Holy Cross Mountains in Poland (Świerczewska-Gładysz 1994) indicates that this species was indeed already present at this time.

Balanus veneticensis Seguenza, 1873

*1873	*Balanus veneticensis* Seguenza, p. 39, pl. 1, figs 4, 4a-c.

Remarks – Seguenza stated that the species was characterised by (translated) “the density and structure of the parietes, the breadth of the radii and all features of the shell, and above all distinguished by various characters of the scutum.” Seguenza stated that the species was very rare and was only found near the village of Venetico, Sicily, and was of Pliocene age. Its affinities remain problematical, and no further specimens have been collected. Newman & Ross (1976) and Pitombo (2002) recorded the species under Balanidae *incertae sedis*. The exterior of the scutum (Seguenza, 1873, pl. 1, fig. 4b) bears a resemblance to that of *Balanus darwinii* (Seguenza, 1876, pl. 10, fig. 11a) in the presence of a ridge subparallel with the tergal margin.

Balanus spongicola Brown, 1827

1873	*Balanus spongicola* Brown – Seguenza, p. 23, pl. 1, figs 3, 3a.
1876	*Balanus spongicola* Brown – Seguenza, p. 24, pl. 9 figs 9-17 only.

Remarks – Seguenza (1873) figured one specimen (a shell) from the Pliocene limestone of San Filippo and another from Barcellona, near Messina, both from the “lower Zanclean”. In 1876, he illustrated a larger suite of material, including terga (his pl. 9, figs 12, 15a, b) and scuta (pl. 9, figs 12, 14, 16). These compare well with material of extant specimens (*e.g.*, Darwin, 1854b, pl. 4, fig. 1a-d; Davadie, 1963, pl. 27) particularly in the crenulated occludent margin of the scutum, and the deep tergal depressor pit. The terga are also similar, in the shallow, well-defined spur fasciole and the blunt truncation of the tergal spur. The large tergum figured (Seguenza, 1876, pl. 9, fig. 15, 15a) with a long tergal spur, strongly grooved on the internal face, is perhaps from an old individual. Menesini (1984) recorded the species as appearing in the Oligocene of the Mediterranean region, and persisting to the present day. The geographical range of living specimens extends along the eastern Atlantic seaboard, from the southern United Kingdom down to South Africa (Young, 1998, fig. 32).

Balanus balanus Linnaeus, 1758

1876	*Balanus porcatus* Da Costa – Seguenza, p. 41.

Remarks – Seguenza recorded one specimen, from Astian strata near Barcellona, Messina. De Alessandri (1906 p. 304) also recorded the species from Messina. It is known to occur quite widely in the Miocene-Pliocene of the Mediterranean and northwest Europe (Italy, France, Germany, Russia, Belgium, Sweden, United Kingdom; Davadie, 1963, p. 69). It is absent from the present-day Mediterranean (Koukouros & Matsa, 1998), but does occur extensively in the North Atlantic and North Pacific (Newman & Ross, 1976).

Genus *Concavus* Newman, 1982

Type species – *Balanus concavus* Bronn, 1831

Concavus concavus (Bronn, 1831)

1873	*Balanus concavus* Bronn – Seguenza, p. 32, pl. 1, fig. 5, 5a-5f.

1876 *Balanus concavus* Bronn – Seguenza, pl. 10, figs 1, 3-10 only.
1953 *Balanus concavus* Bronn – Davadie, p. 101, pl. 6, fig. 5.
1982 *Concavus* (*Concavus*) *concavus* (Bronn) – Newman, fig. 1c.
1992a *Concavus concavus* (Bronn) – Zullo, p. 5, fig. 3.1-8.

Remarks – The opercular plates figured by Seguenza (1873, 1876) under this name mostly fall within the range of the species as illustrated by Zullo (1992a, fig. 3.1-8), characterised particularly by the deeply overfolded spur fasciole and long tergal spur. However, the tergum illustrated by Seguenza (1876, pl. 10, fig. 2) is quite different, in the extraordinarily broad scutal and carinal surfaces, flat on the exterior, which do not compare with any known concavine taxon (Zullo, 1992a); this specimen can possibly be referred to *Megabalanus coccopoma* (Darwin, 1854b). Seguenza recorded *B. concavus* from the "lower Zanclean" of Masse. According to Menesini (1984), *C. concavus* first occurred in the late Oligocene of the Mediterranean region, and is found commonly through the Miocene and Pliocene, until it became extinct at the end of the early Pleistocene. However, Zullo (1992a, p. 5) doubted the assignation of pre-Pliocene specimens to this species, and these require further study. The subspecies called *B. concavus rubescens* by Seguenza (1873, unfigured) probably falls within the morphological range of the species.

Concavus scutorum (Seguenza, 1876)

*1876 *Balanus scutorum* Seguenza, p. 78, pl. 9, figs 5-8.
1952 *Balanus* (*Balanus*) *concavus* Bronn *scutorum* (Seguenza) – Moroni Ruggieri, p. 67, pl. 1, figs 5, 6; pl. 2, figs 9-13.
1976 *Balanus concavus scutorum* Seguenza – Newman & Ross, p. 61.

Remarks – Seguenza's figured material includes two shells (his pl. 9, figs 5, 6), a tergum (pl. 9, fig. 7) and a scutum (pl. 9, fig. 8). The tergum has a strongly convex occludent margin and an open spur furrow, which narrows apically. The scutum has the outline of an isosceles triangle, and the external face is dominated by commarginal growth lines, lacking radial striae. The species differs from *C. concavus* in the broader occludent surface of the tergum, the convex occludent margin and the open spur furrow. The scutum differs from that of congeners in lacking strong radial striations. The species in Seguenza's material came from Testa del Prato, near Reggio, and Altavilla, near Palermo, Sicily. Moroni Ruggieri's (1952) material came from the lower Pleistocene of Cojano, Toscana, Italy.

Genus *Megabalanus* Hoek, 1913

Type species – *Lepas tintinnabulum* Linnaeus, 1758

?Megabalanus coccopoma (Darwin, 1854b)

1876 *Balanus concavus* Bronn – Seguenza, pl. 10, figs 2, 2a only.

Remarks – A single tergum, figured by Seguenza (1876, pl. 10, fig. 2, 2a), can possibly be referred to this species (compare Shadadi *et al*., 2014, fig. 12i, j). This appears to be the first fossil record of the species, which at the present day occurs widely in the Indo-Pacific and Atlantic oceans (Henry & McLaughlin, 1986; Shadadi *et al*., 2014). However, the unusual morphology may perhaps be related to the exceptional size of the specimen rather than specific characteristics.

Megabalanus tintinnabulum (Linnaeus, 1758)

1876 *Balanus tintinnabulum* Linnaeus – Seguenza, pl. 9 figs 1, 1a.

Remarks – The single scutum from Terreti, near Reggio, in Calabria, recorded by Seguenza (1876, pl. 9, fig. 1), is insufficient to confirm the presence of this species. In comparison with scuta of the species as figured by Henry & McLaughlin (1986, fig. 5a-c, g, h, k), the basal margin is evenly convex, rather than angled and, on the interior surface, the articular ridge is elongated, rather than short and apical in position. The tergum figured by De Alessandri (1906, pl. 15, fig. 22) from Tuscany certainly belongs to this species. Menesini (1984) stated that the species first appeared in the late Oligocene in northern Italy, and extended its geographical range during the early Miocene to occur in France, Spain and Sardinia. Its range contracts in the late Miocene and Pliocene to local occurrences in Algeria and Apulia (southern Italy). It occurs very locally during the early Pleistocene of the Mediterranean Basin, and then disappears. It occurs widely in the Atlantic Ocean, from Gibraltar to the Cape of Good Hope, and is also present in the Pacific and Indian oceans. According to Seguenza (1876, Appendix 2) and Menesini (1984) records of living *M. tintinnabulum* in the Mediterranean Sea (*e.g.*, Koukouras & Matsa, 1998) are introductions from shipping, more recently possibly as Lessepsian migrants through the Suez Canal.

Megabalanus tulipiformis (Ellis, 1758)

1873 *Balanus tulipiformis* Ellis – Seguenza, p. 19, pl. 1, figs 1, 1a, 1b.
1876 *Balanus tulipiformis* Ellis – Seguenza, pl. 9, figs 2, 3.
1953 *Balanus tulipiformis* Ellis – Davadie, p. 97, pl. 5, figs 1-6; pl. 6, fig. 6.

Remarks – Seguenza (1873, 1876) figured three shells which he identified as belonging to this species, and a scutum (1876, pl. 9, fig. 3), all from Faro. This is similar in shape to a scutum of *M. tulipiformis* figured by Henry & McLaughlin (1986, fig. 14a, b) and also agrees in the form of the articular ridge and the tergal depressor pit. De Alessandri (1906, pl. 4, figs 1-5) figured material of this species from Tuscany and Calabria. According to Menesini (1984), the species appeared in the middle Miocene of Italy and France, and became abundant in the Miocene and Pliocene of Italy and spread to Algeria. It is found across the present-day Mediterranean (Menesini, 1984; Koukouros & Matsa, 1998, p. 137) and extends along the eastern Atlantic seaboard from the Bay of Biscay south to Angola (Young, 1998b, fig. 33). Seguenza's material came from the "Pliocene" (probably uppermost Piacenzian-Calabrian) of Faro, Sicily.

Genus *Perforatus* Pitombo, 2004

Type species – *Balanus perforatus* Brugière, 1789

Perforatus perforatus (Bruguière, 1789)

1873 *Balanus perforatus* Bruguière – Seguenza, p. 27, pl. 1, fig. 2, 2a.
1876 *Balanus perforatus* Bruguière – Seguenza, pl. 9, figs 18-22.

Remarks – The morphology of the tergum and scutum figured by Seguenza (1876, pl. 9, figs 20, 21) compares well with extant examples figured by Davadie (1963, pls 16-18) in the deep, almost closed spur fasciole, the elongated tergal spur, the strong scutal adductor ridge on the scutum and the deep lateral scutal depressor scar on the scutum. The conical shells with a narrow orifice (Seguenza, 1876, pl. 9, figs 18, 19, 22) are also typical of the species (*e.g.*, Southward, 2008, fig. 27). Seguenza recorded the species from Caltanisetta, Altavilla and Masse in Sicily. According to Menesini (1984), the species appeared in the earliest Oligocene of the Mediterranean; it survives to the present day across the Mediterranean (Koukouros & Matsa, 1998, p. 137).

Family Pyrgomatidae Gray, 1825

Diagnosis – Wall of 4, 6 plates or wholly concrescent; parietes solid or tubiferous; when tubiferous tubes occur between outer lamina and sheath, or between external ribs of wall; interlaminate figures complex, radii solid; basis calcareous, rarely tubiferous, membranous in *Pyrgospongia*. All species of this family are highly specialised to symbiosis in corals or sponges (Anderson, 1994). This has affected many extreme morphological specialisations in some clades.

Remarks – The precise age of the fossil pyrgomatids recorded by Seguenza (1873), Moroni (1952) and those figured herein, probably all from Capo Milazzo, is unknown.

Subfamily Megatrematinae Holthuis, 1982

Diagnosis – Wall single plated, conical, hemispherical or discoidal, opercular plates separable; scutum balanoid; tergum saggitate or trapezoidal (after Ross & Pitombo, 2002 p. 58).

Genus *Adna* Sowerby, 1823

Type species – *Adna anglica* Sowerby, 1823

Adna anglica J. de C. Sowerby, 1823

1873 *Pyrgoma anglicum* Sowerby – Seguenza, pl. 2, figs 4a, 4b.
2002 *Adna anglica* Sowerby – Ross & Pitombo, p. 58.

Remarks – Seguenza only figured a single scutum of this species (refigured here as Fig. 10/4a-b), although he evidently had more material. The interior of the scutum is comparable with that of the specimen figured by Darwin (1854b, pl. 12, fig. 4b) in shape and the depressed region adjacent to the lower tergal margin. The species is recorded as living in the western Mediterranean (Koukouros & Matsa, 1998).

Genus *Pyrgomina* Bałuk & Radwański, 1967

Type species – *Pyrgomina seguenzai* Bałuk & Radwański, 1967

Pyrgomina costatum (Seguenza, 1873)
Plate 13, figs 1, 4

*1873 *Pyrgoma costatum* Seguenza, p. 52, pl. 2, figs 5a-c, e.
1967 *Pyrgoma costatum* Seguenza – Moroni, p. 40, pl. 10, fig. 1a-d; pl. 13, fig. 1-h.
1967 *Creusia costata* (Seguenza) – Bałuk & Radwański, p. 484.
1976 *Ceratoconcha costata* (Seguenza) – Newman & Ross, p. 58.
2002 *Pyrgomina costatum* (Seguenza) – Ross & Pitombo, p. 60.

Diagnosis – *Pyrgomina* in which 29-31 ribs are present; ribs low, acutely rounded and separated by as much or more than their own width.

Types – Seguenza's specimens (Fig. 10/5a-c, d) from the "Zanclean" of Capo Milazzo are lost, but Moroni (1967, pl. 10, fig. 1) designated a neotype from the same locality. The whereabouts of Moroni's material are unknown.

Material – Two specimens from the Gelasian-Calabrian of Capo Milazzo (PMC. R. 1. CIR-105cm, 108cm).

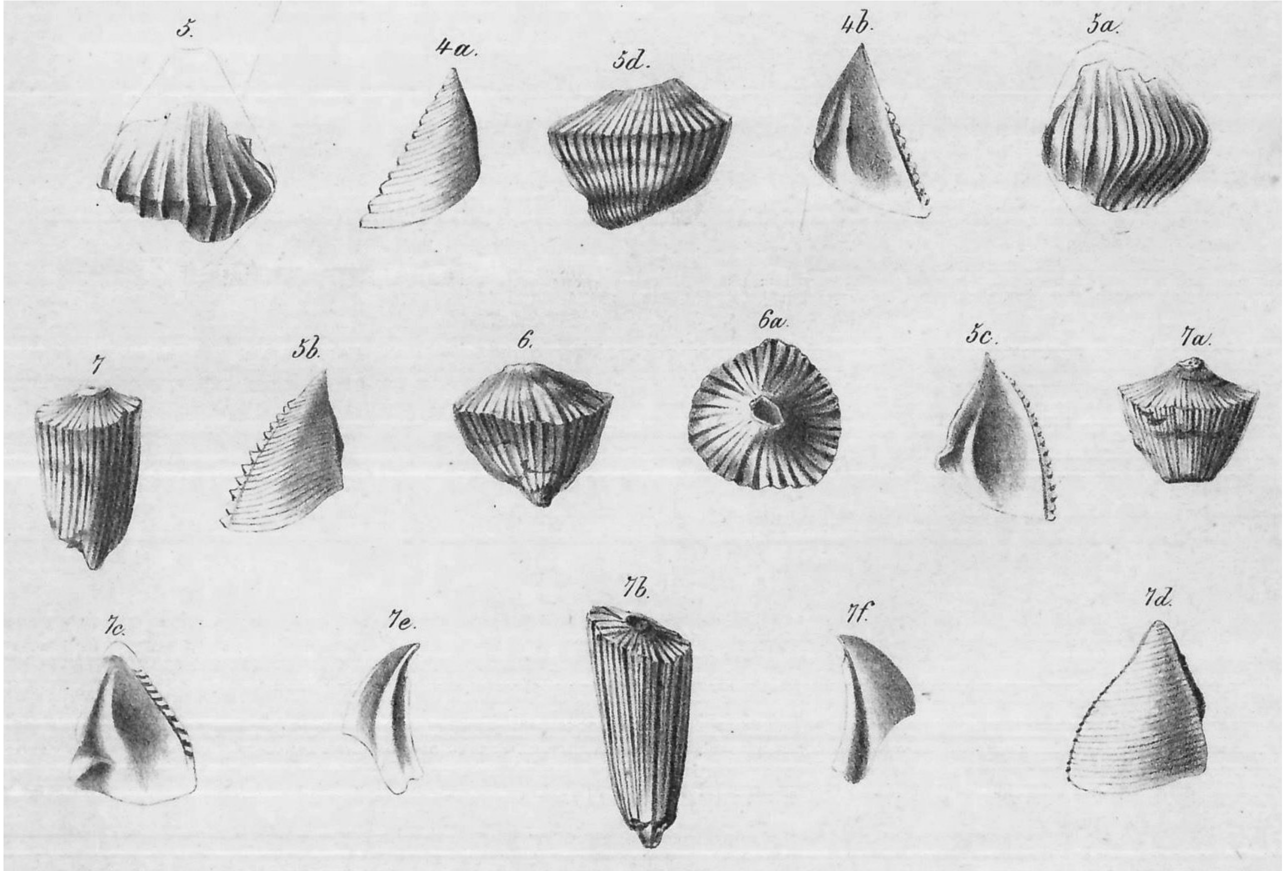


Figure 10. Pyrgomatidae, the originals of Seguenza (1873, pl. 2, figs 4-7): 4a, 4b. *Adna anglica* J. de C. Sowerby, 1823, scutum, external and internal views; 5a-c, e. *Pyrgomina costata* (Seguenza, 1873); 5, 5a. fragmentary shell; 5b, 5c. external and internal views of scutum; 5d. *Pyrgomina elargatum* (Seguenza, 1873), lateral view of shell; 6, 6a. *Pyrgomina diploconus* (Seguenza, 1873), lateral and apical views of shell; 7, 7a-f. *Ceratoconcha milticostata* (Seguenza, 1873); 7, 7b. lateral views of shells; 7c, d. scutum, interior and interior views; 7e, 7f. interior and exterior views of tergum.

