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RESEARCH PAPER

The ostracod genus *Eucytherura* G.W. Müller and the '*Cythere complexa* Brady' problem

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Abstract
The marine ostracod genus *Eucytherura* G.W. Müller, 1894 was described from the Gulf of Naples and four species were assigned to it, three new (*Eucytherura angulata*, *E. alata*, *E. gibbera*) and one previously described (*Cythere complexa* Brady, 1867); however, no type species was selected. A subsequent designation of *C. complexa* Brady as a type species, without discussion, has been followed uncritically ever since, but identification of that species has been uncertain due to the brevity of Brady's original (unillustrated) description and the poor quality of some subsequent illustrations. *Eucytherura* is a diverse and stratigraphically long-ranging genus, and stabilizing its taxonomy is clearly important. We verify, with reference to syntypic specimens illustrated with SEM images for the first time, that Müller's *E. complexa* (Brady) is indeed conspecific with Brady's species. However, its confirmed status as the type species of *Eucytherura* remains problematic because Müller's original description of the genus relied more on another congeneric species, *Eucytherura gibbera*; it is recommended that particular attention should be paid to the latter, for which both carapace morphology and soft parts were well described and figured by Müller, as a characteristic representative of *Eucytherura*, whereas *E. complexa* is much less well-known.

Keywords Ostracoda · Taxonomy · Type species

Introduction

The great natural scientist Sir Isaac Newton is quoted as saying "If I have seen further, it is by standing on the shoulders of giants." (letter to Robert Hooke, 15 February 1676, cited in Turnbull (1959)). We understand these words to mean that Newton's own advances in 'natural philosophy' were built on the work and discoveries of earlier scholars interested in the natural world. We recognise the same pattern in modern science, but the process is underpinned by trust in the results and conclusions of earlier workers, coupled with healthy scepticism. In modern science, it is clearly impossible for a worker to repeat all the classical experiments to convince themselves of the reliability of published data. Similarly, in the world of taxonomy, assigning a species to genus X involves confidence in earlier decisions about the definition of that taxon, and with a diverse fauna or flora it is clearly impossible to check every genus or species to its original description and its subsequent history. In this paper, we look at the genus *Eucytherura* G.W. Müller, 1894, originally described on the basis of living species from the Gulf of Naples and now believed to have a long and diverse fossil record from the Triassic to the present day. Some indication of its fossil and living diversity is given by Kempf's (1986) listing of 143 species; later Kempf (1995) added a further 23 species and there are certainly more. Such a diverse and apparently long-lived group of species gathered under the name *Eucytherura* must be securely based on a well-described and illustrated type species that serves as a fundamental reference point for comparative purposes. There are consequences, not only with regard to modern biodiversity but also in deep time. We were surprised, therefore, to find that the type species of *Eucytherura* was still poorly known

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This is a contribution to the special issue honouring Professor Ekkehard Herrig on his 90th birthday.

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and the whereabouts of its type specimens uncertain. We have recently worked on the genus *Microceratina* Swanson, 1980 which, like *Eucytherura*, is an extant taxon with a long evolutionary history from the Early Jurassic (Danielopol et al. 2023) and a member of the family Cytheruridae. That study involved comparative morphological analysis of carapace features of three *Eucytherura* species: *E. alata* G.W. Müller, 1894, *E. complexa* (Brady, 1867), *E. mistrettai* Sissingh, 1972, which drew our attention to the uncertain identification of *E. complexa* and its subsequent and unchallenged designation as the type species of *Eucytherura*. This led to the present investigation aimed at resolving these issues by locating and illustrating type specimens of *E. complexa* with Scanning Electron Microscope (SEM) images.

Eucytherura—a taxonomic journey

The first reference to the genus *Eucytherura* occurs in Müller (1893, p. 364): "In the genera *Eucytherura* (n. gen) and *Hestoleberis* [a misspelling of *Xestoleberis*] the first antennae serve mainly for touching, with which a grasping forward may be associated; it is also sometimes used for removing obstacles that are pushed outwards and upwards." (translated from the original German). As there is no further description or illustration the name is *nomen nudum*, although the World Ostracoda Database gives the genus as *Eucytherura* G.W. Müller, 1893 (https://www.marinespecies.org/ostracoda/aphia.php?p=taxdetails&id=127611).

The full and formal description of the new genus *Eucytherura* is in Müller's (1894, p. 305) monograph on the Gulf of Naples; however, no type species was designated. Four species assigned to the new genus are described and illustrated; they are, in order of appearance:

Cythere complexa Brady 1867
Eucytherura angulata n. sp.
Eucytherura alata n. sp.
Eucytherura gibbera n. sp.

We reproduce here Müller's description of the genus (translated from the original German, our additions in []):

Genus *Eucytherura* nov. gen.
(Pl. 19 Fig. 21–26; Plate 20 Fig. 13, 14, 16–20; Plate 21 Fig. 1–3).

Shell rough, rather short, very short in front, cut off almost vertically, extended into a short point posteriorly. The profile is so similar in the species known to me that I have refrained from reproducing it for all species (compare the description of *complexa*). The inner margin and the line of adhesion [concrescence] are difficult to see, only from the inside it is possible to trace the inner margin: it runs parallel to the shell margin, at a moderate distance from it; the line of adhesion seems to coincide completely with the inner margin. Marginal pore canals only very sporadic. Margin narrow, the whole margin is entire [uniform], membranous, covered by the overhanging calcified lip. Lateral eyes are very distinct, large, the middle one small, not always certainly detectable. Hinge only with an anterior and posterior tooth of the right shell [valve], sometimes finely denticulated in between.—Antenna 1 rather slender, indistinctly 6-limbed [limbs = segments/podomeres] (limb 4 and 5 not sharply separated), bristles moderately long, partly as long as the four last limbs, slender, some more strongly developed. Antenna 2 is 4-limbed. Mandible with slender seta bearing few long, pointed teeth at tip; palp 3-limbed, limbs 1 and 2 fused. Branchial plate with one long and one very short bristle. Maxilla [Maxillula] with slender setae, the two orally directed rays of the branchial plate almost equal in length. Legs 1–3 [P_{1-3} = L5–L7] long and slender, especially the terminal claw, P_1 and P_2 with one bristle on the anterior margin, a double bristle on the posterior margin of the 1st limb, P_3 with or without bristle on the anterior, with one bristle on the posterior margin (the bristles on the anterior margin always without those at the end of the 1st limb). Furca of ♀ with four bristles, posterior end of body extended into a long, slender point.

Müller's (1894) description of the genus is clearly based on observations of at least two (if not all four) of the species that he assigned to it. For *Eucytherura complexa* (subsequently designated type species) Müller illustrated only a left valve external lateral view and a carapace dorsal view, and of the appendages only a male hemipenis; this evidence of the presence of soft parts means it can be considered "living" and is so far the only known living record of *E. complexa*. For *Eucytherura gibbera* he illustrated a left valve external lateral view, a carapace dorsal view, a left valve internal lateral view, and appendages: antennula, antenna, mandibula, maxillula, legs (L5, L6, L7), furca, male brush-shaped organ and hemipenis. Note that Danielopol et al. (2023, p. 334) mistakenly attributed these appendage illustrations to *E. complexa*. For the other two species (*E. alata* and *E. angulata)* only carapace dorsal views were illustrated. His description of the new genus therefore relies on *E. gibbera* for the details of the inner parts of the valve (calcified inner lamella, line of concrescence/inner margin, marginal pore canals) and all appendages except the hemipenis (which is not mentioned in the description of the genus). Despite illustrating male hemipenes of two species, Müller did not mention any sexual dimorphism of the shell.

