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Pliocene distribution of the cirripede *Verruca stroemia* (O.F. Müller, 1776) and revised definitions of the verrucid genera *Verruca*, *Metaverruca* and *Priscoverruca* (Thoracica, Crustacea)

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ABSTRACT:

Gale, A.S. and Sadorf, E. 2025. Pliocene distribution of the cirripede *Verruca stroemia* (O.F. Müller, 1776) and revised definitions of the verrucid genera *Verruca*, *Metaverruca* and *Priscoverruca* (Thoracica, Crustacea). *Acta Geologica Polonica*, **75** (1), e39.

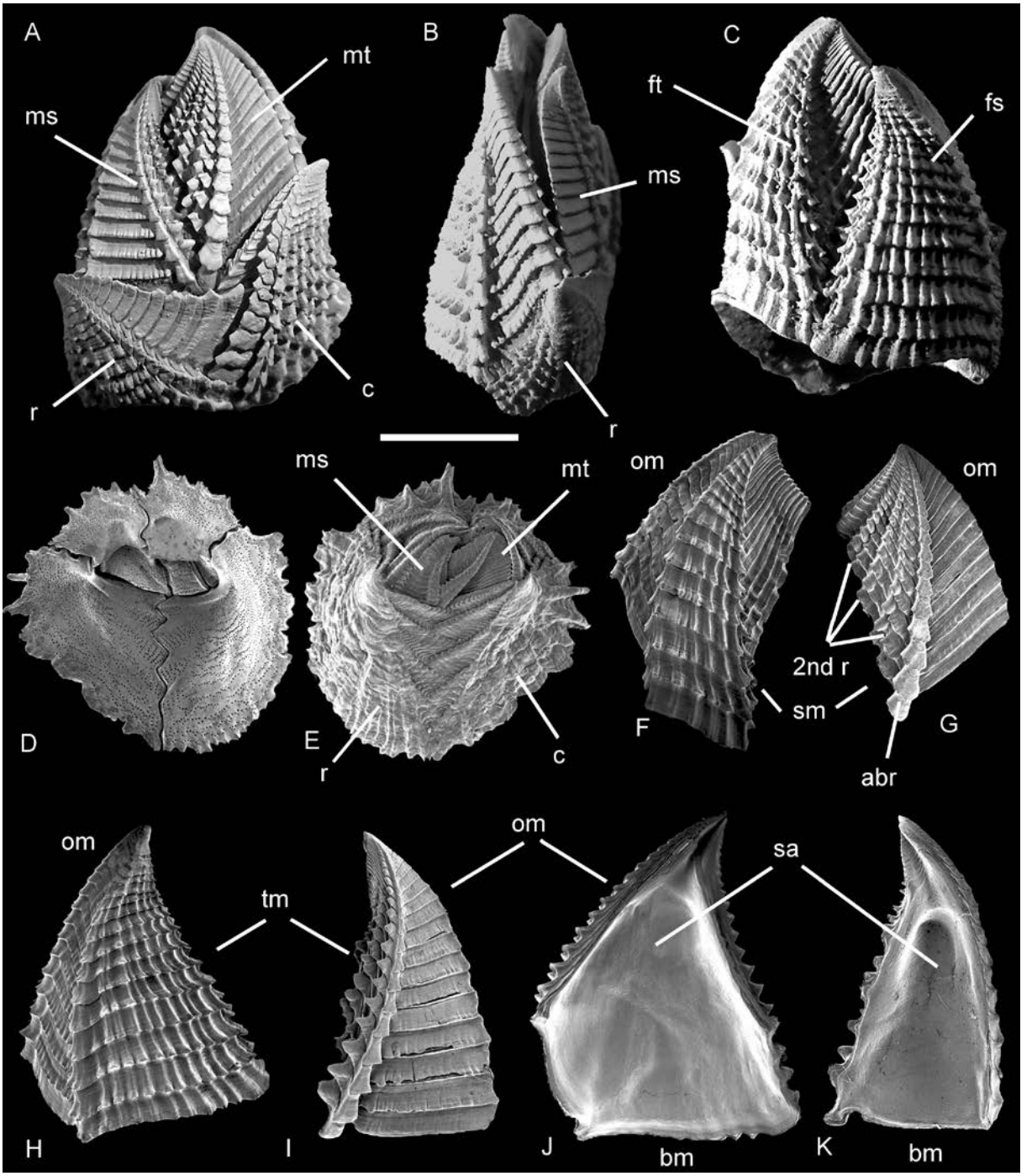
The small, shallow-marine verrucid barnacle *Verruca stroemia* (O.F. Müller, 1776), a characteristic element of the northeast Atlantic Pliocene to present-day fauna, is recorded as occurring abundantly in the upper Pliocene (mid-Piacenzian) Rushmere Member of the Yorktown Formation in North Carolina, the first record (fossil or extant) of the species from the northwest Atlantic or its coastal plain. It is shown here that *Verruca koikei* Tanaka, Kawase, Narita and Karasawa in Koike *et al*., 2006 from the Pliocene of Japan is a synonym of *V. stroemia*, as is *Verruca alaskana* Pilsbry in MacNeil *et al*., 1943 from the Pliocene of Alaska, USA. Revised morphological definitions of the genera *Verruca* Schumacher, 1817, *Metaverruca* Pilsbry, 1916 and *Priscoverruca* Gale, 2014, are provided and the affinities of living and fossil species assigned to these genera reassessed. The presence of *V. stroemia* in the upper Pliocene of the north Pacific was enabled by the open Bering Strait, and the extended geographical range of the species, in both the Atlantic and Pacific, is approximately coincident with the mid-Piacenzian Warm Period (mPWP).

Key words: Verrucid cirripedes; Pliocene; Mid-Piacenzian Warm Period.

INTRODUCTION

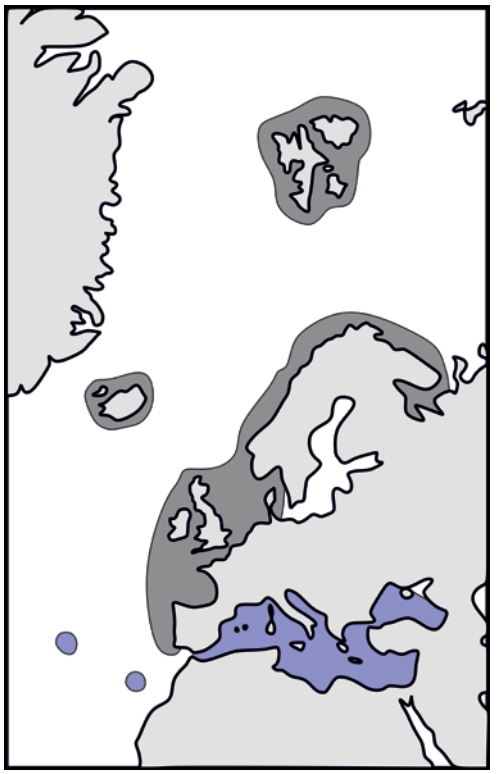
The verrucids are small, asymmetrical cirripedes which have a four-plated shell wall constructed from one scutum, one tergum (both fixed), the carina and the rostrum; an opercular lid is formed by the moveable scutum and tergum (Darwin 1854; Pilsbry 1916; Young 1998; Gale 2014; Text-fig. 1). At the present day, verrucids are most diverse and abundant in the deep sea, but one genus, *Verruca* Schumacher, 1817, occurs commonly in shallow-marine habitats in the northeast Atlantic, the Mediterranean and the western coast of South America. The phylogeny of verrucids has lately been discussed by Gale (2014) and Gale and Vidovic (2023), who described the fossil occurrences and traced the lineage back to the ancestral Late Cretaceous genus *Eoverruca* Withers, 1935.

One living species, *Verruca stroemia* (O.F. Müller, 1776), occurs abundantly in shallow-marine Pliocene and Pleistocene strata in northwest Europe (UK, Belgium, The Netherlands) and at the present day, it extends from southern Portugal north to the White



Text-fig. 1. Nomenclature for verrucid cirripede shells. A–C, F–K – *Gibbosaverruca* sp., present day, off Madagascar; A – view of free side; B – ventral view; C – view of fixed side; F – external view of fixed tergum; G – external view of free tergum; H, I – external views of fixed and moveable scuta, respectively; J, K – internal views of fixed and moveable scuta, respectively. D, E – *Verruca stroemia* (O.F. Müller, 1776), present day, Donegal, Ireland, in basal and apical views, respectively. Abbreviations: abr – apicobasal ridge; bm – basal margin; c – carina; fs – fixed scutum; ft – fixed tergum; ms – moveable scutum; mt – moveable tergum; om – occludent margin; r – rostrum; sa – scar of scutal adductor muscle; sm – scutal margin (of tergum); tm – tergal margin (of scutum); 2nd r – secondary ridges on moveable tergum. Scale bar equals 10 mm.

Sea (Russia) and is also present around Spitsbergen and Iceland (Young *et al.* 2003; Text-fig. 2). *Verruca stroemia* is most commonly found attached to roots of the alga *Laminaria* sp. in shallow subtidal hab-



Text-fig. 2. Map to show the present-day distribution of *Verruca stroemia* (O.F. Müller, 1776) (grey) and *Verruca spengleri* Darwin, 1854 (blue) (after Young *et al.* 2003, fig. 1).

itats (Southward 2008). In the Mediterranean and around east-central Atlantic islands, it is replaced by *V. spengleri* Darwin, 1854. Until now, *V. stroemia* had never been recorded, living or fossil, from the Atlantic seaboard of North America (Pilsbry 1916). Recently, one of us (ES) discovered abundant valves of this species in the upper Pliocene (Piacenzian) of North Carolina and sent the material to AG for identification and description. This material forms the basis of the present paper, which also discusses the definitions and identification of the closely related verrucid genera *Verruca*, *Metaverruca* Pilsbry, 1916, and *Priscoverruca* Gale, 2014.

LOCALITY AND GEOLOGY

Specimens were collected from spoil piles at the Martin-Marietta Fountain Quarry near the town of Fountain, North Carolina, USA (Text-fig. 3). The quarry produces aggregate excavated from an exposed granite monadnock, the only exposed igneous rock in the area (Brown 1959). Cretaceous and younger strata were deposited around the monadnock. The quarry scrapes this sediment and dumps it to the side to access the granite beneath. Snyder and Katrosh (1979) determined that a shell bed on top of the weathered granite surface was early Pleistocene in age, based on the shape of the bivalve *Noetia variabilis* (MacNeil, 1938). Farrell and Keyworth (2003) mentioned thin slivers of Cretaceous deposits (Cape Fear Formation and Black Creek Group), Pliocene Yorktown Formation equivalents, upper Pliocene Bacons Castle Formation, and the upper Pliocene or lower Pleistocene Moorings Unit exposed above the granite at Fountain Quarry.

