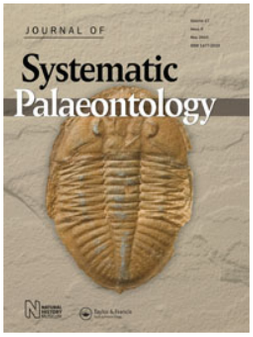

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Eocene shallow-marine ostracods from Madagascar: southern end of the Tethys?

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Twenty-five genera and 32 species of Eocene shallow-marine ostracods from Madagascar were examined for taxonomy and palaeobiogeography. Eight new species – *Paijenborchellina madagascarensis* sp. nov., *Neocyprideis polygonoreticulata* sp. nov., *Alciella irizukii* sp. nov., *Neomonoceratina afroangulosa* sp. nov., *Muellerina eocenica* sp. nov., *Stigmatobradleya hunti* gen. et sp. nov., *Uroleberis paranuda* sp. nov., *Xestoleberis renemai* sp. nov. – and one new genus – *Stigmatobradleya* gen. nov. – are described. Eocene Malagasy ostracods showed a strong affinity to the Eocene East Tethyan fauna in Arab-Africa and Indo-Pakistan. They also showed certain affinity to the Eocene West Tethyan fauna in Europe. One species, *Pokornyella lamarckiana* sensu lato, showed a very wide Eocene geographical distribution, covering Europe, Indo-Pakistan, Arab-Africa, Japan and perhaps North America. These results indicate that the East African, Arabian, and Indo-Pakistan regions constitute the East Tethyan palaeobiogeographical sub-realm, with considerable faunal similarity found across the regions. This sub-realm extends to south-eastern Africa in the south and is a part of the broader Tethyan palaeobiogeographical realm with certain, but less, palaeobiogeographical similarity. The spatial extent of the Tethys palaobiogeographical realm *sensu lato* includes Asia-Oceania in the east and eastern America in the west. Based on our results, we suggest a need to update the scheme of global ostracod biogeographical division.

http://zoobank.org/urn:lsid:zoobank.org:pub:C98E65A2-FEB8-4D63-B294-7A1A22C51F5E

Keywords: global palaeobiogeography; Cenozoic; Palaeogene; Africa; Ostracoda; Crustacea

Introduction

One of the most important features of the Eocene ocean is a large shallow-marine habitat or palaeobiogeographical realm, the Tethys Sea, centred on the circum-Mediterranean region (including northern and Mediterranean European, northern African, Arabian, Indo-Pakistani and Indo-Pacific regions) (Premoli Silva *et al.* 1995; Harzhauser *et al.* 2002; Renema *et al.* 2008), and in a broad sense extending to eastern America (= tropical western Atlantic) in the west and Asia-Oceania in the east (Keij 1976; McKenzie 1982; 1991a, b). The Eocene Tethyan fauna is important because it includes ancestors of modern species that constitute tropical biodiversity and its hotspots (Renema *et al.* 2008; Leprieur *et al.* 2016). However, global- and sub-global-scale Eocene shallow-marine palaeobiogeography is relatively poorly understood, mainly because of the paucity of in-depth modern syntheses (Premoli Silva *et al.* 1995; Popov *et al.* 2001; Renema *et al.* 2008). This is especially true compared to post-Eocene shallow-marine palaeobiogeography of which intensive and extensive synthesis studies were recently conducted by Harzhauser and colleagues for the circum-Mediterranean region (Harzhauser *et al.* 2002, 2007).

Among taxonomic groups, ostracod crustaceans are a comparatively well-understood component of Eocene shallow-marine palaeobiogeography, as data were recently compiled and summarized by several researchers (Yamaguchi 2006; Yamaguchi & Kamiya 2009). However, in Eocene south-eastern Africa, shallow-marine fossils remain poorly investigated, not only for ostracods (Dingle 1976; Ahmad *et al.* 1991) but in general (Premoli Silva *et al.* 1995; Renema *et al.* 2008; Squires 2013). There have only been two comprehensive Eocene shallow-marine ostracod studies in south-eastern Africa: Dingle (1976) in South Africa, and Ahmad *et al.* (1991) in Tanzania. Both studies showed the affinity of the Eocene south-eastern African ostracod fauna with the

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fauna in Pakistan, which is within the eastern Tethyan region. Dingle (1976) revealed little similarity between Eocene South African ostracods and those from other regions, including south-eastern USA, north-eastern Europe, and western and northern Africa. Ahmad *et al.* (1991) suggested a link, albeit relatively weak, between Eocene Tanzanian ostracods and Cenozoic ostracods in Tethyan regions in a broad sense (including the Caribbean, Indo-Pacific, Pacific and Mediterranean regions). However, data were too limited to conduct further comprehensive palaeobiogeographical comparisons at that time. Since then, there have been no Eocene shallow-marine ostracod studies in south-eastern Africa, whereas in other regions, such as Europe, northern Africa and Indo-Pakistan, a considerable amount of data has been accumulated over the last ~30 years. Here, we investigate Eocene shallow-marine ostracods from Madagascar, and conduct detailed comparisons of Eocene shallow-marine ostracods between Madagascar and other regions to discuss their palaeobiogeography. Our results show considerable similarity between the Eocene Madagascan fauna and Eocene faunas of the Indo-Pakistani and Arab-African regions, but our Eocene Madagascan fauna also shows certain similarity to Eocene faunas of Europe and the broader Tethys. This indicates that Eocene south-eastern Africa is a part of the East Tethyan palaeobiogeographical sub-realm that belongs to the broader Tethyan palaeobiogeographical realm. Our results suggest that the global scheme of ostracod palaeobiogeographical division should be updated.

Geological setting

Madagascar is geologically diverse, with formations ranging from marine and terrestrial sediments to igneous and metasediments (Besaire 1946). Mesozoic to Palaeogene limestones and sandstones form a broad, shallowly dipping plateau in the south-west of the island, intersected by occasional basalt intrusions and overlain by recent sands. Following rifting during the Cretaceous, Madagascar was relatively stable tectonically during the Palaeogene, allowing the development of a shallow, stable carbonate platform. Eocene carbonate sediments outcrop in a broad band at the most south-westerly point of the plateau in the region of Toliara (Fig. 1). Accessible outcrop is generally scarce due to the low topography and spiny forest flora; however, coastal sections and quarries sampled during 2014 as part of a field campaign to examine the larger benthic foraminiferal biodiversity of the region give some insight into the Eocene stratigraphy. The sediments in the region comprise larger benthic foraminiferal limestones dominated by alveolinids and *Nummulites*, carbonate sandstones, and thick oyster beds (Cotton *et al.* in prep); clay deposits, however, are rare. Molluscan fossils and echinoids are also very common.

Samples examined in this paper are from the rare clay horizons and were only found at two of nine sites sampled during the 2014 fieldwork. The two sites, TOL2 and TOL4, are situated approximately 0.5 km from each other and are on either side of the main road into Toliara (Fig. 1). Site TOL2 is a 6 m-high exposure, comprising larger foraminiferal packstones with abundant *Alveolina*. Oysters and oyster fragments are common, along with occasional coral and gastropod moulds. The ostracod-bearing sample (TOL2-LC2A) was taken from a thin clay bed (<5 cm thick) and consisted of a dark grey clay with no visible macrofossils. Site TOL4 is a 7 m high outcrop comprising soft, sandy carbonates which weather orangeish. Oysters are particularly abundant at this site, with some beds consisting of thick deposits of intact shells. However, unlike the TOL2 section, larger foraminifera including *Alveolina* were only found in the lowermost bed of the section and are comparatively uncommon. The ostracod sample TOL4-LC4 came from a small bed, <10 cm thick, consisting of pale grey, sandy clay, which showed some orange weathering. No macrofossils were visible in the clay bed. Sample TOL4-LC2 was collected from the matrix of one of the oyster beds slightly below the TOL4-LC4 horizon. All clay samples were checked for nannofossils prior to washing, which would have been useful to further constrain the age model. However, all were barren. The presence of *Alveolina* indicates an Early–Middle Eocene age (Hottinger 1974; Serra-Kiel *et al.* 1998). The mixture of *Alveolina* and oysters suggests a very shallow marine, coastal environment, transitioning from carbonate to clastic deposition (Cotton *et al.* in prep.).

Material and methods

The three clay samples from sites TOL2 (sample TOL2-LC2A) and TOL4 (samples TOL4-LC2 and TOL4-LC4) were wet-sieved through a 63 μm sieve and then dried in an oven at < 40°C. Since the samples were ostracod-rich, the residue samples were split into fractions using a splitter to obtain >300 specimens. All specimens in a split were picked from the >150 μm size fraction, sorted, identified and counted. The number of specimens refers to valves and carapaces. Full information about the samples and specimens used for the present study is given in Table 1 and Supplementary Table S1. Uncoated ostracod specimens were digitally imaged with a Hitachi S-3400N variable pressure scanning electron microscope (SEM) in low-vacuum mode, at the Electron Microscope Unit, University of Hong Kong.

For the higher classification, we mainly referred to the World Ostracoda Database (Brandão *et al.* 2017), Whatley *et al.* (1993) and Horne *et al.* (2002).

Repository. Figured specimens are deposited in the Naturalis Biodiversity Center, Leiden, the Netherlands (**RGM**),

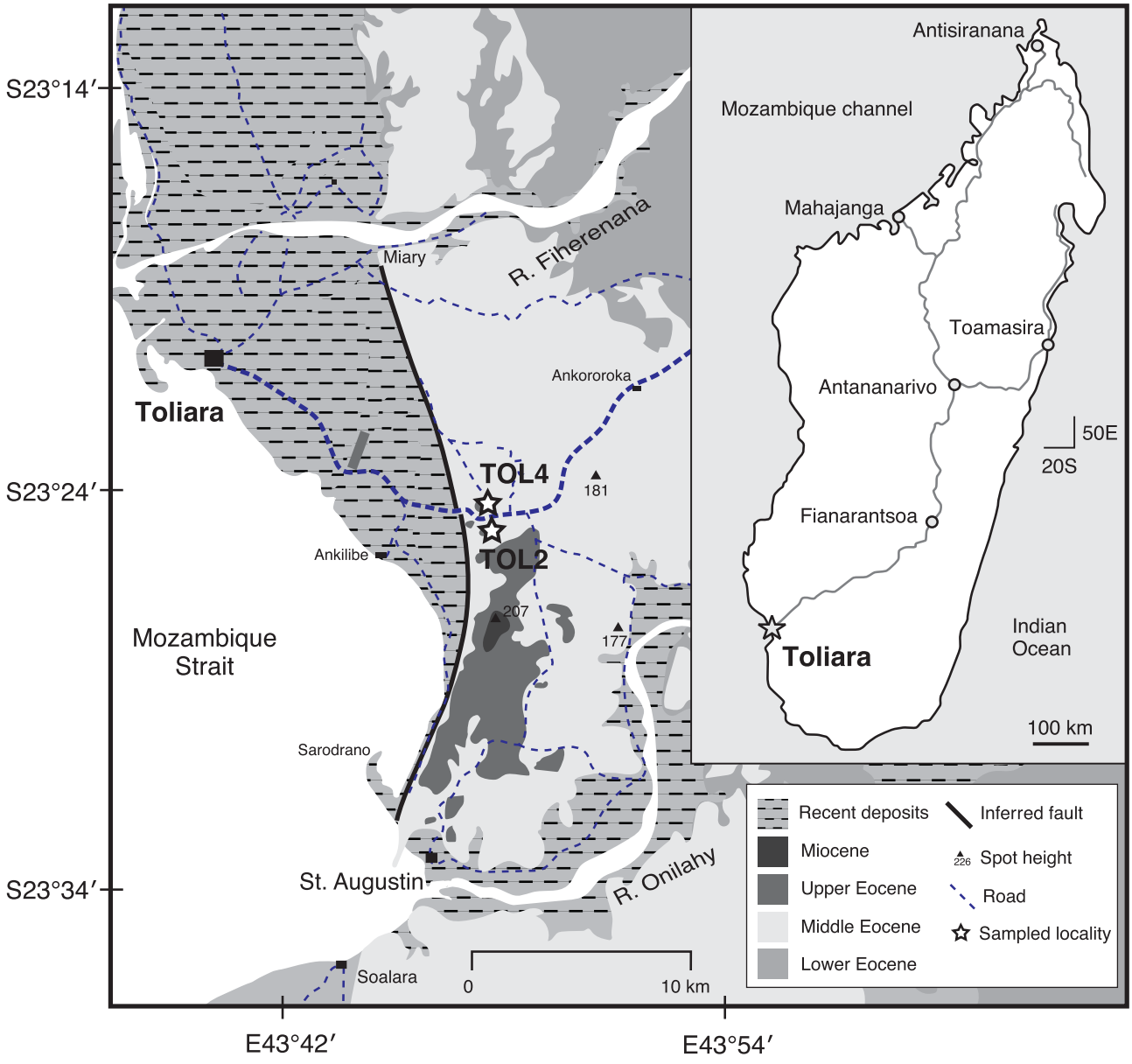


Figure 1. Index and locality maps. Index map shows the location of Toliara in Madagascar. Locality map is a close-up showing locations of sites TOL2 and TOL4 in the Toliara area.

under catalogue numbers RGM.1349541–RGM.1349634. MY's personal catalogue numbers (prefixed LC2A, LC2 and LC4 indicating samples from TOL2-LC2A, TOL4-LC2 and TOL4-LC4, respectively, from which a number-bearing specimen comes) are also shown.

Abbreviations. LV, left valve; RV, right valve; L, length (mm); H, height (mm).

Systematic palaeontology

Class **Ostracoda** Latreille, 1802
Subclass **Podocopa** Sars, 1866
Order **Platycopina** Sars, 1866
Superfamily **Cytherelloidea** Sars, 1866
Family **Cytherellidae** Sars, 1866
Genus ***Cytherella*** Jones, 1849

Type species. *Cytherina ovata* Roemer, 1841, designated by Ulrich (1894).