Remarks – This species was redescribed by Moroni (1967) and placed in *Pyrgomina* by Bałuk & Radwański (1967). Ross & Pitombo (2002) discussed Seguenza's species *P. costatum* and *P. elargatum*, and concluded that both were valid and could be distinguished by the number of ribs (29-31 in *costatum*, about 40 in *elargatum*). The problem with the material is that although one specimen has 29 ribs (Pl. 13, fig. 1a-c) and falls within the range of *P. costatum*, the other two have 33 and 38 ribs (Pl. 13, figs 3a-c, 5). These are provisionally referred to *P. elargatum* (see below). The scutum associated with the tallest specimen (Pl. 13, fig. 4a, b) has a gently convex occludent margin and a deep notch for the tergum, and closely resembles Seguenza's scutum of *Pyrgomina costata* (Seguenza, 1873, pl. 2, fig. 5b, c). It has been bored by a gastropod in the region of the depressor scar. Resolution of this taxonomic uncertainty must await discovery of more material.

Pyrgomina elargatum (Seguenza, 1873)
Plate 13, figs 2, 3

*1873 *Pyrgoma elargatum* Seguenza, p. 317, pl. 2, fig. 5d.
1876 *Pyrgoma elargatum* Seguenza, pl. 10, fig. 23.
1967 *Pyrgoma costatum* Seguenza – Moroni, p. 17, pl. 11, figs 7, 9, 10; pl. 17, fig. 7b only.
2002 *Pyrgomina elargatum* (Seguenza) – Ross & Pitombo, p. 60.

Diagnosis – *Pyrgomina* with numerous (33-40), very narrow ribs, separated by less than their own width.

Type – The specimen (now lost) figured by Seguenza (1873, pl. 2, fig. 5d, refigured here as Fig. 10/5d) from Capo di Milazzo, Sicily.

Material – Two specimens from the Gelasian-Calabrian of Capo Milazzo, Sicily (PMC. R. 1. IPI. CIR-106cm, 107cm).

Remarks – Ross & Pitombo (2002) differentiated Seguenza's species from material referred to *P. costatum* by Moroni (1967) as a form with 40 ribs, which are separated by less than their own width. Of the four specimens available from recent collecting, the rib numbers are 26, 28, 33 and 38. Those with 33 and 38 ribs are provisionally assigned to *P. elargatum*, but clearly a larger sample is needed to look statistically at variation in rib number in order to assess the possibility that there is a broad range of variation within a single species, *P. costatum*.

Pyrgomina diploconus **(Seguenza, 1873)**

*1873	*Pyrgoma diploconus* Seguenza, p. 58, pl. 2, figs 6, 6a.

Type – The specimen (now lost) from Fondaco nuovo (Messina) and figured by Seguenza (1873, pl. 2, fig. 6, 6a, refigured here as Fig. 10/6. 6a) is here designated lectotype.

Remarks – This species does not appear to have been discussed since its original description. Seguenza's illustrated specimen (1873, pl. 58, figs 6, 6a) is a biconical form that has 34 ribs, falling between *P. costatum* and *P. elargatum* in rib number. The species is retained provisionally, because Ross & Pitombo (2002), in their major review, were convinced of the taxonomic value of rib number. A larger suite of specimens are needed to study variation in *Pyrgomina*.

Subfamily Ceratoconchinae Newman & Ross, 1976
Genus *Ceratoconcha* Kramberger-Gorjanovic, 1889

Type species – Creusia krambergeri Bałuk & Radwański, 1967

Ceratoconcha multicostata **(Seguenza, 1873)**

*1873	*Pyrgoma multicostatum* Seguenza, p. 55, pl. 2, fig. 7.
?1873	*Pyrgoma multicostata latum* Seguenza, p. 57, pl. 2, fig. 7a.
1905	*Pyrgoma multicostatum* Seguenza – De Alessandri, pl. 6, figs 15-22.
1967	*Creusia multicostata* (Seguenza) – Bałuk & Radwański, p. 484.
1976	*Ceratoconcha rangi rangi* (Des Moulins) – Newman & Ross, p. 59.

Type – The specimen (now lost) from near Rometta (Sicily), figured by Seguenza (1873, pl. 2, fig. 7, refigured here as Fig. 10/7) is here designated lectotype.

Remarks – Seguenza's name was placed in synonymy with *C. rangi* (Des Moulins, 1875) by Duvergier (1922) and subsequently by Newman & Ross (1973, 1976, p. 59). The first illustration of a specimen as *C. rangi* was by Duvergier (1922), showing a broad shell (height approximately equal to breadth) with a very low parietal wall, quite different from the material from Italy figured by Seguenza and De Alessandri (1906). Their specimens have a tall, conical basis (height 2-3 times greater than breadth), and it appears that *P. multicostatum* is probably a valid name. Seguenza figured both a scutum (1873, pl. 2, fig. 7c, d) and a tergum (fig. 7e, f) of his *P. multicostatum*; the tergum appears to be typical of *Ceratoconcha* (compare with Young, 1989, fig. 1e, g) in the concave scutal margin, the convex occludent margin, the moderately elongated tergal spur and the apicobasal ridge on the interior of the spur. However, Seguenza's scutum (refigured by De Alessandri, 1906, pl. 6, fig. 21) is curious in having a sigmoidal occludent margin and a deep lateral scutal depressor scar set on a short process.

Discussion

Composition of the Plio-Pleistocene cirripede fauna from Sicily

The species described by Seguenza (1873, 1876) and the new material which we have studied is listed in Table 2. A total of 41 taxa are recorded, the majority of which come from the upper Piacenzian to Calabrian, although it is not possible to determine the detailed age of much of Seguenza's material. The fauna is composed of calanticids (three species), scalpellids (five species), lepadids (two species), verrucids (six species) and balanomorphs (25 species). Of these, only 8 (19.5%) are still living in the Mediterranean Sea, and 18 species are extinct (44%). The fauna is remarkably diverse, and some taxa are exceptionally abundant locally (*e.g.*, *Pachylasma giganteum, Scillaelepas carinata*), forming a significant part of the sediment.

Lepadids are epipelagic forms, attached to floating detritus, while coronulids and chelonibiids attach to whales and turtles (sometimes to crustaceans), respectively. All other taxa are benthic. The depth ranges of extant species found in the Plio-Pleistocene fauna of Sicily, based on present Atlantic and Mediterranean data, are as follows (in part from Young, 1998a, b, 2003; Southward, 2008):

Amphibalanus amphitrite	(intertidal)
Perforatus perforatus	(intertidal-40 m)
Balanus spongicola	(25-30 m)
Megabalanus tulipiformis	(25-250 m)
Pachylasma giganteum	(80-650 m)
Adna anglica	(subtidal to 80 m)
Rostratoverruca romettensis	(441-1,135 m)
Metaverruca zanclea	(240-2,100 m)
Scalpellum spp.	(0-400 m)
Arcoscalpellum michelottianum	(740-3,000 m)
Scillaelepas carinata	(727-2,420 m)
Aurivillialepas ornata	(340-900 m)
Calantica zancleana	(140-890 m)

A significant part of the Sicilian fossil fauna (Table 2) can be ascribed to the upper bathyal zone (200-600 m), including the calanticids, some scalpellids (*A. michelottianum*), *Pachylasma* and most verrucids. The depth occurrences of verrucid genera were tabulated by Young (2002a, fig. 30), who showed *Rostratoverruca* as a relatively shallow taxon (predominantly 100-500 m) and *Metaverruca* predominantly beneath 250 m. Only two

Nr	Family	Name in Seguenza (1873, 1876)	Present name	Key reference	Remarks
1	Calanticidae	*Scillaelepas carinata* (Philippi, 1835)	*Scillaelepas carinata* (Philippi, 1835)	Withers (1953); this paper	living in Atlantic
2	Calanticidae	*Scillaelepas ornata* Seguenza, 1876	*Aurivillialepas ornata* (Seguenza, 1876)	Withers (1953); this paper	living in Atlantic
3	Calanticidae	*Scalpellum zancleanum* Seguenza, 1876	*Calantica zancleana* (Seguenza, 1876)	Withers (1953)	living in Indo-West Pacific
4	Lepadidae	*Lepas mallandriniana* Seguenza, 1876	*Lepas mallandriniana* Seguenza, 1876	Withers (1953)	
5	Lepadidae	*Lepas hilli* (Leach, 1818)	*Lepas hilli* (Leach, 1818)	Seguenza (1876), Withers (1953)	record uncertain
6	Scalpellidae	*Scalpellum molinianum* Seguenza, 1876	*Scalpellum molinianum* Seguenza, 1876	Withers (1953)	
7	Scalpellidae	*Scalpellum sigmoideum* Withers, 1953	*Scalpellum sigmoideum* Withers, 1953	Withers (1953)	
8	Scalpellidae	*Scalpellum* sp. indet.		this paper	
9	Scalpellidae	*Scalpellum fragmentarium* Seguenza, 1876	*Scalpellum* sp. indet.	Withers (1953)	indeterminate
10	Scalpellidae	*Scalpellum michelottianum* Seguenza, 1876	*Arcoscalpellum michelottianum* (Seguenza, 1876)	Withers (1953)	cosmopolitan in deep oceans, present day
11	Verrucidae		*Gibbosaverruca milazzoensis* sp. nov.	this paper	Gelasian
12	Verrucidae	*Verruca romettensis* Seguenza, 1873	*Rostratoverruca romettensis* (Seguenza, 1873)	this paper	Calabrian; living in Atlantic and Mediterranean
13	Verrucidae	*Verruca crebricosta* Seguenza, 1873	*Rostratoverruca crebricosta* (Seguenza, 1873)	this paper	
14	Verrucidae	*Verruca zanclea* Seguenza, 1873	*Metaverruca zanclea* (Seguenza, 1873)	this paper	cosmopolitan in deep oceans, present day
15	Verrucidae	*Verruca dilatata* Seguenza, 1873	*Metaverruca dilatata* (Seguenza, 1873)	this paper	living in Atlantic
16	Verrucidae	*Verruca stroemia* (O.F. Müller, 1776)	*Verruca* sp.	this paper	Seguenza's material indeterminate
17	Pachylasmatidae	*Pachylasma giganteum* (Philippi, 1836)	*Pachylasma giganteum* (Philippi, 1836)	Darwin (1854b); this paper	living in Atlantic and Mediterranean
18	Chelonibiidae	*Chelonibia depressa* Seguenza, 1873	*Chelonibia* sp.		not illustrated; status uncertain
19	Chelonibiidae		*Platylepas mediterranea* Collareta, Reitano, Rosso, Sanfilippo, Bosselaers, Bianucci & Insacco, 2019		Gelasian, Capo Milazzo
20	Coronulidae	*Coronula bifida* Bronn, 1831	*Coronula bifida* Bronn, 1831	Collareta et al. (2018)	extinct whale barnacle
21	Acastinae	*Acasta muricata* Seguenza, 1873	"*Acasta*" sp.	this paper	specific status doubtful
22	Archaeobalanidae	*Balanus stellaris* Brocchi, 1814	*Balanus stellaris* Brocchi, 1814	Seguenza (1873); Menesini (1984)	
23	Archaeobalanidae	*Balanus milensis* Seguenza, 1873	*Solidobalanus milensis* (Seguenza, 1873)	Moroni (1967)	Gelasian-Calabrian
24	Archaeobalanidae		*Solidobalanus digeronimoi* sp. nov.	this paper	
25	Balanidae	*Balanus amphitrite* Darwin, 1854b	*Amphibalanus amphitrite* (Darwin, 1854b)	Menesini (1984)	

Nr	Family	Name in Seguenza (1873, 1876)	Present name	Key reference	Remarks
26	Balanidae	*Balanus darwinii* Seguenza, 1876	*Balanus darwinii* Seguenza, 1873	De Alessandri (1906)	poorly known species
27	Balanidae	*Balanus veneticensis* Seguenza, 1873	*Balanus veneticensis* Seguenza, 1873		poorly known species
28	Balanidae	*Balanus spongicola* Brown, 1827	*Balanus spongicola* Brown, 1827	Menesini (1984)	living sponge-dwelling species
29	Balanidae	*Balanus crenatus* Bruguière, 1789	*Balanus crenatus* Bruguière, 1789	Davadie (1953)	living species absent from Mediterranean
30	Balanidae	*Balanus porcatus* Da Costa, 1778	*Balanus balanus* Linnaeus, 1758	Menesini (1984)	living species absent from Mediterranean
31	Balanidae	*Balanus concavus* Bronn, 1831	*Concavus concavus* (Bronn, 1831)	Zullo (1992a)	extinct
32	Balanidae	*Balanus scutorum* Seguenza, 1876	*Concavus scutorum* (Seguenza, 1876)	Moroni Ruggieri (1952)	
33	Balanidae	*Megabalanus coccopoma* (Darwin, 1854b)	*?Megabalanus coccopoma* (Darwin, 1854b)	this paper	uncertain record
34	Balanidae	*Balanus tintinnabulum* Linnaeus, 1758	*Megabalanus tintinnabulum* (Linnaeus, 1758)	Menesini (1984)	uncertain record
35	Balanidae	*Balanus tulipiformis* Ellis, 1758	*Megabalanus tulipiformis* (Ellis, 1758)	Menesini (1984)	living in Mediterranean
36	Balanidae	*Balanus perforatus* Bruguière, 1789	*Perforatus perforatus* (Bruguière, 1789)	Menesini (1984)	living in Mediterranean
37	Pyrgomatidae	*Pyrgoma costata* Seguenza, 1873	*Pyrgomina costata* (Seguenza, 1873)	Ross & Pitombo (2002)	coral barnacle
38	Pyrgomatidae	*Pyrgoma elargatum* Seguenza, 1873	*Pyrgomina elargatum* (Seguenza, 1873)	Ross & Pitombo (2002)	coral barnacle
39	Pyrgomatidae	*Pyrgoma anglica* J. de C. Sowerby, 1823	*Adna anglica* (J. de C Sowerby, 1823)	Ross & Pitombo (2002)	coral barnacle
40	Pyrgomatidae	*Pyrgoma diploconus* Seguenza, 1873	*Pyrgomina diploconus* (Seguenza, 1873)	this paper	status uncertain
41	Pyrgomatidae	*Pyrgoma multicostata* Seguenza, 1873	*Ceratoconcha multicostata* (Seguenza, 1873)	this paper	

Table 2. Cirripedes from the Piacenzian-Gelasian of Sicily, combining Seguenza's records with those based on recent collecting.

of the fossil species (*Arcoscalpellum michelottianum* and *Scillaelepas carinata*) are exclusively lower bathyal in distribution at the present day.

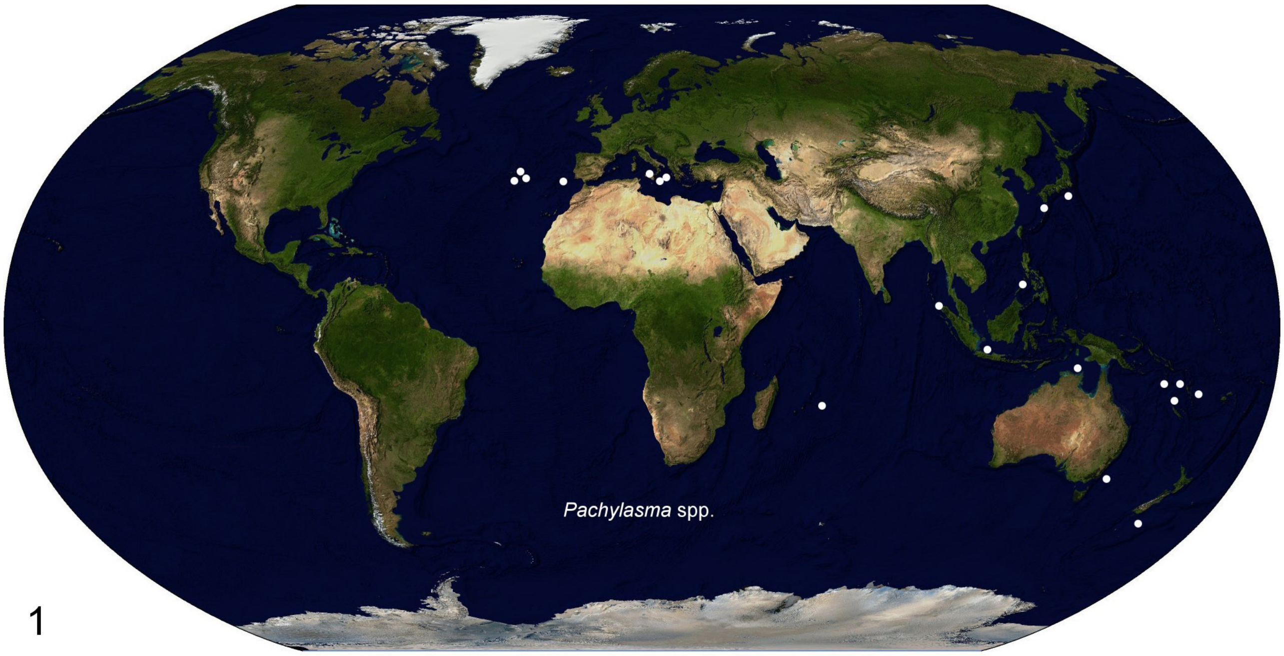
However, there are a number of shallower, warm-water elements, including coral barnacles (Pyrgomatidae, <50 m) and various balanids recorded by Seguenza which live in intertidal (*A. amphitrite*) to shallow-sublittoral environments (*Perforatus perforatus, Balanus spongicola*). These are apparently uncommon and were possibly transported into deeper environments. However, the precise age of these is not known (see above).