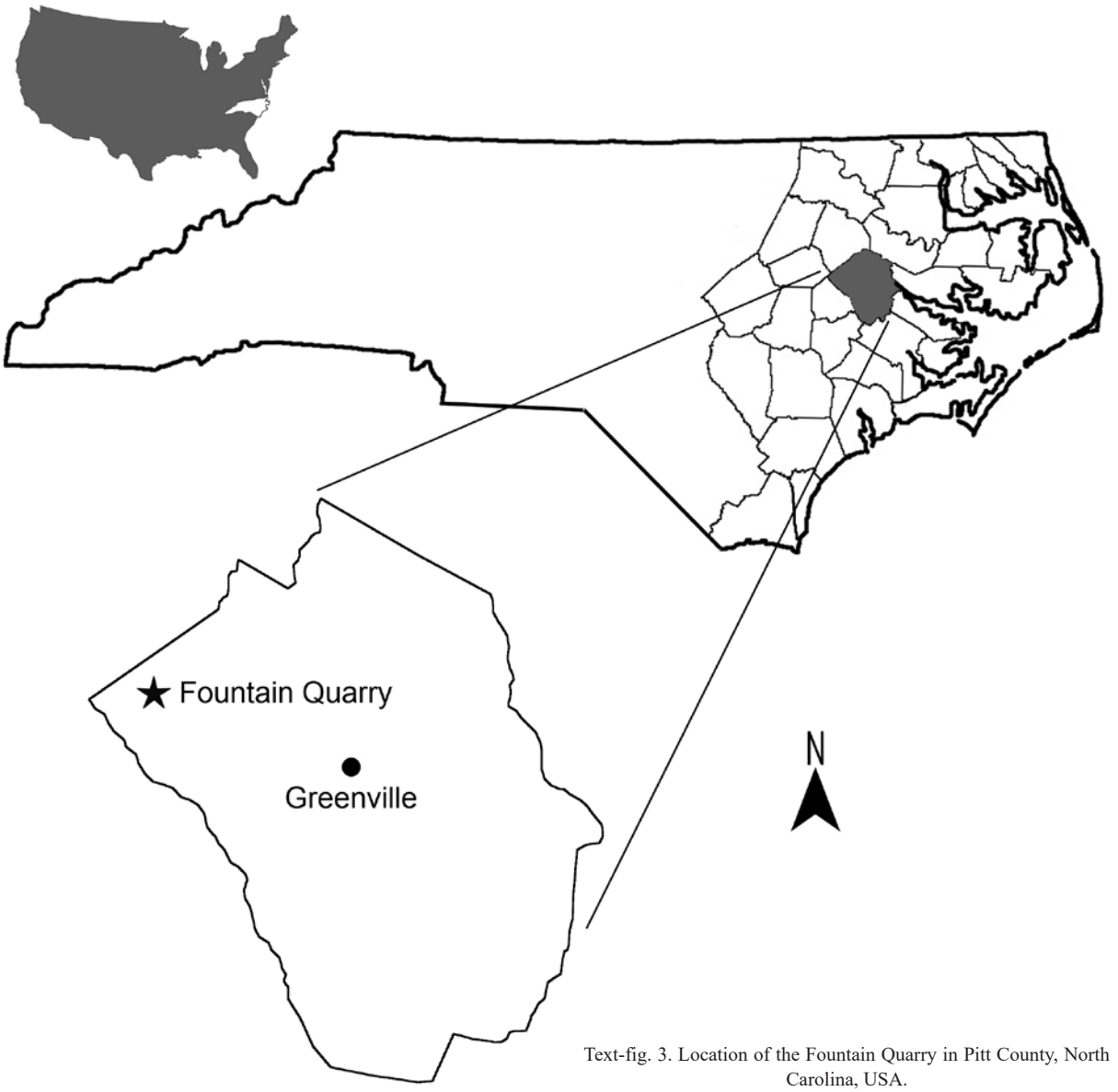
The spoil heaps consist of silty sand with abundant molluscs, including the age-indicative gastropod *Ecphora quadricostata* (Say, 1824) that occurs in the Pliocene Yorktown Formation and its equivalents (Wilson 1987; Campbell and Campbell 1995) as well as the enigmatic cashew-shaped fish bone that Emmons (1858) considered to be a fish tooth. These later became known as "Emmons' Fish Tooth" and are found in the Rushmere Member of the Yorktown Formation (Ray and Bohaska 2001; Ward 2007). Dowsett *et al.* (2019, 2021) equated the Rushmere Member with the mid-Piacenzian Warm Period (mPWP), dated to 3.3–3.2 Ma.

MATERIAL AND METHODS

Three bulk samples, approximately 10 kg each, were collected from different spoil heaps around the quarry. These were sieved using a 1.0-mm-mesh screen, and the residue was searched using magnification. Verrucid barnacle plates proved to be common in one of the samples but lacking in the other two. The material that passed through the 1.0-mm-mesh was later sieved using a 0.6-mm-mesh, and the resulting residue was searched under a microscope to collect small barnacle plates, including moveable terga and scuta, for identification.

Institutional abbreviations:

AU, Auckland University Geology Department Collection, Auckland, New Zealand.
GS, Geological Survey of New Zealand, Lower Hutt, New Zealand.
MNHN, Muséum national d'Histoire naturelle, Paris, France.
NHMUK, The Natural History Museum, London, UK.
OU, Otago University, Geology Department Collection, Dunedin, New Zealand.



Text-fig. 3. Location of the Fountain Quarry in Pitt County, North Carolina, USA.

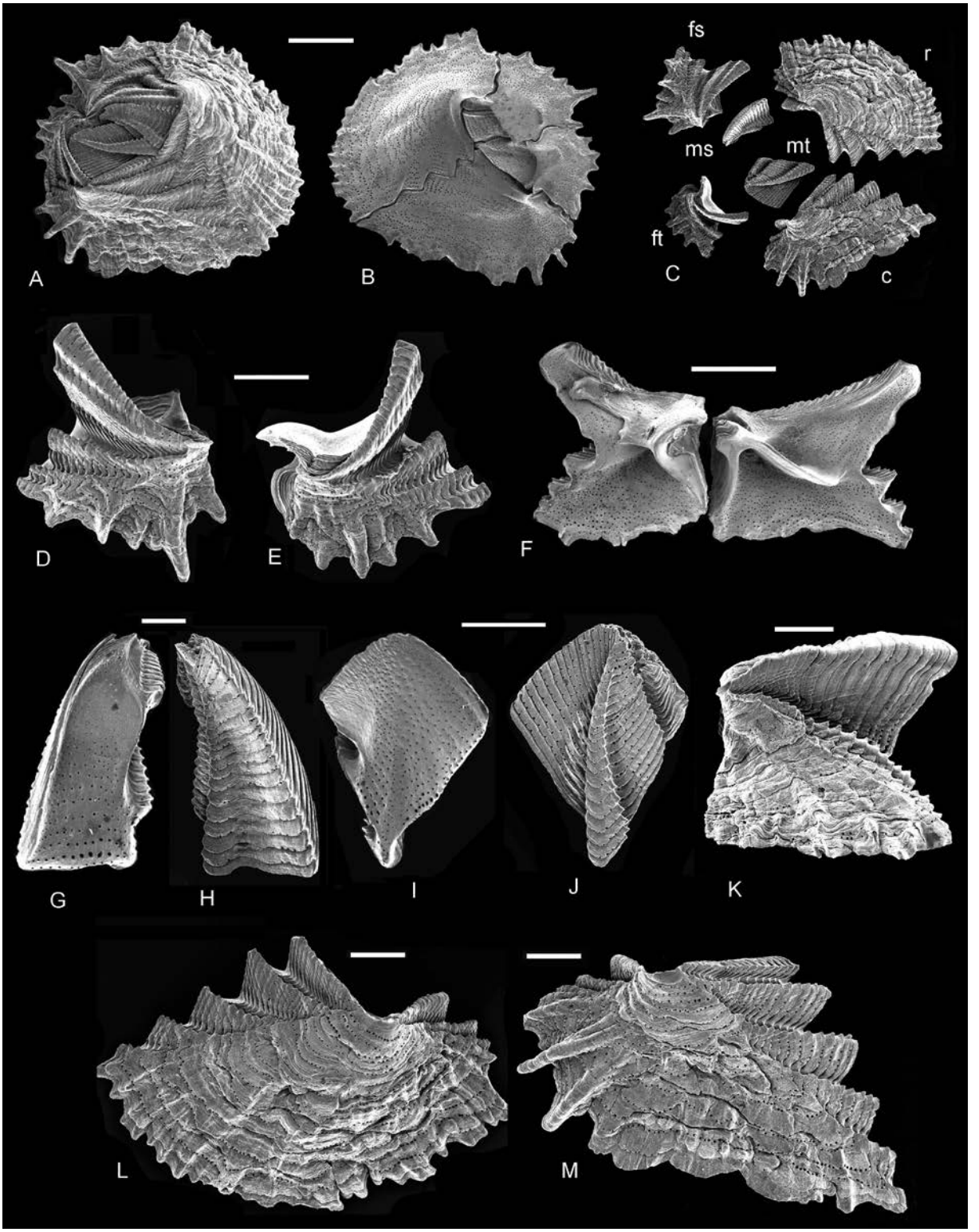
PMC, Museum of Palaeontology of the University of Catania, Sicily, Italy.
SFMCA, Shinshushinmachi Fossil Museum, Nagano Prefecture, Japan.
USNM, United States National Museum, Washington DC, USA.