Cytherella cf. ***kimensis*** Bhandari, Singh & Rana, 2005
(Fig. 2A, B)

Remarks. This species is very similar to *Cytherella kimensis* Bhandari, Singh & Rana, 2005, but the latter has a flat 'belt' along the anterior margin and stronger punctation. It is also similar to *Cytherella hastata*

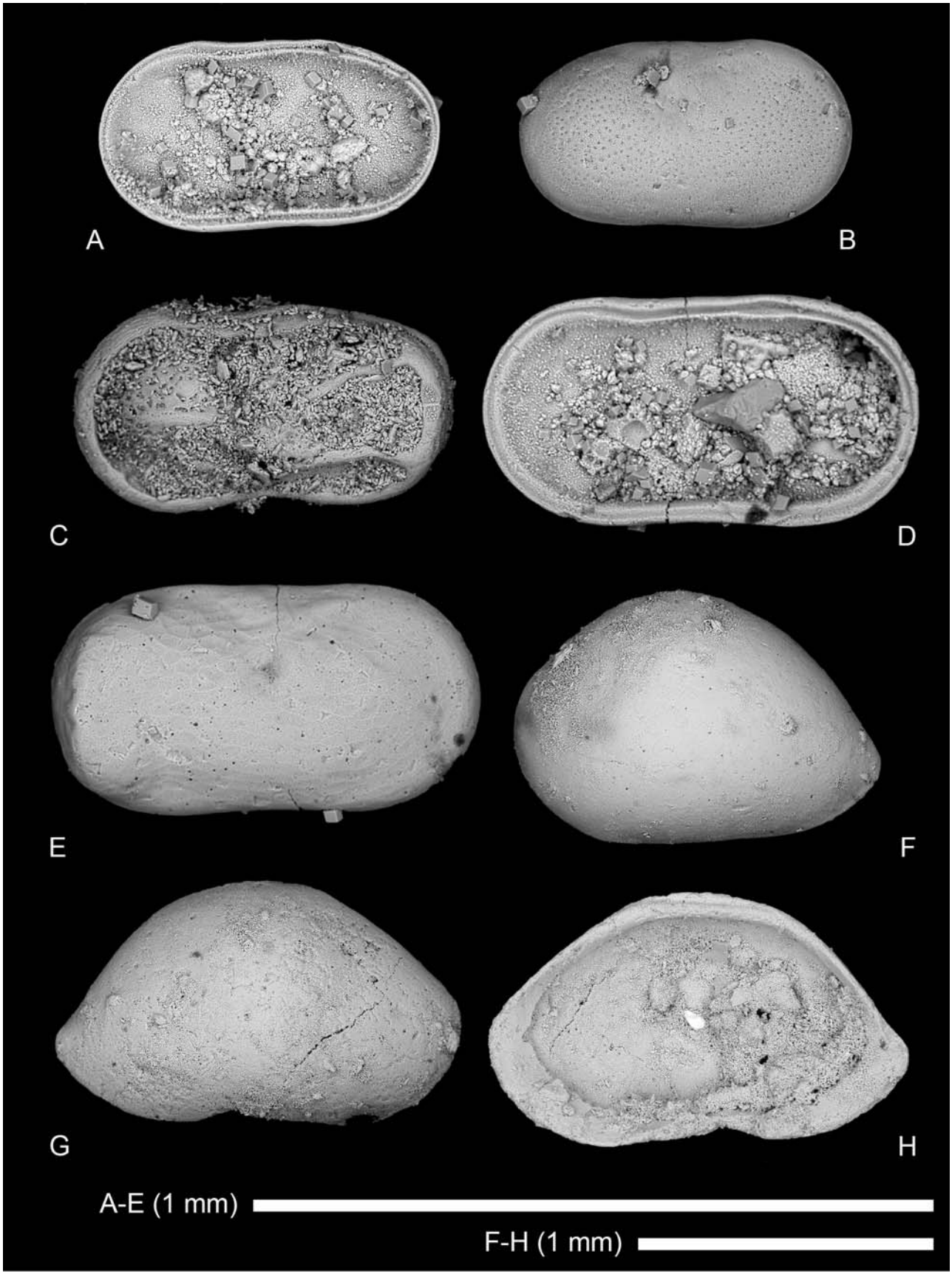

A
B
C
D
E
F
G
H
A-E (1 mm)
F-H (1 mm)

Table 1. Eocene Madagascar ostracod data summary.

Ostracod taxon	TOL4-LC2	TOL4-LC4	TOL2-LC2A
Alciella irizukii	2		
Argilloecia? sp. 1	1		
Bairdoppilata ilaroensis sensu lato	10	3	
Cytherella cf. *kimensis*	2	14	
Cytherelloidea sp. 1	1		
Cytherelloidea sp. 2		2	
Cytherois sp. 1	2		
Echinocythereis sahnii	1		
Hermanites cf. *percultus*	10	1	
Hermanites sp. 1	2		
Kingmaina? sp. 1		1	
Loxoconcha loculus	8	2	1
Muellerina eocenica	6		
Neocyprideis armata sensu lato	123	249	279
Neocyprideis polygonoreticulata	2		
Neocyprideis sp. 1	4		
Neomonoceratina afroangulosa	20		
Paijenborchellina madagascarensis	63	34	15
Paracytheridea sp. 1		1	8
Phlyctenophora cf. *chauhani*	2	11	14
Pokornyella lamarckiana sensu lato	2		
Pontocythere sp. 1	1		
Reticuloquadracythere apostolescui sensu lato	15	1	
Schizocythere cf. *prolata*			2
Semicytherura sp. 1		4	
Stigmatobradleya hunti	9	1	1
Urocythereis? sp. 1	1	1	
Uroleberis paranuda	22	1	
Xestoleberis renemai	11	1	
Xestoleberis sp. 1	3	1	
Gen. et sp. indet. 1	1		
Gen. et sp. indet. 2	1		
Total	325	328	320
Number of species	27	17	7

Neale & Singh, 1985, but the outline is slightly different (*Cytherella hastata* is more slender), and to *Cytherella ahlmadoensis* Bassiouni & Luger, 1996, but the carapace of our species is evenly covered by punctation, whereas *C. ahlmadoensis* lacks punctation in the central part of carapace.

Genus ***Cytherelloidea*** Alexander, 1929

Type species. *Cytherella williamsoniana* Jones, 1849.

Remarks. We consider *Keijcyoidea* Malz, 1981 a junior synonym of *Cytherelloidea* Alexander, 1929, following Titterton & Whatley (2006a).

***Cytherelloidea* sp. 1**
(Fig. 2C)

Remarks. This species is similar to *Cytherelloidea keiji* McKenzie, 1967, but the latter has better developed ridges and polygonal reticulation.

Figure 2. Scanning electron microscope (SEM) images of *Cytherella*, *Cytherelloidea* and *Bairdoppilata* species. **A, B,** *Cytherella* cf. *kimensis* Bhandari, Singh & Rana, 2005, RGM.1349541 (LC4010), RV. **C,** *Cytherelloidea* sp. 1, RGM.1349542 (LC2033), carapace. **D, E,** *Cytherelloidea* sp. 2, RGM.1349543 (LC4009), RV. **F–H,** *Bairdoppilata ilaroensis* sensu lato (Reyment & Reyment, 1959); **F,** RGM.1349544 (LC2007), juvenile LV; **G, H,** RGM.1349545 (LC2008), adult RV. B, E–G: lateral views; C: left lateral view of a carapace; A, D, H: internal views.

***Cytherelloidea* sp. 2**
(Fig. 2D, E)

Remarks. This species is very similar to *Cytherelloidea pandora* (Kornicker, 1963) but is distinguished by having a distinct vertical ridge along the posterior margin. It is also similar to *Cytherella strangulata* Ducasse, 1967 (for SEM image, see Ducasse *et al.* 1985), *Cytherella pustulosa* Keij, 1957 (for SEM image, see Guernet *et al.* 2012), *Cytherelloidea venusta* (Brady, 1880) (for SEM images of the lectotype and paralectotype specimens, see Titterton *et al.* 2001), and *Cytherella dictyon* Malz & Jellinek, 1989 but *Cytherella strangulata*, *Cytherella pustulosa*, *Cytherelloidea venusta*, and *Cytherella dictyon* have much more elongate polygonal fossae and posterior extremity dorsally.

Order **Podocopida** Sars, 1866
Suborder **Bairdiocopina** Gründel, 1967
Superfamily **Bairdioidea** Sars, 1866
Family **Bairdiidae** Sars, 1866
Genus ***Bairdoppilata*** Coryell, Sample & Jennings, 1935

Type species. *Bairdoppilata martyni* Coryell, Sample & Jennings, 1935.

Bairdoppilata ilaroensis s. l. (Reyment & Reyment, 1959)
(Fig. 2F–H)

1959 *Bairdia ilaroensis* Reyment & Reyment: 61, pl. 1, figs 1–7, text-figs 1a, b, 3a–n, 5a–h.
1981 *Bairdia ilaroensis* Reyment & Reyment; Reyment: 56, pl. 9, figs 6, 7.
1983 *Bairdoppilata ilaroensis* (Reyment & Reyment); Foster, Swain, & Petters: 109, pl. 1, figs 5, 7–11.
1987 *Bairdia ilaroensis* Reyment & Reyment; Okosun: 26, pl. 20, figs 7, 9–10.
1990 *Bairdia ilaroensis* Reyment & Reyment; Bassiouni & Luger: 780, pl. 1, fig. 15.
1990 *Bairdoppilata ilaroensis* (Reyment & Reyment); Carbonnel, Alzouma, & Dikouma: 674, pl. 1, fig. 19.
non 1991 *Bairdoppilata ilaroensis* (Reyment & Reyment); Carbonnel & Oyede: 5, pl. 1, fig. 1.
1991 *Bairdia amygdaloides* (Brady) *oblongata* van den Bold; Ahmad, Neale, & Siddiqui: 187, pl. 3, fig. 12 (?non pl. 4, figs 1–3).
non 1992 *Bairdia ilaroensis* Reyment & Reyment; Ismail: 45, pl. 1, fig. 5.
1992 *Bairdia ilaroensis* Reyment & Reyment; El-Waer: 47, pl. 4, figs 4–9.
1994 *Bairdia* gr. *ilaroensis* Reyment & Reyment; Keen, Al-Sheikly, Elsogher, & Gammudi: pl. 16.1, fig. 5.
1996 *Bairdia ilaroensis* Reyment & Reyment; Bassiouni & Luger: 8, pl. 1, figs 10–13.
1996 *Bairdia* sp aff. *Bairdia ilaroensis* Reyment & Reyment; El Sogher: 295, pl. 4, figs 1–5.
1998 *Bairdoppilata ilaroensis* (Reyment & Reyment); Colin, Tambareau, & Krasheninnikov: 291, pl. 1, figs 4, 5.
?2000 *Bairdia ilaroensis* Reyment & Reyment; Shahin: 292, fig. 4.15.
2003 *Bairdia ilaroensis* Reyment & Reyment; Morsi & Speijer: 70, pl. 1, fig. 5.
non 2005 *Bairdia ilaroensis* Reyment & Reyment; Ismail & Ied: 123, pl. 1, figs 15, 16.
non 2005 *Bairdia ilaroensis* Reyment & Reyment; Shahin: 755, pl. 1, figs 14, 15.
2008 *Bairdia ilaroensis* Reyment & Reyment; Morsi, Faris, Zalat, & Salem: 165, pl. 1, figs 11, 13, 14.
?2008 *Bairdia ilaroensis* Reyment & Reyment; Shahin, El Halaby, & El Baz: 129, pl. 1, fig. 11.

Remarks. *Bairdoppilata ilaroensis* (Reyment & Reyment, 1959) was originally described from the Paleocene of Nigeria, and has been widely reported from African and Arabian regions (Bassiouni & Luger 1996). Our specimens look conspecific with two paratype specimens of *Bairdoppilata ilaroensis* shown in plate 1, figure 1a, b of the original description; however, the holotype looks slightly different from these paratypes in outline, being more slender (Reyment & Reyment 1959). We tentatively consider that this difference is due to sexual dimorphism. *Bairdoppilata ilaroensis* is similar to *Bairdoppilata poddari* Lubimova & Mohan in Lubimova, Guha & Mohan, 1960 reported from the Early Eocene of India (for SEM images and synonymy, see Bhandari 1996) and *Bairdoppilata gliberti* Keij, 1957 reported from the Middle Eocene of Belgium and France, but it is distinguished by the straight (instead of concave) dorsal half of the anterior margin. The synonym list is modified after Bassiouni & Luger (1996), Morsi *et al.* (2008), and Shahin *et al.* (2008), in which there is certain variation in outline (e.g. concave/straight dorsal half of the anterior margin) and surface ornamentation (smooth or punctate). Thus, we call our material *Bairdoppilata ilaroensis* sensu lato, which may include the above-mentioned species from India and Europe. Indeed, *Bairdoppilata gliberti* [as *Bairdia* (*Bairdoppilata*) *glibarti*] reported in Ducasse *et al.* (1985, pl. 72, figs 7, 8) looks conspecific with our species. The synonymy between *Bairdoppilata ilaroensis* and *Bairdoppilata gliberti* should be carefully considered by investigating specimens from the type locality using SEM given that both species were described before SEM, was available. One of our specimens (Fig. 2F) is probably a juvenile (A-1) showing a more rounded outline compared to the adult specimen (Fig. 2G, H).

Suborder **Cypridocopina** Jones, 1901
Superfamily **Cypridoidea** Baird, 1845

Family **Candonidae** Kaufmann, 1900
Genus ***Phlyctenophora*** Brady, 1880

Type species. *Phlyctenophora zealandica* Brady, 1880 [junior synonym of *Macrocypris orientalis* Brady, 1868: see Whatley & Zhao (1987) and Wouters (1999)].

Remarks. The type species and its close relatives (e.g. *Phlyctenophora* cf. *zealandica*) have been widely reported in the Indo-Pacific region (Kingma 1948; van Morkhoven 1963; Hartmann 1978, 1981; Jain 1978, 1981b; Howe & McKenzie 1989; Yassini *et al.* 1993; Yassini & Jones 1995; Dewi 1997). Although some researchers consider *Phlyctenophora* Brady, 1880 a junior synonym of *Paracypris* Sars, 1866 (Müller 1912; Hartmann 1963; Benson & Maddocks 1964), we consider them separate genera following van Morkhoven (1963), McKenzie (1967), and Maddocks (1988). Regarding carapace morphology, *Paracypris* Sars, 1866 is much more triangular in outline with a sharply acuminate and prominent posterior margin. Internal details such as subcentral muscle scars, marginal pores and vestibule are similar in the two genera (Maddocks 1969, 1988; Wouters 1999).

Phlyctenophora cf. ***chauhani*** Khosla, 1978
(Fig. 3A–J)

Remarks. This species is very similar to *Phlyctenophora chauhani* Khosla, 1978, but *Phlyctenophora chauhani* has a more slender outline. It is also similar to *Paracypris darrorensis* Bassiouni & Luger, 1996, *Bythocypris* sp. A of El Sogher (1996), and *Paracypris* aff. *Paracypris* sp. A Esker, 1968 of El Sogher (1996). However, *Paracypris darrorensis* has more acuminate posterior margin and straighter dorsal margin, *Bythocypris* sp. A is more slender, and *Paracypris* aff. *Paracypris* sp. A has a more acuminate posterior margin. As partly shown above, similar species (i.e. those with a less acuminate posterior margin compared to true *Paracypris* species: see the Remarks for the genus above) have been broadly considered either *Phlyctenophora* Brady, 1880 or *Paracypris* Sars, 1866 (or even *Bythocypris* Brady, 1880, belonging to a different family) in the Palaeogene–Miocene of the European, Arabian, African, and Indian regions (e.g. Khosla 1978; Ducasse *et al.* 1985; Bassiouni & Luger 1996; Bhandari 1996; El Sogher 1996; Shahin *et al.* 2008). Most are probably the same genus and we prefer to assign them to *Phlyctenophora* at least tentatively.

Superfamily **Pontocypridoidea** Müller, 1894
Family **Pontocyprididae** Müller, 1894
Genus ***Argilloecia*** Sars, 1866

Type species. *Argilloecia cylindrica* Sars, 1866.

Argilloecia? **sp. 1**
(Fig. 4A)

Remarks. The specimen is poorly preserved and thus its generic assignment is uncertain.

Suborder **Cytherocopina** Gründel, 1967
Superfamily **Cytheroidea** Baird, 1850
Family **Cushmanideidae** Puri in Hartmann & Puri, 1974
Genus ***Pontocythere*** Dubowsky, 1939

Type species. *Pontocythere tchernjawskii* Dubowsky, 1939.

Remarks. Following van Morkhoven (1963), Hulings (1966), Garbett & Maddocks (1979) and Athersuch (1982), we consider *Pontocythere* Dubowsky, 1939 and *Cushmanidea* Blake, 1933 separate genera.

Pontocythere **sp. 1**
(Fig. 4B, C)

Family **Cytheridae** Baird, 1850
Genus ***Paijenborchellina*** Kusnetzova in Mandelstam, Schneider, Kuznetsova, & Katz, 1957

Type species. *Paijenborchellina excelens* Kusnetzova in Mandelstam, Schneider, Kuznetsova, & Katz, 1957.

Paijenborchellina madagascarensis sp. nov.
(Figs 5A–K, 6A–H)

Derivation of name. From the type locality, Madagascar.