Unfortunately, there is a mismatch between the information given by Müller on the plate explanations and the plate/figure numbers cited in the text. According to the plate explanations, *E. complexa* only has a hemipenis illustrated

(Müller 1894, pl. 21, fig. 3) but no shell. According to the text (p. 306), however, plate 20, figs. 13 and 17 should show the shell of *E. complexa*, but the explanation for plate 20 lists a fifth species, *Eucytherura dilatata* for these two figures. The name *dilatata* does not appear in the text; presumably Müller had intended to describe a new species, *dilatata*, but then decided that it was Brady's *Cythere complexa*. Despite being corrected by Müller (1912, p. 280) this error seems to have been overlooked by subsequent authors (except for Mistretta, 1967). Van Morkhoven (1963, p. 357) commented that Müller (1894) "…only describes and illustrates the copulatory organ" of *Cythere complexa* Brady and apparently did not notice the mismatch between text and figure explanations; he suggested, furthermore, that Müller (1894) may have intended *E. gibbera* to be the type species because that is one of the four species for which all appendages were described and illustrated.

Müller (1908, p. 114–117) described two new species: *Eucytherura punctata* and *E.*? *antarctica* but without any discussion of the genus. Müller (1912, p. 279–281) corrected the Plate 20 error in his 1894 monograph but did not discuss the genus further, he did not explain "*dilatata*", neither did he designate a type species.

The most significant systematic development for *Eucytherura* occurred when Alexander (1936, p. 592) stated "Genotype, *Cythere complexa* Brady, 1867". No discussion or rationale for the designation of *C. complexa* as a type species ("genotype" in the terminology of the time) was given in this publication or in any other of Alexander's publications; we assume that *C. complexa* Brady was selected simply because it was first in the list of Müller's species in the 1894 publication. Alexander gave a short description of the genus together with species-level comparative remarks about *Cythere chelodon* Marsson, 1880 which he assigned to *Eucytherura*.

Weingeist (1949, p. 364 and 365) gave English translations of Müller's descriptions of *Eucytherura* and of the species *complexa*, and (p. 366) of supplementary remarks about the genus by Müller (1912, p. 279). Weingeist's paper is important because it reviews the systematic development of *Eucytherura*, with helpful translations of Müller (1894, 1908, 1912), Lienenklaus (1900), Mehes (1936), Van Veen (1938) and Bonnema (1941); however, the discussion focuses on species level differentiation as a prelude to the author describing twelve new *Eucytherura* species of his own from the Upper Cretaceous and Cenozoic of the Gulf Coast U.S.A.

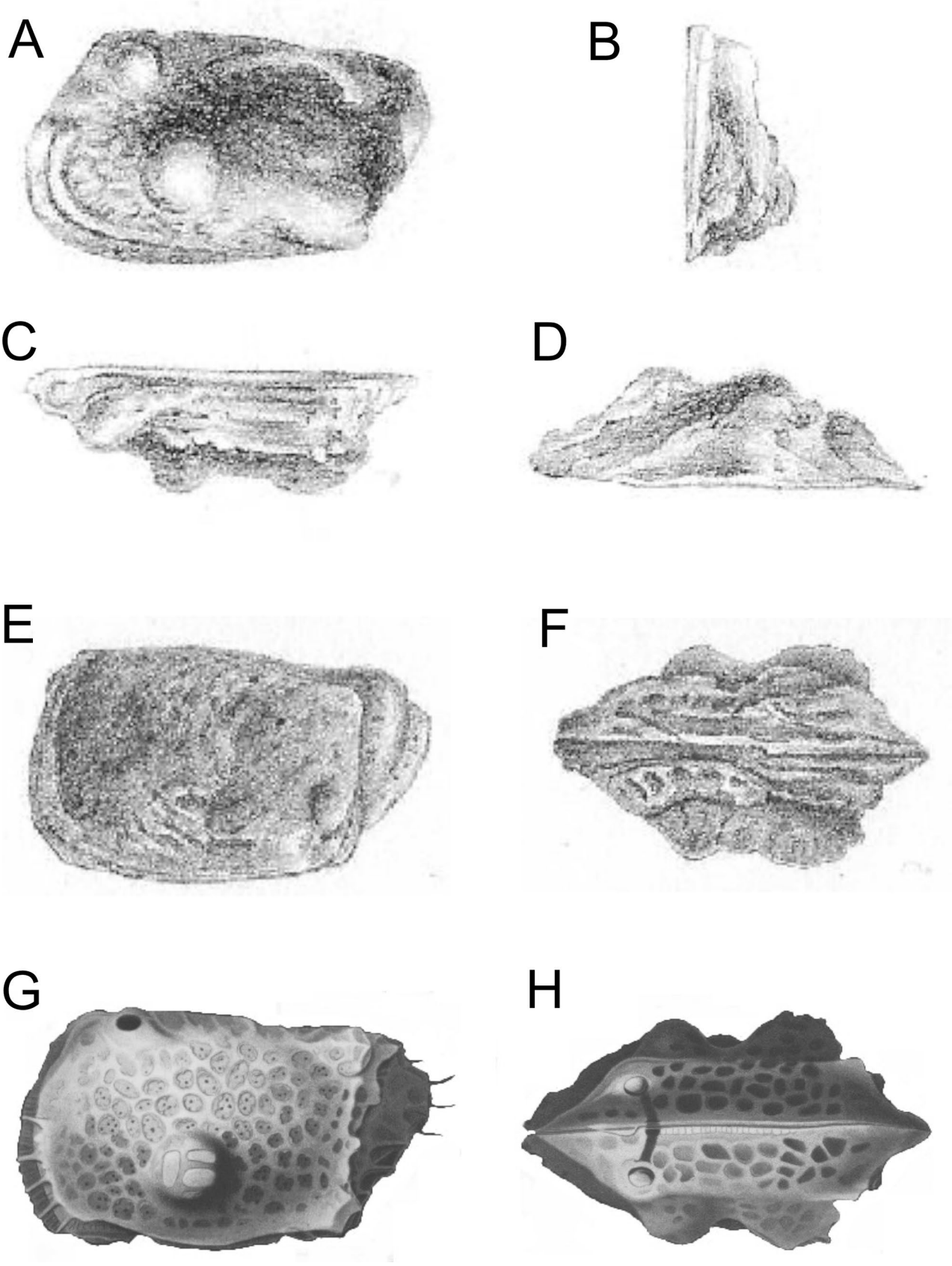
Subsequent authors have followed Alexander's designation of *Cythere complexa* Brady as the type species of *Eucytherura*. The treatise (Moore 1961) says *complexa* is a type species "SD Alexander 1936" (SD = subsequent designation). Van Morkhoven (1963, p. 355) also gives *complexa* as type species and on p. 358 cites Weingeist (1949) for a discussion of the history of *Eucytherura*. The erroneous citation of "*Cythere complanata* Brady, 1867" as a type species by Ballent & Whatley (2009, p. 195) must have been the result of a typing error.

Maddocks and Steineck (1987) elevated the cytherurine tribe Eucytherurini Puri, 1974 to subfamily status, to include living and fossil genera of which at least two (*Eucytherura* and *Xylocythere* Maddocks & Steineck, 1987) have living species for which appendages have been described. A key diagnostic character of the Eucytherurinae is the pore clusters in the sola (fossae) of the external reticulate ornament which penetrate the valve and are visible internally, mentioned by Wengeist (1949) and discussed in detail by Maddocks and Steineck (1987; p. 323) who observed that (in *Xylocythere*, at least) sensilla are absent from the pore clusters, sensillum-bearing simple normal pores being restricted to the muri of the reticulum.