SYSTEMATIC PALAEONTOLOGY

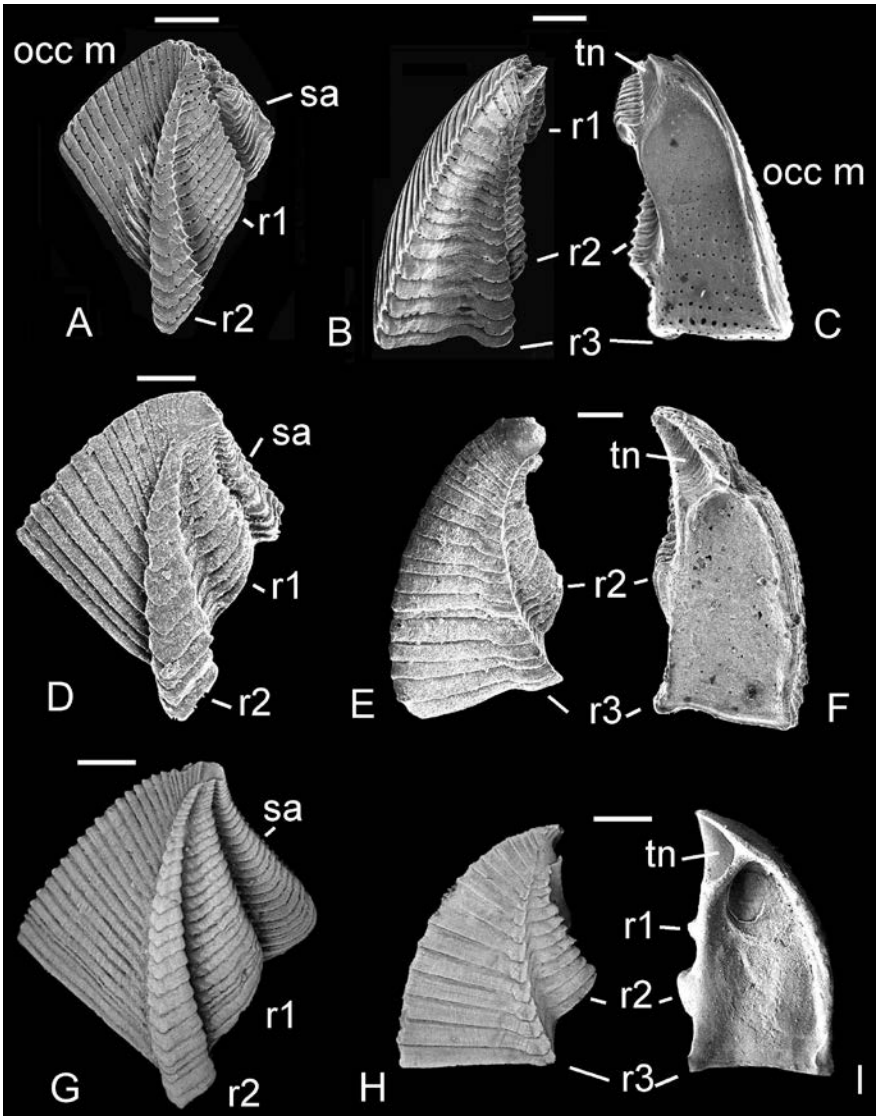
Family Verrucidae Darwin, 1854
Genus *Verruca* Schumacher, 1817

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

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

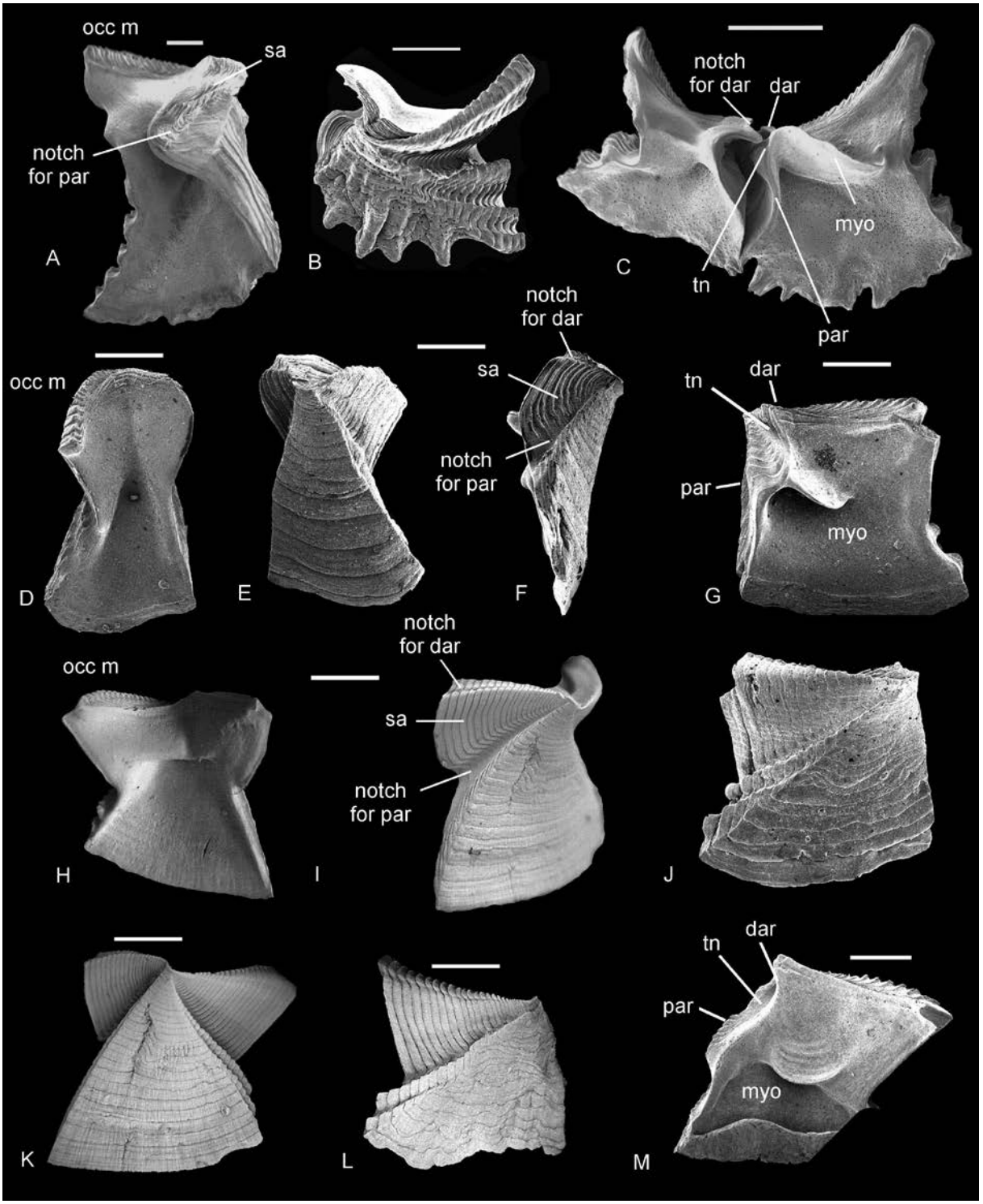


Text-fig. 4. *Verruca stroemia* (O.F. Müller, 1776), present day, Murvagh beach, County Donegal, Ireland. A, B – articulated shell in apical and basal views, respectively; C – disarticulated shell to show plates; D – fixed scutum in lateral-apical view; E – fixed tergum in lateral-apical view; F – paired fixed scutum and tergum in internal view; G, H – moveable scutum in internal and external views, respectively; I, J – moveable tergum in internal and external views, respectivey; K – fixed scutum in lateral view; L – rostrum in external view; M – carina in external view. Scale bars equal 1 mm (A, B) and 0.5 mm (D–M). C not to scale.

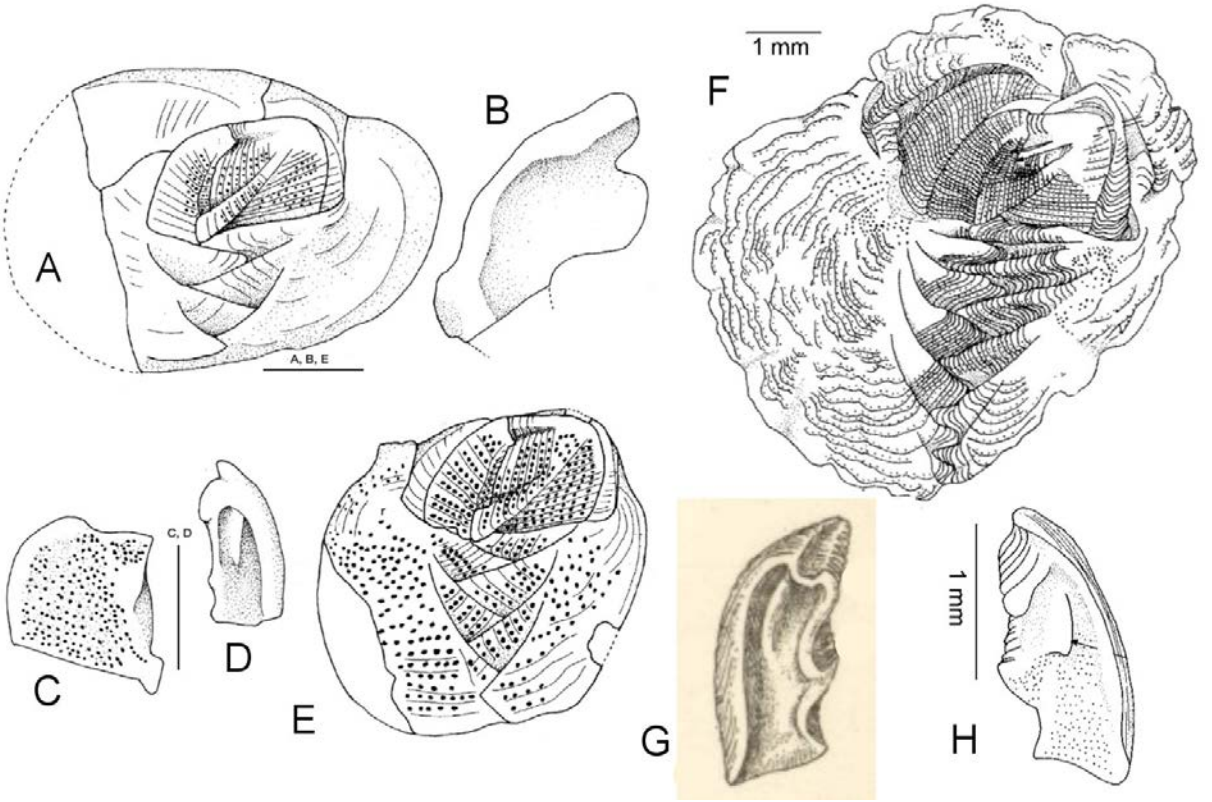


Text-fig. 5. Morphology of moveable scuta and terga in *Verruca*, *Priscoverruca*, and *Metaverruca*. A–C – *Verruca stroemia* (O.F. Müller, 1776), present day, Murvagh beach, County Donegal, Ireland; A – moveable tergum in external view, to show sa, r1, r2; B, C – moveable scutum in external and internal views, respectively, to show shallow tn and strongly developed, prominent ridges r1 and r2. D–F – *Priscoverruca prisca* (Bosquet, 1854), upper Campanian, Norwich, Norfolk, UK; D – moveable tergum in external view, NHMUK PI In 64893, the original of Gale and Vidovic (2023, fig. 20P); E – moveable scutum in external view, NHMUK PI In 64888, the original of Gale and Vidovic (2023, fig. 20F); F – moveable scutum in internal view, NHMUK PI In 64890, the original of Gale and Vidovic (2023, fig. 20K); note triangular, concave tn and absence of r1. G–I – *Metaverruca zanclea* (Seguenza, 1873), lower Pleistocene, Gelasian, Catallarga Hill, near Grammichele, Sicily, Italy; G – moveable tergum in external view, PMC. R. I. lPl. CIR-73, the original of Gale *et al*. (2021, pl. 8, fig 7); H, I – moveable scutum in external and internal views, respectively, PMC. R. I. lPl. CIR-72, the original of Gale *et al*. (2021, pl. 8, fig 6A); note the large sa, the triangular, concave tn and the short r1. Scale bars equal 0.5 mm.