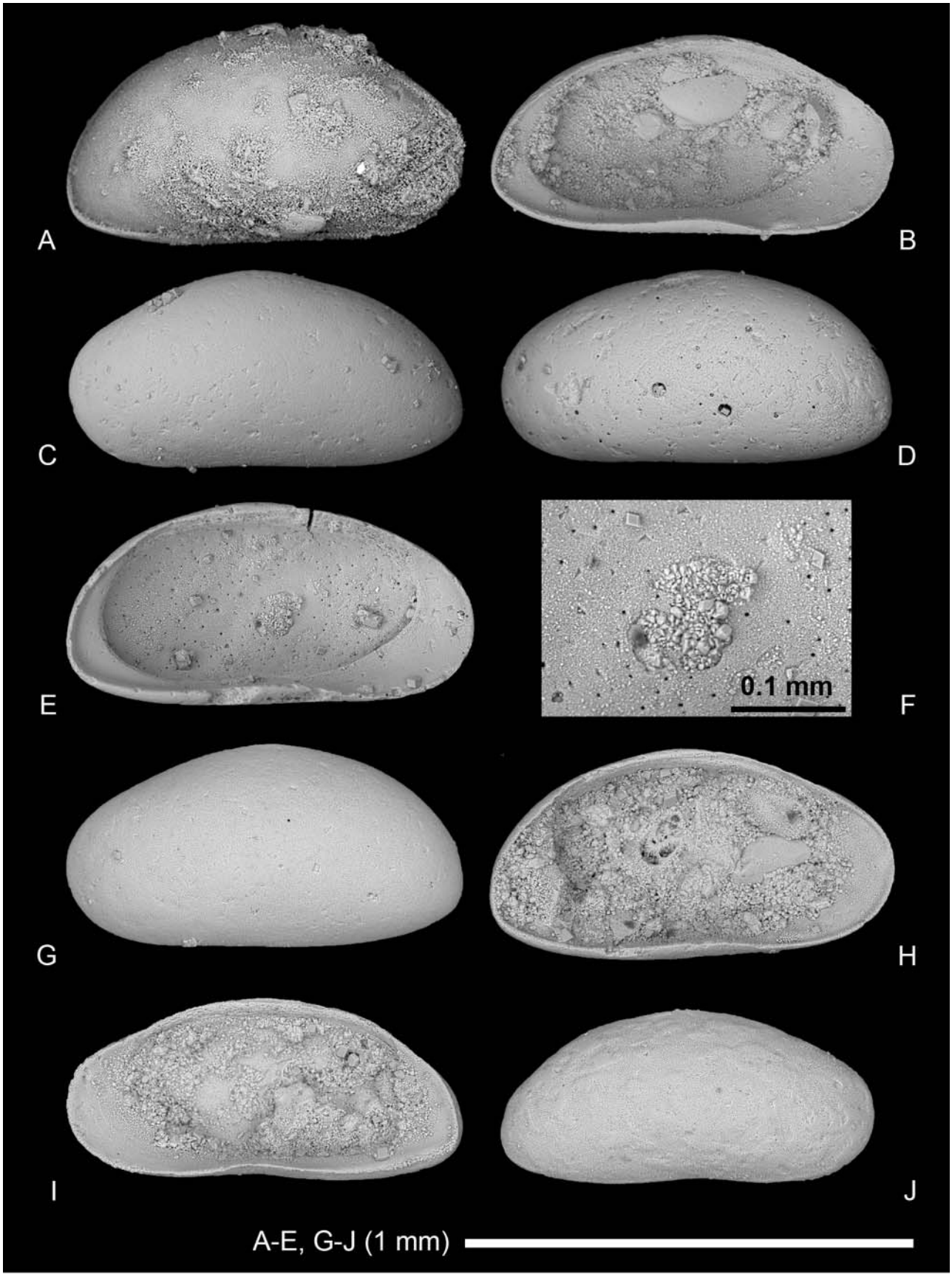
Material. Holotype: RV, RGM.1349561 (LC4016) (Fig. 6E, F). Paratypes: LV, RGM.1349553 (LC2022) (Fig. 5A); LV, RGM.1349554 (LC2023) (Fig. 5B, C); RV, RGM.1349555 (LC2024) (Fig. 5D, E); RV, RGM.1349556 (LC2025) (Fig. 5F, G); RV, RGM.1349557 (LC2048) (Fig. 5H, I); LV, RGM.1349558 (LC2049) (Fig. 5J, K); LV, RGM.1349559 (LC4014) (Fig. 6A, B); LV, RGM.1349560 (LC4015) (Fig. 6C, D); RV, RGM.1349562 (LC4017) (Fig. 6G, H).

Type locality and horizon. Southern Madagascar, Early–Middle Eocene.

Dimensions. RGM.1349561 (LC4016) (holotype): L = 0.663 mm, H = 0.296 mm. RGM.1349559 (LC4014) (paratype): L = 0.764 mm, H = 0.312 mm. RGM.1349558 (LC2049) (paratype): L = 0.747 mm, H = 0.322 mm.

Diagnosis. A well-calcified *Paijenborchellina* species with very well-developed primary reticulation and ventrolateral, median lateral, and dorsolateral ridges.

Description. Carapace well calcified, moderate in size, highest at anterodorsal corner. Outline elongate and subtriangular in lateral view; anterior margin obliquely


A
B
C
D
E
0.1 mm
F
G
H
I
J
A-E, G-J (1 mm)

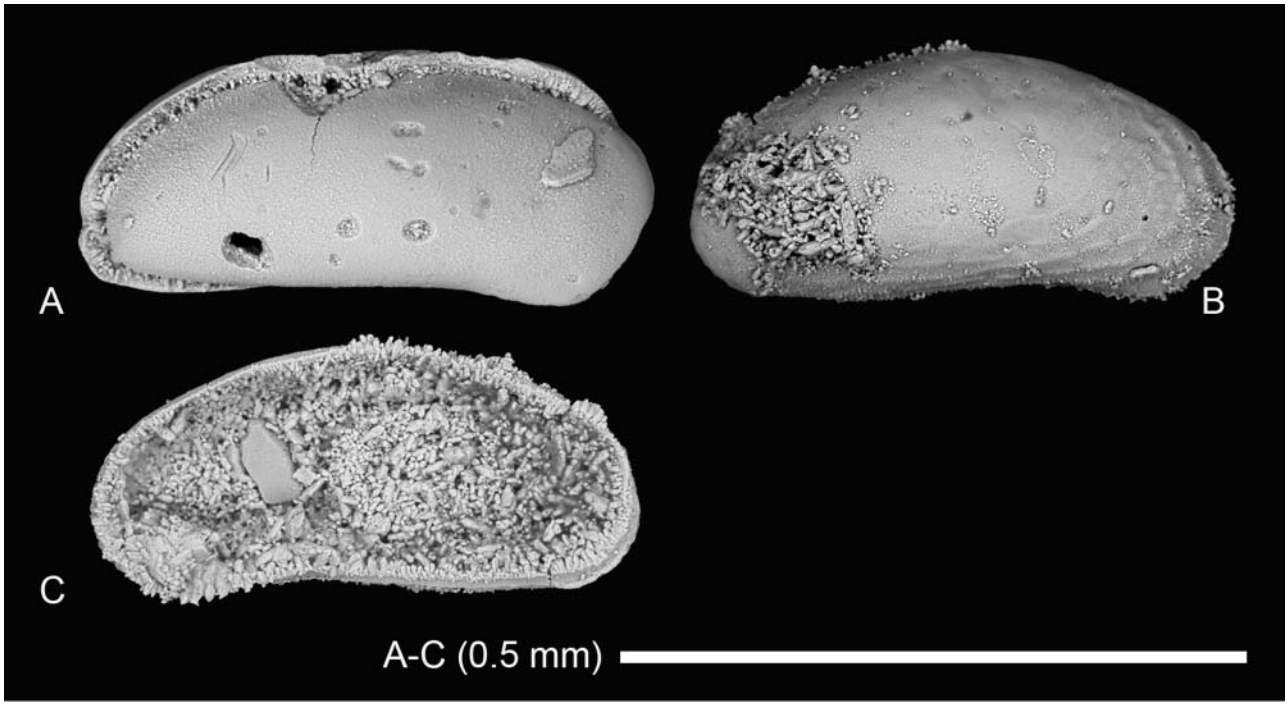


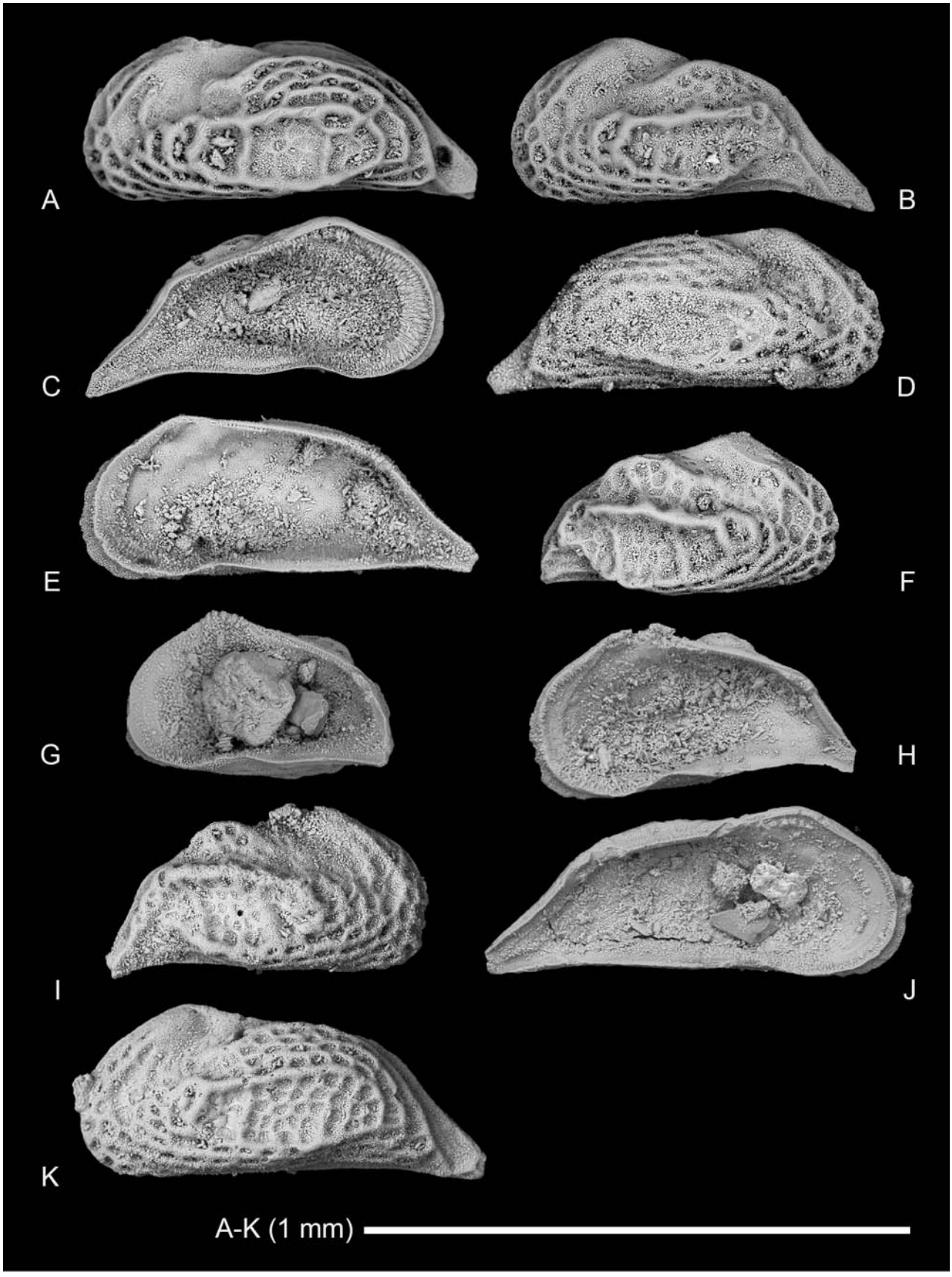
Figure 4. Scanning electron microscope images of *Argilloecia*? and *Pontocythere* species. **A,** *Argilloecia*? sp. 1, RGM.1349551 (LC2030), carapace; **B, C,** *Pontocythere* sp. 1, RGM.1349552 (LC2032), adult? RV. A: right lateral view of carapace; B: lateral view; C: internal view.

rounded; caudal process prominent, long, acute, downturned, pointed ventrally; dorsal margin almost straight, dorsolateral ridge extending above dorsal margin; ventral margin almost straight or slightly concave. Anterodorsal corner angular; posterodorsal corner weakly angular. Surface primary reticulation well developed overall, except dorsomedian sulcus. Ventrolateral, median lateral, and dorsolateral ridges well developed. Ventrolateral and median lateral ridges compose an elongate loop. Dorsolateral ridge curved. Dorsomedian sulcus well developed. Terminal elements of hingement look crenulate. Other internal features not clearly observable. Sexual dimorphism distinct.

Remarks. *Paijenborchellina madagascarensis* sp. nov. is very similar to *Paijenborchellina venosa* Gurney, 1979 (*Paijenborchellina indoarabica* Jain, 1981a is a junior synonym of *Paijenborchellina venosa*; see Mostafawi 2003), but is distinguished by having distinct ridges. *Paijenborchellina venosa* is known from very shallow and hypersaline environments with salinity >40 (Bate 1971; Al-Abdul-Razzaq *et al.* 1982; Mostafawi 2003). Bate (1971) considered *Paijenborchellina venosa* (his *Paijenborchellina* sp.) a salinity-tolerant (i.e. euryhaline) species showing morphological variation (e.g. development of ventrolateral ridge) under varying environmental conditions. This species also shows considerable morphological variation in the development of surface ornamentation (Figs 5, 6).