Ayress et al. (1995, p. 205) noted the proposal of a subfamily Eucytherurinae by Maddocks and Steineck (1987) but retained *Eucytherura* in the Cytherurinae Sars, 1925 without discussion. They gave an emended diagnosis of *Eucytherura* as follows (below), which "allows us to synonymise *Typhlocythere* Bonaduce, Ciampo & Masoli, 1975 [sic], *Typhloeucytherura* Colalongo & Pasini, 1980 and *Parahemingwayella* Dingle, 1984" and consequently they moved all species of those three genera to *Eucytherura*. The paper then described seven deep sea "Cainozoic to Recent" *Eucytherura* new species, as well as three? *Eucytherura* and *Eucytherura* sp. 1 to sp. 3. None of the "Recent" material was mentioned as having soft parts, and the emended diagnosis deals only with hard parts (i.e., carapace morphology).

Emended Diagnosis (Ayress et al. 1995): "A genus of the subfamily Cytherurinae with a small carapace of subrectangular, quadrate or subtriangular lateral outline. Ventral margin gently sinuous, often obscured by posteroventral tumidity or tubercle. Eye tubercle present or absent. Surface very ornate with reticulation, tubercles or ridges. Normal pore canals are usually of two types: those emergent through mural pore conuli; and those arranged in groups through the solum of the reticulation. Muscle scars consist of four subovate adductor scars in a vertical row and a subreniform frontal scar ahead of the row. Hinge, in right valve, consists of a small but prominent circular or ovate tooth on anterior and posterior ends, with a finely locellate median groove very narrow at mid-length and often flexured or sinuous."

Subsequent authors (e.g., Swift 2003; Ballent and Whatley 2009) have followed this amended diagnosis. Forel et al. (2019, p. 17 of 30) say: "Genus *Eucytherura* Müller, 1893 emend. Ayress, Whatley, Downing & Millson, 1995. Type species. *Cythere complexa* Brady, 1867 by subsequent designation by Müller, 1893", which implies, incorrectly, that the subsequent designation was by Müller (and in the year preceding the formal description of the genus and species).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◂**Fig. 1** Earliest illustrations of *Eucytherura complexa* (Brady), not to scale. **A**–**D**: from Brady (1868; pl. 31, figs. 43–46) as "*Cythere limicola* Left valve (young)", **A**, external lateral, **B**, anterior, **C**, dorsal, **D**, ventral; **E**, **F**: from Brady and Norman (1889, pl. 19, figs. 31, 32) as "*Cythere complexa*", **E**, carapace left side external lateral, **F**, dorsal; **G**, **H**: from Müller (1894, pl. 20, figs. 13, 17) as "*Eucytherura dilatata*", **G**, LV external lateral, **H**, carapace dorsal

Whatley and Boomer (2000) made a major and much-needed reorganisation of Triassic and Early Jurassic Cytheruridae on the basis of their carapace morphology, which resulted in 13 genera and subgenera being synonymized into *Eucytherura* which they preferred to retain in the subfamily Cytherurinae Sars, 1925 (despite acknowledging the creation of the subfamily Eucytherurinae by Maddocks and Steineck 1987).

The form identified as *E. complexa* by Ishizaki and Gunther (1974, fig. 26 and pl. 2, figs. 1, 3) from the Pacific side of the Panama isthmus has differences from Atlantic *E. complexa*, including a more elongate (and more tapered towards the posterior) adult carapace shape, minor differences in the reticulum pattern and (most importantly) distinct anterior and posterior vestibula in contrast to Müller's (1894) description which indicates no vestibula (line of concrescence coincident with inner margin). Weingeist's (1949, p. 370) description of the genus *Eucytherura* includes a comment about the difficulty of tracing the line of concrescence, which "generally appears to coincide with the inner margin throughout but may depart from it at the anterior and posterior ends"; it is the separation of the line of concrescence from the inner margin that defines a vestibulum. Mistretta's (1967) treatment of fossil (Quaternary) *Eucytherura* from Sicily argued that vestibula are characteristic of the genus although in some species they are greatly reduced, but no examples were illustrated. The presence or absence of vestibula as a generic characteristic of *Eucytherura* needs further investigation.

Cythere complexa Brady, 1867

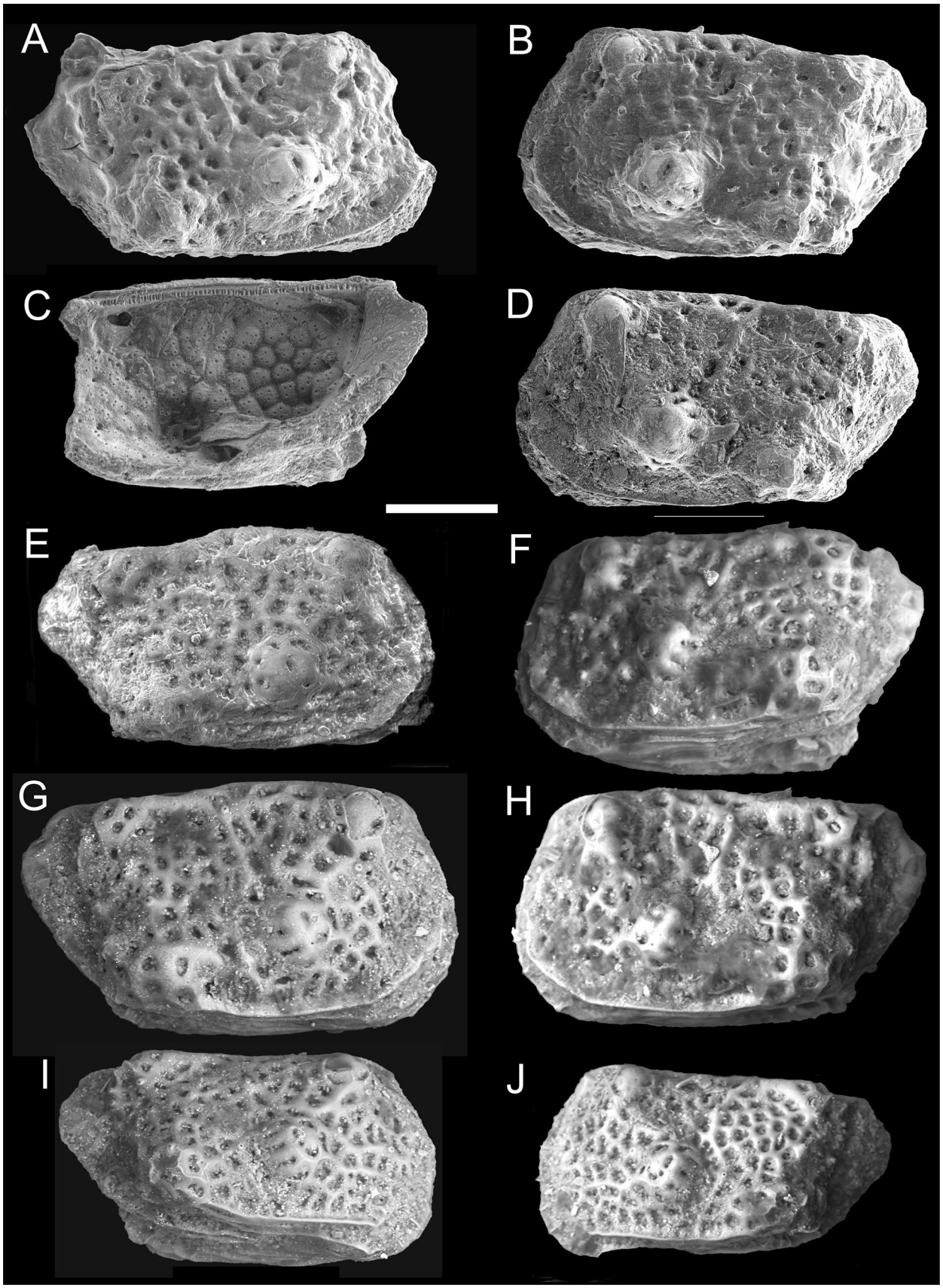
The history of *Cythere complexa* Brady is complicated. It was described but not figured by Brady in 1867 in a *Report of the British Association for the Advancement for Science* for the year 1866, and confusingly 'Report—1866' appears at the top of the first and third pages of the paper. Brady (1867, p. 210) described it as follows:

"Rhomboidal, excessively tumid below, somewhat higher in front than behind; greatest height equal to two-thirds of the length. Anterior margin rounded; posterior obliquely truncate below, and produced into a short blunt beak above; dorsal margin straight, slightly sloping from the front; ventral margin straight. Seen from above the outline is triangular, with deeply constricted sides, pointed in front, and centrally mucronate behind. Surface rather coarsely reticulated; one tubercle situated near the anterior hinge, and two larger ones with an intermediate connecting ala a little above the ventral margin. Length 1/66 in. *Hab*. Uncertain (probably Loch Alsh)." [in. = inch. *Hab*. = habitat].