Palaeobiogeography and closure of Tethys: Tethyan cirripede relics?

A group of deep-water species present in the upper Neogene and lower Pleistocene in the Mediterranean have strong affinities with Indo-southwest Pacific taxa which are not currently represented in the Atlantic. These include *Calantica zancleana*, abundant in the Plio-Pleistocene of the Mediterranean, and still living in the southwest Pacific (Fig. 11/2). The genus *Pachylasma* is diverse in the southwest Pacific (Jones, 2000), but one species occurs in the central-eastern Atlantic (Azores) and in the Miocene-Pliocene to present-day Mediterranean (Fig. 11/1). The genus also occurred in the Pleistocene of the western Indian Ocean (Gale, 2020b). *Pachylasma giganteum* has a long history in the Mediterranean (Burdigalian to present). The survivor of a Mesozoic stock, *Pycnolepas paronae*, occurs in the Miocene of Italy and Spain (Fig. 11/2) and is found in the Pleistocene of the Rodrigues Ridge, western Indian Ocean (Gale, 2020b). Finally, species of *Rostratoverruca* from the Eocene-Miocene of the Mediterranean show affinities with living *Rostratoverruca krugeri* (Broch, 1922) of the Indo-West Pacific.

Mediterranean fossil records with affinities to Indo-West Pacific species which pre-date the closure of the eastern Mediterranean at about 16 Ma (*Pycnolepas paronae, Ros-*

1



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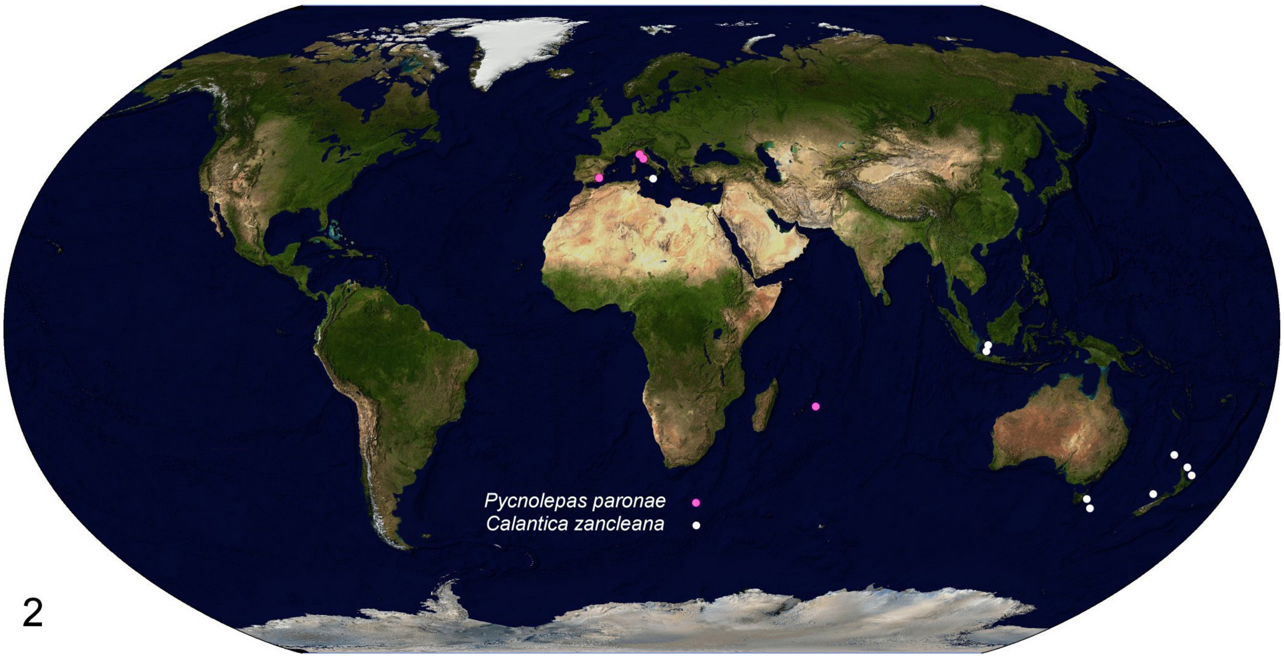

Figure 11. Distribution maps of thoracican cirripede species. 1.Distribution of the balanomorph *Pachylasma* spp.; at the present day, most species inhabit the Indo-West Pacific, but a single species, *P. giganteum* (Philippi, 1836) is found in the Miocene–Pleistocene of Italy and living in the central Mediterranean and the east-central Atlantic. 2. Distribution of extinct *Pycnolepas paronae* (De Alessandri, 1895), found in the Miocene of the Mediterranean and the Pleistocene of the Rodrigues Ridge, Indian Ocean (Gale, 2020b). *Calantica zancleana* (Seguenza, 1876), found fossil in Sicily, inhabits the Java Sea and occurs off Australia and New Zealand.

tratoverruca spp.) can be explained by an original distribution across Tethys, and local survival after closure of the seaway (Gale, 2020b). The genus *Pachylasma* probably also had a similar distribution across Tethys (Fig. 11/1), and after closure, *P. giganteum* speciated and survived in the Mediterranean and east-central Atlantic; the genus subsequently radiated in the southwest Pacific. *Calantica zancleana* can perhaps be regarded as a very long-lived species (>20 myr) with an originally broad Tethyan distribution which survived until the early Pleistocene in the Mediterranean, and still lives in the southwest Pacific (Fig. 11/2). However, the impossibility of recolonisation from the Indo-Pacific means that *C. zancleana* must have recolonised the Mediterranean from now extinct (or undiscovered, living) Atlantic populations.

The balanomorph family Tetraclitidae Gruvel, 1903 is common and abundant in the Indo-Pacific, and the genus *Tesseropora* Pilsbry, 1916 includes species with a wide range, extending from Australasia and southeast Asia to the east African coast (Newman & Ross, 1976, 1977). A single living species, *T. atlantica* Newman & Ross, 1977, is present in the Atlantic, extending from the Bahamas to the Azores and Madeira. The genus is represented by three extinct species in the Mediterranean region (Italy, France); these range in age from Oligocene to Pliocene (Carriol, 1993). *Tesseropora* thus represents another example of a genus, in parallel with *Pachylasma*, with an original distribution across Tethys, interrupted by the closure of the eastern Mediterranean. The genera survived in the Mediterranean and Atlantic, but were neither diverse nor abundant there.

History of Mediterranean cirripedes

The ranges of cirripede species which can be readily fossilised (*i.e.*, having solid calcitic shell plates) in the Mediterranean is summarised in Figure 12 and listed in Table 3. This is based on a compilation of data from De Alessandri (1906), the review of Withers (1953, which dealt systematically with all pedunculated taxa and listed the sessile forms) and papers by Moroni Ruggieri (1952), Moroni (1967), Menesini (1972, 1982, 1984), Menesini & Casella (1988), Davadie (1953, 1963), Collareta *et al.* (2018), plus information from the present paper. The review of the distribution of many balanomorph taxa by Menesini (1984) has proved to be particularly useful. However, some verrucid and balanomorph species have not been revised since the papers of De Alessandri (1895, 1906). The major difficulty encountered in making this compilation has been the changing concepts and definitions of stages and periods through the 20th and 21st centuries. The definitions used here are those from Gradstein *et al.* (2020); stage usage from the older literature has been updated as far as possible, but there remain many uncertainties and possible errors. The age of the major fauna from the Torino Hills (northern Italy) has now been determined as Burdiganian-Langhian (Zunino & Pavia, 2009) and the extensive faunas from Sicily can be shown to be of late Piacenzian to Calabrian age, based on work at Rometta (Di Stefano *et al.*, 2007) and Capo Milazzo (Violanti, 1988; updated by Borghi *et al.*, 2014).

Eocene and Oligocene faunas are rather poorly represented in the Mediterranean region, and only three scalpellids, three verrucids and six balanomorph species have been recorded to date (Fig. 12; Tab. 3). Many more species (30+) appeared in the early Miocene (Aquitanian-Langhian), but most are only known from one small region in northern Italy (Torino Hills), which has yielded an exceptional fauna (De Alessandri, 1906; Withers, 1953). The wider geographical and stratigraphical distribution of these species is therefore unknown. However, eleven of these species do not extend higher than the Langhian (Fig. 12; Tab. 3); one of these, *Pycnolepas paronae*, continued into the Pleistocene in the Indian Ocean (Gale, 2020b). Although a number of the calanticid, verrucid and balanomorph taxa evidently have close affinities with extant Indo-Pacific faunas, the impact of the closure of the eastern Mediterranean (Harzhauser *et al.*, 2002, 2009) on cirripede faunas is not clear, largely because few fossil cirripedes have been described from eastern Tethys. There are no gastropod species in common between the Aquitanian of Kutch and western Tethys, suggesting initial closure at about 22 Ma, but in the Burdigalian 6% of species are found both in eastern and western Tethys (Harzhauser *et al.*, 2009) and demonstrate some connection, broken by final closure 4-5 myr later (17-18 Ma). The absence of northwest Indian gastropod species in the Burdigalian of Europe argues against early Miocene migrations from western Tethys (Harzhauser *et al.* 2009). It is therefore probable that the diverse cirripede faunas of the Burdigalian-Langhian (*e.g.*, De Alessandri, 1906; Withers, 1953) were present in the Mediterranean from a much earlier date, but have no fossil record, perhaps because of the non-preservation of suitable deeper-water facies.

The Messinian Salinity Crisis resulted from the closure of the Betic and Rif straits, with the Mediterranean becoming a hyposaline evaporitic basin from about 6.3 Ma, then a restricted freshwater to brackish environment, the Lago Mare, in the latest Messinian. The base of the Pliocene at 5.33 Ma (*e.g.*, Taviani, 2002; Roveri *et al.*, 2014) marked a renewed connection with the Atlantic and the reappearance of normal marine faunas across the Mediterranean. Considerable controversy surrounds the possible temporary existence of normal marine conditions during the Messinian (Roveri *et al.*, 2014), but the consensus is that the closure and hyposaline conditions resulted in the temporary loss of the stenohaline fauna, and subsequent recolonisation from the Atlantic (Taviani, 2002). There are no extinctions in the cirripede fauna across the Messinian Salinity Crisis (Fig. 12; Tab. 3), so it appears that the fauna recolonised from the eastern Atlantic in the Pliocene, also documented for some bryozoans (Rosso & Di Martino, 2015; Rosso & Sciuto, 2019).

Zanclean and early Piacenzian cirripede faunas are poorly known in the Mediterranean region, possibly because of non-preservation of suitable facies, or alternatively, because recolonisation from the Atlantic was slow. However, the Gelasian-Calabrian fauna redescribed in the present paper, best known from Sicily, is abundant and highly diverse, representing both shallow-marine and bathyal taxa. A total of 41 species, known from the Piacenzian-Gelasian of eastern Sicily, represent by far the most diverse cirripede faunas known from the entire Cainozoic of the Mediterranean region.

The diverse fauna of the Gelasian-Calabrian underwent a loss of 64% in the late Calabrian across the Mediterranean; of these, 20% survived elsewhere and 51% became extinct. The precise date of this dramatic reduction is difficult to estimate, in the absence of continuous, datable successions from this interval which have been sampled for cirripedes. Only two bathyal taxa survive in the Mediterranean to the present day from the Gelasian (*i.e.*, *Pachylasma giganteum* and *Rostratoverruca romettensis*), with the complete loss of calanticids (three species), scalpellids (2), most verrucids (4) and many balanomorphs (11). All coral barnacles of the genera *Pyrgomina* and *Ceratoconcha* completely disappeared from the Mediterranean, having appeared first in the Miocene (Fig. 12; Tab. 3).

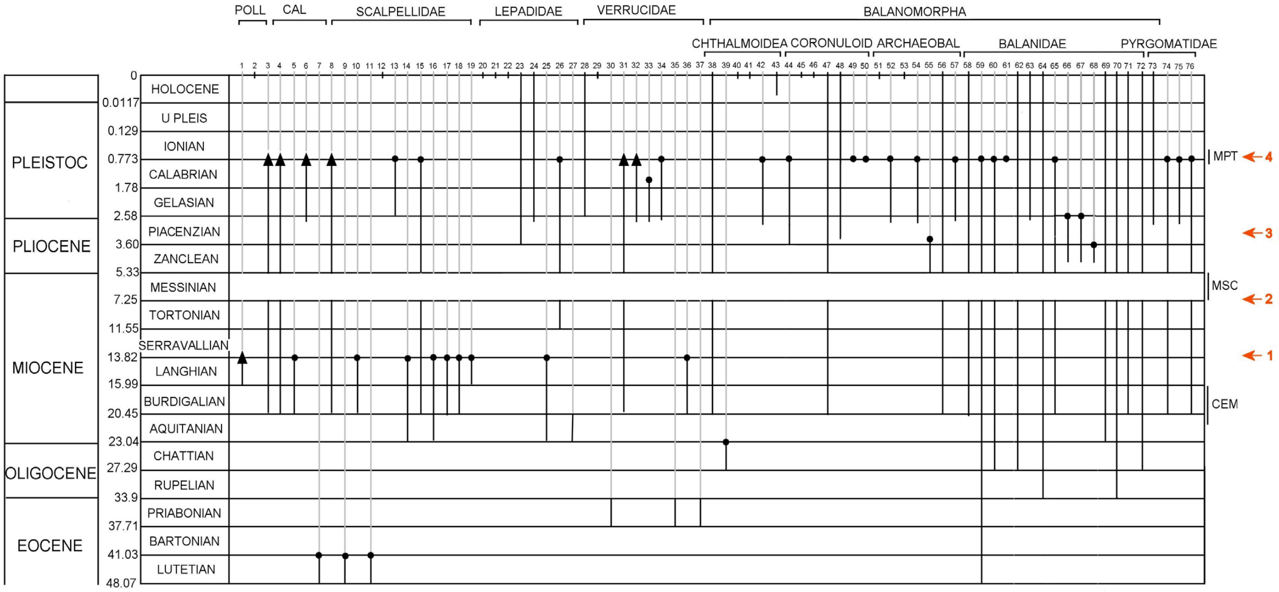

Figure 12. Distribution of cirripede taxa in the Mediterranean region during the Cainozoic; numbers are those used in Table 3. Black lines represent ranges, dots extinctions, and arrows indicate that the species survived elsewhere. Some data are from Menesini (1984), De Alessandri (1906) and the present paper; modern distribution is based largely on Koukouras & Matsa (1998). CEM, closure of eastern Mediterranean; MSC, Messinian Salinity Crisis; MPT, Middle Pleistocene Transition. Red arrows: 1. Apparent extinctions at the end of the Langhian; 2. Base of salinity crisis; 3. Appearance of new taxa in the Pliocene; 4. Extinction at the top of the Calabrian. Abbreviations: POLL, Pollicipedidae; CAL, Calanticidae; ARCHAEOBAL, Archaeobalanidae. Note that species concept of *Concavus concavus* provisionally follows that of Menesini (1984), as a long-ranging taxon, not that of Zullo (1992a), who considered any pre-Pliocene records to be dubious. The records of *Balanus trigonus* follow Menesini (1984) and Davadie (1963).

Nr	Family	Taxon	Reference	Notes
1	Pollicipedidae	*Capitulum italicum* Withers, 1953	Withers (1953)	Burdigalian?, Baldissero, Turin
2	Pollicipedidae	*Pollicipes pollicipes* (Gmelin, 1789)	Koukouros & Matsa (1998)	Lusitanian/warm-water species; rare in Mediterranean
3	Calanticidae	*Calantica zancleana* (Seguenza, 1876)	Withers (1953)	extinct in Mediterranean; living in Java Sea and off Australasia
4	Calanticidae	*Aurivillialepas ornata* (Seguenza, 1876)	Withers (1953)	living in Atlantic, extinct in Mediterranean
5	Calanticidae	*Scillaelepas paronae* De Alessandri, 1906	Withers (1953)	Burdigalian?, Baldissero, Turin
6	Calanticidae	*Scillaelepas carinata* (Philippi, 1835)	Withers (1953); this paper	living in Atlantic, extinct in Mediterranean
7	Calanticidae	*Euscalpellum romanorum* Withers, 1953	Withers (1953)	Lutetian, Gassino, near Turin
8	Scalpellidae	*Arcoscalpellum michelottianum* (Seguenza, 1876)	Withers (1953)	extinct in Mediterranean; cosmopolitan deep sea
9	Scalpellidae	*Arcoscalpellum raricostatum* Withers, 1953	Withers (1953)	Lutetian, Gassino, near Turin
10	Scalpellidae	*Amigdaloscalpellum turinensis* (Withers, 1953)	Withers (1953)	Burdigalian?, Baldissero, Turin
11	Scalpellidae	*Arcoscalpellum gassinensis* (De Alessandri, 1895)	Withers (1953)	Lutetian, Gassino, near Turin
12	Scalpellidae	*Scalpellum scalpellum* (Linnaeus, 1758)	Koukouros & Matsa (1998)	Lusitanian/Boreal species

Table 3. Cainozoic record of cirripedes in the Mediterranean region, based on a survey of the literature and new records presented here.