Bassiouni & Luger (1996) considered *Gibborchella* Gründel, 1976 a junior synonym of *Paijenborchellina* Kusnetzova, 1957. The only difference between *Paijenborchellina* and *Gibborchella* is the presence vs absence of a 'transverse furrow and longitudinal rib' on the valve surface (Gründel 1976; Szczechura 1980). Gründel (1976) erected the new genus *Gibborchella* for the species without this structure. Both Szczechura (1980) and Bassiouni & Luger (1996) considered the difference insufficient to divide genera. This structure is only known from the type species *Paijenborchellina excelens* Kusnetzova, 1957, making this genus monospecific if we accept *Gibborchella* as a valid genus, and is rather schematically illustrated in the original description. Since no microscopic or SEM image of *Paijenborchellina excelens* is available, further details are uncertain, preventing comparison between *Paijenborchellina* and *Gibborchella*. However,

Figure 3. Scanning electron microscope images of *Phlyctenophora* cf. *chauhani* Khosla, 1978. **A**, RGM.1349546 (LC2013), carapace; **B, C**, RGM.1349547 (LC4028), adult LV; **D–F**, RGM.1349548 (LC4011), adult LV; **G, H**, RGM.1349549 (LC4030), adult LV; **I, J**, RGM.1349550 (LC4031), adult RV. C, D, G, J: lateral views. A: right lateral view of a carapace; B, E, F, H, I: internal views; F: closeup of subcentral muscle scars (details not observable).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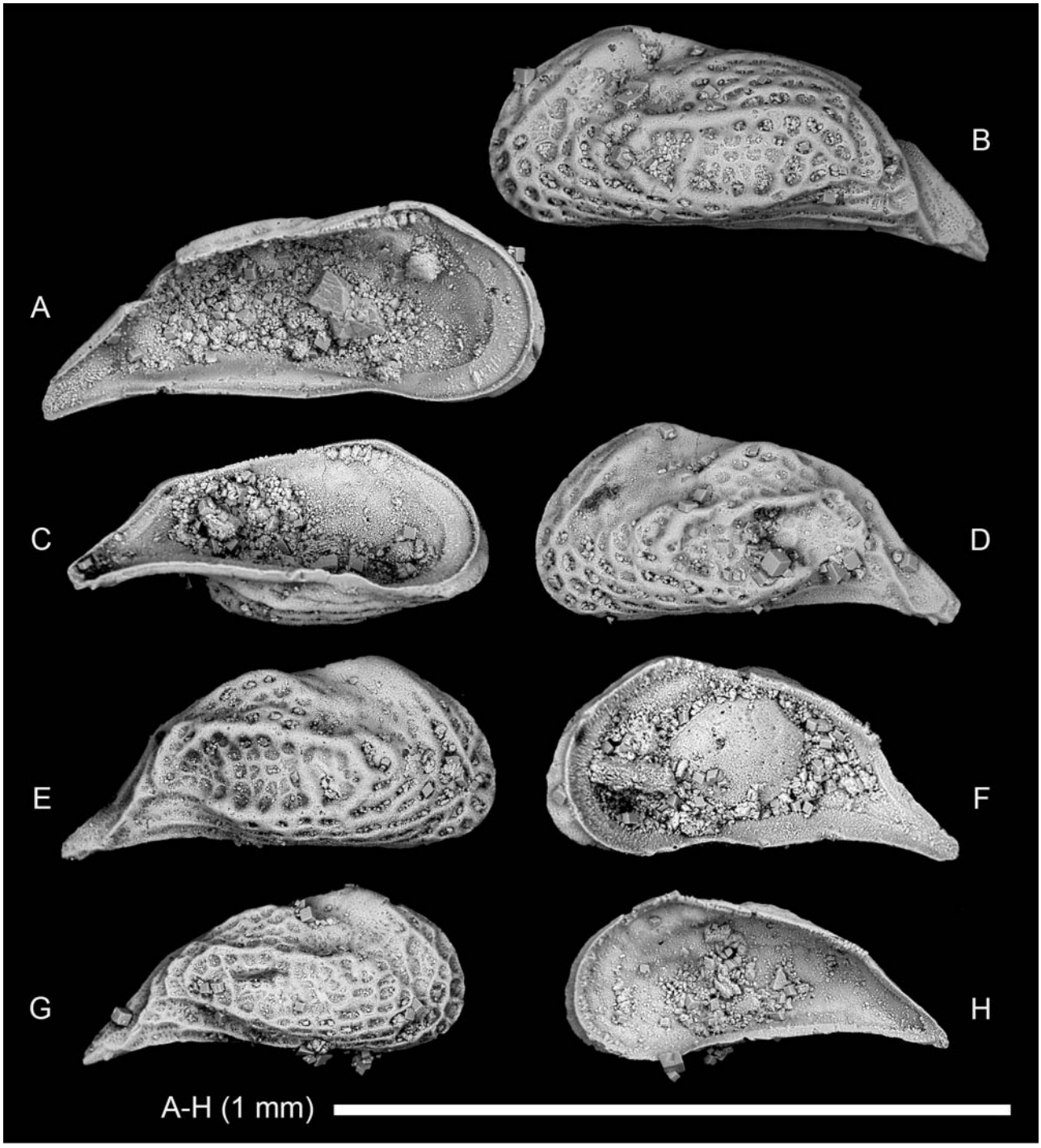


Figure 6. Scanning electron microscope images of *Paijenborchellina madagascarensis* sp. nov. **A, B,** RGM.1349559 (LC4014), adult male LV; **C, D,** RGM.1349560 (LC4015), adult female LV; **E, F,** RGM.1349561 (LC4016), adult female RV; **G, H,** RGM.1349562 (LC4017), A-1 juvenile RV. A, C, F, H: internal views; B, D, E, G: external views.

Figure 5. Scanning electron microscope images of *Paijenborchellina madagascarensis* sp. nov. **A,** RGM.1349553 (LC2022), adult male LV; **B, C,** RGM.1349554 (LC2023), adult female? LV; **D, E,** RGM.1349555 (LC2024), adult male RV; **F, G,** RGM.1349556 (LC2025), adult female RV; **H, I,** RGM.1349557 (LC2048), adult female RV; **J, K,** RGM.1349558 (LC2049), adult male LV. A, B, D, F, I, K: lateral views; C, E, G, H, J: internal views.

our discovery of a second species with this structure strongly supports Szczechura's (1980) and Bassiouni & Luger's (1996) opinions. The elongate loop composed of ventrolateral and median lateral ridges of our species probably corresponds to the 'transverse furrow and longitudinal rib' of *Paijenborchellina excelens*. High-quality SEM images (Figs 5, 6) show clear similarity of our species with the other '*Paijenborchellina'* species that lack this structure (i.e. *Gibborchella*). In particular, our species and *Paijenborchellina venosa* are very similar (except for this structure) and obviously congeneric. Thus, we conclude that *Gibborchella* Gründel, 1976 is a junior synonym of *Paijenborchellina* Kusnetzova, 1957.

Family **Cytherideidae** Sars, 1925
Genus ***Neocyprideis*** Apostolescu, 1956

Type species. *Cyprideis* (*Neocyprideis*) *durocortoriensis* Apostolescu, 1956.

Remarks. There are three closely related genera – *Neocyprideis* Apostolescu, 1956, *Miocyprideis* Kollmann, 1960 and *Bishopina* Bonaduce, Masoli & Pugliese, 1978 – that Titterton & Whatley (1988, 2006b; Titterton *et al.* 2001) considered congeneric, whereas other researchers have tended to separate these genera (Wouters 1981, 2005; Malz & Ikeya 1986; Colin & Carbonel 1990; Colin *et al.* 1990; Jellinek 1993; Mostafawi *et al.* 2005). We abstain from separating these genera by following Titterton and Whatley, at least for now. However, in our opinion the three genera are morphologically distinguishable and have different environmental preferences, as summarized below. Thus, we believe their generic status merits further consideration.

Neocyprideis (type species *Neocyprideis durocortoriensis* Apostolescu, 1956; see Ducasse *et al.* 1985 for SEM images) is distinguished from *Miocyprideis* by having a higher and shorter outline; a much more inflated carapace, especially in the posterior part; an upturned posterior margin; similar height at anterior and posterior cardinal angles (or greater height at posterior cardinal angle than at anterior cardinal angle); and (usually) well-developed dorsomedian sulcus. *Neocyprideis* lacks marginal denticulation that many *Miocyprideis* species have. There are several transitional species that include both '*Neocyprideis'* and '*Miocyprideis'* specimens in a species (e.g. *Neocyprideis simplex* Siddiqui, 2000; *Neocyprideis isoarcuata* Bassiouni & Luger, 1996; *Neocyprideis enkheimensis* Malz, 1973). This variation was interpreted as sexual dimorphism in the original descriptions. However, they may be separate species (i.e. 'females' are a *Neocyprideis* species, and 'males' are a *Miocyprideis* species), especially given the fact that they tend to occur in a stratigraphically transitional stage from *Neocyprideis* to *Miocyprideis* in our taxonomic sense (Siddiqui 2000), or in late or latest stages of *Neocyprideis* occurrence (Malz 1973; Bassiouni & Luger 1996). It merits further investigation whether these are transitional species with inflated carapaces only in females, or whether a *Neocyprideis* species (i.e. females) and a *Miocyprideis* species (i.e. males) were erroneously assigned to a single species. Included species (not exhaustive) are: *Neocyprideis durocortoriensis* Apostolescu, 1956 (see also Ducasse *et al.* 1985); *Neocyprideis* sp. A of Siddiqui (2000); *Neocyprideis simplex* Siddiqui, 2000 [at least the holotype (pl. 1, fig. 4) is included in *Neocyprideis*; the majority of paratypes (pl. 1, figs 2, 3, 5) may be a different species that belongs to *Miocyprideis*, or this difference may be interpreted as sexual dimorphism, as was done by Siddiqui]; *Neocyprideis regularis* Siddiqui, 2000; *Neocyprideis rotundata* Bassiouni & Luger, 1996; *Neocyprideis armata isoarcuata* Bassiouni & Luger, 1996 [at least the holotype (pl. 4, figs 7, 10) is included in *Neocyprideis*; a paratype specimen (pl. 4, fig. 13) may be a different species belonging to *Miocyprideis*, or this difference may be interpreted as sexual dimorphism as done by Bassiouni & Luger]; *Neocyprideis dacquei* Bassiouni & Luger, 1996; *Cyprideis* (*Goerlichia*) *apostolescui* Keij, 1957; *Neocyprideis* cf. *apostolescui* (Keij, 1957) (Ducasse *et al.* 1985); *Cytheridea williamsoniana* Bosquet, 1852 (see also Keij 1957 and Ducasse *et al.* 1985); *Cythere* (*Cytherideis*) *colwellensis* Jones, 1857 (see also Keen 1977a, b, 1978; Lord *et al.* 2009); *Neocyprideis rusaylensis* Keen & Racey, 1991; and *Neocyprideis* (*Neocyprideis*) *enkheimensis* Malz, 1973 [at least the holotype and a paratype (pl. 19, figs 13, 14) are included in *Neocyprideis*; some paratype specimens (pl. 19, figs 11, 12) may be a different species belonging to *Miocyprideis*, or this difference may be interpreted as sexual dimorphism, as was done by Malz].

Miocyprideis (type species *Miocyprideis janoscheki* Kollmann, 1960) is distinguished from *Neocyprideis* by having more elongated outline; less inflated carapace, especially in the posterior part; comparatively downturned posterior margin pointed at the mid-height or below; greater height at anterior cardinal angle than at posterior cardinal angle; inconspicuous dorsomedian sulcus; (usually) marginal denticulation; and (usually) strong overlapped posteroventral margin (i.e. posteroventral flat area outside the margin: Fig. 9E, G). Included species (not exhaustive) are: *Miocyprideis janoscheki* Kollmann, 1960; *Cytheridea spinulosa* Brady, 1868 (= *Clithrocytheridea atjehensis* Kingma, 1948; see Zhao & Whatley 1989b); *Miocyprideis phuketensis* Malz & Ikeya, 1986; *Cyprideis chaudhuryi* Lubimova & Guha in Lubimova *et al.* 1960); *Miocyprideis kachchhensis* Khosla, 1988; *Miocyprideis lyubimovae* Khosla, 1978; *Miocyprideis*

okhaensis Khosla, 1988; *Miocyprideis paravuremis* Khosla, 1988; *Miocyprideis punctata* Khosla, 1988; *Miocyprideis thirukkaruvensis* Guha & Rao, 1976; *Neocyprideis formosa* Siddiqui, 2000; *Neocyprideis armata armata* Bassiouni & Luger, 1996; *Schuleridea bhupendri* Singh & Misra, 1968 (Bhandari 1996); *Cytheridea agilis* Guan *et al.* 1978 (Wouters 2005); *Neocyprideis* sp. 1 of Montenegro, Pugliese & Sciuto (2004); *Neocyprideis polygonoreticulata* sp. nov.; and *Neocyprideis* sp. 1 of this study.

Bishopina (type species *Bishopina mozarti* Bonaduce, Masoli & Pugliese, 1978) is distinguished from *Neocyprideis* and *Miocyprideis* by having a subrectangular outline; truncated posterior margin; vertical posteromarginal (pseudo-)ridge; marginal denticulation; and irregular reticulation (instead of punctation). Included species: *Bishopina mozarti* Bonaduce, Masoli & Pugliese, 1978; *Bishopina vangoethemi* Wouters, 1981; and *Cytheridea timorensis* Fyan, 1916.

The evolutionary history and habitat changes of this lineage can be summarized as follows. *Neocyprideis* is probably the ancestor of *Miocyprideis* (Colin & Carbonel 1990), is known from the Upper Cenomanian to Miocene (Colin *et al.* 1990; Wouters 2005), and is especially well known from the Palaeogene (van Morkhoven 1963; Gerry & Rosenfeld 1973; Keen 1977b; Wouters 2005). This genus tends to be abundant in brackish-water and hypersaline environments, but not in normal marine environments (Keen 1977b, 1990; Keen & Racey 1991; Bassiouni & Luger 1996).

Miocyprideis probably evolved from *Neocyprideis* and is known from the Eocene to Recent (Khosla 1988; Bassiouni & Luger 1996; Mostafawi *et al.* 2005). Siddiqui (2000) might have shown a macroevolutionary sequence from *Neocyprideis* to *Miocyprideis*, via the Paleocene–Early Eocene *Neocyprideis* sp. A and *Neocyprideis regularis* to Upper Eocene *Miocyprideis formosa* (his *Neocyprideis formosa*) with the transitional species *Neocyprideis simplex* in between. In the Eocene, directly following the evolution of this genus, *Miocyprideis* continued to occupy similar habitats to *Neocyprideis* and often coexisted with it. For example, *Miocyprideis* is often dominant in very shallow hypersaline lagoonal environments and coexisted with *Neocyprideis* during the Middle Eocene (Bassiouni & Luger 1996). In younger strata, *Miocyprideis* appears to have become adapted to a fully marine environment. The fossil Neogene Indo-Pakistan species do not show any indication of brackish-water habitats (co-occurrence with brackish-water faunas) (Khosla 1988; Bhandari *et al.* 2001). The extant species are mainly known from tropical, shallow, fully marine environments (typically tropical, fully marine lagoons) in the Indian and Pacific oceans (Malz & Ikeya 1986; Khosla 1988; Babinot & Kouyoumontzakis 1995; Titterton *et al.* 2001; Mostafawi *et al.* 2005). But a few brackish-water species are known in the Recent Indo-Pacific (Montenegro *et al.* 2004; Wouters 2005) and Neogene European regions, including the type species from the Miocene of the Vienna Basin (Kollmann 1960; Zelenka 1990; Aiello *et al.* 2005). Recent brackish-water species show certain intermediate morphological states (i.e. similarity to *Neocyprideis*), including a relatively inflated carapace and/or lack of marginal denticulation, but otherwise are *Miocyprideis* (Montenegro *et al.* 2004; Wouters 2005). Among Recent species, marine species have punctate carapaces (Malz & Ikeya 1986; Khosla 1988; Titterton *et al.* 2001), while brackish-water species have smooth carapaces (Montenegro *et al.* 2004; Wouters 2005).