Although not figured the species is valid under International Code of Zoological Nomenclature Articles 11 and 12 for names published before 1931 (ICZN, 1999). Brady later figured *C. complexa* (Brady 1868, pl. 31, figs. 43–46), providing the first illustrations of the species as recognized by its author. However, he had decided (Brady 1868, p. 405–406) that it was "merely the young of *C. limicola*." (= *Palmenella limicola* (Norman, 1865)), and therefore indicated *C. complexa* Brady as a synonym (with a question mark) of *Cythere limicola* (Norman). In Brady and Norman (1889) he had clearly revised his thinking because *C. complexa* appeared as an established species and was redescribed and figured; a synonymy list showed the incorrect date of 1866 for the first publication of *complexa* and included *Cythere limicola (partim)* from Brady's 1868 "Monograph of the Recent British Ostracoda" also incorrectly dated as 1866. The new description (Brady and Norman 1889, p. 145–146; pl. 19, figs. 31, 32) was:

"Shell, seen laterally, rhomboidal, a little higher in front than behind; height equal to more than half the length; anterior extremity obliquely truncated, rounded off below and obscurely angulated above; posterior very oblique, truncated, forming a projecting beak above the middle, postero-dorsal angle broadly and obliquely truncated, emarginate; dorsal margin almost rectilinear, ventral gently convex. Seen from above, the outline is subhexagonal, the margins very irregular, strongly and sharply mucronate behind and very obtuse in front; greatest width equal to the height, and situated behind the middle; lateral margins very deeply excavated in the middle, converging sharply towards the front, and still more abruptly behind. Surface of the valves irregularly waved and rugose, bordered in front by a broad encircling flange, and near the posterior extremity sinking suddenly in a transverse direction, thus forming with the ventral margin a rectangular ridge. Length .4 mm. Originally described from specimens dredged by the late Dr. Jeffreys and A.M.N. in the Minch. It has been more recently dredged by Dr. Norman in a depth of 126 fathoms at Stoksund, Norway."

The drawings of *Cythere complexa* from Brady (1868) and Brady and Norman (1889) together with Müller's (1894) *Eucytherura complexa* are reproduced herein (Fig. 1). The original record of "probably Loch Alsh" (Brady 1867) refers to the waters between the eastern extremity of the Isle of Skye and the Scottish mainland, while "The Minch" (Brady and Norman, 1889) comprises the waters lying to the north of Skye, contiguous with (but some 60 km from) Loch Alsh via the Inner Sound and the Kyle of Loch Alsh narrows. No depth was mentioned for the Scottish record, but the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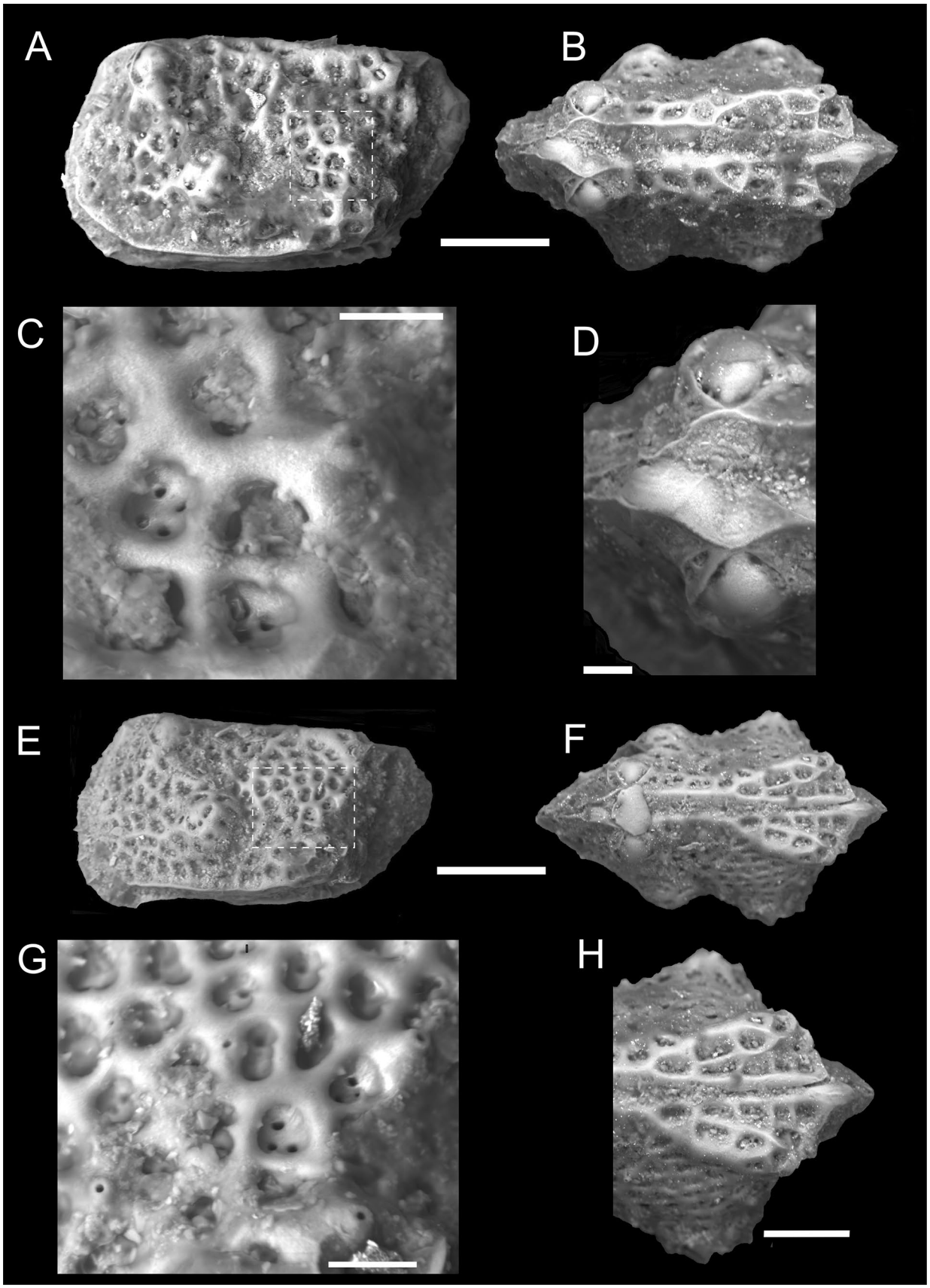
◂**Fig. 2** Scanning Electron Microscope (uncoated) images of *Eucytherura complexa* (Brady) from the Norman Collection, Natural History Museum. **A**–**D** *Cythere complexa* syntypes (1911.11.8. M 3261; The Minch, 1866), **A**, RV external lateral (anterior margin broken; estimated length 360 µm), **B**, LV external lateral (length 340 µm), **C**, RV internal lateral (anterior margin broken, estimated length 360 µm), **D**, LV external lateral (length 360 µm); **E**: RV external lateral (length 350 µm), as *Cythere limicola*, Shetland (young) (1911.11.8. M 3249); **F**–**J**: *Cythere complexa* Brady, Norway, Stoksund (1911.11.8. M 3262), **F**, carapace left side oblique showing ventral surface (length 370 µm), **G** (same as **F**), carapace right side, **H** (same as **F**), carapace left side, **I**, carapace right side oblique showing ventral surface (length 325 µm), **J** (same as **I**), carapace left side. All presumed female except **I**, **J** (possible male). Scale bar (**A**–**J**) 100 µm

Norwegian record from "126 fathoms" is 230.4 m. Note that there is no reference to soft parts.