Text-fig. 6. Distinction between fixed scuta and terga in *Verruca*, *Priscoverruca* and *Metaverruca*. A–C – *Verruca stroemia* (O.F. Müller, 1776), present day, Murvagh beach, County Donegal, Ireland; A – fixed tergum in oblique dorsal view; B – fixed tergum in apical view; C – semi-articulated fixed tergum (left) and fixed scutum (right) in internal view; note the deeply interpenetrant articulation, with the process formed by the par, the myo and the tn on the fs fitting into a corresponding deep notch on the ft, the apical part of which is formed by the sa; the dar fits into a small slot on the ft. D–G, J – *Priscoverruca prisca* (Bosquet, 1854), upper Campanian, Norwich, Norfolk, UK; D–F – fixed tergum in internal (D), external (E), and dorsal (F) views, NHMUK PI In 64891a; G, J – fixed scutum in internal and external views, respectively, NHMUK PI In 64886, the original of Gale and Vidovic (2023, fig. 20D, I); the sa forms a wing-like process, directed internally, with a notch for the par on the fixed scutum (G); the articulation is shallow in comparison with that in *V. stroemia* (A–C) and the myo is small and only extends across half of the fs. H, I, K–M – *Metaverruca zanclea* (Seguenza, 1873); H, I, K – fixed tergum, in internal (H), dorsal (I) and external (K) views, →



PMC. R. I. lPl. CIR-75, the original of Gale *et al*. (2021, pl. 8, fig. 9); L, M – fixed scuta (L is PMC. R. I. lPl. CIR-74; M is PMC. R. I. lPl. CIR-69) in external and internal views, respectively, the original of Gale *et al*. (2021, pl. 8, figs 3, 8), lower Pleistocene, Gelasian, Catallarga Hill, near Grammichele, Sicily, Italy; the structure of the fixed tergum (H, I, K) is essentially similar to that in *Priscoverruca* (D, E, F), but the corresponding structures on the fixed scutum are very different; the tn, par and dar are narrow and elongated, and the myophore forms a short tongue-like descending process; in the lateral view of *M. zanclea* (see below), the par forms a narrow process overlapping the ft, and the tn only covers part of the sa; a similar arrangement is present in all species of *Metaverruca* in which the internal structure is known. Scale bars equal 0.5 mm (A, B) and 1 mm (C–M).



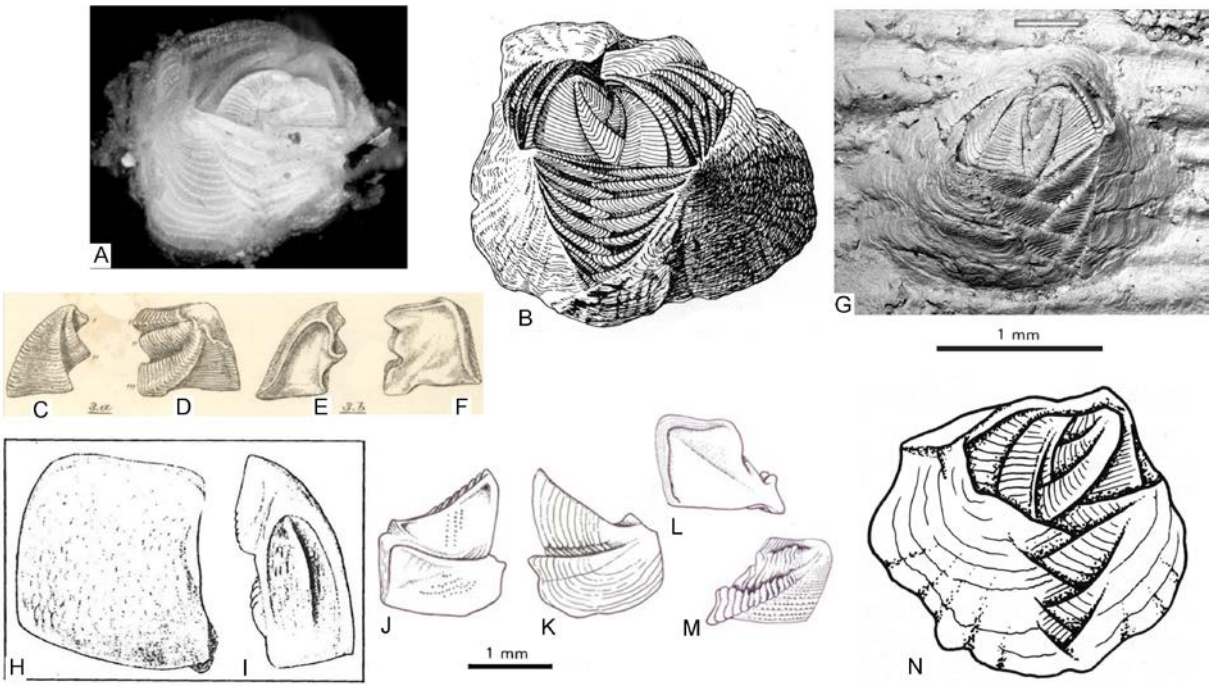
Text-fig. 7. Selected species of *Verruca* Schumacher, 1817. A–E – *Verruca minuta* Young, 2000, present day, Brazil; A, E – shells in apical view; B – fixed scutum in interior view; C – moveable tergum in interior view; D – moveable scutum in interior view, after Young (2000, fig. 4). F–H – *Verruca spengleri* Darwin, 1854; F – entire shell in apical view; G, H – moveable scutum in interior view; F, H after Young *et al*. (2003, fig. 1), present day, Mediterranean; G after Darwin (1854, pl. 21, fig. 2), present day, Madeira. Scale bars equal 1 mm.

wing on fixed tergum (Text-fig. 6A, B); scutal auricle forming depression.

INCLUDED SPECIES: In addition to the type species, the following extant forms: *Verruca spengleri* Darwin, 1854 (Text-fig. 7F–H), *Clitia laevigata* G.B. Sowerby, 1827 (Text-fig. 8A–F), *Verruca minuta* Young, 2000 (Text-fig. 7A–E), *Verruca cookei* Pilsbry, 1927 (Text-fig. 8G, H), and *Verruca jago* Buckeridge, 1997 (Text-fig. 9A–J). Of the fossil taxa, *V. jagti* Gale, 2014, *V. tasmanica tasmanica* Buckeridge, 1983 (Text-fig. 10A–G), *V. sorrellae* Perreault and Buckeridge, 2019, *V. digitali* Buckeridge in Buckeridge and Finger, 2001, *V. veneti* Carriol and Dieni, 2005 (= *Metaverruca euganea* Carriol and Dieni, 2005), *V. withersi* Kruizinga, 1939 (see Jagt and Buckeridge 2005), and *V. vietus* Buckeridge in Buckeridge *et al*., 2014 (Text-fig. 8J–L) are here considered to belong to *Verruca*. *Verruca vermi* Carriol in Carriol and Schneider, 2013, from the Pliocene of Chile, is here held to be a synonym of *Verruca laevigata*.

REMARKS: As defined above, *Verruca* is a sharply demarcated genus, characterised by the presence of tiny pores in all shell plates, the strongly alate, triangular occludent wings on the fixed scuta and terga, the interpenetrate nature of the articulation between these plates and features of the interior of the moveable scutum. However, Perreault and Buckeridge (2019, p. 37) used a much broader definition of the genus, as "verrucids with the operculum nearly parallel to the base, and marginal apices on the rostrum and the carina." The problem with this is that these features are also found in other verrucid genera, including *Metaverruca* and *Priscoverruca*. *Metaverruca*, in particular, is a large genus of worldwide distribution in bathyal and abyssal habitats including at least 16 species (Young 1998).

Following the definition used here, there are five extant species of *Verruca*, which fall into two distinct groups. In one of these, which includes *V. spengleri*, *V. cookie*, and *V. minuta*, there is a short adductor ridge on the moveable scutum which is approximately parallel with the occludent margin of the valve (Text-