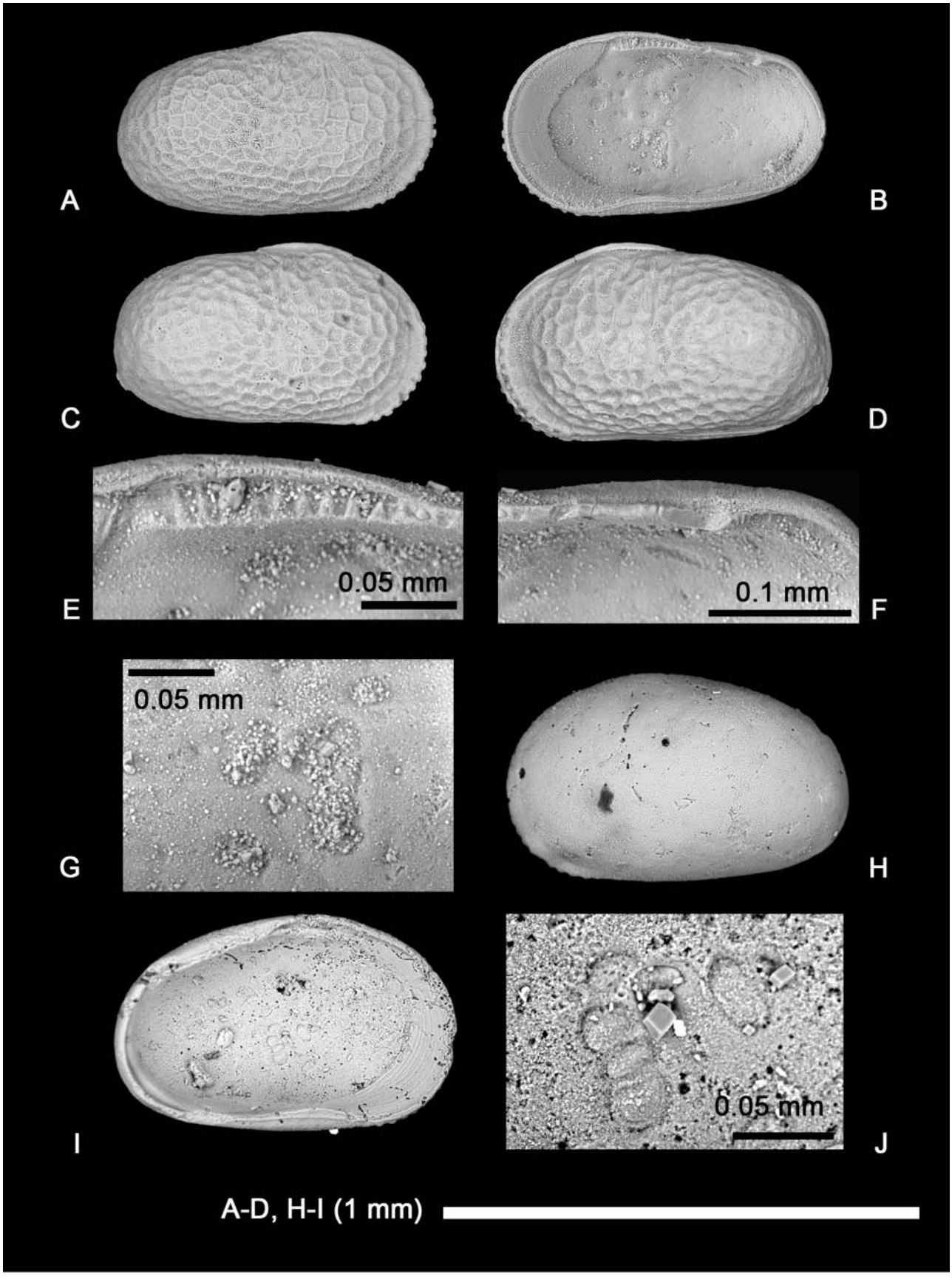
Bishopina probably evolved from *Miocyprideis* and is known only from the Miocene to Recent (Titterton *et al.* 2001). This genus lives in tropical, shallow, fully marine environments (typically tropical, fully marine lagoons) in the Indian and Pacific oceans (Bonaduce *et al.* 1978; Wouters 1981; Malz & Ikeya 1986; Weissleader *et al.* 1989; Titterton *et al.* 2001), the same habitat as Recent *Miocyprideis*.

Neocyprideis armata s. l. Bassiouni & Luger, 1996
(Figs 7H–J, 8A–J, 9A–H, 10A–H, 11A–H)

1996 *Neocyprideis armata* Bassiouni & Luger: 61, pl. 1, figs 1–7, text-figs 1a, b, 3a–n, 5a–h.

Remarks. Our specimens show variations in surface punctation, ranging from the smooth form to the (entirely) punctate form. Punctation of the intermediate form tends to be concentrated in the central part, and to be lacking at the anterior margin and the posterior third. The smooth form of our specimens is identical to the smooth form of *Neocyprideis armata* Bassiouni & Luger, 1996. Although Bassiouni & Luger (1996) described two subspecies of *Neocyprideis armata* – *Neocyprideis armata armata* Bassiouni & Luger, 1996 and *Neocyprideis armata isoarcuata* Bassiouni & Luger, 1996 – we consider these to be separate species, i.e. *Neocyprideis armata* Bassiouni & Luger, 1996 and *Neocyprideis isoarcuata* Bassiouni & Luger, 1996. Although the smooth forms are identical, the punctate form and the intermediate form of our specimens are slightly different from those of *Neocyprideis armata*. *Neocyprideis armata* has finer punctation compared to our specimens. The outline is identical between our specimens and *Neocyprideis armata*. Thus, we prefer to consider our specimens and *Neocyprideis armata* broadly conspecific and refer to them as *Neocyprideis armata* sensu lato, at least for now.

Bassiouni & Luger (1996) did not compare *Neocyprideis armata* with Indian and Pakistani species. *Neocyprideis armata* is very similar to *Neocyprideis chaudhuryi* (Lubimova & Guha in Lubimova *et al.*, 1960). Although the illustration of the original description of *Neocyprideis*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chaudhuryi is not very clear, it seems that the punctate form of *Neocyprideis chaudhuryi* has sparse punctation according to the original description text (stating "Reticules are very infrequent") and subsequent studies that showed microphotographic and SEM images (Guha 1961; Khosla 1978, 1988). In contrast, the punctate form of *Neocyprideis armata* has dense punctation. In addition, the original description of *Neocyprideis chaudhuryi* stated that "Surface of the valves is covered by irregularly oval angular reticules" (Lubimova *et al.* 1960), but *Neocyprideis armata* lacks such irregular-shaped puncta. Note that irregular-shaped punctae are not clearly visible in any illustrations, microphotographic or SEM images of *Neocyprideis chaudhuryi* (Guha 1961; Khosla 1978, 1988), and thus uncertainty remains. (The punctate form of) *Neocyprideis armata* is also very similar to *Neocyprideis formosa* Siddiqui, 2000, but is distinguished by its finer and less intensive punctation and by the presence of anteromarginal denticles. *Neocyprideis okhaensis* (Khosla, 1988) and *Neocyprideis paravurensis* (Khosla, 1988) are distinguished from *Neocyprideis armata* by having coarser punctation and posteromarginal denticles. Thus, although *Neocyprideis armata* shows considerable affinity to the Indo-Pakistan species of *Neocyprideis*, they are separate species.

Neocyprideis polygonoreticulata sp. nov.
(Fig. 7A–G)

Derivation of name. From its polygonal reticulation.

Material. Holotype: RV, RGM.1349563 (LC2001) (Fig. 7A, B, E–G). Paratype: carapace, RGM.1349564 (LC2053) (Fig. 7C, D).

Type locality and horizon. Southern Madagascar, Early–Middle Eocene.

Dimensions. RGM.1349563 (LC2001) (holotype): L = 0.666 mm, H = 0.382 mm. RGM.1349564 (LC2053) (paratype): L = 0.676 mm, H = 0.398 mm.

Diagnosis. A moderately calcified, relatively small *Neocyprideis* species with polygonal reticulation and evenly rounded posterior margin.

Description. Carapace moderately calcified, relatively small in size, highest at anterodorsal corner. Outline rounded, subrectangular in lateral view; anterior and posterior margins evenly rounded; dorsal margin slightly sinuous; ventral margin almost straight. Ventral half of the anterior margin denticulate. Anterodorsal corner very weakly angular; posterodorsal corner rounded. Lateral surface covered by polygonal primary reticulation. Dorsomedian sulcus present. Hingement merodont type. Terminal and median hinge elements crenulate. Subcentral muscle scars are composed on a frontal scar and adductor scars, but the details are not observable.

Remarks. This species is characterized by well-developed primary reticulation with angular, polygonal fossae. This structure is not known from any other species of *Neocyprideis*.

***Neocyprideis* sp. 1**
(Fig. 9I–J)

Remarks. This species is more inflated than *Neocyprideis armata* sensu lato Bassiouni & Luger, 1996.

Family **Cytheruridae** Müller, 1894
Genus ***Semicytherura*** Wagner, 1957

Type species. *Cythere nigrescens* Baird, 1838.

***Semicytherura* sp. 1**
(Fig. 12D, E)

Remarks. Several species of *Semicytherura* are known from the Miocene and Oligocene of Tanzania (Ahmad *et al.* 1991) adjacent to Madagascar, but *Semicytherura* sp. 1 is distinguished from all of these species by having very fine secondary reticulation and upturned caudal process pointing dorsally.

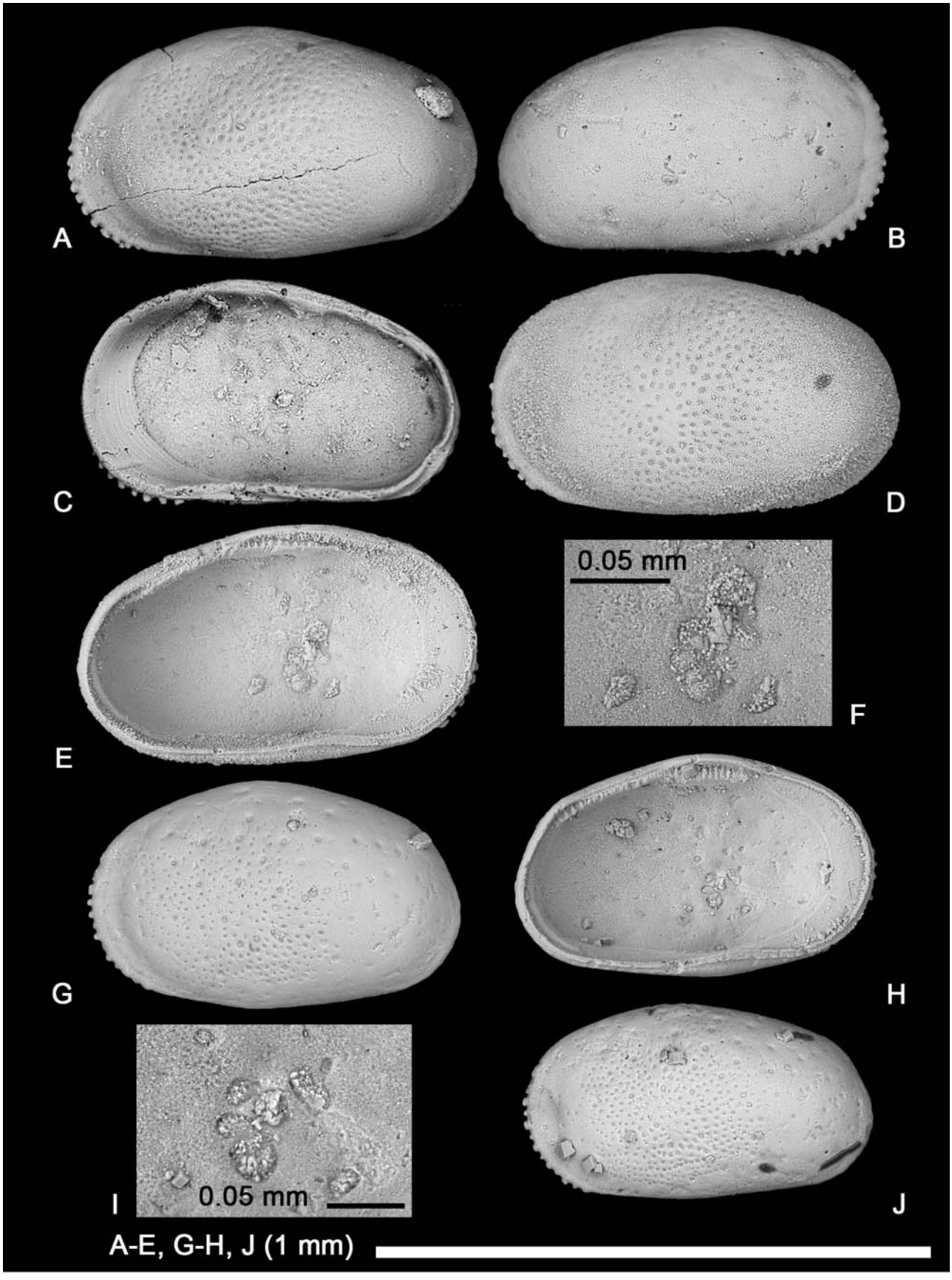
Family **Hemicytheridae** Puri, 1953

Remarks. Hemicytherid and thaerocytherid genera have often been erected monospecifically and/or based on 'old' species that were described in the nineteenth or early twentieth century and involve taxonomic uncertainty because of the lack of SEM and other images showing details of the morphology. This leads to considerable confusion of genus-level taxonomy in these families in our opinion. Taxonomic revision with re-study of the type species of uncertain genera and with a global (palaeo)biogeographical perspective is needed.

Genus ***Alciella*** Liebau, 1991

Type species. *Pataviella* (*Alciella*) *alciensis* Liebau, 1991.

Figure 7. Scanning electron microscope images of *Neocyprideis* species. **A–G,** *Neocyprideis polygonoreticulata* sp. nov.; **A, B, E–G,** RGM.1349563 (LC2001), adult RV; **C, D,** RGM.1349564 (LC2053), adult carapace. **H–J,** *Neocyprideis armata* sensu lato Bassiouni & Luger, 1996, RGM.1349565 (LC2003), adult female LV. A, H: lateral views; C: right lateral view of a carapace; D: left lateral view of a carapace; B, E–G, I, J: internal views; E, F: hingement closeup (all elements crenulate); G, J: close-up of subcentral muscle scars (one frontal and four adductor scars and a fulcral point observable at least in J).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Remarks. *Alciella* Liebau, 1991 is characterized by relatively flat (i.e. less inflated) valves; trapezoidal outline with straight dorsal margin and prominent posterior margin pointed ventrally; moderately developed subcentral tubercle; development of horizontal ridges, especially of dorsolateral, median lateral, and ventrolateral ridges; and regular primary reticulation. Dorsolateral and ventrolateral ridges do not extend above/below the dorsal/ventral margin, leaving a flat margin around the valve. Dorsolateral and median lateral ridges are connected through muri, making an elongate loop-like appearance posterodorsally. The ocular ridge is absent or runs on the anterior marginal rim outside the A fossa or between the A and Z fossae in Liebau's coding scheme (Liebau 1975, 1991; Schornikov & Tsareva 2002). All of these characters are present in our specimen.