Nr	Family	Taxon	Reference	Notes
13	Scalpellidae	*Scalpellum sigmoideum* Withers, 1953	Withers (1953)	lower Pleistocene, Sicily
14	Scalpellidae	*Scalpellum dalpiazi* Withers, 1953	Withers (1953)	Burdigalian?, near Turin
15	Scalpellidae	*Scalpellum molineanum* Seguenza, 1876	Withers (1953)	Tortonian-lower Pleistocene, Italy
16	Scalpellidae	*Scalpellum lovisatoi* De Alessandri, 1895	Withers (1953)	Lower and Middle Miocene, Sardinia, Malta
17	Scalpellidae	*Scalpellum burdigalense* Des Moulins, 1875	Withers (1953)	Burdigalian?, near Turin
18	Scalpellidae	*Scalpellum formae* De Alessandri, 1895	Withers (1953)	Burdigalian?, near Turin
19	Lepadidae	*Poecilasma melitense* (Withers, 1953)	Withers (1953)	Burdigalian, Malta
20	Lepadidae	*Lepas pectinata* Spengler, 1793	Koukouros & Matsa (1998)	Cosmopolitan
21	Lepadidae	*Lepas anatifera* Linnaeus, 1767	Koukouros & Matsa (1998)	Cosmopolitan
22	Lepadidae	*Lepas anserifera* Linnaeus, 1758	Koukouros & Matsa (1998)	Cosmopolitan
23	Lepadidae	*Lepas* cf. *anatifera*	Withers (1953)	dubious record
24	Lepadidae	*Lepas hilli* Leach, 1817	Withers (1953)	dubious record
25	Lepadidae	*Lepas rovasendai* De Alessandri, 1895	Withers (1953)	Aquitanian-Burdigalian, Turin district
26	Lepadidae	*Lepas mallindriana* Seguenza, 1876	Withers (1953)	Tortonian, Messina, Sicily
27	Brachylepadidae	*Pycnolepas paronae* De Alessandri, 1895	Withers (1953); Gale (2020b)	Aquitanian, Chieri, near Turin; Carboneras, Spain
28	Verrucidae	*Rostratoverruca romettensis* (Seguenza, 1873)	this paper	Gelasian, Sicily
29	Verrucidae	*Verruca spengleri* Darwin, 1854b	Young *et al*. (2003)	widespread in Mediterranean
30	Verrucidae	*Verruca venata* Carriol & Dieni, 2005	Carriol & Dieni (2005)	Priabonian, near Padua, Italy
31	Verrucidae	*Metaverruca zanclea* (Seguenza, 1873)	this paper	cosmopolitan, deep water
32	Verrucidae	*Metaverruca dilatata* (Seguenza, 1873)	this paper	living, eastern central Atlantic
33	Verrucidae	*Gibbosaverruca milazzensis* sp. nov.	this paper	Gelasian-Calabrian, Capo Milazzo, Sicily
34	Verrucidae	*Rostratoverruca crebricosta* (Seguenza, 1873)	this paper	Piacenzian-Gelasian, Sicily
35	Verrucidae	*Rostratoverruca seguenzai* Carriol & Dieni, 2005	Carriol & Dieni (2005)	Priabonian, near Padua, Italy
36	Verrucidae	*Rostratoverruca miocrebicosta* (De Alessandri, 1895)	De Alessandri (1906)	Burdigalian?, Baldissero, Turin
37	Verrucidae	*Metaverruca eugenea* Carriol & Dieni, 2005	Carriol & Dieni (2005)	Priabonian, near Padua, Italy
38	Pachylasmatidae	*Pachylasma giganteum* (Philippi, 1836)	Jones (2000); Gale (2020b); this paper	Burdigalian-Recent, Mediterranean-eastern Atlantic
39	Tetraclitidae	*Tesseropora isseli* De Alessandri, 1895	De Alessandri (1906)	Oligocene, Sassello, Italy
40	Chthamalidae	*Euraphia depressa* (Poli, 1791)	Koukouros & Matsa (1998)	
41	Chthamalidae	*Chthamalus montagui* Southward, 1976	Koukouros & Matsa (1998)	
42	Chthamalidae	*Chthamalus liguisticus* De Alessandri, 1895	De Alessandri (1906)	"Pliocene", Albissola, Savona, Italy
43	Chthamalidae	*Chthamalus stellatus* (Poli, 1795)	De Alessandri (1906); Koukouros & Matsa (1998)	Holocene-Recent
44	Coronulidae	*Coronula bifida* Bronn, 1831	Collareta *et al*. (2018)	cosmopolitan Plio-Pleistocene, whale barnacle

Nr	Family	Taxon	Reference	Notes
45	Chelonibiidae	*Stomatolepas elegans* (Da Costa, 1838)	Koukouros & Matsa (1998)	attached to turtles, living only
46	Chelonibiidae	*Chelonibia caretta* (Spengler, 1790)	Koukouros & Matsa (1998)	attached to turtles, living only
47	Chelonibiidae	*Chelonibia patula* (Ranzani, 1813)	Menesini (1984)	attached to turtles, living only
48	Chelonibiidae	*Chelonibia testudinaria* (Linnaeus, 1758)	Menesini (1984)	attached to turtles, living only
49	Chelonibiidae	*Chelonibia depressa* Seguenza, 1873		attached to turtles, living only
50	Chelonibiidae	*Platylepas mediterranea* Collareta, Reitano, Rosso, Sanfilippo, Bosselaers, Bianucci & Insacco, 2019	attached to turtles, living only	
51	Chelonibiidae	*Platylepas hexastylos* (Fabricius, 1798)	Koukouros & Matsa (1998)	attached to turtles, living only
52	Archaeobalanidae	*Solidobalanus milensis* (Seguenza, 1873)	Moroni (1967)	also known from Miocene of Poland
53	Archaeobalanidae	*Solidobalanus fallax* (Broch, 1927)	Koukouros & Matsa (1998)	eastern Atlantic species
54	Archaeobalanidae	*Solidobalanus digeronomoi* sp. nov.	this paper	probable sponge association
55	Archaeobalanidae	*Chirona hameri* (Ascanius, 1767)	Menesini & Casella (1988)	known from Zanclean, southeast Spain
56	Archaeobalanidae	*Conopea calceola* (Ellis, 1758)	Menesini (1984)	
57	Archaeobalanidae	*Balanus darwini* Seguenza, 1876	De Alessandri (1906)	
58	Acastinae	*Acasta* spp.		sponge dwelling
59	Balanidae	*Balanus stellaris* Brocchi, 1814	Menesini (1984)	widespread in Mediterranean region, extinct
60	Balanidae	*Concavus concavus* (Bronn, 1831)	Menesini (1984)	widespread in Mediterranean region, extinct
61	Balanidae	*Concavus scutorum* (Seguenza, 1876)	this paper	
62	Balanidae	*Balanus crenatus* Bruguière, 1789	Davadie (1963); Menesini (1984)	
63	Balanidae	*Balanus trigonus* Darwin, 1854b	Davadie (1963)	fossil records from Italy and Poland
64	Balanidae	*Balanus spongicola* Brown, 1827	Menesini (1984)	sponge dwelling
65	Balanidae	*Balanus balanus* Linnaeus, 1758	Davadie (1963)	
66	Balanidae	*Balanus seguenzai* De Alessandri, 1895	De Alessandri (1906)	
67	Balanidae	*Balanus veneticensis* Seguenza, 1873	Seguenza (1873)	poorly known
68	Balanidae	*Balanus pantanellii* De Alessandri, 1895	De Alessandri (1906)	
69	Balanidae	*Amphibalanus amphitrite* (Darwin, 1854b)	Menesini (1984)	
70	Balanidae	*Perforatus perforatus* (Bruguière, 1789)	Menesini (1984)	
71	Balanidae	*Megabalanus tulipiformis* (Ellis, 1758)	Menesini (1984)	
72	Balanidae	*Megabalanus tintinnabulum* (Linnaeus, 1758)	Menesini (1984)	
73	Pyrgomatidae	*Adna anglica* Sowerby, 1823	Seguenza (1873)	coral barnacle
74	Pyrgomatidae	*Ceratoconcha multicostatum* (Seguenza, 1873)	Seguenza (1873)	coral barnacle
75	Pyrgomatidae	*Pyrgomina costatum* (Seguenza, 1873)	Ross & Pitombo (2002)	coral barnacle
76	Pyrgomatidae	*Pyrgomina elargatum* (Seguenza, 1873)	Ross & Pitombo (2002)	coral barnacle

Causes of extinction

Two main explanations for the Pleistocene extinctions of Mediterranean macrobenthos have been proposed. Raffi & Stanley (1985) invoked climatic cooling as a cause of the large loss of bivalve taxa (61%) between what would now be considered as early Pleistocene and present-day assemblages, and calculated that only 54% of the fauna survived until today. They identified two pulses of extinction, at 3.0-3.2 Ma and a later one at 2.4-2.5 Ma, although the dating needs revision. Di Geronimo *et al*. (1996) documented changes in the Neogene-Quaternary benthic faunas of the Mediterranean and attributed the loss of deep benthos to the increasing restriction of the Gibraltar Sill, the low-nutrient conditions, highly saline, warm deep waters and the effects of Quaternary glacial/ interglacial alternations. Borghi *et al*. (2014) studied the echinoid fauna of the Capo Milazzo section in Sicily and identified the disappearance during the Calabrian of deep-water taxa which currently live in the eastern Atlantic. They attributed this to the loss of deep, cold (psychrospheric) water as the Mediterranean Sea developed a stratified, homothermal structure with warm deep saline water (*e.g*., Emig & Geistdoerfer, 2004).

The Mediterranean has been a semi-restricted, low-nutrient basin, with anti-estuarine circulation since the basal Zanclean flooding through the Gibraltar Strait at 5.33 Ma (Rogerson *et al*., 2012). The basin has been prone to dysoxic events (associated with short eccentricity maxima, precession minima) which deposited organic-rich sapropels, since the middle Miocene (Rohling *et al*., 2015), associated with enhancement of the African monsoon. Sediment drift development in the Gulf of Cadiz, generated by the outflow of saline water, suggests that the modern flowpath was already in place by the onset of the Pleistocene at 2.58 Ma (Rogerson *et al*., 2012, fig. 8).

The Middle Pleistocene Transition (0.7-1.25 Ma) was marked by the amplification of glacial/interglacial cycles driven by the 100-kyr short eccentricity cycle rather than the 40-kyr obliquity cycle (Shackleton & Opdyke, 1976; Clark *et al*., 2006). The interglacials associated with MIS 37, 31, 25, 21 and 19, and the intervening glacials have been identified in cores from the eastern Mediterranean Basin (Ziegler *et al*., 2010) and Peral *et al*. (2020) have recently undertaken a detailed study of the exposed section across the MPT (Calabrian-Ionian) at Montalbano Jonico in southern Italy, which extends from MIS 36 to MIS 17. Using clumped oxygen isotopes and Mg/Ca ratios, they have calculated that the shallow subsurface temperatures attained during interglacials MIS 31 and MIS 19 were closely similar to those obtained nearby at the present day. Temperatures obtained across the glacials studied were very similar, suggesting that the MPT had little effect on the oceanography of the Mediterranean Sea, unless other local factors, such as uplift, came into play.

The significance of these studies for the causes of the late Calabrian extinctions are as follows:

If the present oceanography and circulation pathways of the Mediterranean originated in the Pliocene, and were in place by the earliest Pleistocene (including the thermal stratification, homothermy and generation of saline deep water), then the argument that loss of colder, deep-water environment (psychrosphere) resulted in benthic faunal losses from the end-Calabrian to the present day is not correct.

The onset of major glacials, such as MIS 20 and 22 in the late Calabrian (Peral *et al*., 2020, fig. 2) probably generated surface-water temperatures too cold for some shallow-marine benthos, such as coral barnacles.

We know very little about the mid-late Pleistocene Mediterranean deep benthic faunas during alternate glacial/ interglacial periods, and it is possible that colder-water elements were able to recolonise temporarily during at least some glacials. This could be tested by sampling across glacial/interglacial intervals in outcrops.

A further possibility is that other factors caused indirectly by the MPT, were responsible for faunal impoverishment. The extensive, global extinctions in deep-water, calcareous benthic forams (20%) documented by Hayward *et al*. (2014) at 0.8 Ma were possibly caused by reductions in surface productivity, with calcareous nannoplankton shifting to a more intra-annually variable production (Kender *et al*., 2015).

A number of Atlantic deep-sea cirripedes appear to have undergone both dramatic reductions in abundance and local extinctions at approximately the same time. The calanticid genera *Aurivillialepas* and *Scillaelepas* are nowadays extremely rare and have a scattered distribution in the Atlantic (Fig. 4), and *Calantica zancleana*, which must have been present in the Pliocene in order to re-populate the Mediterranean, is no longer present in the Atlantic, although it survives in the Indo-Pacific (Fig. 11/2; see Withers, 1953; Foster, 1978). The absence of fossil bathyal faunas from the Atlantic precludes any detailed understanding of these changes. Additionally, *Balanus stellaris* and *Concavus concavus*, both of which had a widespread distribution in northwest Europe (Menesini, 1984; Zullo, 1992a), including the North Sea and Germany, went extinct at the end of the early Pleistocene as did the whale barnacle, *Coronula bifida*, which had a nearly global distribution in the Pliocene and early Pleistocene (Buckeridge *et al*., 2018; Collareta *et al*., 2018).

The only other evidence for Pleistocene extinctions in bathyal cirripede faunas comes from the Rodrigues Ridge in the western Indian Ocean (Gale, 2020a, b). Here, extensive faunas of Plio-early Pleistocene age were retrieved from original bathyal depths, and include 43 taxa of which only 16 (37%) survive to the present day.

Present-day Mediterranean cirripedes

The modern cirripede fauna of the Mediterranean includes 27 species with calcite shells, almost all of which are currently living in the eastern Atlantic (Koukouras & Matsa, 1998). Although the mid-Pleistocene to Holocene fossil record in the Mediterranean is poor, it is likely that some of these cirripedes with long histories (Fig. 12; Tab. 3) have survived in the Mediterranean since the early Pleistocene, including many balanids (*Balanus spongicola, Amphibalanus amphitrite, Perforatus perfo-*

ratus, Conopea calceola, Acasta spongites, Adna anglica and *Megabalanus tulipiformis*). Others are demonstrably more recent invaders (*e.g.*, *Lepas* spp., *Pollicipes pollicipes, Scalpellum scalpellum, Chthamalus stellatus, Ch. montagui, Solidobalanus fallax, Megabalanus tintinnabulum, Balanus trigonus* [although this was probably present earlier in the Mediterranean], *Amphibalanus eburneus* and *A. improvisus*). The turtle barnacles *Stomatolepas elegans, Platylepas elegans* and *Chelonibia patula* are also new to the Mediterranean.

The only cirripede species currently endemic to the Mediterranean is *Euraphia depressa* (Poli, 1791), which has now been found in the Red Sea (Achituv & Safriel, 1980) but has no fossil record in either basin. It is interesting that some species still common in the eastern Atlantic and present in the lower Pleistocene of the Mediterranean have not subsequently recolonised the region (*e.g.*, *Balanus crenatus, B. balanus*) and two (*Balanus trigonus, Megabalanus tintinnabulum*) are in the process of doing so.

Conclusions

The remarkable, prescient and detailed taxonomic work in Seguenza's monographs on the cirripede faunas of the Sicilian Pleistocene (1873, 1876) have been largely overlooked by zoologists studying living Atlantic and other species. Although his scalpellid species *Arcoscalpellum michelottianum* (Seguenza, 1876) has been recognised as the valid name for a globally distributed deep-sea taxon (see Young, 2007), the same has not been true of the calanticid and verrucid taxa which he described. We conclude that *Metaverruca zancleana* (Seguenza, 1873) is the correct name for the globally distributed deep-sea species commonly referred to as *Metaverruca recta*. *Metaverruca dilatata* (Seguenza, 1873) is the senior synonym of the living Atlantic species *M. radiata* (Gruvel, 1901) and *Rostratoverruca romettensis* (Seguenza, 1873) is the senior synonym of the species living in the eastern Atlantic and Mediterranean, previously called *Metaverruca imbricata* (Gruvel, 1900).