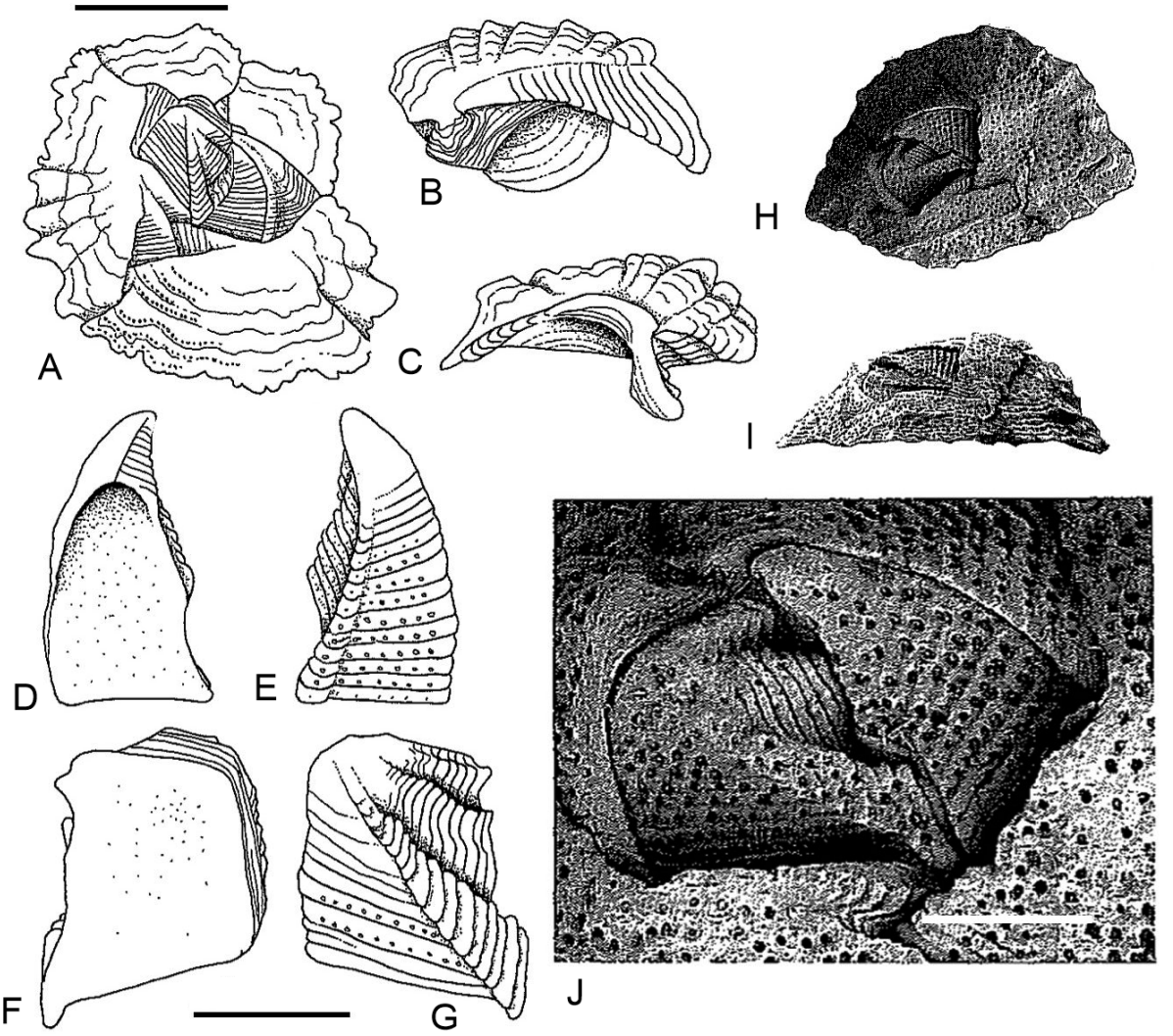
Text-fig. 8. Selected species of *Verruca* Schumacher, 1817. A–F – *Verruca laevigata* G.B. Sowerby, 1827; A – live individual in apical view; B – shell in apical view, after Pilsbry (1916, pl. 8, fig. 2); C, E – moveable scutum, in exterior (C) and interior (E) views, after Darwin (1854); D, F – moveable tergum in exterior (D) and interior (F) views. G – *Priscoverruca rocana* (Steinmann in Wilckens, 1921), apical view of shell, NHMUK PI In 27370, Danian, Roca, Rio Negro, Argentina. H, I – *Verruca cookei* Pilsbry, 1927, internal view of moveable tergum (H) and moveable scutum (I), after Pilsbry (192, fig. 1), present day, Hawaii, USA. J–M – *Verruca vietus* Buckeridge in Buckeridge *et al*., 2014; J, K – internal and external views of fixed scutum, respectively, OU 45259; L, M – internal and external views of moveable tergum, holotype, OU 45258, the originals of Buckeridge in Buckeridge *et al*. (2014, fig. 1A–D), upper Oligocene, Cosy Dell, near Waimumu, Southland, New Zealand. N – *Priscoverruca nuciformis* (Buckeridge, 1983), apical view of holotype, AU6212, lower Miocene, Pakaurangi Point, Auckland, New Zealand, after Buckeridge (1983, fig. 42). Scale bars equal 1 mm.

figs 7D, G, H, 8H, I). The other two extant species, *V. stroemia* and *V. laevigata* (Text-figs 4, 8A–F), lack this feature. Numerous fossil species, including imperforate forms, were placed in the genus *Verruca* by Perreault and Buckeridge (2019). Using the criterion of shell perforation, only *V. tasmanica tasmanica* (Text-fig. 10A–H), *V. sorrellae*, *V. digitali*, and *V. vietus* (Text-fig. 8J–L) belong to *Verruca*. However, there are fossil and living taxa which lack shell perforations, but display the broad myophore flange, the interpenetrant articulation between the fixed scutum and fixed tergum and large occludent wings on the fixed scutum and fixed tergum. These include *Verruca alabamensis* Perreault and Buckeridge, 2019, from the Oligocene of Alabama (USA). It can be difficult to identify specific differences between isolated valves of fossil verrucid species, in part because of the indifferent illustration of valves in varied orientations, and also because preservation is sometimes poor. The placement of the imperforate fossil species is discussed below.

OCCURRENCE: On the basis of the discussion above, *Verruca* occurs very widely from the upper Maastrichtian to the present day in all the world's oceans.

Verruca stroemia (O.F. Müller, 1776)
(Text-figs 4A–M, 5A–C, 6A–C, 11A–T)

*1776. *Lepas strömia* O.F. Müller, p. 251.
1854. *Verruca strömia* Darwin, p. 518, pl. 21, fig. 1a–f.
1855. *Verruca strömia* Darwin, p. 42, pl. 2, fig. 9a, b.
1916. *Verruca strömia* (O.F. Müller); Pilsbry, p. 24.
1943. *Verruca alaskana* Pilsbry in MacNeil *et al*., p. 95, pl. 15, figs 8, 9.
1978. *Verruca stroemia* (O.F. Müller); Nilsson-Cantell, p. 48, figs 23, 24.
1998. *Verruca stroemia* (O.F. Müller); Young, p. 58, figs 15–17.
2003. *Verruca stroemia* (O.F. Müller); Young *et al*., p. 91, fig. 1A, B.



Text-fig. 9. *Verruca jago* Buckeridge, 1997. A, H – apical views of entire shell; B – fixed scutum, in apical view; C – fixed tergum, in apical view; D, E – internal and external views, respectively, of moveable scutum; F and G – internal and external views, respectively, of moveable scutum; I – lateral view of shell; J – enlargement of moveable valves. A–G shows the holotype (MNHN-Ci 2425); I, J is an unregistered specimen in MNHN. Present day, Grande Comore Island, western Indian Ocean. Scale bars equal 1 mm.

2006. *Verruca koikei* Tanaka, Kawase, Narita and Karasawa in Koike *et al*., p. 1, figs 1.1–1.7.

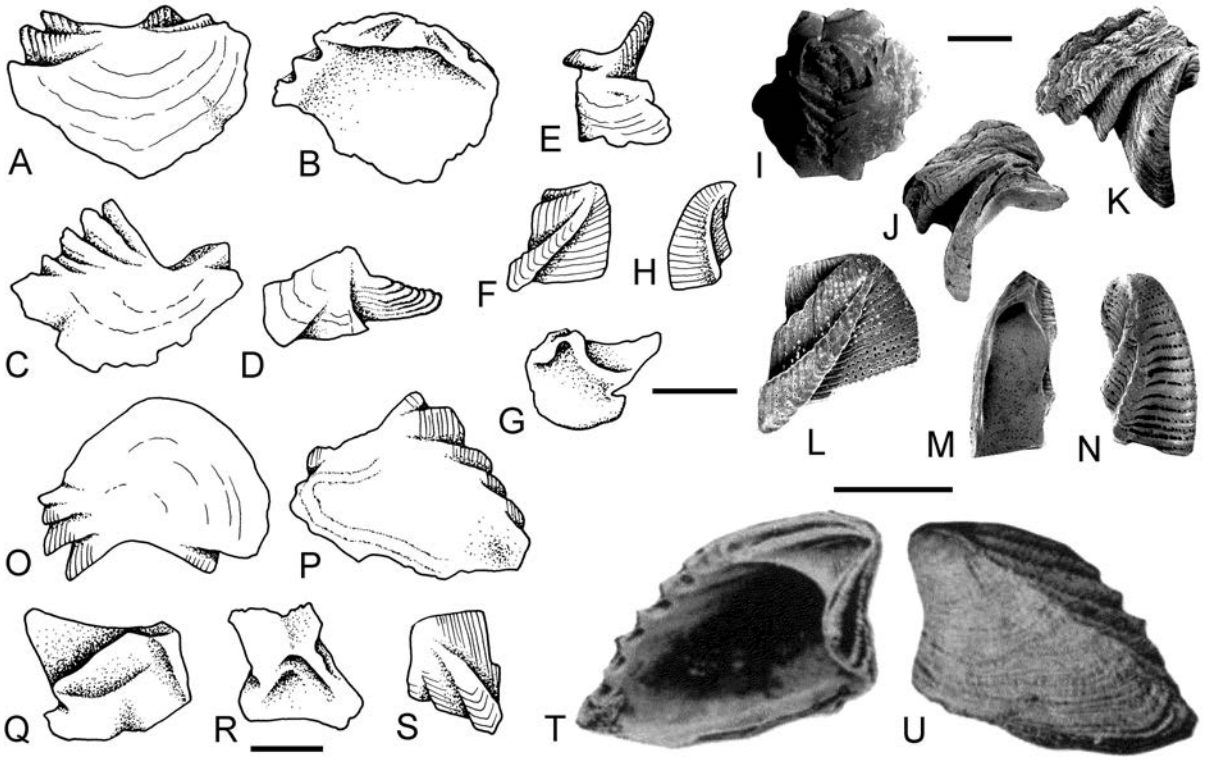
2009. *Verruca stroemia* (O.F. Müller); Marquet *et al*., p. 55, pl. 4, figs 5–7.

TYPE: Unspecified, 'North Sea'.

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

MATERIAL: The assemblage from the Rushmore Member (Yorktown Formation) of Fountain Quarry, Fountain, is illustrated in Text-fig. 11. All plate types are represented; the material can be confidently assigned to *V. stroemia*.