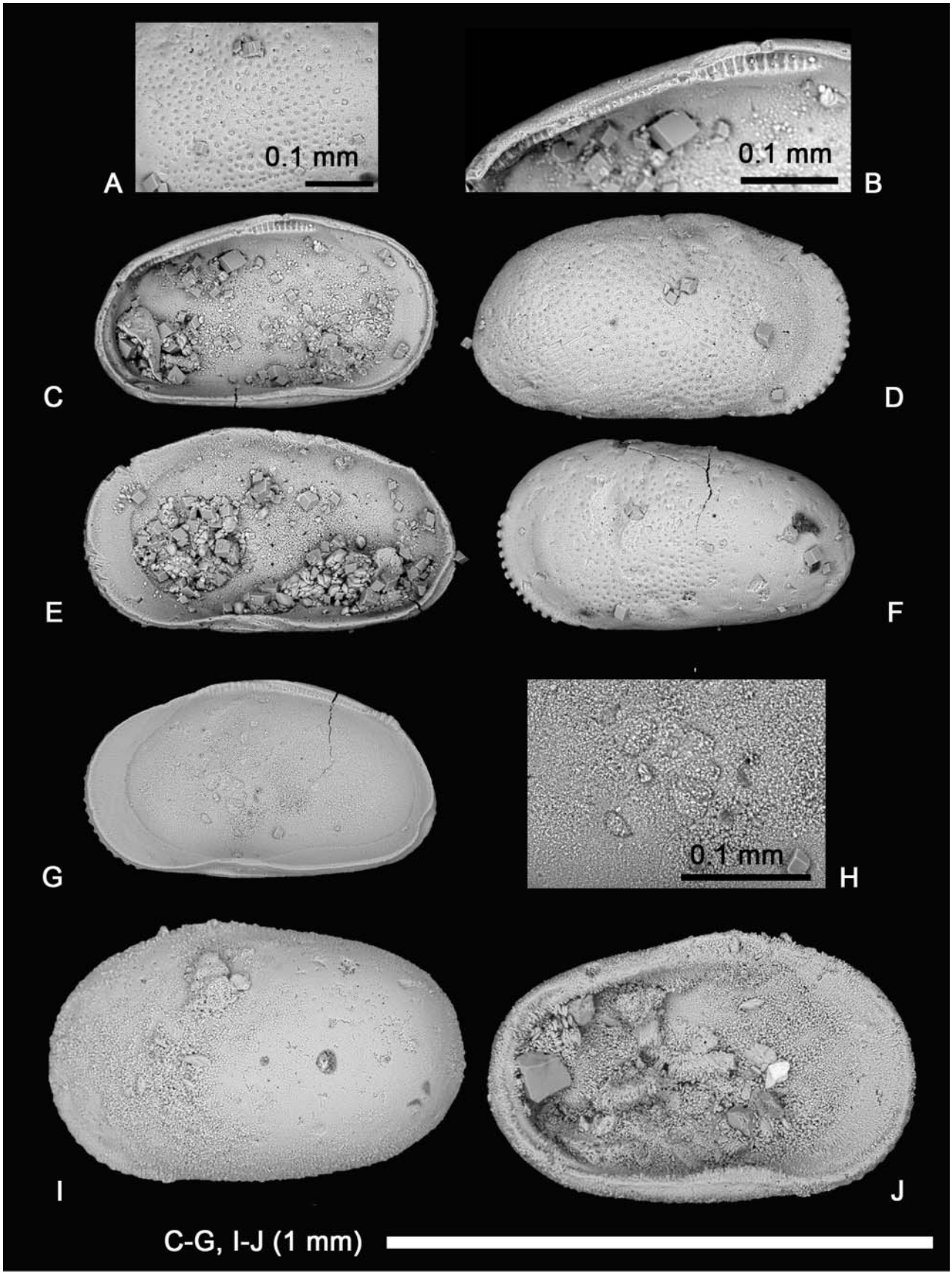
Genera closely related to *Alciella* include *Ambostracon* Hazel, 1962, *Patagonacythere* Hartmann, 1962, *Graptocythere* Ruggieri 1972, and *Tepidiora* Jellinek, 1995. There is no significant difference in the internal details such as hingement (holamphidont) and subcentral muscle scars (three frontal scars and four adductor scars; dorsomedian and ventromedian adductor scars subdivided). Note that there is some uncertainly because of the insufficiency of published images of the type species, especially for internal details (Hartmann 1962; Hazel 1962; Valentine 1976; Valicenti 1977; Whatley *et al.* 1996, 1997, 1998). In addition, there is considerable uncertainty regarding the use of muscle scar details (two or three frontal scars, presence or absence of subdivision of adductor scars) for generic taxonomy of hemicytherids because of their high intraspecific and intrageneric variability (Irizuki 1993). The distributions of normal and marginal pores are of use for the generic taxonomy of hemicytherids (Irizuki 1993), but the normal and marginal pore details are not always shown in taxonomic papers and are not always observable depending on the preservation of fossil specimens. Thus, here we mostly focus on external valve morphology.

Some of these taxa were originally described as genera and others as subgenera, but all are basically divided using external shell characteristics because of the similarity of the internal details. Thus, there is little merit in treating some taxa as genera and others as subgenera, and here we treat all of these taxa as genera.

Both *Ambostracon* Hazel, 1962 and *Patagonacythere* Hartmann, 1962 are similar to *Alciella* in having the posterodorsal loop composed of dorsolateral and median lateral ridges, but are distinguished by having a long, oblique median lateral ridge starting from the posterodorsal corner and reaching to anteroventral area. In addition, the valve is more inflated; the posterodorsal loop is situated more dorsally; the dorsolateral and ventrolateral ridges are better developed and situated closer to the dorsal/ventral margin; and the ventrolateral ridge is longer in *Ambostracon* and *Patagonacythere*.

Ambostracon and *Patagonacythere* are very similar genera. According to Valicenti (1977), the only difference between *Ambostracon* and *Patagonacythere* is the ocular ridge running between the A and B fossae in Liebau's coding scheme (Liebau 1969, 1991; Benson 1972; Irizuki 1993). *Ambostracon* tends to have an ocular ridge and *Patagonacythere* tends not to have it (or it may run on the anterior marginal rim outside the A fossa). Although the original descriptions of the type species of both genera are based on rather schematic drawings (Hartmann 1962; Hazel 1962), subsequent research has included clear SEM images from topotypic regions, supporting the presence of this difference (Valentine 1976; Valicenti 1977; Whatley *et al.* 1996, 1997, 1998). However, the presence or absence of an ocular ridge may not (always) be a diagnostic character to divide hemicytherid genera, and several studies have included species with and without an ocular ridge in the same genus (Brouwers 1993; Irizuki 1993). Thus, because *Patagonacythere* was erected some months after *Ambostracon* according to Titterton & Whatley (2008), *Patagonacythere* can be a junior synonym of *Ambostracon*. However, there are certain differences between closely related species from each type region (the Plio-Pleistocene–Recent of California and the south-western Atlantic). Valentine (1976) illustrated SEM images of 'topotype' specimens of the type species of *Ambostracon*, *Ambostracon costatum* Hazel, 1962, from the Santa Barbara Formation showing the equivalent age to the type locality of the Lomita Marl Member in California, USA and also of many other *Ambostracon* species showing clear affinities to the type species. McKenzie & Swain (1967) also reported similar Recent *Ambostracon* species from nearby Baja California. These 'Californian' *Ambostracon* species tend to show irregular and coarser primary reticulation; better development of not only the major ventrolateral, median lateral and dorsolateral ridges, but also other minor ridges and muri; and an oblique vertical ridge connecting the posterior ends of dorsolateral and ventrolateral ridges. Valicenti (1977) and Whatley and colleagues (Whatley *et al.* 1996, 1997, 1998) depicted SEM images of 'topotype' specimens of the type species of *Patagonacythere*, *Patagonacythere tricostata* Hartmann, 1962, from the south-western Atlantic. Several researchers have reported several similar species to the type species from the south-western Atlantic and Southern

Figure 8. Scanning electron microscope images of *Neocyprideis armata* sensu lato Bassiouni & Luger, 1996. **A,** RGM.1349566 (LC2004), adult male LV; **B, C,** RGM.1349567 (LC2006), adult male RV; **D–F,** RGM.1349568 (LC2005), adult female LV; **G–I,** RGM.1349569 (LC4001), adult female? LV; **J,** RGM.1349570 (LC4002), adult male LV. A, B, D, G, J: lateral views; C, E, F, H, I: internal views; F, I: close-up of subcentral muscle scars (one frontal and four adductor scars and a fulcral point observable at least in I).


A
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B
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J
C-G, I-J (1 mm)

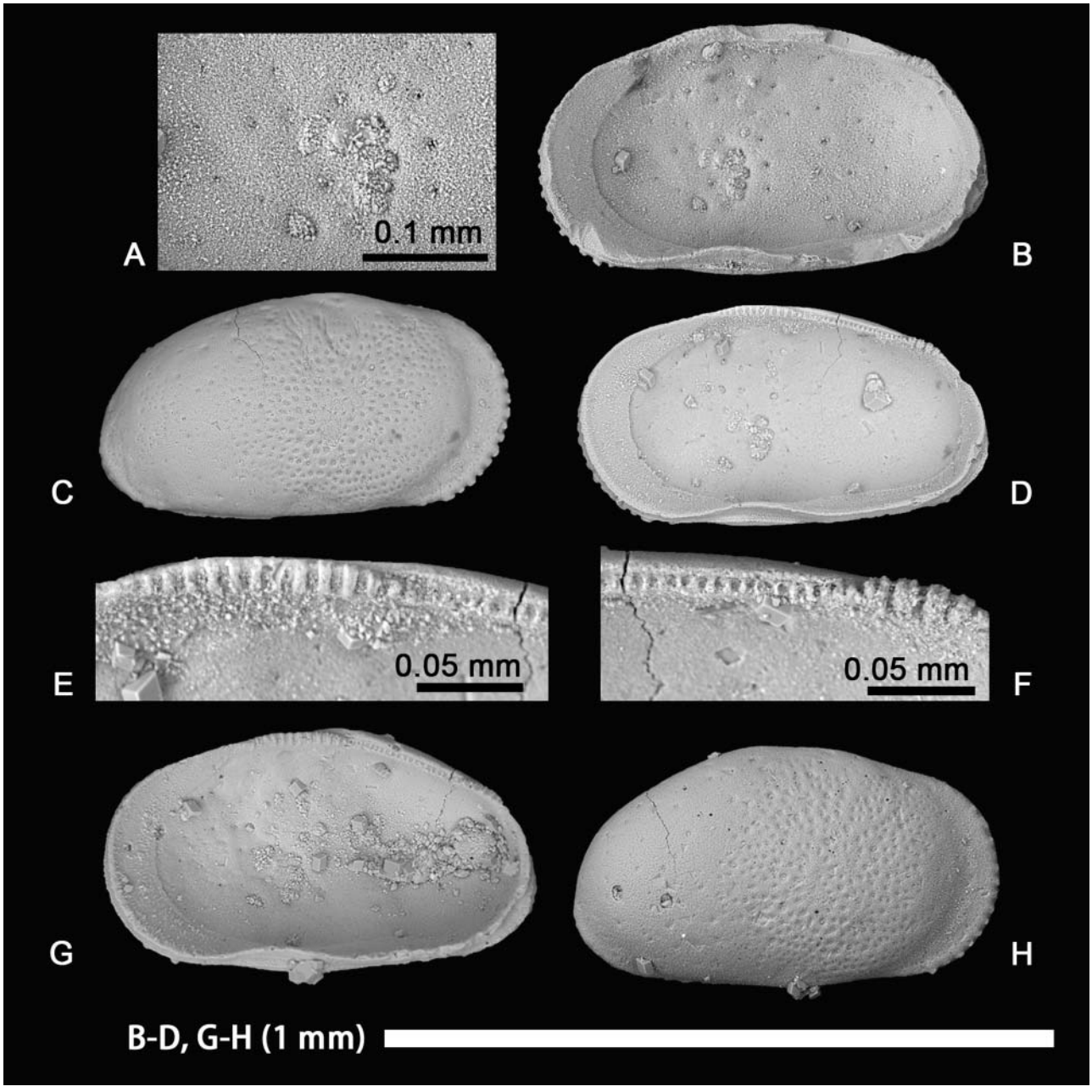


Figure 10. Scanning electron microscope images of *Neocyprideis armata* sensu lato Bassiouni & Luger, 1996. **A, B,** RGM.1349575 (LC2A037), adult female RV; **C–F,** RGM.1349576 (LC4032), adult male RV; **G, H,** RGM.1349577 (LC4027), adult male RV. A, B, D–G: internal views; C, H: lateral views; A: close-up of subcentral muscle scars; E, F: hingement close-up.

oceans, which are the topotypic region in a broad sense (Valicenti 1977; Whatley *et al.* 1996; Majewski & Olempska 2005). These 'south polar' species show regular primary reticulation and subdued ridges and muri other than the major three ridges of ventrolateral, median lateral and dorsolateral ridges, and lack an obliquely vertical ridge connecting the dorsolateral and ventrolateral ridges. Less calcified species have more inconspicuous oblique median lateral ridges while still retaining a trace. Thus, we prefer to consider *Ambostracon* and *Patagonacythere* separate

Figure 9. Scanning electron microscope images of *Neocyprideis* species. **A–H,** *Neocyprideis armata* sensu lato Bassiouni & Luger, 1996; **A–C,** RGM.1349570 (LC4002), adult male LV; **D, E,** RGM.1349571 (LC4003), adult female RV; **F,** RGM.1349572 (LC4004), adult male LV; **G, H,** RGM.1349573 (LC2A036), adult female RV. **I, J,** *Neocyprideis* sp. 1, RGM.1349574 (LC2054), adult female? LV. A, D, F, I: lateral views; B, C, E, G, H, J: internal views; A: close-up showing punctation; B: close-up of hingement; H: close-up of subcentral muscle scars.

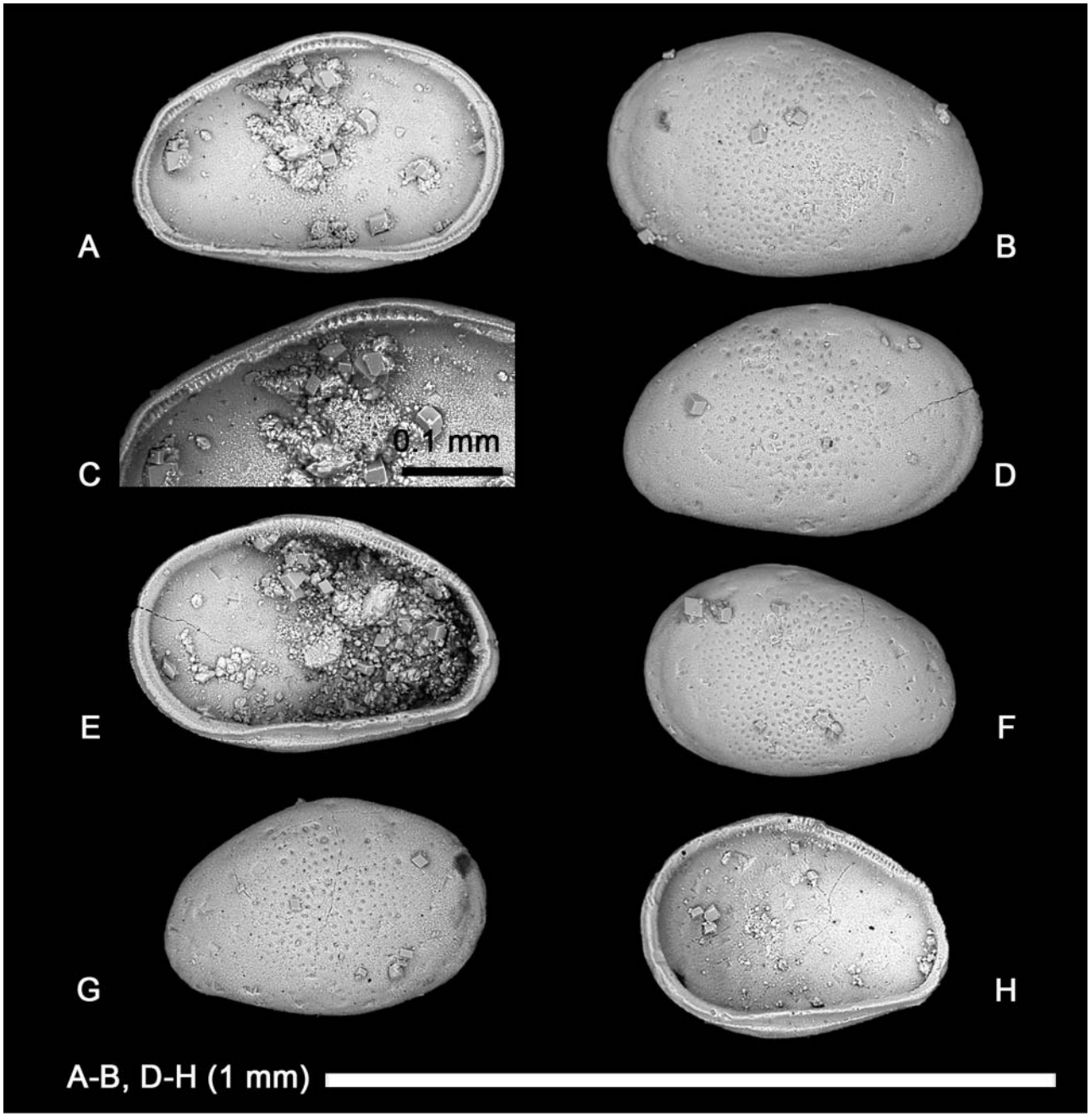


Figure 11. Scanning electron microscope images of *Neocyprideis armata* sensu lato Bassiouni & Luger, 1996. **A–C,** RGM.1349578 (LC4005), A-1 juvenile LV; **D, E,** RGM.1349579 (LC4006), A-1 juvenile RV; **F,** RGM.1349580 (LC4007), A-2 juvenile LV; **G, H,** RGM.1349581 (LC4008), A-2 juvenile RV. A, C, E, H: internal views; B, D, F–G: lateral views; C: hingement close-up.

genera that may be confined to the type regions of the north-eastern Pacific and Southern Ocean/south-western Atlantic, respectively. *Baffinicythere* Hazel, 1967 is also similar to *Ambostracon* and *Patagonacythere* but is distinguished by lacking the median lateral ridge and by the presence of two obliquely vertical ridges connecting the posterior end of the dorsolateral ridge and the posterior end and posterior third of the ventrolateral ridge, respectively, making a triangular loop. *Laperousecythere* Brouwers, 1993 is similar to *Ambostracon*, but lacks the obliquely vertical ridge connecting the posterior ends of dorsolateral and ventrolateral ridges and has better regular primary reticulation. However, the validity of the assignment of the many species from various regions outside the

type regions (e.g. Irizuki 1993; Irizuki *et al.* 2004; Gemery *et al.* 2017) needs to be carefully re-evaluated.