Scillaelepas carinata, described in detail by Seguenza on the basis of Sicilian fossil material, is the senior synonym of living taxa described from the Atlantic variously as *S. gemma, S. superba* and *S. grimaldi*. The species described as *Scillaelepas ornata* Seguenza, 1873 is the senior synonym of *Aurivillialepas calycula*, which is known from scattered records in the eastern Atlantic, and it is possible that the rare living species, *A. bocquetae* Newman, 1980 and *A. falcata* (Aurivillius, 1898) are also synonyms of *A. ornata*.

Few of the balanomorphs recorded by Seguenza (1873) have been rediscovered, but we here record material of *Solidobalanus milensis* (Seguenza, 1873) and a new species, *S. digeronimoi* sp. nov. Seguenza's identification of various shallow-water balanomorph taxa from the Plio-Pleistocene of Sicily is largely confirmed upon review. Fossil material of the Acastinae, including *A. muricata* Seguenza, 1873, awaits re-evaluation in view of Kolbasov's (1993) revision of the subfamily. Likewise, the Pyrgomatidae require revision based upon larger numbers of specimens.

The large fauna recorded from the lower Pleistocene of Sicily by Seguenza and subsequent discoveries consists of 40 taxa, including three calanticids, five scalpellids, two lepadids, six verrucids and 24 balanomorphans. This is the most diverse cirripede assemblage found in the entire Cainozoic record of the Mediterranean Basin. The majority of the taxa probably inhabited the upper bathyal zone, with scarcer shallower-water elements, including coral barnacles, being transported downslope, and rare epizootic and epipelagic components (chelonibiids, coronulids, lepadids). Of these 40 taxa, only eight are still present in the Mediterranean, and 18 are extinct.

A review of the Cainozoic history of cirripedes in the Mediterranean Basin (Fig. 12; Tab. 3) demonstrates that:

The presence of a diverse early Miocene (Serravallian-Langhian) cirripede fauna in the Mediterranean, most of which had disappeared before the onset of the Messinian Salinity Crisis.

The appearance of a new, highly diverse fauna in the Pliocene-lower Pleistocene, which included significant numbers of endemic species.

The presence in the Miocene-lower Pleistocene faunas of genera which can be inferred to have originally been distributed across Tethys before closure of the eastern Mediterranean connection to the Indian Ocean (16-20 Ma), including the deep-water balanomorph genus *Pachylasma* (Fig. 11/1). At least two species probably survived in both regions after closure; the calanticid *Calantica zancleana*, found fossil in the Plio-Pleistocene of Sicily, and still living in the Java Sea and around Australasia probably has a very ancient origin (Fig. 11/2; pre-20 Ma). The brachylepadid *Pycnolepas paronae*, found in the Miocene of Spain and Italy, survived into the early Pleistocene in the western Indian Ocean (Gale, 2020b; Fig. 11/2 here).

A major loss of cirripedes (64%) from the Mediterranean occurred around the end of the early Pleistocene (Gelasian-lower Ionian); of these, only 18% survived elsewhere, and 48.5% became extinct. Possible causes of this extinction are climatic cooling (shallow water) and development of warm deep saline water in the Mediterranean Basin. At the same time, the extinction or permanent loss of some species from the eastern Atlantic precluded the possibility of their recolonising of the Mediterranean, as is inferred to have happened after the Messinian Salinity Crisis (*e.g.*, Taviani 2002). The major benthic extinctions at about 0.8 Ma in ocean basins which has been attributed to changes in primary productivity (Kender *et al.*, 2016) may thus have indirectly affected the Mediterranean faunas.

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Plate 1. *Scillaelepas carinata* (Philippi, 1835), present-day specimens: 1a, b. lateral and ventral views of individual attached to coral; dissociated plates of same individual as follows: 1c, 1d. carina, in dorsal and lateral views; 1e-g, rostrum, in ventral, lateral and internal views, respectively; 1h, 1i. scutum, in external and internal views; 1j. upper latus, in external view; 1k. rostrolatus, in external view; 1l. carinolatus, in external view. Provenance: Porcupine Sea Bight, northeast Atlantic, *51613#M, 2,200-2,240 m. NOC collections, Southampton; 2a-c. large individual, in lateral, ventral and dorsal views, respectively; 3a, 3f. smaller individual, in lateral and ventral views; dissociated plates of this specimen, in external view, as follows: 3b. upper latus; 3c. carinolatus; 3d. carinolatus; 3e. subcarina. Provenance of both specimens: Atlantic, from off Florida coast, station 8-XI-05-1, 28^{o}17.0999’N, 79^{o}36.8593’W, JSL I-4909, depth 727 m (Fig. 2); 6-VI-11-003, 28^{o} 45.497’N, 80^{o}04.283’W, depth 64-88 m (Fig. 3). A.S. Gale collection. Scale bars equal 5 mm (1, 3) and 10 mm (2).

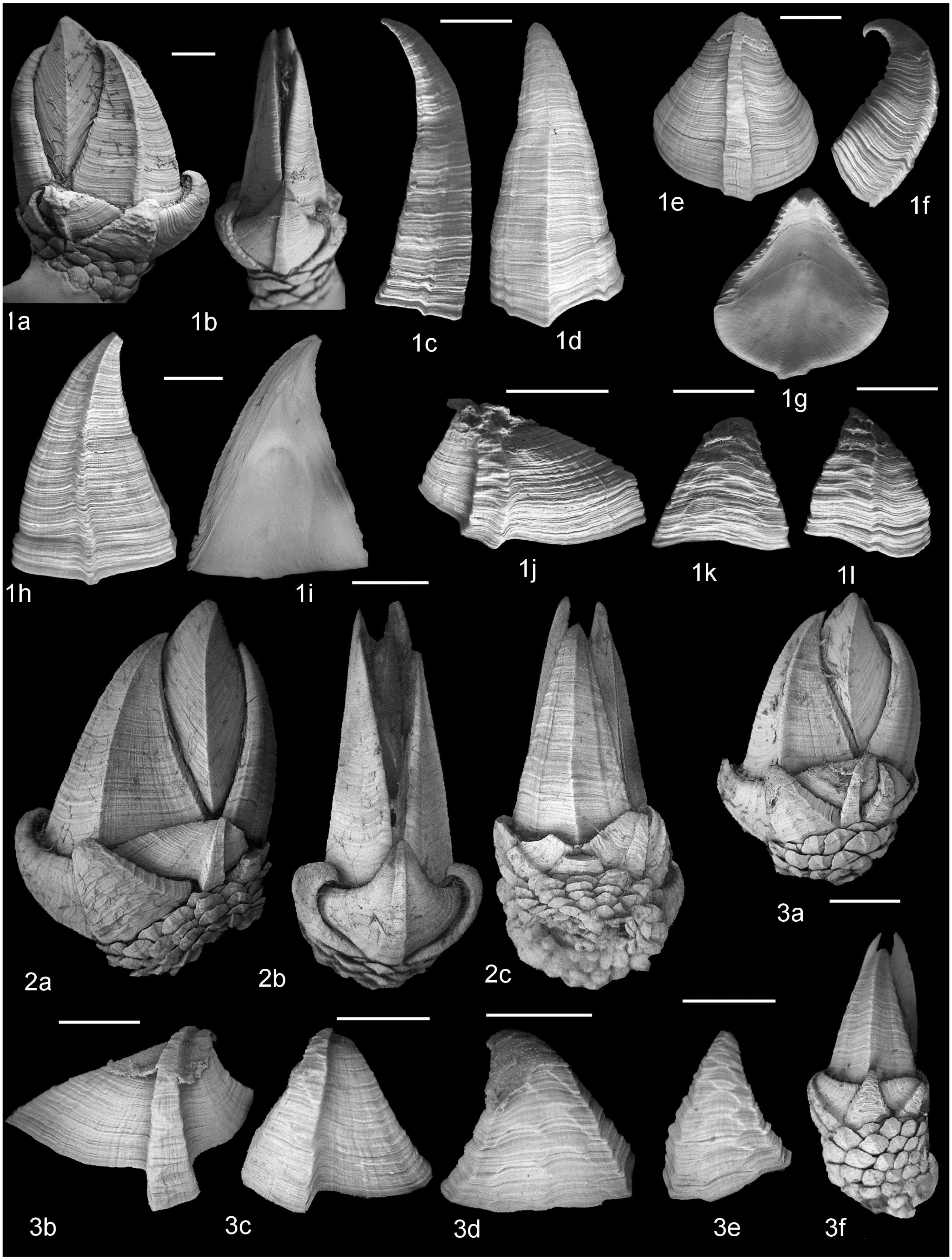

Plate 1

Plate 2. *Scillaelepas carinata* (Philippi, 1835). 1a, b. rostrum (NHMUK In. 33995); 2a, 2b. scuta: 2a. external view (original of Withers, 1953, pl. 16, fig. 5; NHMUK In. 33663), 2b. internal view (original of Withers, 1953, pl. 16, fig. 3b; NHMUK In. 33654); 3a, 3b. carina in dorsal and lateral views (original of Withers, 1953, pl. 16, fig. 2; NHMUK In.33648); 4. large scutum, external view, with internal view of tergum (PMC. R. I. Pl.CIR-1); 5-7. terga, external views: 5 (PMC. R. I. Cal. CIR-2), 6 (NHMUK In.33664) and 7 (original of Withers, 1953, pl. 16, fig. 7; NHMUK In. 33662); 8, 9, 13. upper latera, in external view (PMC. R. I. Cal. CIR-3, 4, 8); 10. subcarina, in external view (PMC. R. I. Cal. CIR-5); 11. rostrum, external view; 12. rostrolatus, in external view (PMC. R. I. Pl. CIR-6; PMC. R. I. Cal. CIR-7); 14, 15. carinolatera, in external view (PMC. R. I. Cal. CIR-9, 10). Provenance: 1-3, 6, 7. Messina, Sicily, no details. Fig. 11, La Montagna, Messina, Sicily. All other specimens from Calabrian, Scoppo, Sicily(SC). Scale bars equal 10 mm (4-7); all others are 5 mm.

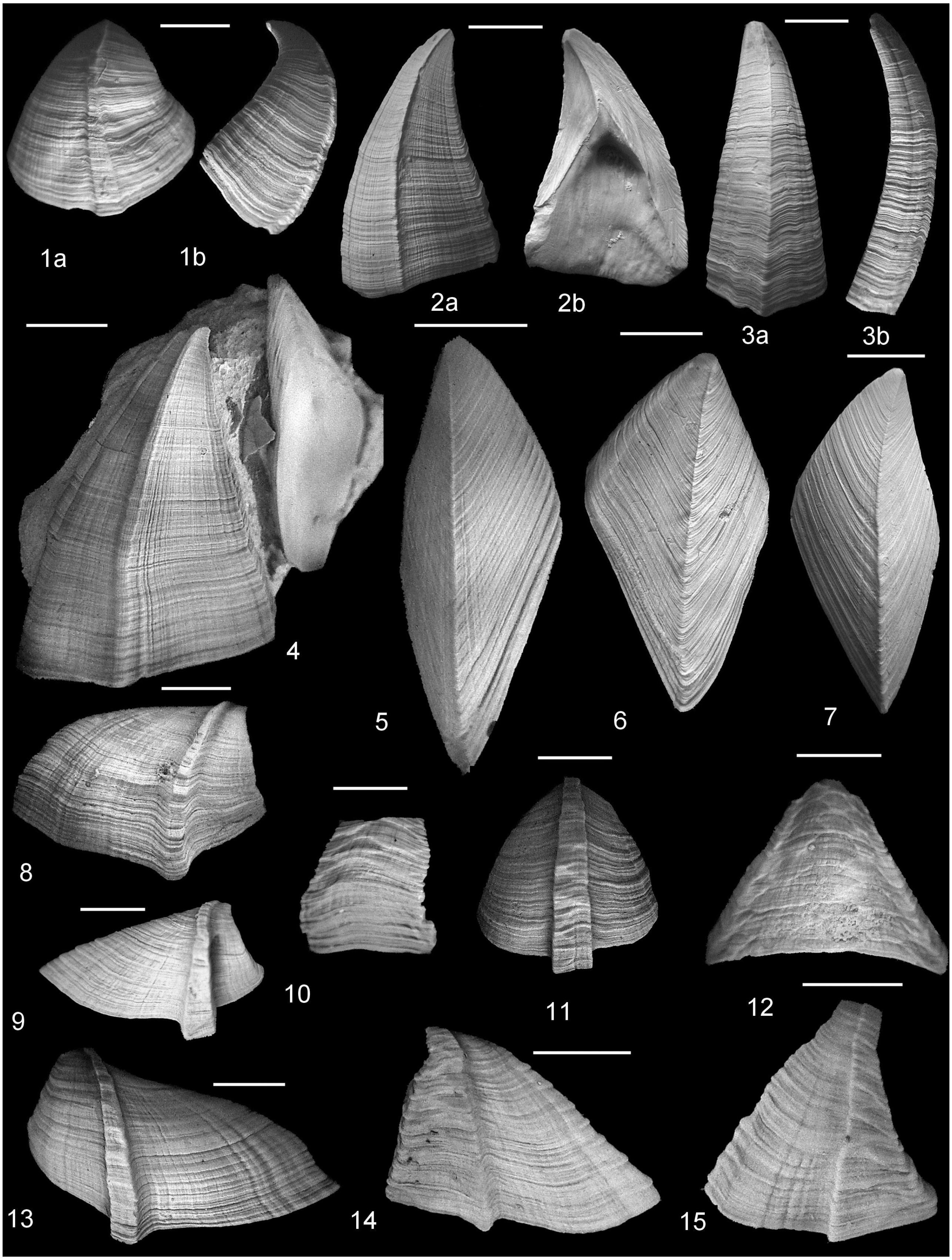

Plate 2

Plate 3. *Aurivillialepas ornata* (Seguenza, 1876): 3. individual (lateral view), original of Innocenti *et al*. (2015, fig. 4, as *A. calycula* (Aurivillius, 1898)); 1, 2, 7, 9, 10, 13, 14. scuta; fig. 1a, 1b. scutum, **neotype**, in external and internal views (original of Withers, 1953, pl. 17, fig. 8; NHMUK In. 33675); 2, 4, 7, 9, 13. small scuta; 7b, 10b, 14b. internal view, all others external view (PMC. R. I. Cal.CIR-15, 18, 20, 24, 75); 10, 14. large, ornate scuta (PMC. R. I. Cal. CIR-21, 25); 4-6, 8. terga, external views; 4. original of Withers, 1953, pl. 17, fig. 9; NHMUK In. 33678; 5, 6, 8. PMC. R. I. Cal. CIR-16, 17, 19; 11. rostrum, in external view (PMC. R. I. Cal. CIR-22); 12. small scutum, in external view (PMC. R. I. Cal. CIR-23). Provenance: 1, 4. from Messina, Sicily; 3. present-day, Banco de Galicia, northeast Atlantic; all others from Calabrian, Scoppo, Sicily (SC). Scale bars equal 5 mm (1, 3-6, 8, 10, 14) and 1 mm (2, 7, 9, 11-13).