DESCRIPTION: Shell profile of low dome, outline irregularly oval, maximum diameter less than 10 mm. Weak and highly irregular apicobasal ridges, variably nodose, present on wall, sometimes extending as short processes on margin, notably on fixed scutum, fixed tergum and on tergal margin of carina (Text-fig. 4A,

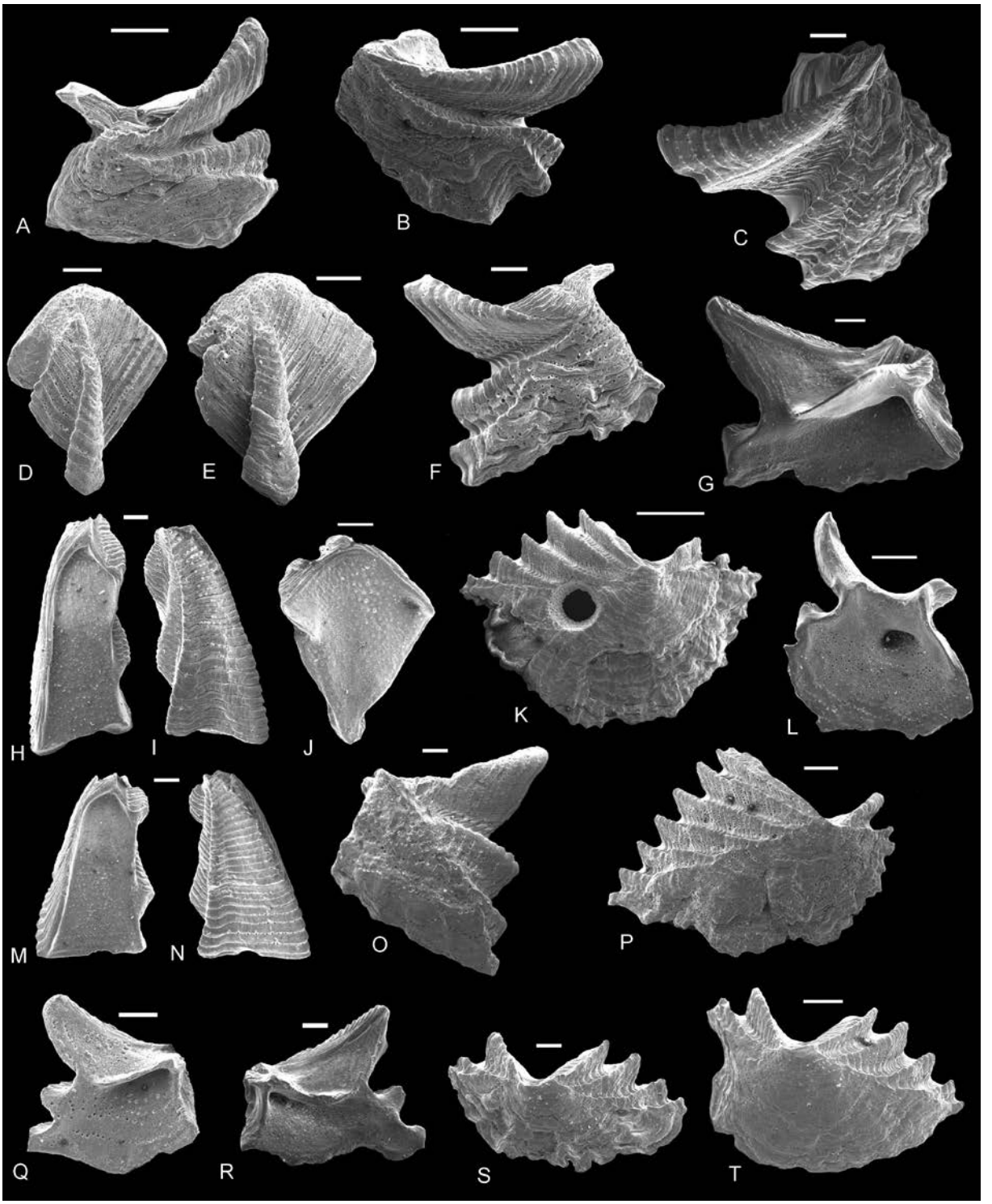


Text-fig. 10. Selected species of *Verruca* Schumacher, 1817. A–H – *Verruca tasmanica chatheca* Buckeridge, 1983, GS 11580, CH/f227; Chatham Island, New Zealand, after Buckeridge (1983, fig. 44), Eocene, Thanetian–Ypresian; A, B – rostra, in external and internal views, respectively; C – external view of carina; D, G – fixed scuta in external and internal views, respectively; E – external view of fixed tergum; F – external view of moveable scutum; H – external view of moveable scutum. I–N – *Verruca stroemia* (O.F. Müller, 1776), after Koike *et al*. (2006, fig. 1, as *V. koikei*), Pliocene, Ogikubo Formation, Nakagumi, Nagano City, Nagano Prefecture, Japan; I – apical view of shell, SFMCA-0013; J – fixed tergum, SFMCA-0015; K – fixed scutum, SFMCA-0014; L – external view of moveable tergum, SFMCA-0016; M, N – moveable scutum, SFMCA-0017, in internal and external views, respectively, after Tanaka *et al*. in Koike *et al*. (2006, fig. 1). Scale bars equal 1 mm.

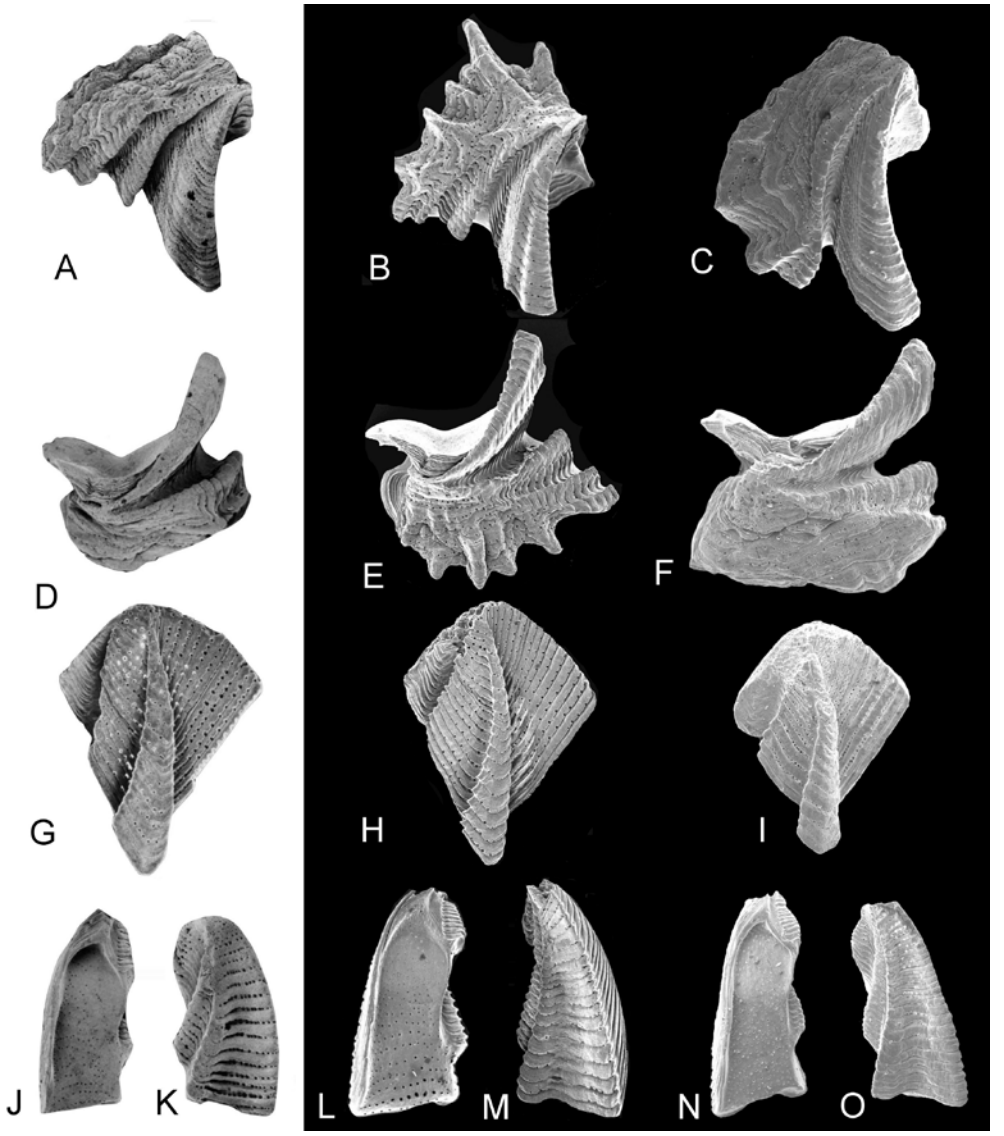
B). Some individuals have smooth carinae and rostra. Imbricate growth lines very irregular, bearing 5–10 μm pores on basal margins of increments which are variably visible on exterior of shell, but conspicuous on interior (Text-fig. 4B). Opercular plates (moveable scutum, moveable tergum) parallel with base, operculum less than half rostrocarinal diameter.

Rostrum rhombic, concavo-convex, asymmetrical (broader on carinal margin), apex elevated, articulating with rostrum by 4–5 strong interpenetrant ridges and grooves and with fixed scutum by 2–3 similar ridges and grooves (Text-fig. 4L). Carina flatter, basal-carinal angle acute, elongated, apex less prominent than that of rostrum (Text-fig. 4M). Fixed scutum bearing tall, incurved, triangular occludent wing, the inner margin of which articulates with the ventral margin of moveable scutum. The wing is separated from the body of the valve by a deep groove, into which a rib from the rostrum fits (Text-fig. 4D). Interior of fixed scutum with a sheet-like, horizontal myophore which is confluent with proximal articular ridge on the dorsal margin of the valve, forming a horizontal, inverted V-shaped structure with a central cavity (Text-fig. 4F). The tergal notch forms a protuberant process and is separated from the distal articular ridge by a narrow slit. The fixed tergum is similar in shape to the fixed scutum, often less broad; a deep groove separates the occludent wing from the body of the valve, which accommodates a rib from the carina. The fixed scutum-fixed tergum articulation is highly modified, as in all *Verruca*. The scutal auricle is inflected inwards and is set in a deep groove which accommodates a raised tergal notch on the fixed scutum (Text-fig. 4F). A flat process on the apical margin of the fixed tergum fits into the narrow slit adjacent to the tergal notch on the fixed scutum and articulates with its distal articular ridge on its upper surface.