Alciella is very similar to *Graptocythere* Ruggieri 1972 in general appearance, but *Graptocythere* has a very well-developed ocular ridge between the A and Z fossae and a continuous circular dorsolatera-posterolateral-ventrolateral-ocular ridge (Jellinek 1995; Gross & Piller 2006). European species assigned to *Ambostracon* by Whatley and Maybury (Maybury & Whatley 1986a, b; Whatley & Maybury 1986a, b) do belong to this genus in our opinion.

Alciella is also similar to *Tepidiora* Jellinek, 1995, but *Tepidiora* has a well developed ocular ridge between the A and Z fossae and four (instead of three) lateral ridges (i.e. dorsolateral, dorsal median lateral, ventral median lateral and ventrolateral ridges) (Jellinek 1995). *Auradilus* Jellinek, 1995 has a more *Aurila*-like outline and subcentral loop on the ventrolateral ridge (Jellinek 1995). *Hemicythere* Sars, 1925 lacks a median lateral ridge, and the internal details (especially hingement) are different (Athersuch & Whittaker 1981). Externally, *Pataviella* Liebau, 1991 is more similar to *Hornibrookella* Moos, 1965 (see Al-Furaih 1975) than to *Alciella* Liebau, 1991. Regarding the subcentral muscle scars, *Pataviella* has three frontal scars and four adductor scars with the dorsomedian and ventromedian scars divided, whereas *Hornibrookella* has two frontal scars and four adductor scars with the dorsomedian and ventromedian scars undivided. See Jellinek (1995), Bonaduce *et al.* (1987), and Pokorný (Pokorný

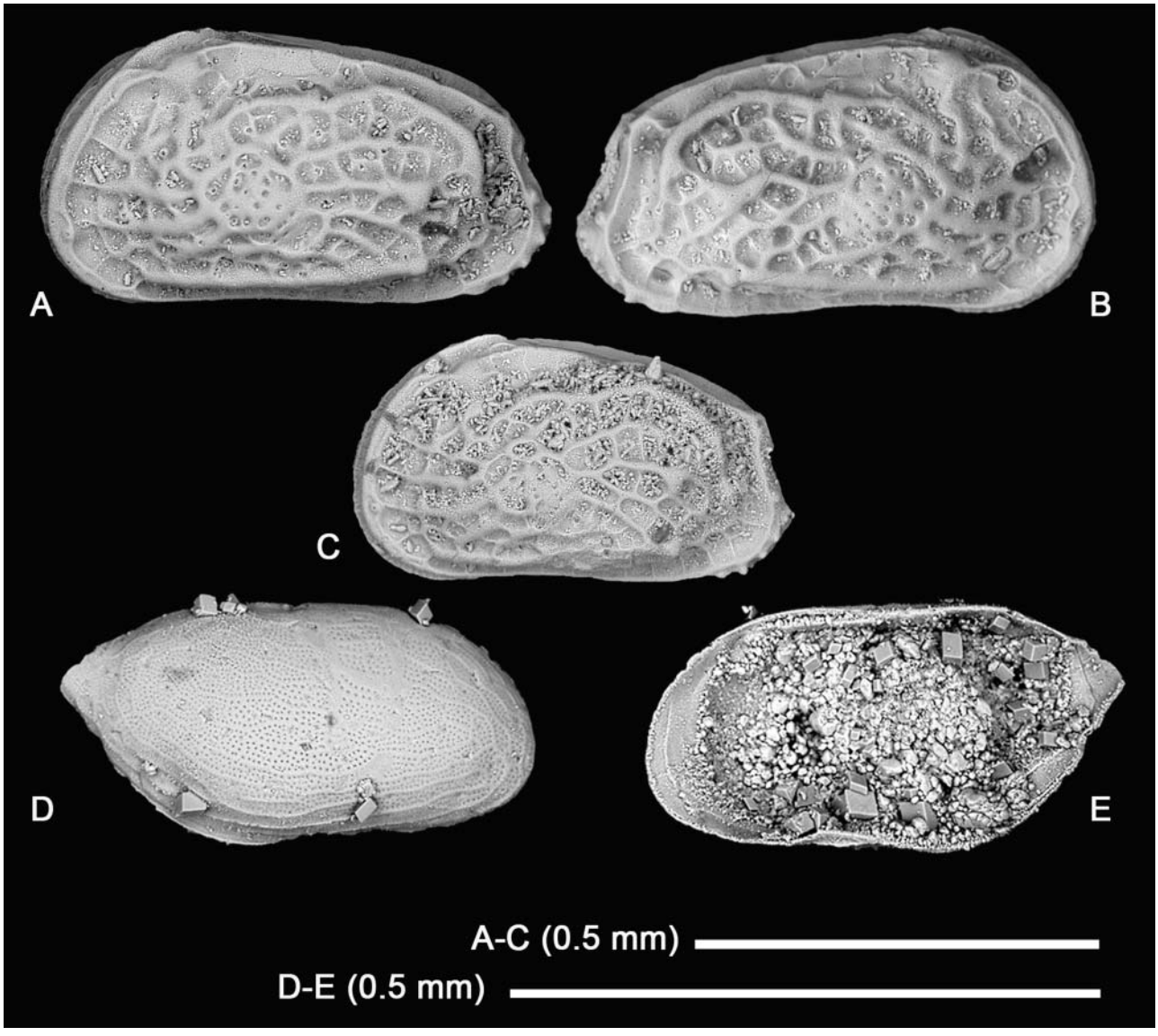
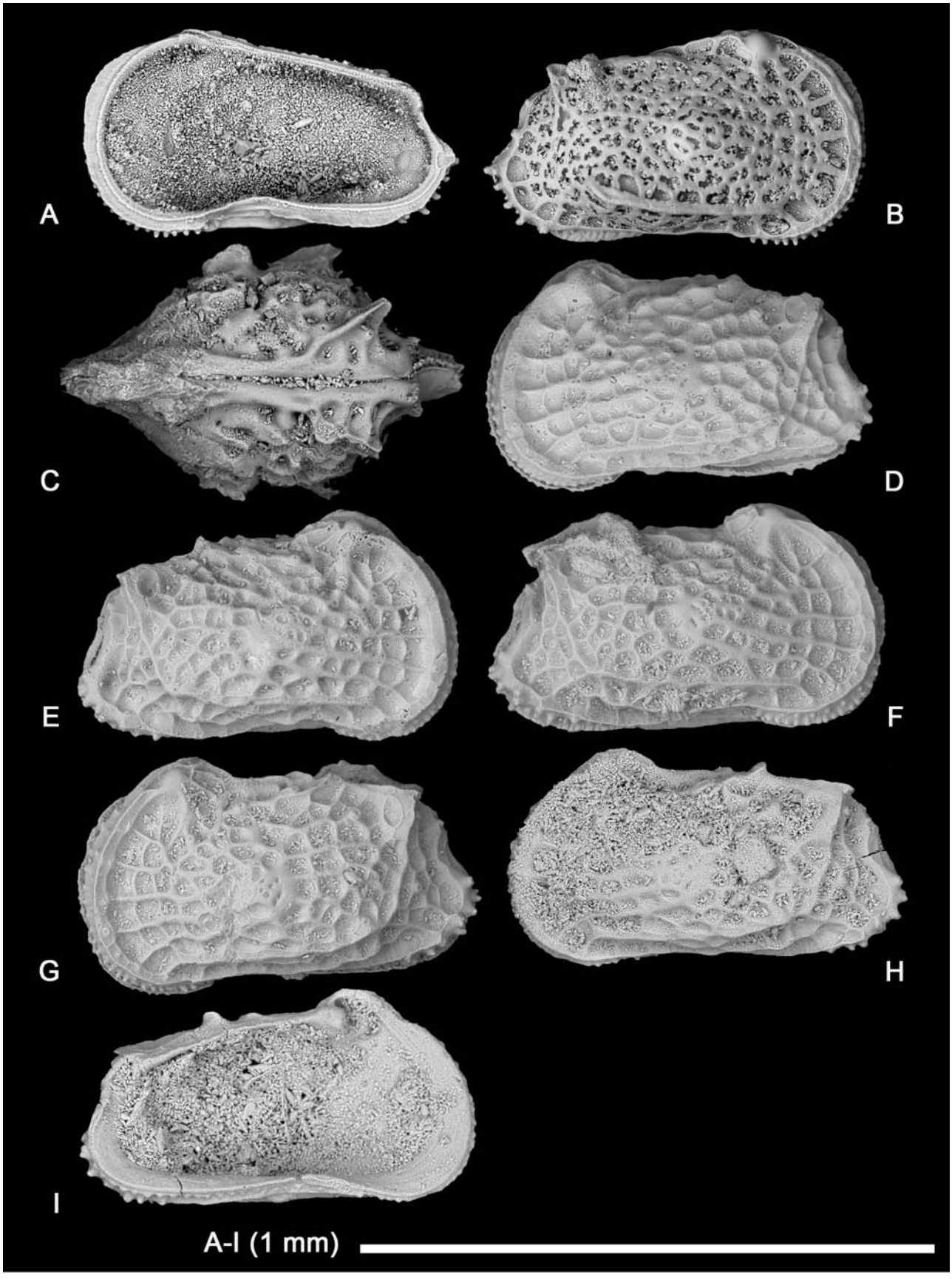


Figure 12. Scanning electron microscope images of *Alciella* and *Semicytherura* species. **A–C,** *Alciella irizukii* sp. nov.; **A, B,** RGM.1349582 (LC2021), adult? carapace; **C**, RGM.1349583 (LC2058), juvenile? carapace. **D, E,** *Semicytherura* sp. 1, RGM.1349584 (LC4021), adult? RV. A, C: left lateral views of carapaces; B: right lateral view of a carapace; D: lateral view; E: internal view.


A
B
C
D
E
F
G
H
I
A-I (1 mm)

1969a, b) for descriptions of more distantly related genera such as *Mutilus* Neviani in Howe, 1955 and *Radimella* Pokorný, 1969b. This genus is known from the Eocene and Oligocene of Europe.

Species included are: *Pataviella* (*Alciella*) *alciensis* Liebau, 1991; *Pataviella* (*Alciella*) *gracilis* Liebau, 1991; *Pataviella* (*Alciella*) sp. LA 56 of Liebau (1991); *Hazelina*? *parisiensis* Guernet, 1984; *Pokornyella*? *bicostata* Monostori, 1998; *Pataviella*? sp. of Guernet *et al.* (2012); and *Alciella irizukii* sp. nov.

Alciella irizukii sp. nov.
(Fig. 12A–C)

Derivation of name. In honour of Toshiaki Irizuki, Shimane University (Japan), for his work on hemicytherid ostracods.

Material. Holotype: carapace, RGM.1349582 (LC2021) (Fig. 12A, B). Paratype: carapace, RGM.1349583 (LC2058) (Fig. 12C).

Type locality and horizon. Southern Madagascar, Early–Middle Eocene.

Dimensions. RGM.1349582 (LC2021) (holotype): L = 0.639 mm; H = 0.344 mm. RGM.1349583 (LC2058) (paratype): L = 0.564 mm; H = 0.314 mm.

Diagnosis. An *Alciella* species with well-developed primary reticulation, muri and ridges, and dorsolateral ridge situated distantly from the dorsal margin.

Description. Carapace moderately calcified, highest at anterodorsal corner. Outline trapezoidal; anterior margin rounded; caudal process moderately developed and pointed ventrally, bearing spines in its ventral half; dorsal margin almost straight; ventral margin slightly concave; ventrolateral ridge straight and relatively short; median lateral ridge thicker in its posterior end; dorsolateral ridge curved and situated distantly from the dorsal margin; subcentral tubercle well developed; anterior and posterior marginal rims and sulci present; eye tubercle well developed. Median lateral and dorsolateral ridges constitute irregular-shaped loop. Anterodorsal and posterodorsal corners moderately angular. Lateral surface ornamented with primary reticulation; muri thick and well developed. Internal features not observable.

Remarks. This species is very similar to *Alciella parisiensis* (Guernet, 1984) (= *Hazelina*? *parisiensis* Guernet, 1984) but *Alciella parisiensis* has a better developed median lateral ridge and smoothly arched dorsolateral ridge that continues into the posteromarginal ridge. It is also similar to *Alciella bicostata* (Monostori, 1998) (= *Pokornyella*? *bicostata* Monostori, 1998) but is distinguished by the almost straight dorsal margin, more prominent posterior margin, and better developed ridges and muri. *Pataviella*? sp. of Guernet *et al.* (2012), which belongs to *Alciella*, is distinguished from this species by having a more continuous median lateral ridge and irregularly developed primary reticulation.