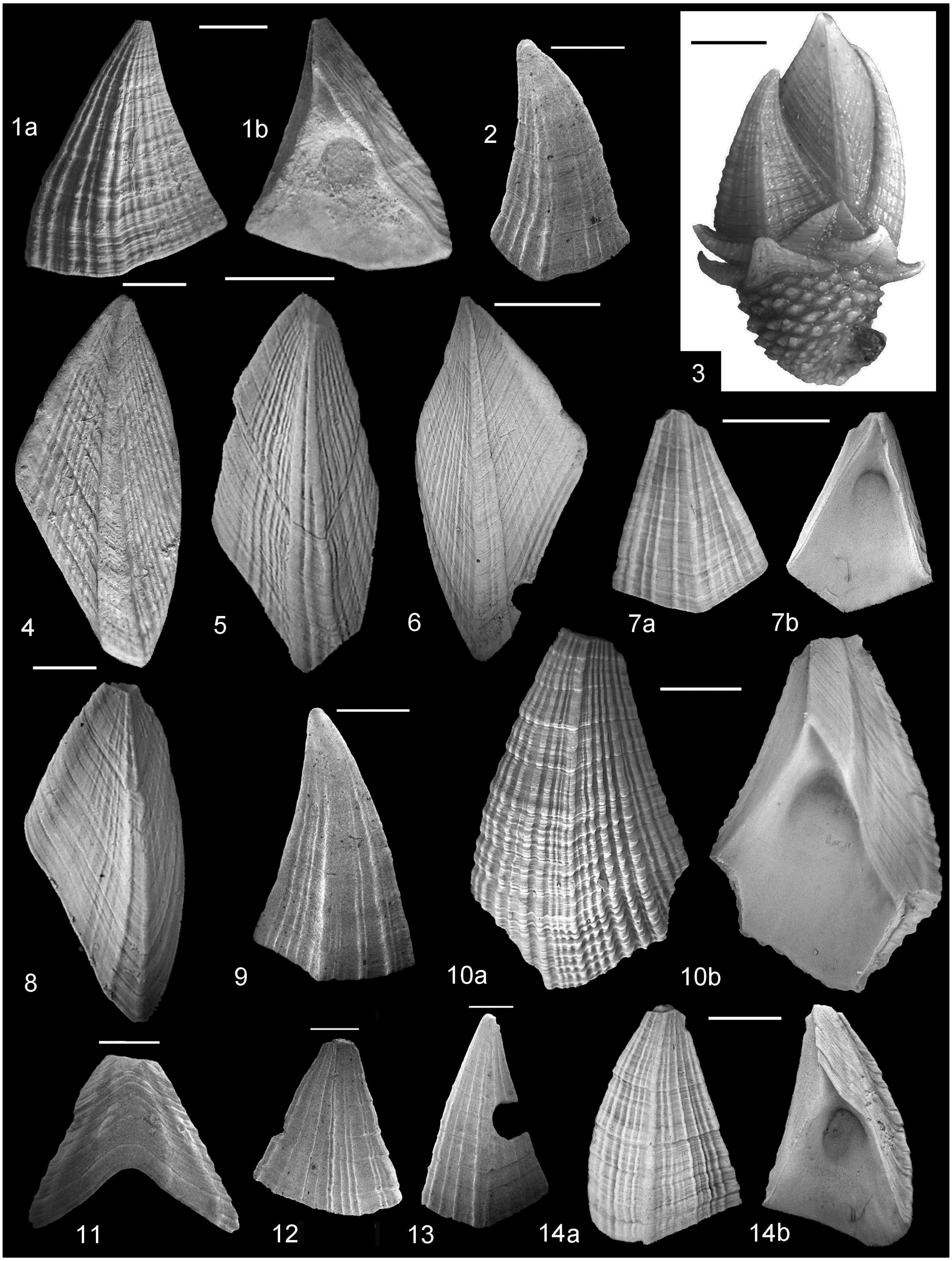

Plate 3

Plate 4. *Aurivillialepas ornata* (Seguenza, 1876): 1a-c. subcarina (PMC. R. I. Cal. CIR-26), in external, lateral and internal views, respectively; 2. subcarina (PMC. R. I. Cal. CIR-27), in external view; 3a-c. subrostrum (PMC. R. I. Cal. CIR-28), in external, lateral and internal views, respectively; 4. carina (PMC. R. I. Cal. CIR-29) in external view; 5a-c. rostrum (PMC. R. I. Cal. CIR-30), in external, lateral and internal views, respectively; 6a, b. carina (PMC. R. I. Cal. CIR-31), in external and lateral views; 7. carina (PMC. R. I. CIR-32), in external view; 8, 12, 13. upper latera (PMC. R. I. Cal. CIR-33, 37, 38), in external views; 9. rostrolatus (PMC. R. I. Cal. CIR-34), in external view; 10, 11. carinolatera (PMC. R. I. Cal. CIR-35, 36), in external views; 14a, b. carina (NHMUK In. 33674, the original of Withers, 1953, pl. 17, fig. 7), in external and lateral views. Provenance: 7, Gelasian, Messina, Sicily; all others are from the Calabrian, Scoppo, Sicily (SC). Scale bars equal 1 mm (1-6, 8-13) and 5 mm (7, 14).

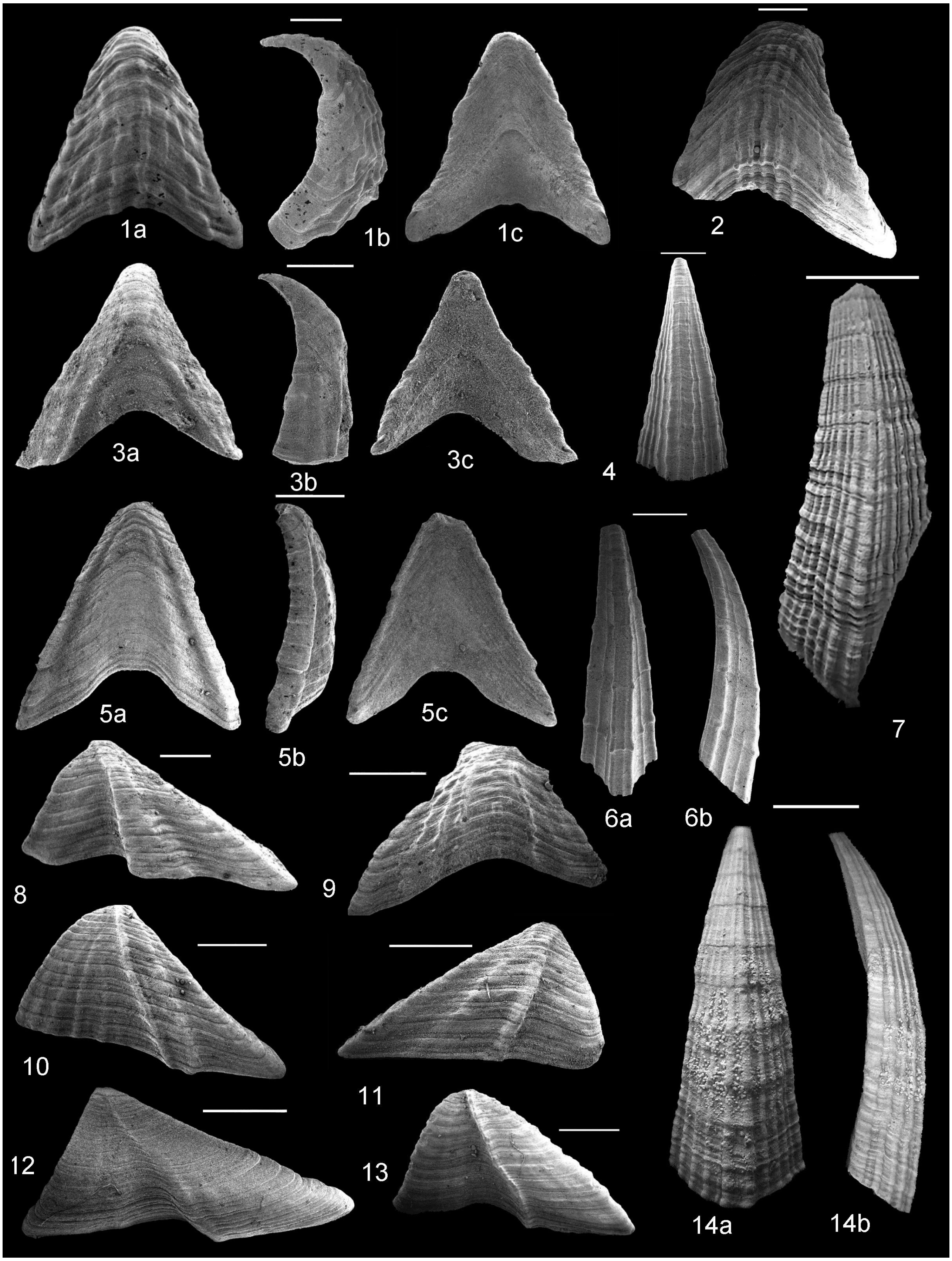

Plate 4

Plate 5. 1-3. *Scalpellum* sp.: 1. fragmentary scutum (PMC. R. I. CIR-39c); 2, 3. carinae (2a lateral, 2b dorsal view), 3 (dorsal view) (PMC. R. I. Cal. CIR-40, 41); 4. *Arcoscalpellum michelottianum* (Seguenza, 1876), carina, in dorsal and lateral views (PMC. R. I. Cal. CIR-42); 5-19. *Rostratoverruca romettensis* (Seguenza, 1873). 5, 8, 11, 14, 16. fixed terga in external view, to show variation (PMC. R. I. Cal. CIR-43, 47, 49, 52, 54); 6, 9, 12, 15, 17. fixed scuta, internal view, to show variation in proportionate height, position and development of scutal adductor scar (PMC. R. I. Cal. CIR-44, 47, 50, 53, 55); 7, 10. shells, in apical (7b, 10b) and lateral (scutal-tergal, 7a, 10a) views (PMC. R. I. R CIR-45, PMC. R. I. Cal. 48); 13. shell, lacking moveable plates, in scutal-tergal (13a) and apical (13b) views (PMC. R. I. CIR-51); 18, 19. articulated rostrum/carina (PMC. R. I. Cal. CIR-56, 57). Provenance: 7, present-day, off Sicily (Medicore 25); all other specimens from Calabrian, Scoppo, Sicily (SC). Scale bars equal 1 mm (1, 7, 10, 13); all others are 0.5 mm.

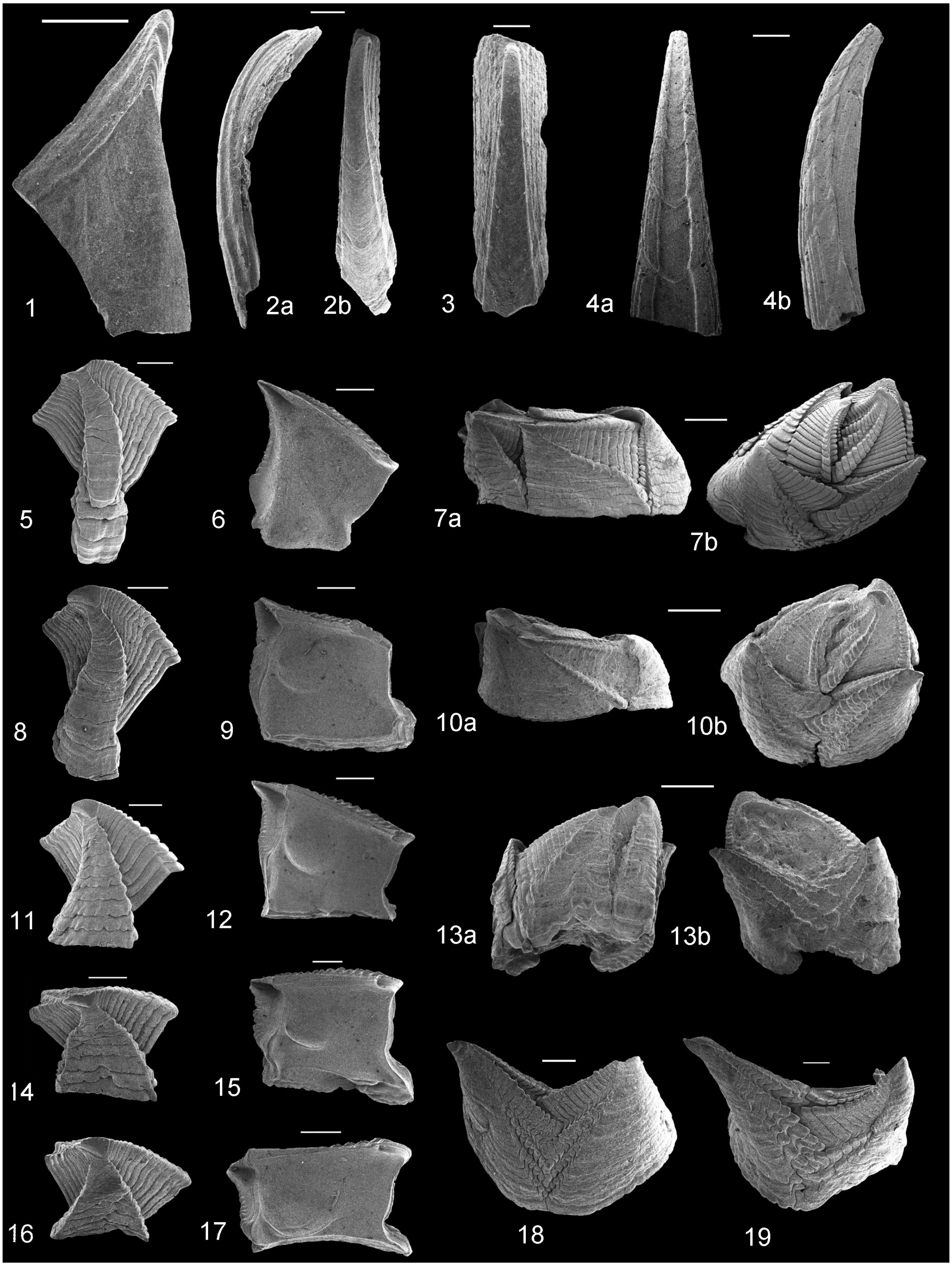

Plate 5

Plate 6. *Rostratoverruca romettensis* (Seguenza, 1873): external view of fixed tergum (1a), internal view of fixed scutum (1b), external views of moveable scutum (1c) and moveable tergum (1d) (PMC. R. I. R. CIR-58); 2, 5. external views of moveable terga (PMC. R. I. Cal. CIR-59, 62); 3, 4. external views of moveable scuta (PMC. R. I. Cal. CIR-60, 61); 6, 7, 9. fixed scuta, in external (6, 9) and internal (7) views (PMC. R. I. Cal. CIR-63, 64, 66); 8. fixed tergum, in external view (PMC. R. I. Cal. CIR-65); 10. paired fixed scutum-tergum, in internal view (PMC. R. I. Cal. CIR-67). Provenance: 1. Present-day. MEDCOR 25; 2-10. Calabrian, Scoppo, Sicily (SC). Scale bars equal 0.5 mm.

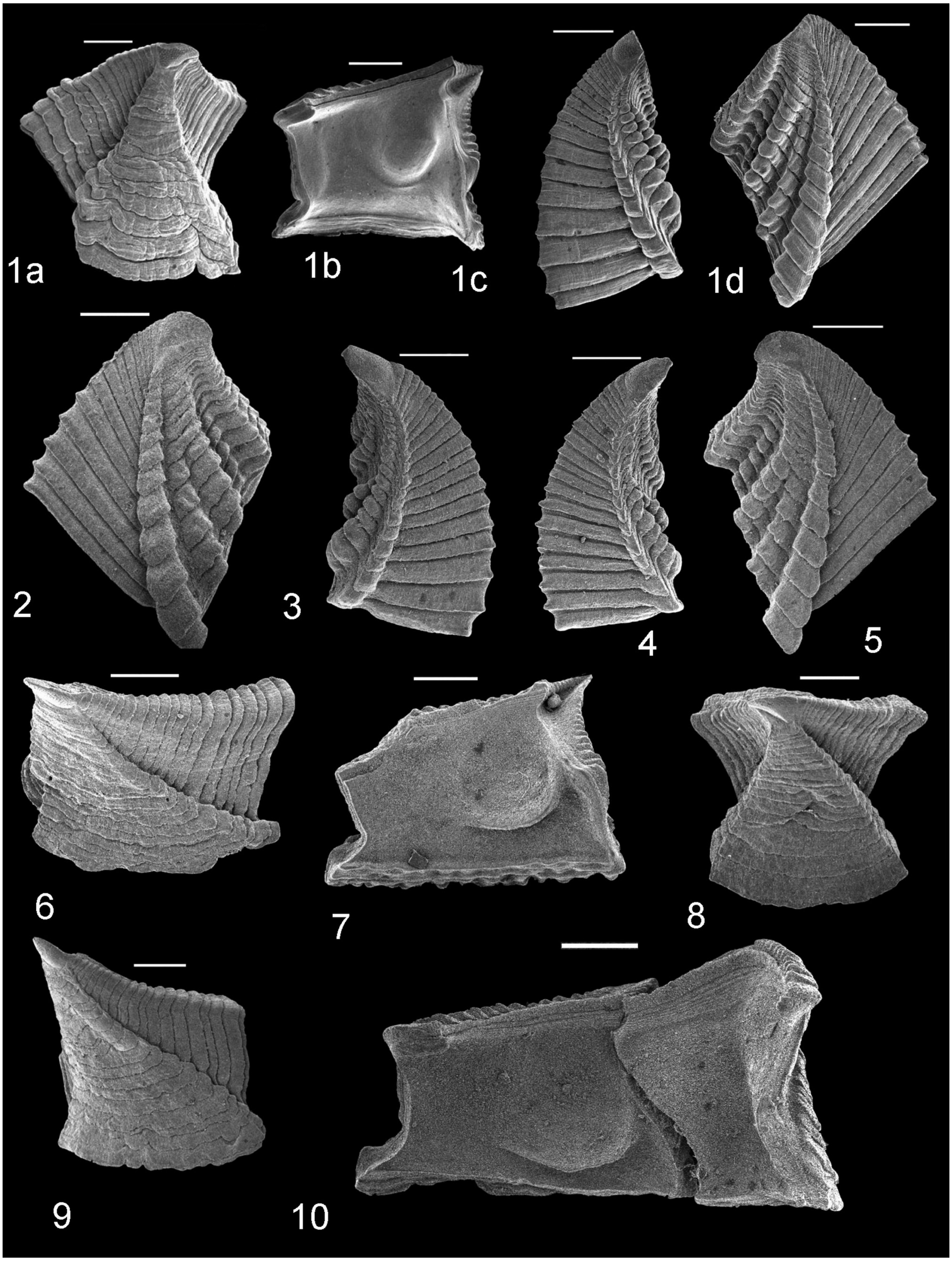

Plate 6

Plate 7. Species of *Gibbosaverruca*. 1-10, 12, 13, 16. *Gibbosaverruca milazzensis* sp. nov.: 1-4. fixed terga, in external view; 1. **holotype** (PMC.CIR.18.1.202.1a); 2-4. **paratypes** (PMC.CIR.18.1.2021.b1-b3); 5, 10. fixed scuta, **paratypes**, in external and internal views, respectively (PMC.CIR.18.1.2021.b4, b9); 6, 9. moveable terga, in external view (PMC.CIR.18.1.2021.b6, b8); 7, 8. moveable scuta, in external view (PMC.CIR.18.1.2021.b6, b7); 13, 16. carinae (PMC.CIR.18.1.2021.b10, b11). 11, 14, 15, 17, 18. *Gibbosaverruca nitida* (Hoek, 1883): external views of moveable scutum (11b) and moveable tergum (11a); 14. carina, original of Gale (2020a, pl. 15, fig. 7; NHMUK IC 1786); 15. rostrum, original of Gale (2020a, pl. 15, fig. 4; NHMUK IC 1792); 17. fixed scutum, original of Gale (2020a, pl. 15, fig. 5; NHMUK IC1784); 18. fixed tergum, original of Gale (2020a, pl. 15, fig. 3; NHMUK IC 1782). Provenance: 1-10, 12, 13, 16. Gelasian, Capo Milazzo to Punta Mazza (PM6), Sicily; 11. Present-day, southwest Pacific; 14, 15, 17, 18. Plio-Pleistocene, Rodrigues Ridge, Indian Ocean. Scale bars equal 1 mm (1, 3, 4, 12) and 0.5 mm (2, 5-11, 13-18).