The moveable scutum is triangular, flat, height twice the breadth, occludent margin gently convex



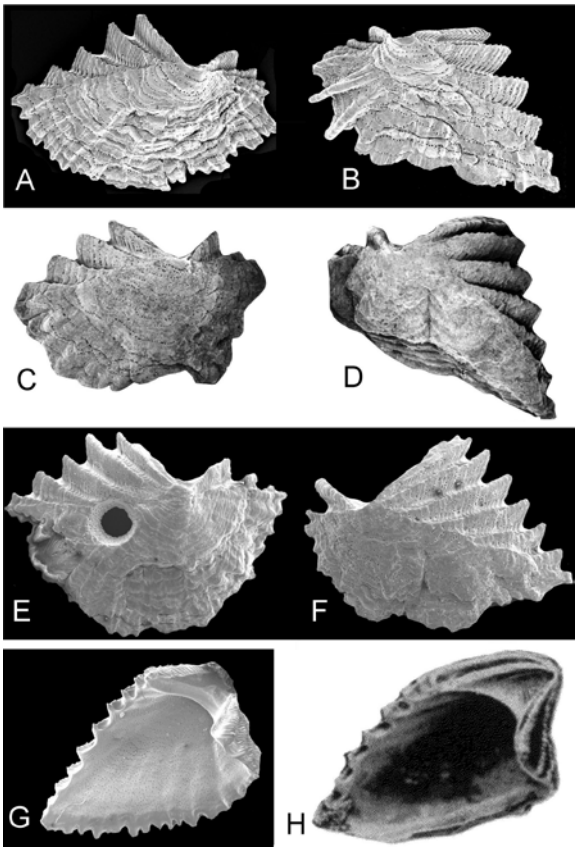
Text-fig. 11. *Verruca stroemia* (O.F. Müller, 1776). A, F, L – fixed terga in apical (A, F) and internal views (L), NHMUK PI In 66388a, 66392, 66397; B, C, G, O, Q, R – fixed scuta in apical (B, C), internal (G, Q, R), and lateral external views (O), NHMUK PI In 66388, 66389, 66393, 66399, 66401, 66402; D, E, J – moveable terga in external (D, E) and internal views (J), NHMUK PI In 66390, 66391, 66395; H, I, M, N – moveable scuta in internal (H, M) and external views (I, N), NHMUK PI In 66394, 66398; K, S, T – rostra in external views, NHMUK PI In 66396, 66403, 66404; P – carina in external view, NHMUK PI In 66400. Rushmere Member, Yorktown Formation, upper Pliocene, Fountain Quarry, Fountain, Pitt County, North Carolina, USA. Scale bars equal: 1 mm (K), 0.4 mm (P, T), 0.3 mm (L), and 0.2 mm in all others.



Text-fig. 12. Comparative morphology of geographically and temporally separate assemblages of *Verruca stroemia* (O.F. Müller, 1776). A–C – fixed scuta; D–F – fixed terga; G–I – moveable terga; J–O – moveable scuta. A, D, G, J, K are from the Pliocene, Ogikubo Formation, Nakagumi, Nagano City, Nagano Prefecture, Japan, after Koike *et al*. (2006, fig. 1, as *V. koikei*); B, E, H, L, M are present day, Murvagh beach, Donegal, County Donegal, Ireland; C, F, I, N, O are from the Rushmere Member, Yorktown Formation, upper Pliocene, Fountain Quarry, Fountain, Pitt County, North Carolina, USA. Dodać: Not to scale.

(Text-fig. 4G, H). Tergal margin bearing three ridges (r1–3) forming an interpenetrate contact with corresponding structures on the ventral margin of the moveable tergum. R1 and r2 protuberant, obliquely angled and bearing short transverse ridges. Tergal notch short, shallow. Moveable tergum kite shaped, upper (occludent) carinal and lower carinal margins set at 90º, carinal surface flat, triangular (Text-fig. 4I, J). Central rib (r2) broadening basally, protruding from basal margin of valve. First rib (r1) flat, broad. Scutal auricle narrow, protruding from scutal margin. Moveable scutum and moveable tergum with evenly spaced regular terracing.

REMARKS: *Verruca stroemia* differs from *V. spengleri* (and also from *V. cookei* and *V. minuta*) in the absence of an adductor ridge on the interior of the moveable scutum, the less conspicuous pores on the exterior of the shell, and from *V. spengleri* in minor differences in the relative width of ridges on the moveable tergum



Text-fig. 13. Comparative morphology of geographically and temporally separate assemblages of *Verruca stroemia* (O.F. Müller, 1776). A, C, E – rostra in external views; B, D, F – carinae in external views; G, H – rostra in internal views. A, B, G are present day, Murvagh beach, Donegal, County Donegal, Ireland; C, D are from the Pliocene, Ogikubo Formation, Nakagumi, Nagano City, Nagano Prefecture, Japan (after Koike *et al*. 2006, fig. 1, as *V. koikei*); E, F are from the Rushmere Member, Yorktown Formation, upper Pliocene, Fountain Quarry, Fountain, Pitt County, North Carolina, USA; H is after Pilsbry in MacNeil *et al*., 1943 (pl. 15, fig. 8), holotype of *Verruca alaskana* Pilsbry, 1943, intermediate beach, Nome, Alaska, USA (USNM 499109). Not to scale.

(Young *et al.* 2003). It may be differentiated from *V. laevigata* by the more elongated rhombic shape of the moveable tergum and the fewer interpenetrant ridges uniting the wall plates. It differs from *V. jago* in lacking extensive external pores. We are unable to find any morphological differences between *V. stroemia* and *V. koikei* from the lower Pliocene of Japan (Koikei *et al*. 2006) or *V. alaskana* from the Pliocene of Nome, Alaska, USA (Text-figs 12, 13).

Verruca stroemia occurs commonly in the Pliocene Coralline Crag Formation (Zanclean) and less commonly in the Pliocene Red Crag Formation (Piacenzian) of the UK (Darwin 1855; Collins *et al*. 2014; Gale 2025), the Lillo Formation (Oorderen Member, Piacenzian) of northern Belgium (Marquet *et al*. 2009; Gale *et al*. in prep.). At the present day, the range extends from southern Portugal northwards along the Atlantic and North Sea coasts to the White Sea (Russia) and around Iceland and Spitsbergen (Text-fig. 2). It is here recorded from the upper Pliocene (mid-Piacenzian) of North Carolina (USA) and from the Pliocene of Japan (see Discussion below). It is present in the Breidavik Group (upper Pliocene–lower Pleistocene) of northern Iceland (Símonarson and Eríksson 2021) and the upper Pleistocene (Eemian) of the Archangelsk region of Russia (Funder *et al*. 2002).

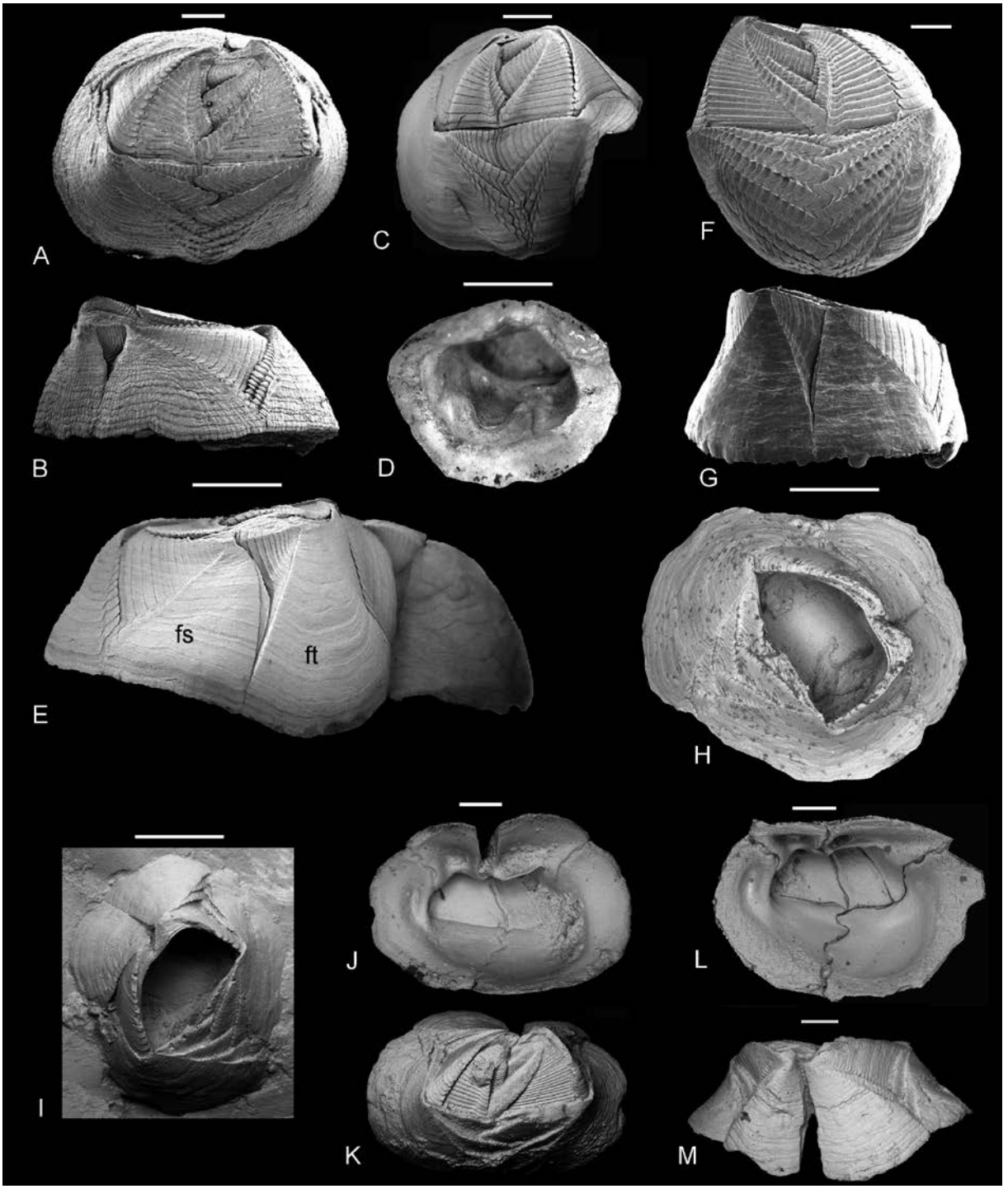
Genus *Metaverruca* Pilsbry, 1916

TYPE SPECIES: *Verruca zanclea* Seguenza, 1873 (= senior synonym of *Verruca recta* Aurivillius, 1898; see Gale *et al*. 2021).