Brady and Norman's (1889) description of *C. complexa* is an improvement on Brady's (1867) unillustrated original description but the two sets of figures published by Brady (1868, pl. 31, figs. 43–46) and Brady and Norman (1889, pl. 19, figs. 31, 32) are poor (probably due to the small size of the specimens) and might even be considered to represent two different species. It seems likely that subsequent identifications of *E. complexa* have relied on Müller's (1894) excellent, detailed illustrations. An important (and apparently long-ignored) question, therefore, is whether *Eucytherura complexa* (Brady) of Müller (1894) is truly conspecific with *Cythere complexa* Brady, 1867; this can only be answered by re-illustrating type specimens. No type specimens of *C. complexa* could be located in the G.S. Brady Collection, formerly in the Hancock Museum in Newcastle-upon-Tyne (renamed the Great North Museum: Hancock in 2009) but now kept in the Great North Museum Resource Centre at the Discovery Museum in the same city. However, a search of the A.M. Norman Collection at the Natural History Museum in London produced three micropalaeontological slides. The first (1911.11.8. M 3261), labelled "*Cythere complexa* Brady Types. The Minch 1866.", contains two right valves and two left valves; we are confident that these are specimens on which Brady's (1867) original description was based and thus constitute syntypes of *C. complexa*. The second (1911.11.8. M 3249), labelled "*Cythere limicola.* The Minch 1866." and "Shetland (young)", contains a right valve adult *Palmenella limicola* (Norman, 1865) and a smaller right valve that we identify as *C. complexa.* The third (1911.11.8. M 3262), labelled "*Cythere complexa* Brady. Norway, Stoksund", contains two carapaces corresponding to the material cited by Brady and Norman (1889, p. 146). The specimens were imaged, uncoated in a low vacuum, by placing each entire slide (with glass cover-slip removed) in the Scanning Electron Microscope. On the basis of the resulting SEM images (Figs. 2 and 3) we confirm that *Eucytherura complexa* (Brady) of Müller (1894) is conspecific with *Cythere complexa* Brady, 1867. Three of the valves are mounted to display external lateral views (Fig. 2A, B, D); clearly evident are the three tubercular swellings in the posterodorsal, posteroventral and central muscle scar positions, and the prominent eye tubercle. The reticulate ornament is to some extent obscured by adhering dirt. A prominent murus (ridge) runs sub-parallel to the outer margin from above mid-height anteriorly, curving down to run almost straight ventrally to join the posteroventral tubercle overhanging and obscuring the posterior half of the ventral outer margin. This overhang is clearly evident in one right valve (with a damaged anterior margin) mounted to display the internal view (Fig. 2C), which also shows the hinge with rounded terminal teeth and locellate median element. Particularly noteworthy are the pore clusters visible in the sola of the reticulum in the external view, also seen in the internal view in which the externally slightly concave sola present convex surfaces giving the inner side of the outer lamella a quilted appearance. Our SEM image of the RV from Shetland, considered by Brady to be a juvenile of *Palmenella limicola*, confirms its identity as *C. complexa.* The two carapaces from Stoksund are mounted with a slight "lean" towards the dorsal margin due to the posteroventral tubercular swelling, so that the sub-marginal murus does not appear to overhang the posteroventral outer margin; the larger of these two specimens (Fig. 2G, H) is a good match with the syntypes, but the smaller differs (Fig. 2I, J) in being less high relative to length and the submarginal murus is absent from the anterior region, only running ventrally; we consider it likely that this is a male, all of the others being females, but we are unable to verify this at present.

Eucytherura complexa has been found in North Atlantic waters from the Iberian peninsula (the western Algarve continental shelf, S Portugal, and the Mira River estuary, SW Portugal: Cabral and Loureiro 2013; and the Basque Basin, N Spain: Rodríguez-Lázaro et al. 2018) to NW Scotland and Norway around latitude 64ºN (Brady 1867, 1868; Brady and Norman 1889). It has also been recognized and figured from Mediterranean waters: the Gulf of Naples (Müller 1894), the Adriatic Sea (Bonaduce et al. 1976; Breman 1976) and the Tyrrhenian Sea (Aiello et al. 2022). Seemingly anomalous records from the Gulf of Panama, on the Pacific side of the Panama Isthmus (Ishizaki and Gunther 1974), could perhaps be explained as the result of transport by shipping passing through the Panama Canal from the Atlantic to the Pacific.

All of these records are of Recent material and, therefore, assumed to represent living populations, although none has been shown, by the presence of soft parts, to have been alive at the time of collection except Müller's (1894) from the Gulf of Naples for which only a hemipenis was illustrated (Fig. 4); the other appendages of *E. complexa* are, as yet, unknown. Fossil occurrences have also been reported, such as Mistretta's (1967) record from Quaternary deposits at Palermo, Sicily, and Mostafawi's (1989) records from the Upper Pliocene and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◂**Fig. 3** Scanning Electron Microscope (uncoated) images of *Eucytherura complexa* (Brady) from the Norman Collection, Natural History Museum. **A**–**H** *Cythere complexa* Brady, Norway, Stoksund (1911.11.8. M 3262) (**A**–**D** same as Fig. 2**G**; **E**–**H** same as Fig. 2**I**); **A**, carapace left side, **B**, carapace dorsal, **C**, detail of (**A**) showing reticulum with pore clusters in sola, **D**, detail of (**B**) showing eye tubercles, **E**, carapace left side, **F**, carapace dorsal, **G**, detail of (**E**) showing reticulum with pore clusters in sola, **H**, detail of (**F**) showing reticulum. Scale bars 100 µm (**A**, **B**, **E**, **F**), 50 µm (**H**), 20 µm (**C**, **D**, **G**)

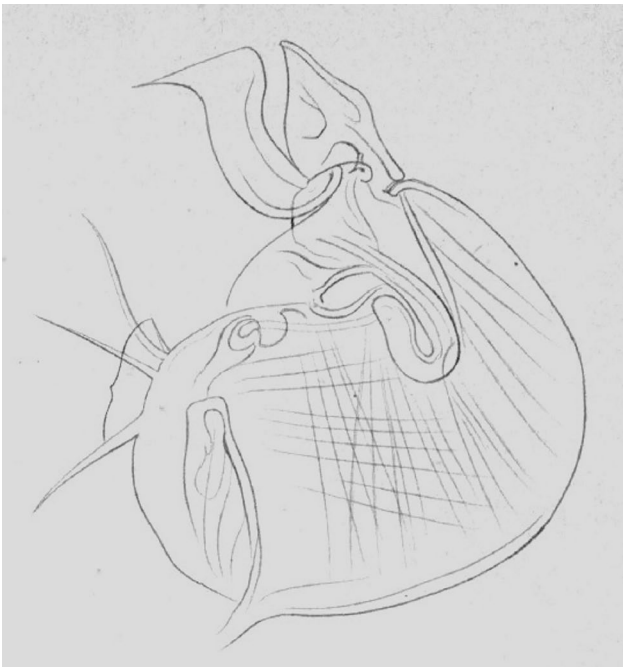

Fig. 4 *Eucytherura complexa* (Brady), male hemipenis, from Müller (1894, pl. 21, fig. 3)

Lower Pleistocene of Rhodes Island. It should be noted that some aspects of the carapace morphology of *E. complexa* appear variable, not only with their relative development on individual valves but also according to their precise orientation when viewed and imaged. For example, the prominent murus running sub-parallel to the ventral and anterior margins may be developed more in some specimens so that in external lateral view it overhangs and obscures more of the outer margin (see, e.g., Aiello et al. 2022, pl. 4, fig. 11). We also cannot rule out the possibility that this murus has been reduced, in some specimens, by post-mortem abrasion.