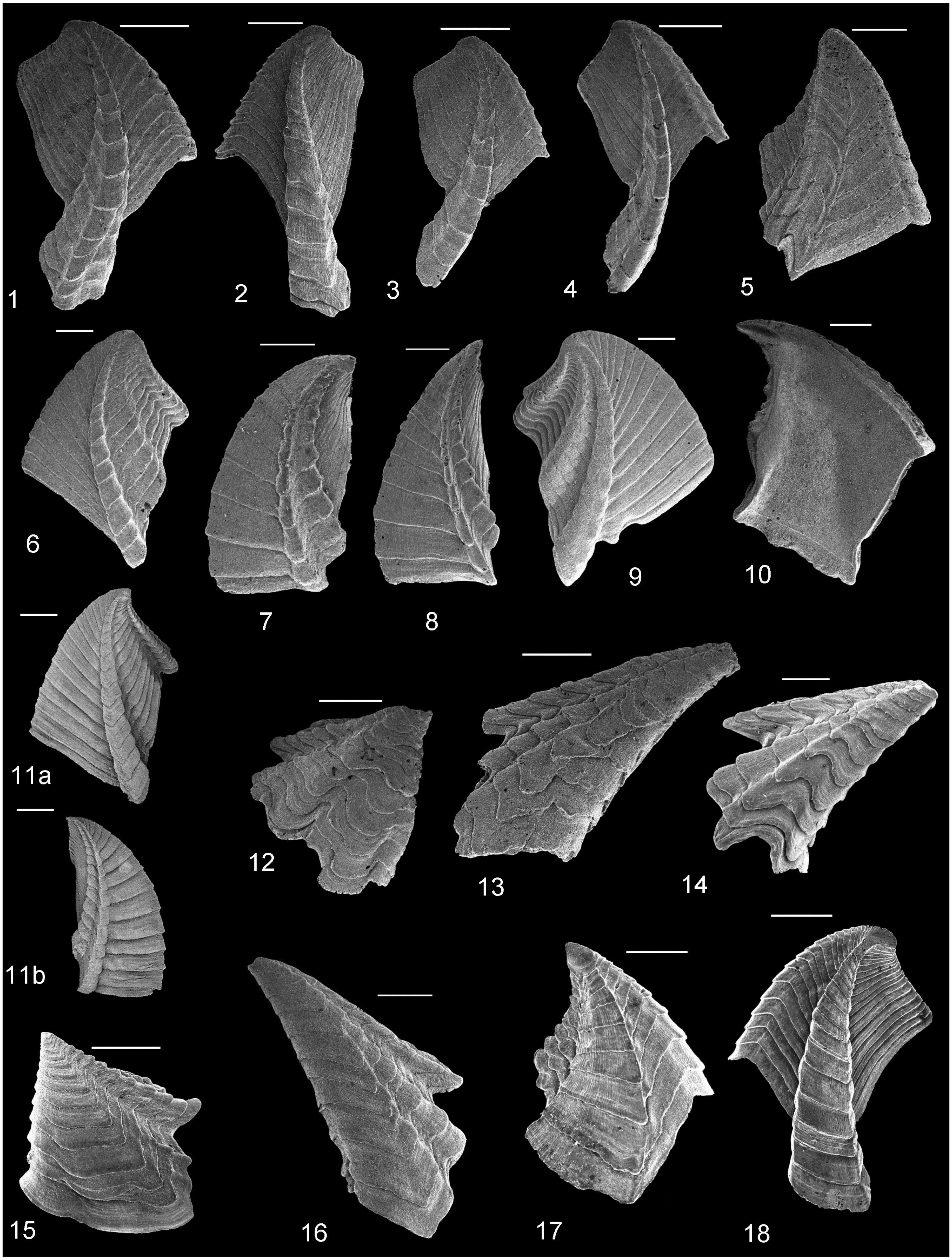

Plate 7

Plate 8. *Metaverruca zanclea* (Seguenza, 1873): 1a, b. fixed scutum, in internal and external views; 2. shell, in apical view, moveable plates missing (PMC. R. I. lPl. CIR-68); 3, 5, 8. fixed scuta, in internal (3, 5) and external (8) views (PMC. R. I. lPl. CIR-69, 71, 74); 4. carina, in external view (PMC. R. I. lPl. CIR-70); 6a. moveable scutum; 6b. moveable tergum, in external view; 7. moveable tergum, in external view (PMC. R. I. lPl. CIR-73); 9. fixed tergum, in external view (PMC. R. lPl. CIR-75); 10. rostrum, in external view (PMC. I. lPl. R. 1. CIR-76). Provenance: 1, 6. Recent, southwest Pacific; 2. Lower Pleistocene, Capo Milazzo, Sicily; 3-5, 7-10. Lower Pleistocene, Catallarga Hill, near Grammichele, Sicily. Scale bars equal 1 mm (2), 2 mm (3, 5, 6); all others are 5 mm.

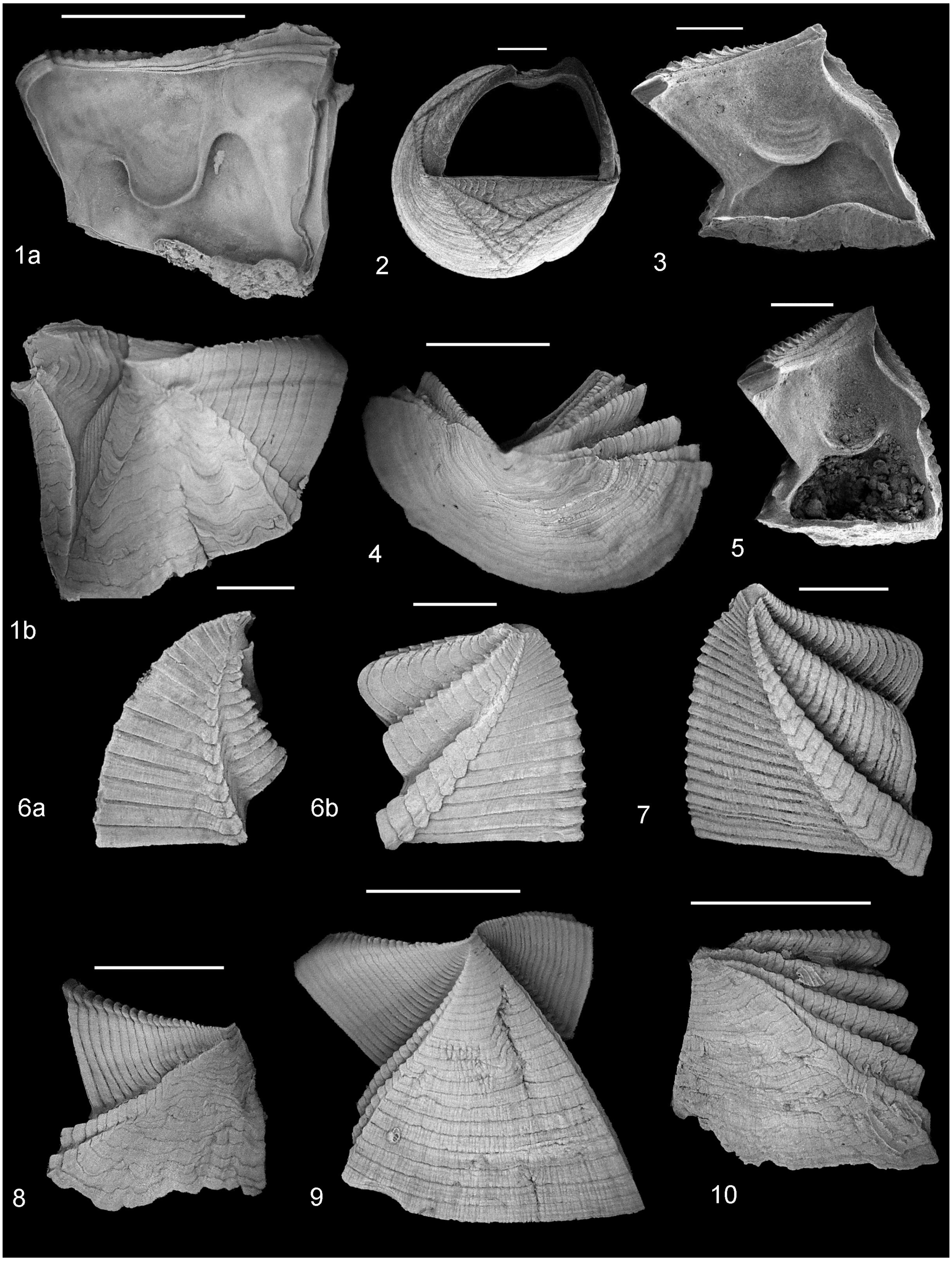

Plate 8

Plate 9. *Metaverruca dilatata* (Seguenza, 1873): 1. fixed scutum and tergum, in lateral external view (PMC. R. I. lPl. CIR-77); 2, 5, 6. rostra, in external view (PMC. R. I. lPl. CIR-78, 81, 82); 3. carina, in external view (PMC. R. 1. IPl. CIR-110); Fig. 3, carina (PMC. R. I. lPl. CIR-79); 4. shell, lacking moveable plates (PMC. R. I. lPl. CIR-80); 7, 9. fixed terga, in external view (PMC. R. I. lPl. CIR-83, 85); 8. fixed scutum, in external view (PMC. R. I. lPl. CIR-84); 10. moveable scutum, in external view (PMC. R. I. lPl. CIR-86); 11, 12. moveable terga, in external views (PMC. R. I. lPl. CIR-87, 88). Provenance: lower Pleistocene, Catallarga Hill, near Grammichele, Sicily. Scale bars equal 2 mm.

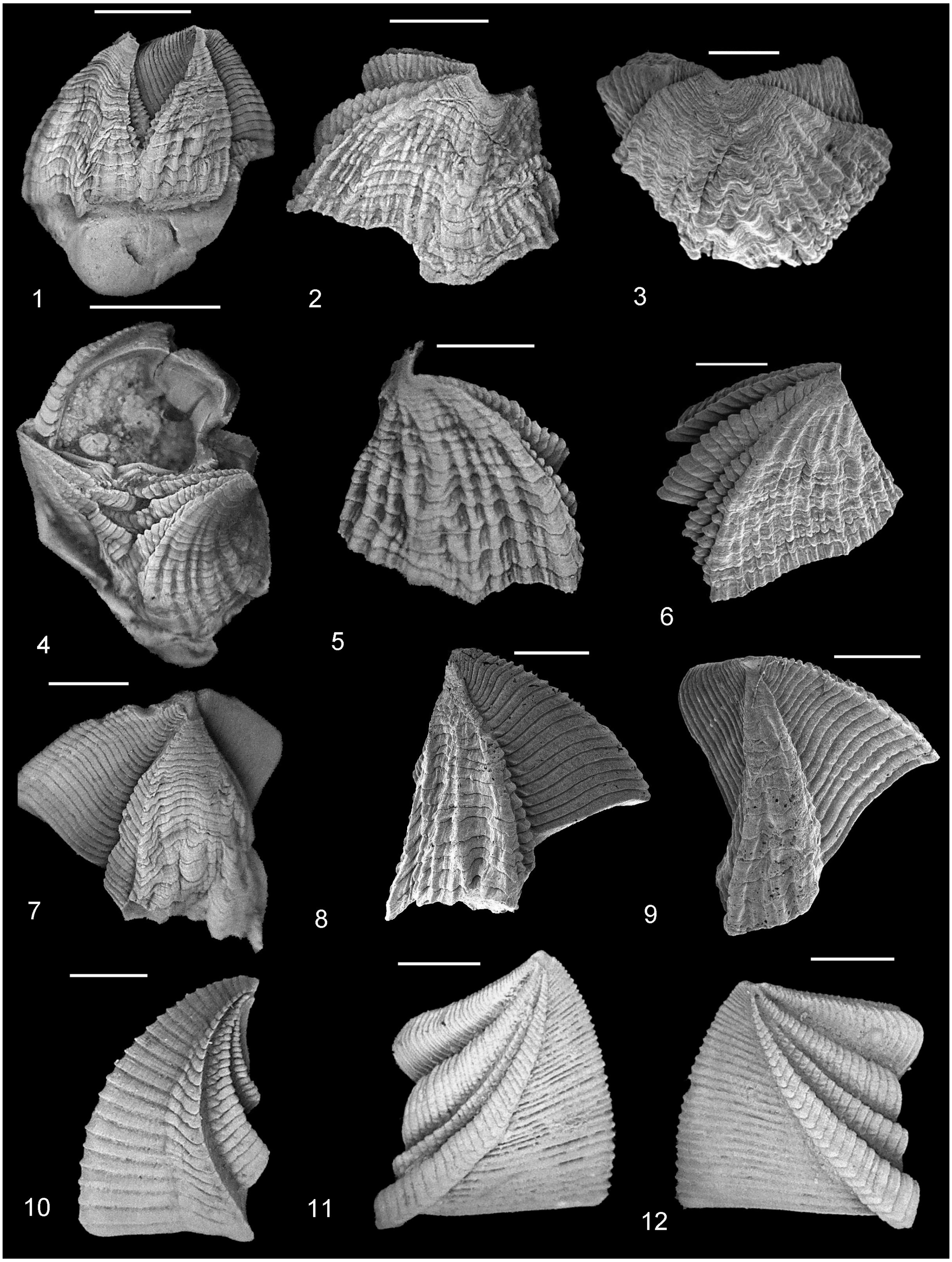

Plate 9

Plate 10. *Pachylasma giganteum* (Philippi, 1836): 1a, b. shell (PMC. R. I. R. CIR-89), in lateral and apical views; 1c, d. tergum in external and internal views; 1e, f. scutum in external and internal views; 2a, b. tergum (PMC. R. I. lPl. CIR-90), in external and internal views; 3, 7. scuta, 3a (external view) and 3b, 7 (internal views) (PMC. R. I. lPl. CIR-91, 95); 4a, b. marginal plate in external and internal views (PMC. R. I. lPl. CIR-92); 5, 6. carinae, in external and internal views (PMC. R. I. lPl. CIR-93, 94); 8, 9a, b. rostral plates, in internal (8, 9b) and external (9a) views (PMC. R. I. lPl. CIR-96, 97); 10. carinomarginal, in internal view (PMC. R. I. lPl. CIR-98). Provenance: 1. Present-day, Mediterranean; 2-10. Lower Pleistocene, La Montagna, Sicily (LM). Scale bars equal 10 mm (1, 3), all others are 5 mm.