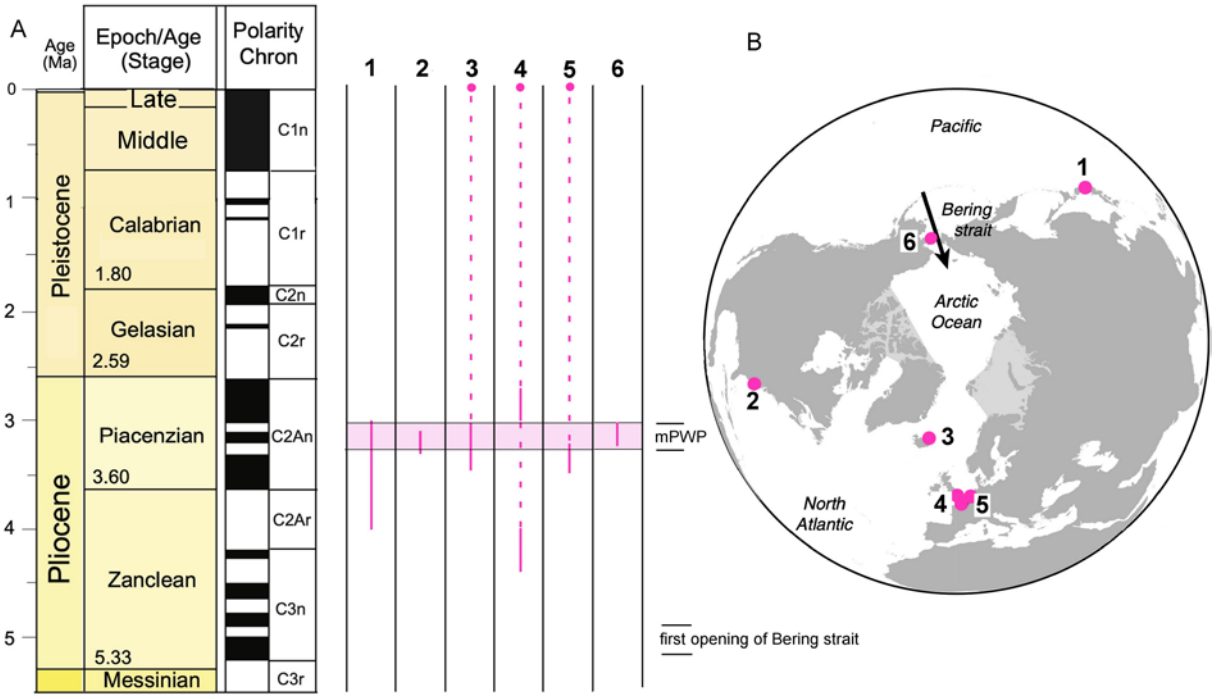
DIAGNOSIS: Shell imperforate, box like, breadth approximately twice height (Text-fig. 14A–G), wall plates nearly vertical, basal margin not splayed. Operculum large, D-shaped, extending over most of rostrocarinal diameter of apical surface of shell. Fixed scutum subrectangular to trapezoidal, articulation with fixed tergum comprising an elongated tergal notch defined by narrow proximal and distal articular ridges. Myophore centrally placed, oval, projecting basally. Moveable scutum (Text-fig. 5G, H) with deep tergal notch and weak rl. Fixed tergum with triangular exterior wall and subequally sized, inset occludent wing and scutal auricle which project laterally (Text-fig. 6H, I, K). Basal margin of wall plates inflected, forming an internal rim (Text-figs 6M, 14D). Wall plates fused in fully grown individuals.

INCLUDED SPECIES: *Verruca dilatata* Seguenza, 1873 (= senior synonym of *V. radiata* Gruvel, 1901), *V. macani* Stubbings, 1936, *V. aequalis* Aurivillius, 1898, *V. cornuta* Aurivillius, 1898, *V. trisulcata* Gruvel, 1900, *Metaverruca defayae* Buckeridge, 1994, *M. norfolkensis* Buckeridge, 1994, *M. plicata* Buckeridge, 1994, *M. maclaughlinae* Buckeridge, 1997, *M. sensibilis* Young, 1998, and *M. reunioni* Foster and Buckeridge, 1994.

REMARKS: In many species referred to *Metaverruca*, the myophore is a short, oval tongue positioned more or less in the centre of the fixed scutum (*M. zanclea*, Text-fig. 6M; *M. norfolkensis*, *M. cor-*



Text-fig. 14. Selected verrucid species. A, B – *Metaverruca defayae* Buckeridge, 1997, shell in apical (A) and lateral (B) views; present day, New Caledonia. C–G – *Metaverruca zanclea* (Seguenza, 1873); C–E – shell in apical (C), basal (D) and lateral (E) views, present day, off Rodrigues, Indian Ocean, the original of Gale (2020a, pl. 12, fig. 2); F–G – shell in apical (F) and lateral (G) views, present day, New Caledonia, the original of Gale (2020, pl. 17, fig. 3a, b). H–M – *Priscoverruca prisca* (Bosquet, 1854); H, I – shells lacking moveable plates in apical view; H is NHMUK PI In 27155, I is NHMUK PI In 27156, the original of Withers (1935, figs 41, 42); J, K – entire shell, NHMUK PI In 62170, in internal (J) and apical (K) views, the original of Jagt and Collins (1989, fig. 4g) and Gale (2014, fig. 23E, F); L – shell, NHMUK PI In 63640, in internal view; M – shell, NHMUK PI In 62171, in lateral view, the original of Jagt and Collins (1989, fig. 4e) and Gale (2014, fig. 21A). H, I are from the upper Campanian, Norwich, Norfolk, UK; J–M are from the upper lower Maastrichtian, Vijlen Chalk Member (Gulpen Formation), Haccourt, Belgium. Scale bars equal 1 mm.



Text-fig. 15. Pliocene–present day timescale (A), after Raffi *et al*. (2020), to show the occurrences of *Verruca stroemia* (O.F. Müller, 1776) at the following localities (B): 1 – Rushmere Member, Yorktown Formation, Piacenzian, Fountain Quarry, Fountain, Pitt County, North Carolina, USA; 2 – Ogikubo Formation, Pliocene, Nakagumi, Nagano City, Nagano Prefecture, Japan; 3 – Breidavik Group (upper Pliocene–lower Pleistocene) of northern Iceland; 4 – Coralline and Red Crag formations, eastern England (Suffolk, Essex); 5 – Oorderen Formation, Piacenzian, Antwerp area, Belgium; 6 – Nome, Alaska, USA. Note that the present-day distribution (Text-fig. 2) is restricted to the northeast Atlantic.

nuta, *M. sensibilis*). In these species, an inflected basal rim is also present (Text-fig. 14D). However, in *M. plicata* (Gale, 2020a, pl. 12, fig. 4b) and a specimen referred to *M. recta* (Gale 2020a, pl. 12, fig. 1c) the myophore forms a broad sheet extending ventrally from the articulation with the fixed tergum almost to the ventral margin of the valve, similar to the condition in *Verruca* itself (e.g., Text-fig. 6C). A similar development is present in the Eocene *V. alabamensis* (Perreault and Buckeridge 2019, pl. 2, fig. A). There is no inflected basal margin in these forms and the wall plates are not fused.

OCCURRENCE: *Metaverruca* ranges from the Eocene to the present day and is common in the Plio-Pleistocene deposits of eastern Sicily, where it is represented by *M. dilatata* and *M. zanclea* (Gale *et al.* 2021). In deposits of approximately coeval age, off Rodrigues in the Indian Ocean, *M.* cf. *zanclea*, *M. reunion*, and *M.* cf. *norfolkensis* are present (Gale 2020a). The genus is widespread and common globally in the deep sea (Young 1998; Chan *et al.* 2009, 2010).

Genus *Priscoverruca* Gale, 2014

TYPE SPECIES: *Verruca prisca* Bosquet, 1854.

DIAGNOSIS: Shell imperforate, basal margin splayed without inflected rim, opercular valves occupying half of rostrocarinal diameter of apical surface (Text-fig. 14H–M). Fixed scutum rectangular, occludent wing low, short, myophore extending across half of valve interior (Text-fig. 6G). Occludent wing and scutal auricle of fixed tergum subequal (Text-fig. 6D–F), fixed scutum-fixed tergum articulation shallow, not interpenetrant. Moveable scutum lacking rl ridge, tergal notch triangular, concave (Text-fig. 5E, F).

INCLUDED SPECIES: In addition to the type species, *Verruca rocana* Steinmann in Wilckens, 1921 from the Paleocene (Danian) of Argentina and *V. nuciformis* Buckeridge, 1983 from the Miocene of New Zealand. *Verruca punica* Buckeridge and Jagt in Buckeridge *et al.* (2008) from the Paleocene of Tunisia and *V. sauria* Buckeridge, 2011 from the Upper Cretaceous of New Zealand also probably belong to this genus.

REMARKS: *Priscoverruca* differs most importantly from *Verruca* in its imperforate shell, short, low occludent wings on the fixed scutum and fixed tergum, the relatively flat articulation between the fixed tergum and fixed scutum, the narrow myophore and large tergal notch on the fixed scutum. From *Metaverruca*, it differs in the proportionately smaller opercular valves and the splayed basal margin which is not inflected. In a number of respects, *Priscoverruca* is intermediate between *Metaverruca* and *Verruca*. The dominant occurrence of *Priscoverruca* is in the upper Campanian and Maastrichtian (Gale and Vidovic 2023), but the genus survived into the Paleocene (*P. rocana*; Text-fig. 8G) and Miocene (*P. nuciformis*, Text-fig. 8N).

DISCUSSION

The small cirripede *Verruca stroemia* is recorded for the first time from North America, occurring commonly in the Rushmore Member of the Yorktown Formation (upper Pliocene) in North Carolina. The range of the species, currently restricted to the Atlantic seaboard of northwest Europe, in the Pliocene extended to the Atlantic seaboard of the USA. The species is also present in the Pliocene of the North Pacific, in the Nagano Prefecture of Japan, where it was described as *V. koikei* by Tanaka *et al*. in Koike *et al*. (2006). *Verruca alaskana*, from the Pliocene of Alaska, is also referred to *V. stroemia*. The distribution of fossil examples of the taxon is shown in Text-fig. 15B.

The oldest known occurrence of *V. stroemia* is in the Zanclean Ramsholt Member of the Coralline Crag Formation of Suffolk, England, dating to approximately 4.4 Ma (Johnson *et al*. 2022). Although the precise ages of some of the occurrences of the species are poorly known (Text-fig. 15A), the Rushmore Member in North Carolina can be precisely dated to 3.15–3.2 Ma (Dowsett *et al*. 2021) and falls within the mid-Piacenzian Warm Period (mPWP) as defined by Dowsett *et al*. (2019). The initial opening of the Bering Strait, allowing interchange of Atlantic and Pacific faunas, can now be dated precisely to the Miocene–Pliocene boundary (4.9–5.2 Ma; Hall *et al*. 2023), based on radiometric dates derived from northern Iceland lavas coincident with the initial appearance of Pacific molluscs in Iceland. It seems possible that the mid-Piacenzian warming permitted *V. stroemia* to extend its range to the Arctic Ocean, and during the late Pliocene, briefly colonise the North Pacific by migration through the Bering Strait.

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