The question of the type species

Examination of syntypes of *Cythere complexa* Brady confirms that Müller's (1894) *E. complexa* (Brady) is indeed Brady's species, but it is clear that his *E. gibbera* contributed more to the characterisation of the new genus than did *E. complexa*. Weingeist (1949) suggested that Müller may have intended *E. gibbera* as the type species because it was illustrated in most detail, noting that although *E. complexa* was the first to appear in the text after the description of the new genus, and the only one of the four *Eucytherura* species described in the monograph that was actually mentioned in the generic description, Müller's use of a question mark in synonymy for Brady's original (unillustrated) description of *C. complexa* indicated uncertainty about whether the name was applicable to the Gulf of Naples species presented as *E. complexa*. Nevertheless, the International Code of Zoological Nomenclature (1999: 4th edition) is clear: "In the absence of a prior type fixation for a nominal genus or subgenus, an author is deemed to have designated one of the originally included nominal species as type species, if he or she states (for whatever reason, right or wrong) that it is the type or type species, or uses an equivalent term, and if it is clear that that author accepts it as the type species." (ICZN 69.1.1). We must, therefore, accept Alexander's (1936) designation of *C. complexa* (Brady) as the type species of *Eucytherura* Müller, but we recommend careful attention to the role of *E. gibbera* in defining the genus. To this end we have copied and assembled (Fig. 5) Müller's (1894) original illustrations of adult *E. gibbera*. We have omitted the dorsal view of a carapace that he indicated as a juvenile because, if the magnifications are correct (all shell illustrations of *Eucytherura* species on his pl. 20 being indicated as 216x), the "juv." specimen (op. cit., pl. 20, fig. 16) is slightly longer than any of the adults of *Eucytherura* species! It is also (contrary to the adult *E. gibbera*) prominently alate and lacks a dorsal row of tubercles; we consider it likely that this is the result of errors in the plate explanation, so that the "juvenile" is really the adult of *E. alata*, and another (smaller) dorsal view (pl. 20, fig. 18) presented as adult *E. alata* is actually a juvenile of that species. Useful SEM images of *E. gibbera* have been published by Aiello et al. (2018) from Holocene deposits at Pozzuoli on the northwestern coast of the Gulf of Naples, and Aiello et al. (2022) associated with a hydrothermal vent system in the Tyrrhenian Sea.

Consequences

Whatley and Boomer (2000) made a major and much-needed reorganisation of Triassic and Early Jurassic Cytheruridae on the basis of their carapace morphology, which resulted in 13 genera and subgenera being synonymized into *Eucytherura* but, given the unsoundness of the definition of that genus, this now seems unfortunate. They cited *complexa* and Alexander's (1936) Subsequent Designation, the overview of Weingeist (1949), plus the emended diagnosis of Ayress et al. (1995). One of us (ARL) unwisely added a

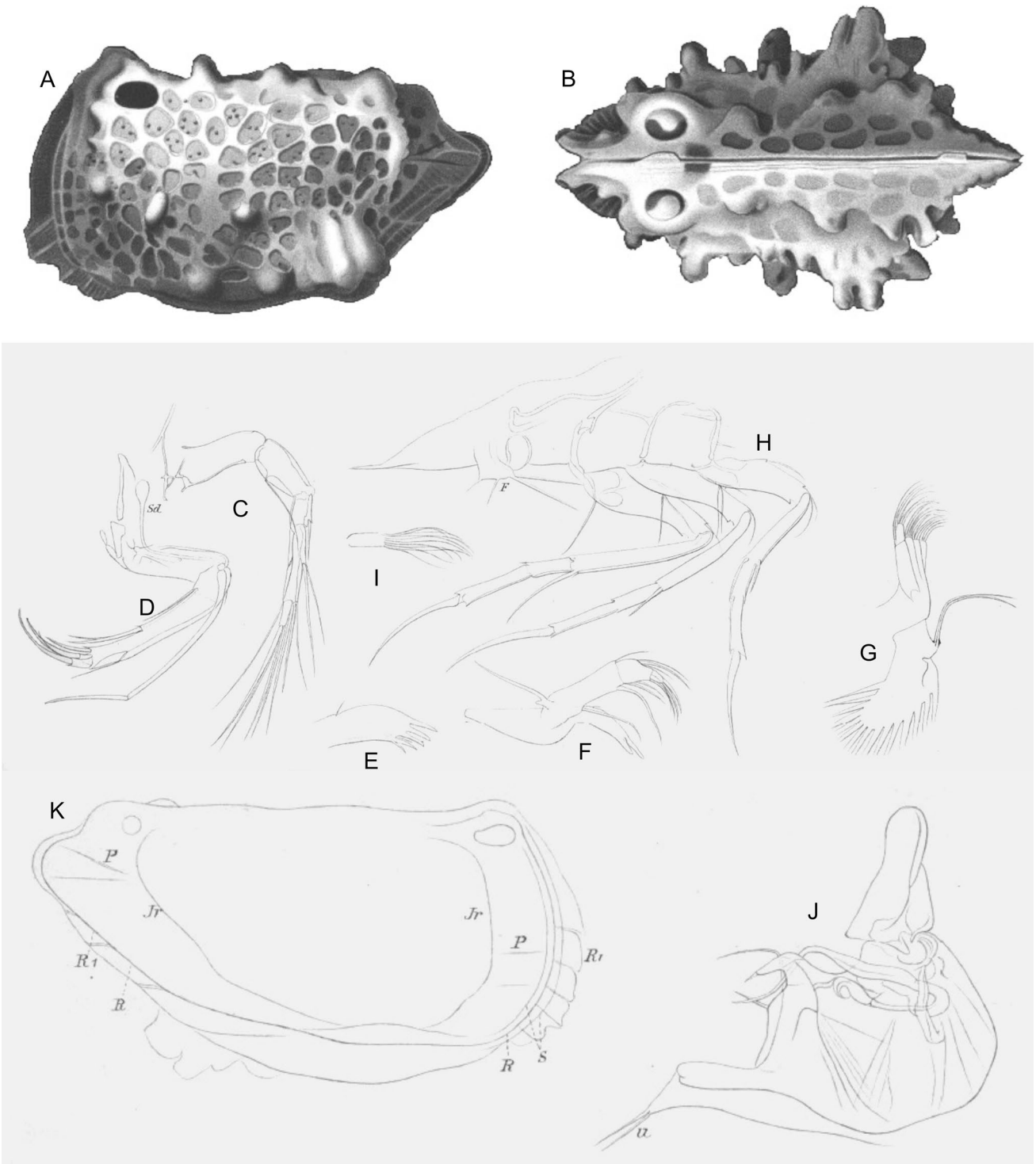

Fig. 5 *Eucytherura gibbera* Müller: illustrations of carapace and appendages from Müller (1894) pl. 19, figs. 21–26 (**C**–**I**), pl. 20, figs. 14, 19 (**A**, **B**), pl. 21, figs. 1, 2 (**K**, **J**), not to scale. **A**, carapace left side; **B**, carapace dorsal view; **C**, antennula; **D**, antenna; **E**, toothed termination of mandibular coxa; **F**, mandibular coxa and palp; **G**, maxillula; **H**, walking legs (L5, L6, L7), furca and posterior extremity of body; **I**, male brush-shaped organ; **J**, male hemipenis; **K**, left valve internal lateral view; all presumed female except **I**, **J**

remark to Danielopol et al. (2023, p. 334): "The palaeontological evidence shows that both *Eucytherura* and *Microceratina* are phylogenetic lineages of great longevity, both existing since the early Mesozoic. *Eucytherura* originated in the Triassic (Whatley & Boomer 2000) and *Microceratina* we document here from the early Jurassic, and it may be that

Eucytherura is ancestral to *Microceratina*." Perhaps these ancient "*Eucytherura*" are not *Eucytherura* at all? In recent years the scanty knowledge of Triassic ostracod assemblages has dramatically improved and links to later Mesozoic taxa are becoming better understood (see, e.g., Forel et al., 2019). Fully comprehensive reviews of published citations of *E. complexa* and the numerous fossil species assigned to (and genera synonymised with) *Eucytherura* are well beyond the scope of the present paper but will, we hope, be facilitated by our illustrations of syntypes of *C. complexa* Brady. Our synonymy of *E. complexa* (see Systematics section below) is restricted to key references and examples reviewed in the writing of this paper.