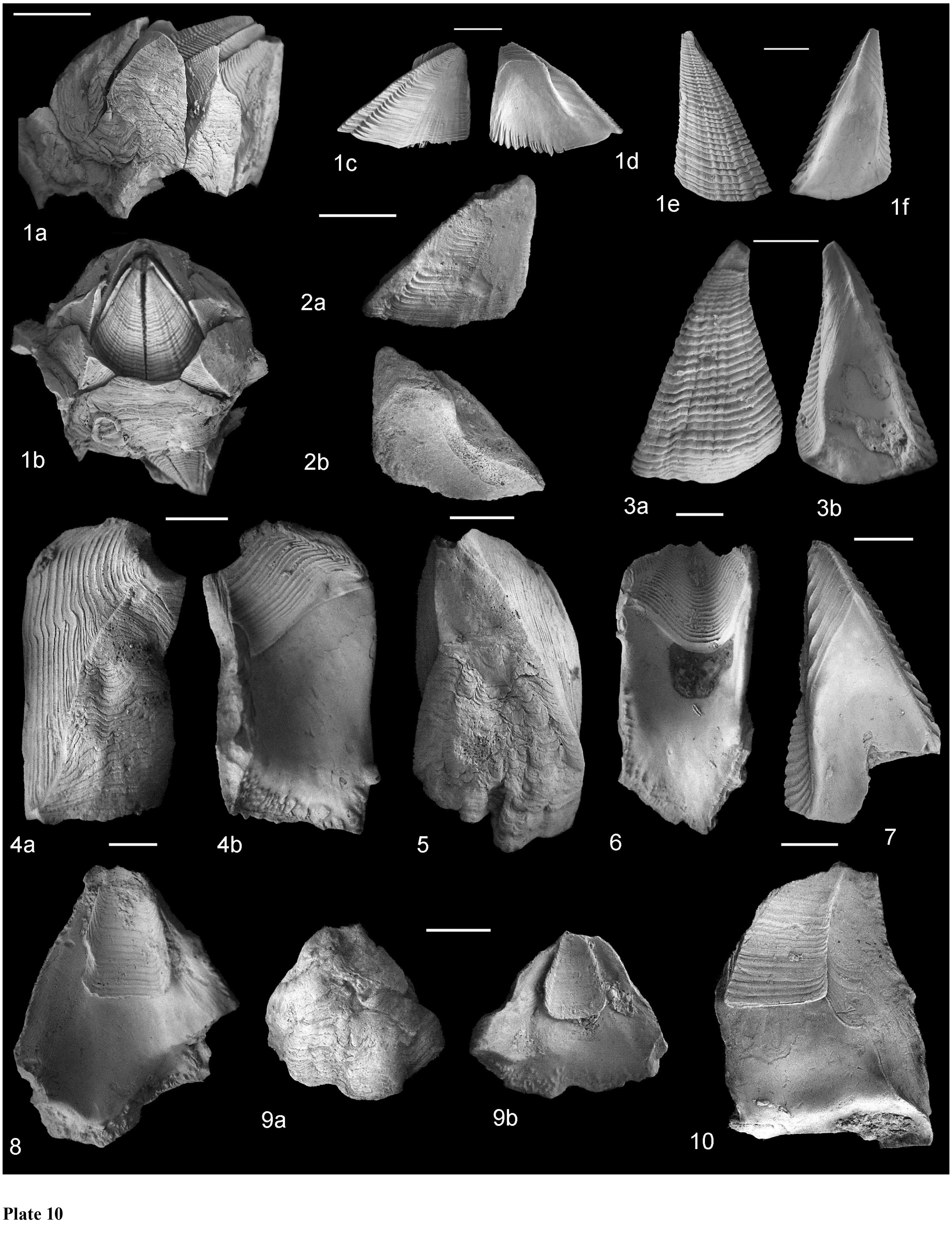

Plate 10

Plate 11. *Solidobalanus digeronimoi* sp. nov.: 1a, b. marginal plate (**holotype**, PMC.CIR.18.1.2021a), in external and internal views (1c, enlargement of sculpture); 2a, b. rostral plate (**paratype**, PMC.CIR.18.1.2021b1), in external and internal views; 3a, b. carina (**paratype**, PMC.CIR.18.1.2021b2), in external and internal views; 4. rostral plate (**paratype**, PMC.CIR.18.1.2021b3), in external view; 5a, b. carinomarginal plate (**paratype,** PMC.CIR.18.1.2021b4) in external and internal views; 6. articulated marginal and carinomarginal plates (**paratype**, PMC.CIR.18.1.2021b5), in external view; 7a-c. marginal plate, with attached fragment of carinomarginal (**paratype**, PMC.CIR.18.1.2021b6), in external and internal views (7c, enlargement of basis to show pores). Provenance: all are from the Gelasian of Capo Milazzo-Punta Mazza Camp 6 (PM6). Scale bars equal 2 mm (1a, b, 2-5), 1 mm (6, 7a, b) and 0.2 mm (1c, 7c).

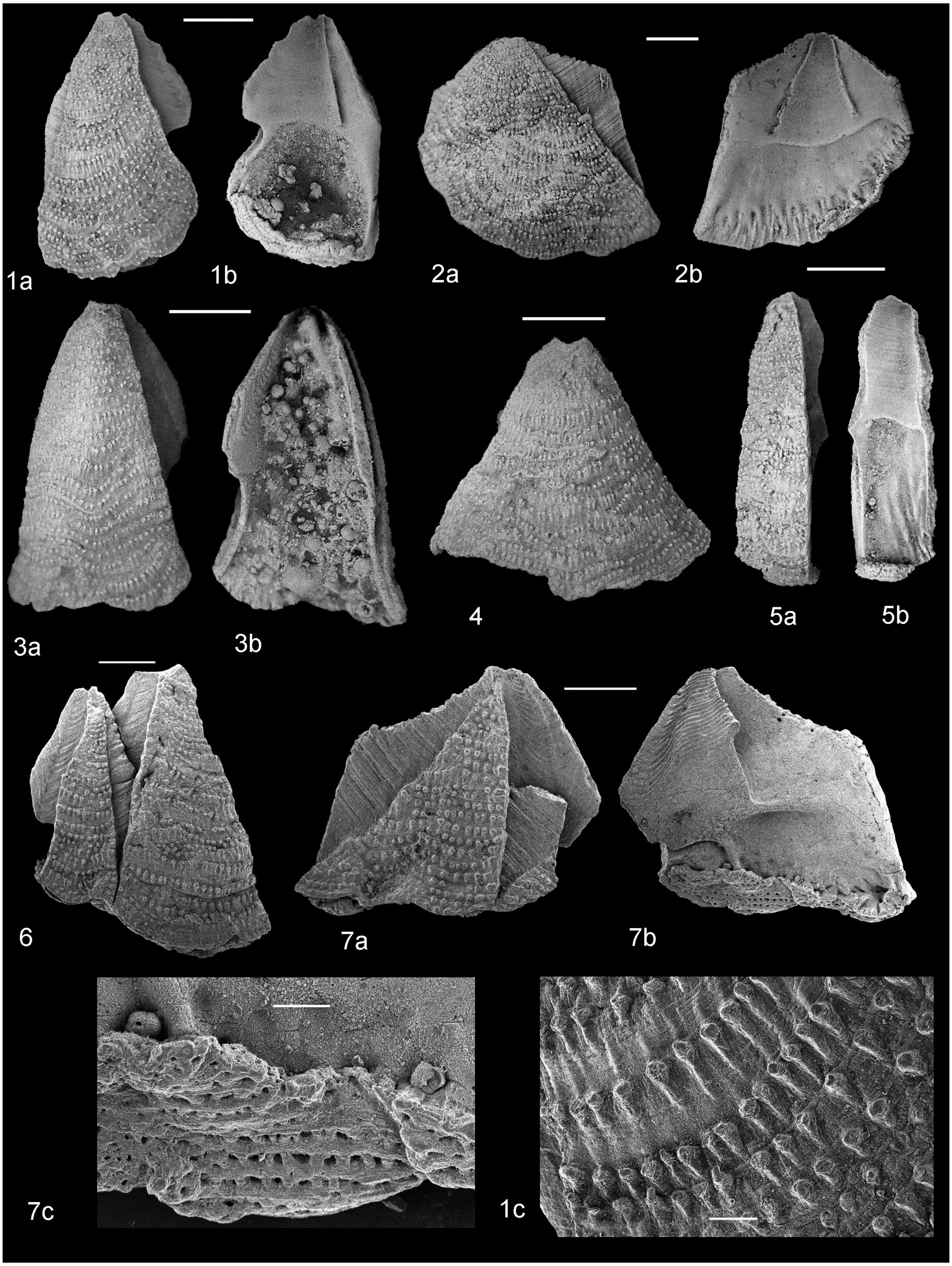

Plate 11

Plate 12. 1-4. *Solidobalanus digeronimoi* sp. nov: 1, 2, scuta (**paratypes**, PMC.CIR.18.1.2021b7, b8), in external and internal views; 3a, b., tergum, **paratype** (PMC.CIR.18.1.2021b9), in external and internal views; 4, **paratype** rostral plate (PMC. CIR.18.1.2021b10), in external view; 5-7, 9, *Solidobalanus milensis* (Seguenza, 1873): 5a, b. marginal plate (PMC. R. I. lPl. CIR-99) of small individual, in external and internal views; 6a, b. rostral plate (PMC. R. I. lPl. CIR-100), in external view; 7a, b. partial shell (PMC. R. I. lPl. CIR-101), consisting of articulated rostral, marginal and carinomarginal plates, with basis, in internal and external views; 9. marginal plate (PMC. R. I. lPl. CIR-103), in external view; 8, 10, "*Acasta*" sp.: 8a, b. marginal plate (PMC. R. I. Cal. CIR-102), in external and internal views; 10a, b. carina (PMC. R. I. lPl. CIR-104), in internal and external views. Provenance: 1-7, 9, 10 are from Capo Milazzo; 8 from the Calabrian of Scoppo (SC). Scale bars equal 2 mm (8), 1 mm (1-3, 7, 10) and 0.5 mm (4-6, 9).

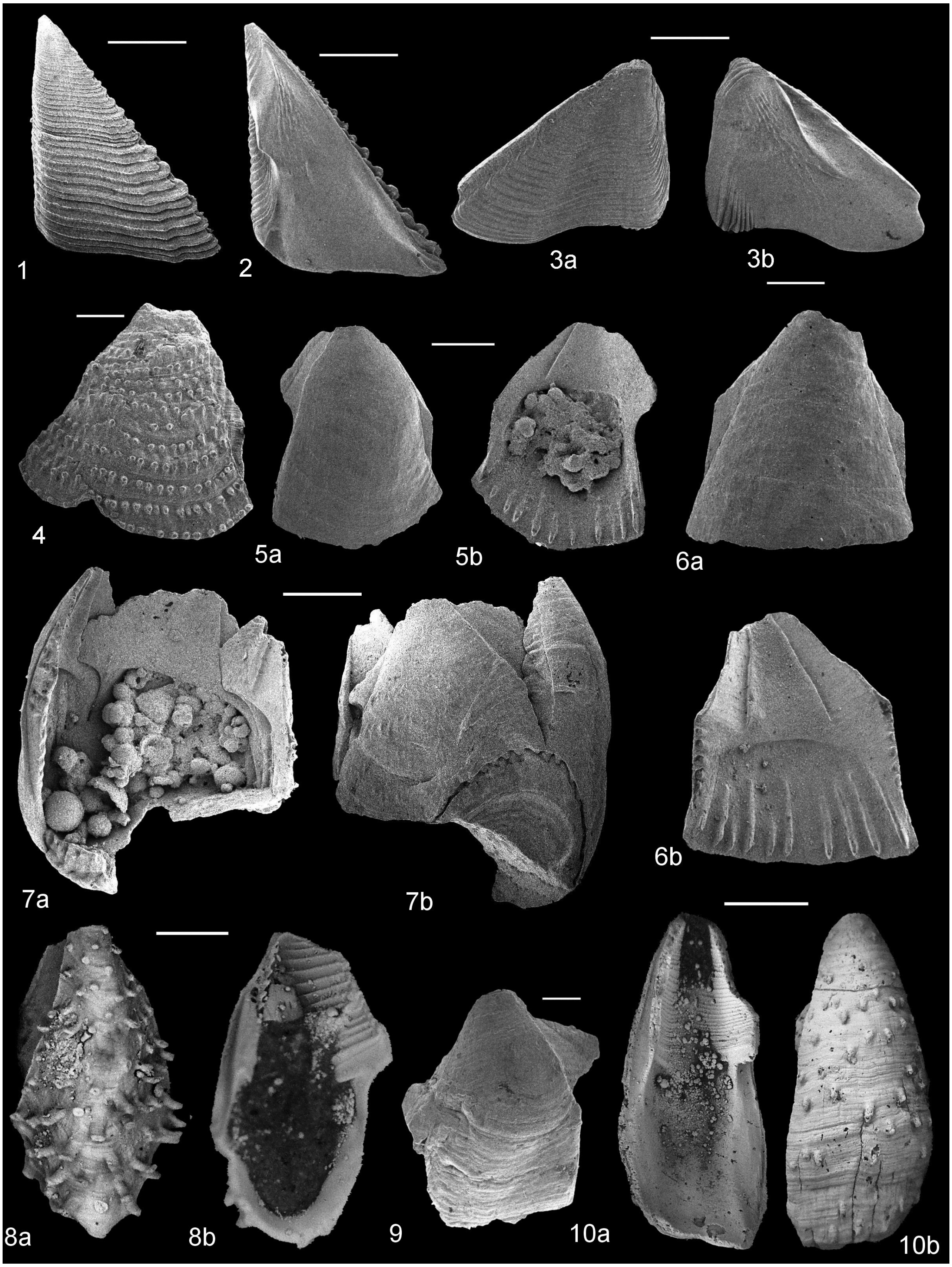

Plate 12

Plate 13. Species of *Pyrgomina*. 1, 4. *Pyrgomina costata* (Seguenza, 1876): 1a-c. shell (PMC. R. I. lPl. CIR-105), in oblique lateral, apical and basal views, respectively; 4a-d. scutum (PMC. R. I. lPl. CIR-108), in external (a) and internal (b) views and shell in lateral (c) and basal (d) views; 2, 3. *Pyrgomina elargatum* (Seguenza, 1876): 2. parietal wall (PMC. R. I. lPl. CIR-106) lacking basis in basal (2a) and apical (2b) views; 3a-c. shell (PMC. R. I. lPl. CIR-107) in lateral, apical and basal views, respectively; 5. *Pyrgomina* sp. (PMC. R. I. lPl. CIR-109), fragment of wall, to show structure. Provenance: all are from the Calabrian–Gelasian of Capo Milazzo, Sicily. Scale bars equal 4 mm (2), 2 mm (1, 3, 4c, 4d), 1 mm (5) and 0.5 mm (4a, b).

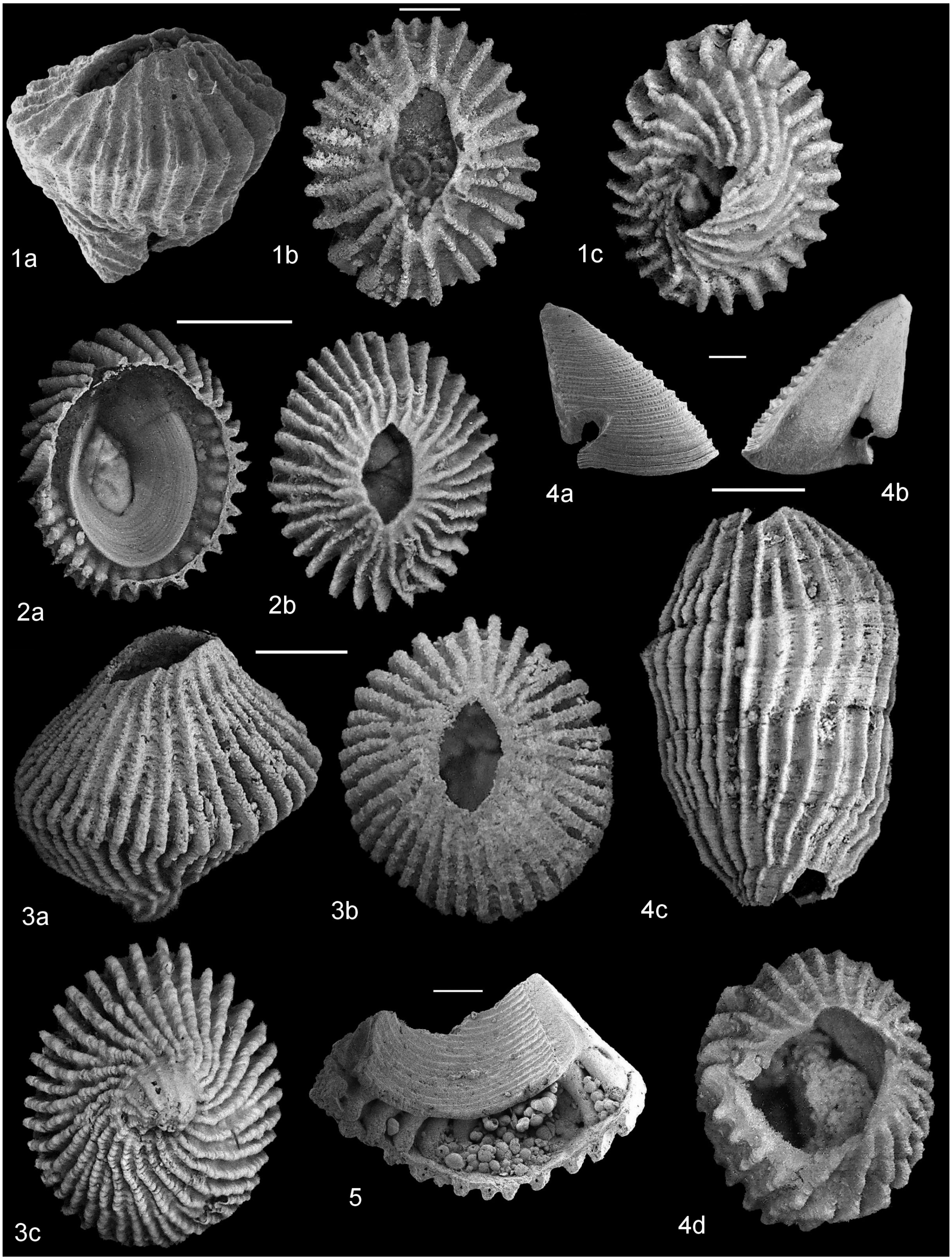

Plate 13