The way forward for *Eucytherura*?

It is necessary to recognise that:

1. There is a valid species group with a long and diverse evolutionary history and characterized by certain "*Eucytherura*" morphological traits such as pore clusters in the sola of the reticulum.
2. The type species of *Eucytherura, Cythere complexa* Brady, remains poorly known in spite of our new SEM images of syntypic valves.
3. Müller's *Eucytherura gibbera* is the most thoroughly described and illustrated of his new species on which he based the description of his new genus *Eucytherura*, and is still the only member of the genus for which all appendages have been illustrated.
4. Müller's (1894) material exists (Diebel 1962) but it is decalcified (Athersuch 1976) and therefore of no use for carapace characteristics.
5. Revisions of *Eucytherura* by subsequent authors have focused on carapace morphology and ignored appendages.

We recommend, therefore, that future efforts should include revision of the numerous species hitherto assigned to *Eucytherura*, taking account of our illustrations of the syntypes of the type species and applying our emended diagnosis of the genus (see Systematic section, below), including (where possible) attention to appendage as well as carapace morphology.

Systematic section

Family **Cytheruridae** G.W. Müller, 1894
Subfamily **Eucytherurinae** Puri, 1974 emend Maddocks & Steineck, 1987

Genus ***Eucytherura*** G.W. Müller, 1894

Type species (by subsequent designation). Cythere complexa Brady, 1867

Emended diagnosis. A genus of the subfamily Eucytherurinae with a small (typically c. 400 µm long) carapace of subquadrate, subtrapezoidal or subtriangular lateral outline, with a short caudal process situated above mid-height. Anterior margin gently convex to almost straight. Ventral margin gently sinuous or smoothly convex, often overhung and obscured in lateral view by ventral to posteroventral tumidity, tubercle or ridge. Eye tubercle present or absent. Surface is very ornate with reticulation, tubercles or ridges. Normal pore canals usually of two types: those emergent through muri of the reticulation, sometimes with pore conuli, simple and each bearing a sensillum; and those arranged in groups in the sola of the reticulation, simple and without sensilla. Four subovate adductor muscle scars in a vertical row and a subreniform frontal scar. Hinge, in right valve, with a prominent circular or ovate tooth at each end and with a finely locellate median groove narrow at mid-length and often flexured or sinuous (i.e., lophodont). Calcified inner lamella relatively broad anteriorly and posteriorly with anterior and posterior vestibula present or greatly reduced (if not absent), narrow ventrally; marginal pore canals few, simple. Antennula with six podomeres, the fourth and fifth fused, the rest articulated. Antenna with four articulated podomeres. Mandibular coxa ventrally slender, toothed; exopodite branchial plate with one long and one greatly reduced setae. Maxillular branchial plate with c. 15 rays and two anteriorly-directed setae. Setal formulae of walking leg protopodites: L5 1 + 2 + 2; L6 1 + 1 + 2; L7 1 + 1 + 1. Female furcal (caudal) rami each very short and bearing up to four setae of varying lengths. Posterior extremity of the body is slender and pointed.

Remark. Translations of Müller's (1894) descriptions of *Eucytherura gibbera* and *E. complexa* are given in Appendices 1 and 2 respectively.

Eucytherura complexa (Brady, 1867)

1867 *Cythere complexa* n. sp.—Brady: p. 210. Adult, Recent, The Hebrides.
1868 *Cythere limicola* (Norman) (pars): Brady p. 405–406, pl. XXXI, figs. 43–46 (non pl. XXXI figs. 38–41 = *Palmenella limicola* (Norman)). Adult, Recent, coastal waters of Scotland; depth unknown but maximum depth of The Minch is c. 120 m.
1889 *Cythere complexa* G.S. Brady—Brady and Norman: p. 145–146, pl. XIX, figs. 31, 32. Adult, Recent, The

Minch (max. depth c. 120 m) and Stoksund, Norway (126 fathoms = 230.6 m).

1894 *Eucytherura complexa* Brady [sic]—G.W. Müller: p. 306–307, pl. 20, figs. 13, 17 [given in figure caption as *Eucytherura dilatata*, error corrected by Müller (1912)], pl. 21 fig. 30. Adult, Recent, Gulf of Naples, Italy.

1967 *Eucytherura complexa* (Brady)—Mistretta: p. 2–3, fig. 2e, pl. 1, fig. 4. Adult, Quaternary, Palermo (Sicily).

?1974 *Eucytherura complexa* (Brady)—Ishizaki and Gunther: p. 44–45, fig. 26, pl. 1 figs. 1–3, pl. 2 figs. 1–2. Adult, Recent, Gulf of Panama, depths 27–262 m.

1976 *Eucytherura complexa* (Brady, 1867)—Breman: p. 68, pl. X, fig. 142. Adult, Recent, Adriatic Sea, depths 90–800 m.

1976 *Eucytherura complexa* (Brady, 1866) [sic]—Bonaduce et al.: p. 85, pl. 48, figs. 6–14. Adult, Adriatic Sea, Recent, depths beyond 70 m.

1989 *Eucytherura complexa* (Brady, 1866) [sic]—Mostafawi: pl. 3, fig. 49. Adult, Rhodes Island, Damatria Formation, Upper Pliocene and Vasfi Formation, Lower Pleistocene.

2013 *Eucytherura complexa* (Brady, 1867)—Cabral and Loureiro, p. 140, pl. 2, fig. 7. Juvenile, Recent, western Algarve continental shelf off Portugal and Mira River estuary, SW Portugal (transported); Holocene, Tagus River estuary, Lisboa, Portugal.

2018 *Eucytherura complexa* (Brady, 1867)—Rodriguez-Lazaro et al.: p. 151, fig. 5d. Juvenile, Recent, Basque Basin, Bay of Biscay, eastern North Atlantic continental shelf, depths 110–170 m.

2022 *Eucytherura complexa* (Brady, 1867)—Aiello et al.: pl. 4, fig. 11. Adult, Recent, Tyrrhenian Sea.

2023 *Eucytherura complexa* (Brady, 1867)—Danielopol et al.: p. 308, 320, 323, fig. 11A-F. Juvenile, Recent, eastern North Atlantic continental shelf off Portugal, depth 105–110 m.

Emended Diagnosis. Female carapace subtrapezoidal in lateral view, with well-developed reticulum and prominent reticulate tubercles posteroventrally and posterodorsally. Pore clusters in the sola of the reticulum typically with 2–4 pores. Eye tubercles prominent. Each valve externally with a prominent ridge running subparallel to the anterior and anteroventral margins, converging with the ventral margin to connect with a posteroventral tubercle overhanging the outer margin. Internally the outer margin outline is subtriangular, the convex ventral margin curving smoothly into the posterior margin to meet the caudal process well above mid-height. In dorsal view, the posteroventral tubercles are more inflated than those in the central muscle scar and posterodorsal regions. Male (?) carapace less high in relation to length, with the prominent ridge running only from the posteroventral tubercle to terminate close to the anterior end of the ventral margin.

Syntypes. Two right valves and two left valves, all assumed adult female, in the Norman Collection, Zoology Department, the Natural History Museum, London, UK, on slide 1911.11.8. M 3261 labelled "*Cythere complexa* Brady Types. The Minch 1866."

Type locality. The Minch, The Hebrides, Scotland (approx. lat. 58° N, long. 6 ° W). Brady (1867) gave the locality as "Uncertain (probably Loch Alsh)"; subsequently Brady & Norman (1889, 146) stated: "Originally described from specimens dredged by the late Dr Jeffreys and A.M.N. in the Minch. It has been more recently dredged by Dr Norman in a depth of 126 fathoms [230.4 m] at Stoksund, Norway.". Since the type specimens were evidently collected by A.M. Norman and remain in his collection at the Natural History Museum, London, we assume that The Minch is the correct type locality. Loch Alsh lies between the eastern extremity of the Isle of Skye and the Scottish mainland, approximately 60 km south of The Minch and connected with it via the Inner Sound and the Kyle of Loch Alsh narrows.

Remarks. Distinguishing between adult and at least the larger juvenile specimens is made difficult by the strongly developed external ornament which does not seem to change significantly in the final moult, but we suggest that in external lateral view the adult dorsal and ventral margins (the latter being mainly the overhanging ventral murus and not the true margin) are approximately parallel, while in juveniles they are distinctly convergent towards the posterior. Juveniles can also be recognized more easily by their narrow calcified inner lamellae, provided that separate valves are available to view internally (only adults have relatively broad calcified inner lamellae anteriorly and posteriorly); pore conuli and pore clusters may be differently distributed in adults and juveniles. Applying these criteria, adult length range is 0.33–0.40 mm and juveniles are < 0.32 mm long. Specimens illustrated by Cabral and Loureiro (2013) and Rodriguez-Lazaro et al. (2018) are juveniles (Cristina Cabral pers. comm. 09/08/2023; Julio Rodriguez-Lazaro pers. comm. 23/01/2023). Good external and internal views showing adult characteristics were illustrated by Bonaduce et al. (1976).

Conclusions

1. The genus *Eucytherura* Müller, 1894 was based on living material from the Gulf of Naples and has subsequently been interpreted as representing an important,

diverse and numerous group of marine species ranging from the Early Mesozoic to the present.
2. Müller's (1894) original description of *Eucytherura* relied mainly on his new species *E. gibbera,* which remains the only species of the genus for which the appendages (other than the male hemipenis) have been described.
3. Müller (1894) did not designate a type species; Alexander (1936), by subsequent designation, established *Cythere complexa* Brady 1867 as the type species, probably because it was the first species to be described by Müller in his monograph.
4. Comparison of the type material of *Cythere complexa* Brady with Müller's (1894) excellent figures of *Cythere complexa* Brady confirms that the two are conspecific.
5. Future taxonomic studies of *Eucytherura* species should take into consideration the morphological characteristics of not only the type species (*E. complexa* (Brady) but also *E. gibbera* Müller, 1894.
6. An emended diagnosis of *Eucytherura* is provided, including appendage morphology and internal details of the valves overlooked by authors since Müller (1894).

Appendix 1

Translation of Müller's (1894) description of *Eucytherura gibbera.*

Species *Eucytherura gibbera* n. sp.
(Pl. 19 Fig. 21–26; Pl. 20 Fig. 14, 16, 19; Pl. 21 Fig. 1, 2 ; Pl. 20 Fig. 16 juvenile).

Shell similar in profile to that of *complexa*, very bumpy, the upper margin broken up into a series of ridges, some of which overhang the rim of the shell in profile. Behind the extensive eye bulge [tubercle] is a smaller, strongly upturned one, which in profile overhangs the upper rim of the shell. After a clear gap there is then a group of 2 or 3 bulges, the last of which forms the posterior border of the upper rib. At the level of the sphincter [closing muscles, not anus?], a middle row of 3 bulges [tubercles?]: one each, about the same width as the anterior and posterior margins of the eye tubercle, and a 3rd, lying behind the closing muscle attachments; the 2nd and 3rd, are quite extensive. In the lower edge [margin] we also find a row of bulges: one, which is visible in the view from above between 2 and 3 of the middle row and is not very prominent, furthermore a whole group of not sharply separated bulges, which form the rear outer corner. Also to be mentioned is a bulge at the front edge of the eye boss [tubercle]; the rear descending edge also appears as a double bulge in the view from above. Quite opaque, chalky white to orange-yellow.—Penis: Attachment broader at base than tip of basal piece, with bluntly rounded tip; mating tube (?) protruding in profile as a long, slender, downward-curved process on inner side. The basal piece forms a distinct corner at the inner margin, which is extended into a strong process curving inwards and downwards.

Size. 0.36–0.4 mm.

Occurrence. Especially among calcareous algae, also among detritus of Posidonia, not rare.

Appendix 2

Translation of Müller's (1894) description of *Eucytherura complexa* Brady.

Species *Eucytherura complexa* Brady.
(Pl. 20 Fig. 13, 17; Pl. 21 Fig. 3).

? *Cythere complexa* Brady 3 pag. 210; *limicola* (partim) Brady 8 pag. 405, Pl. 31 Fig. 38–41; *complexa* Brady & Norman pag. 145, Pl. 19 Fig. 31, 32.

Shell in profile rather short and stocky, height to length about = 1: 1.6, dorsal margin straight, slightly sloping posteriorly, ventral margin also straight, anterior margin forming a very shallow arc, sharply separated from the dorsal and ventral margins at an angle slightly greater than a right angle; the lower corner only slightly in front of the upper. The edge [anterior margin] is surmounted by a broad lip with radial striations and individual stronger ribs. The posterior margin is also sharply set off from the dorsal and ventral margin, its lower end is clearly in front of the upper, it forms about a right angle with a blunted tip, this would be about 2/3 of the shell height; it too is surmounted by a calcified, striped lip. The broad median surface is sharply defined against a narrower dorsal surface and a broader ventral surface, finally against the posterior end of the shell. The upper edge runs approximately at the same height as the upper edge of the shell, in profile it almost completely coincides with it or covers it; in the view from above it delimits a field which begins in the region of the eye and whose margins extend backwards parallel to the hinge margin to about the posterior limit of the dorsal margin, most sharply defined in the eye region and at the posterior end, and are rounded in between. The lower [inner] margin begins slightly above the anterior end of the ventral margin; in its further course it coincides in profile with the ventral margin or covers it; in its posterior half it forms approximately a hemispherical extension, in which the overlying part of the shell also participates; the anterior half of its edge is covered from above by a hemispherical bulge, into which the closing muscles

enter. This creates a double, semi-circular extension in the view from above, which is characteristic of the species. The shell is quite evenly full of roundish, sharply defined pits, which look like a cloverleaf or rosette due to the flat, pointed projections of the edge. In each pit there are one or a few strongly refractive, quite conspicuous dots, apparently pore canals, I have never seen the associated hairs. Shell rather cloudy, especially the strongly protruding edges, as well as the ribs between the shallow pits, freshly chalky to yellowish.—Penis rather broad and short, with a second sacral attachment arising from the tip, the outer half of which is directed straight upwards and simply pointed, the inner half of which is curved in the opposite direction and extended into a fine, inwardly turned tip. The mating tube seems to arise in the upper half in the middle of the surface, freely protruding, but I have not identified its position and shape with certainty; in the lower half 3 larger and 1 smaller bristle arise at the inner edge, which correspond to the furca.

Size. 0.33–0.35 mm.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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