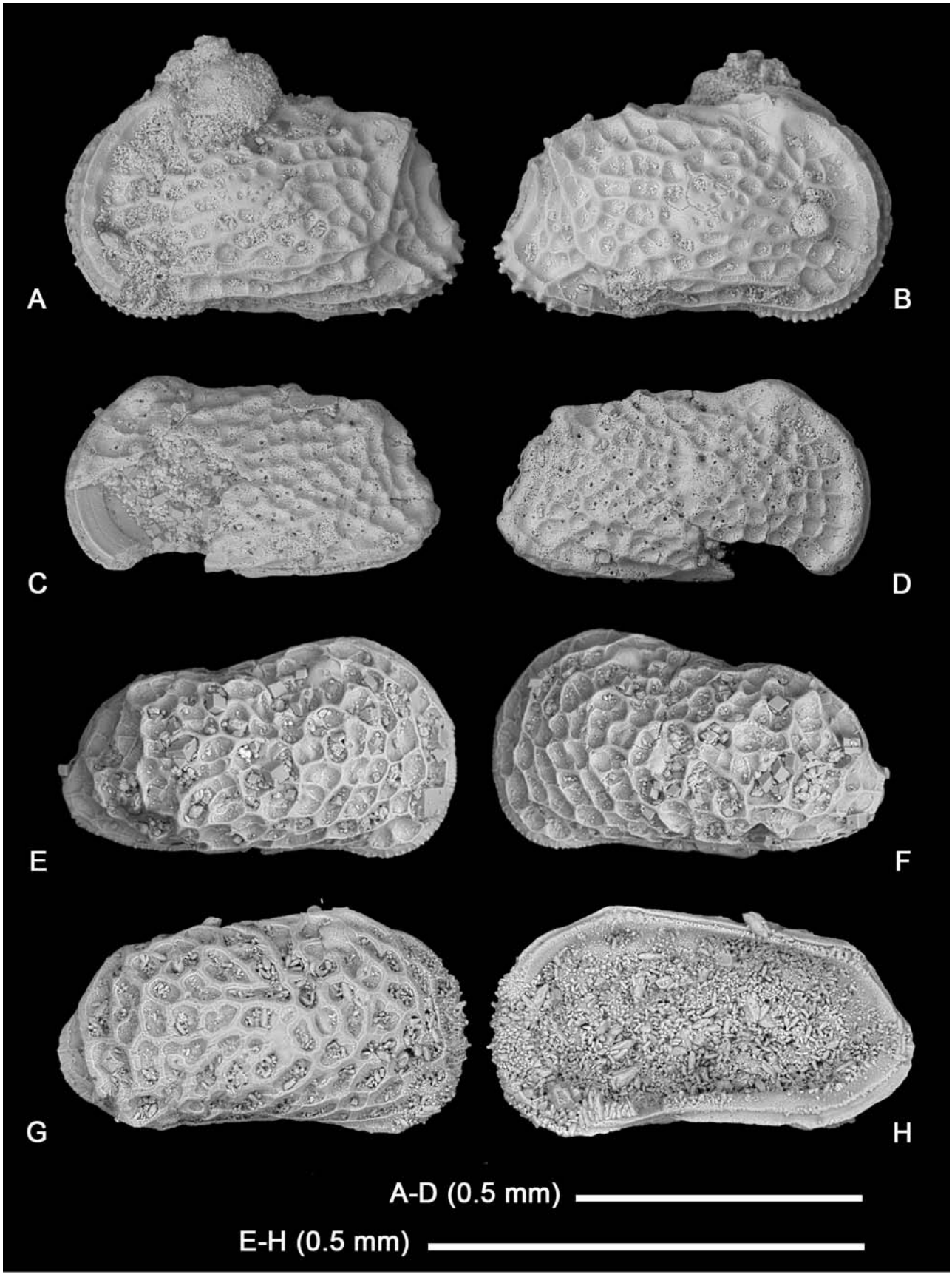
Hazelina Moos, 1966 has a V-shaped frontal muscle scar, and does not show much similarity to any species discussed above, except for the presence of ventrolateral, median lateral and dorsolateral ridges that are common characteristics of many hemicytheird and trachyleberidid genera. *Pokornyella* Oertli, 1956 has an almond-shaped outline and undivided ventromedian adductor scars, and also lacks ridges on the valve surface (Oertli 1956; Keij 1957; Hazel 1967).

Genus ***Hermanites*** Puri, 1955

Type species. *Hermania reticulata* Puri, 1954.

Remarks. An SEM image of a paratype specimen of the type species was shown by Benson (1972), and further details on this genus can be found in Warne & Whatley (2016) and Hazel (1968). Very similar genera to *Hermanites* Puri, 1955 have been erected based on species that were formerly included in *Hermanites* (van Morkhoven 1963), including *Grinioneis* Liebau, 1975 (type species *Hermanites paijenborchiana* Keij, 1957) and *Dameriacella* Liebau, 1991 (type species *Hermanites dameriacensis* Keij, 1958). We prefer to use *Hermanites* in a broad sense to include all of these genera, at least for now. *Hornibrookella* Moos, 1965 may also be a junior synonym of *Hermanites* in our opinion. The only major difference may be the divided dorsal adductor scar in *Hornibrookella* (Al-Furaih 1975; Liebau 1991) compared with the undivided scar in *Hermanites* (Hazel 1968; van Morkhoven 1963), but muscle scar details of the type species of *Hermanites* are not well known (Puri 1954; van Morkhoven 1963; Benson 1972) and the dorsal adductor scar is now always divided even in the type species of *Hornibrookella* (Al-Furaih 1975). Re-study of the type species of these genera, of which the details are often poorly known (especially for *Hermanites*), will help to evaluate the validity of these genera. *Quadracythere* Hornibrook, 1952 and *Tenedocythere* Sissingh, 1972 have a much higher and shorter carapace (showing

Figure 13. Scanning electron microscope images of *Hermanites* species. **A, B,** *Hermanites* sp. 1, RGM.1349585 (LC2016), juvenile? RV. **C–I,** *Hermanites* cf. *percultus* Ahmad, Neale & Siddiqui, 1991; **C,** RGM.1349586 (LC2017), adult carapace; **D, E,** RGM.1349587 (LC2041), adult carapace; **F, G,** RGM.1349588 (LC2042), adult carapace; **H, I,** RGM.1349589 (LC2057), adult LV. A, I: internal views; B, H: lateral view; C: dorsal view; D, G: left lateral views of carapaces; E, F, right lateral views of carapaces.


A
B
C
D
E
F
G
H
A-D (0.5 mm)
E-H (0.5 mm)

quadrate outline) than *Hermanites* which has a comparatively elongate outline.

Hermanites cf. ***percultus*** Ahmad, Neale & Siddiqui, 1991
(Figs 13C–I, 14A–D)v

Remarks. This species is characterized by strongly prominent anterodorsal and posterodorsal corners. Similar *Hermanites* species in this regard are known from Tanzania (*Hermanites percultus* Ahmad, Neale & Siddiqui, 1991) and Europe [*Hermanites orbignyana* (Bosquet, 1852), *Hermanites vahrenkampi dudarensis* (Monostori, 1998), *Hermanites vermiculata* (Bosquet, 1852)]. Although the type species of *Hermanites* lacks the strongly prominent anterodorsal and posterodorsal corners, such intrageneric variation in outline is common in hemicytherid and thaerocytherid genera, e.g. in the well-defined genus *Poseidonamicus* Benson, 1972 in which several species have strongly prominent anterodorsal and posterodorsal corners showing concave dorsal margins and others have angular but not prominent dorsal corners showing straight dorsal margins resulting in a trapezoidal outline (Whatley *et al.* 1986; Hunt 2007).

This species is very similar to and may be conspecific with *Hermanites percultus.* Our specimens and *Hermanites percultus* have an almost identical reticulation pattern and ridge arrangement, but *Hermanites percultus* has a better calcified carapace and better developed ridges and miri as well as a more subrectangular outline (Ahmad *et al.* 1991) (our specimens have a slightly more subtriangular appearance: Figs 13C–I, 14A–D). Thus, we prefer to call them *Hermanites* cf. *percultus*. *Hermanites orbignyana* (Bosquet, 1852) and *Hermanites vahrenkampi dudarensis* (Monostori 1998) are also very similar to this species, but have more irregular primary reticulation (Keij 1957; Ducasse *et al.* 1985; Monostori 1998). *Hermanites vermiculata* (Bosquet, 1852) is distinguished from this species by having better developed ridges and muri, and a more prominent posterior margin (Keij 1957; Ducasse *et al.* 1985). *Bradleya*? sp. B of Ahmad *et al.* (1991) is distinguished from this species by the position of the eye tubercle more distant from the anterodorsal margin.

Hermanites **sp. 1**
(Fig. 13A, B)

Remarks. Our specimen is probably a juvenile, judging by the narrow inner lamella, weak hingement and relatively small size, and may be an A-1 juvenile of *Hermanites* cf. *percultus* Ahmad, Neale & Siddiqui, 1991.

Genus ***Urocythereis*** Ruggieri, 1950

Type species. *Cytherina favosa* Roemer, 1838.

Urocythereis? **sp. 1**
(Fig. 14E–H)

Remarks. Generic assignment is uncertain, but our species shows considerable similarity to the type species of *Urocythereis* Ruggieri, 1950, *Cytherina favosa* Roemer, 1838 (Keij 1957). Thus, we questionably include this species in *Urocythereis*.

Family **Loxoconchidae** Sars, 1925
Genus ***Loxoconcha*** Sars, 1866

Type species. *Cythere rhomboidea* Fischer, 1855.

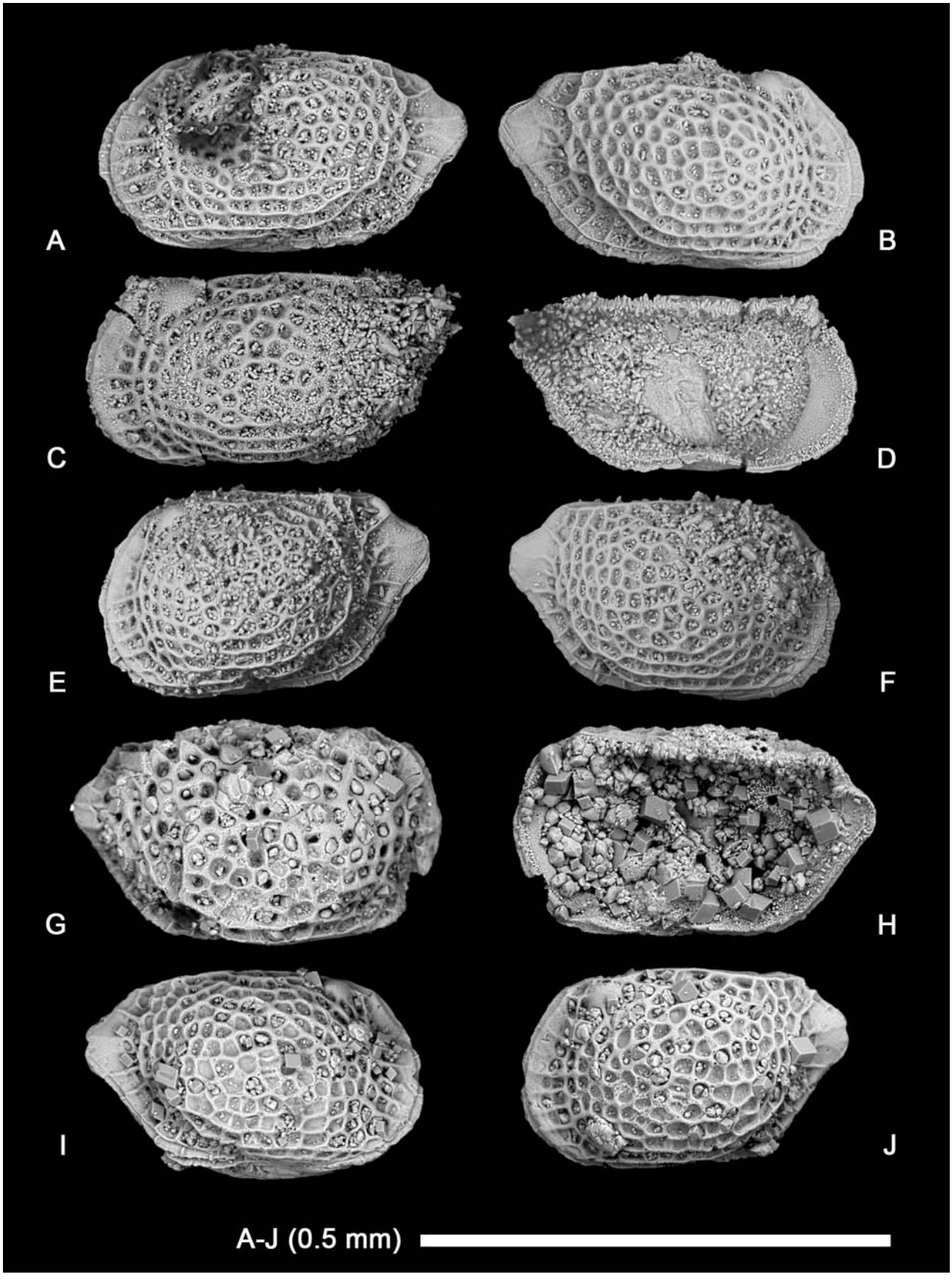
Loxoconcha loculus (Ahmad, Neale & Siddiqui, 1991)
(Fig. 15A–J)

1991 *Loxoconcha* (*Myrena*) *loculus* Ahmad, Neale & Siddiqui: 245, pl. 30, figs 10–12.

Remarks. The rounded, short, and high outline, and flat anterior and posterior margins of *Loxoconcha loculus* (Ahmad, Neale & Siddiqui, 1991) show considerable similarity to *Myrena* Neale, 1967 (*sensu* Mazzini 2005) and *Palmoconcha* Swain & Gilby, 1974. However, we prefer to put this species in *Loxoconcha* Sars, 1866 because of the well-developed eye tubercle that is lacking or inconspicuous in *Myrena* and *Palmoconcha*. Although all known species of *Myrena* are deep-sea forms that naturally lack an eye tubercle regardless of genus, shallow-water species of a closely related genus, *Kuiperiana* Bassiouni, 1962, have no or inconspicuous eye tubercles. Many shallow-marine *Palmoconcha* species are known, including the type species, and they have no or inconspicuous eye tubercles. Internal details of our specimens are not well preserved (Fig. 15D, H).

Myrena, *Kuiperiana*, and *Palmoconcha* have only subtle known differences. All of them have a smooth (or weakly crenulate) median hinge element (Bassiouni 1962; Ishizaki & Gunther 1976; Maybury 1990; Mazzini 2005). *Myrena* and *Kuiperiana* share the same posterior terminal hinge element in the RV, i.e. one arched tooth composed of a large knob with a thin, crenulate, arched tail anteriorly, showing a ‘comma-like’ appearance (Bassiouni 1962; Maybury 1990; Mazzini 2005; Yamaguchi & Kamiya 2007). *Palmoconcha* has a similar, but slightly

Figure 14. Scanning electron microscope images of *Hermanites* and *Urocythereis*? species. **A–D,** *Hermanites* cf. *percultus* Ahmad, Neale & Siddiqui, 1991; **A, B,** RGM.1349590 (LC2043), adult carapace; **C, D,** RGM.1349591 (LC4029), adult carapace. **E–H,** *Urocythereis*? sp. 1; **E, F,** RGM.1349592 (LC4025), carapace; **G, H,** RGM.1349593 (LC2059), adult? RV. A, C, F: left lateral views of carapaces; B, D, E: right lateral views of carapaces; G: lateral view; H: internal view.


A
B
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J
A-J (0.5 mm)

different, posterior terminal hinge element in the RV, that has more of a 'telephone receiver-like' appearance composed of two large knobs connected by an arched ridge (Ishizaki & Gunther 1976; Athersuch & Horne 1981; Horne & Kilenyi 1981; Horne & Whatley 1985). Comparing the external views of the type species of these genera, *Kuiperiana* is elongated, and *Myrena* and *Kuiperiana* are short, high, and rounded in outline; anterior and posterior flat margins are broad in *Myrena* and *Palmoconcha*, but very narrow in *Kuiperiana*; the caudal process is more prominent and angular in *Palmoconcha* than the others, and pointed at mid-height instead of above mid-height; all are covered by regular and primary reticulation, but the reticulation is comparatively more angular and irregular in *Myrena* and *Kuiperiana* and more rounded and regular in *Palmoconcha*; the straight part of the dorsal margin (i.e. hinge line) is shorter in *Palmoconcha* than in *Myrena* and *Kuiperiana* (Bassiouni 1962; Swain & Gilby 1974; Ishizaki & Gunther 1976; Uffenorde 1981; Mazzini 2005).

Many but not all researchers have considered *Myrena* to be a junior synonym of *Kuiperiana* (Maybury 1990; Ayress 1992; Mazzini 2005; Yamaguchi & Kamiya 2007). Numerous species currently assigned to *Palmoconcha* seem better placed in *Myrena*, e.g. *Loxoconcha semistriata* Kingma, 1948 and *Loxoconcha parapontica* Zhou, 1995, that clearly have a '*Myrena'* external appearance and hingement (Zhao & Whatley 1989b; Zhou 1995; Yamaguchi & Kamiya 2007). There are also many species currently assigned to *Kuiperiana* that may be better placed in *Myrena* (if *Myrena* is not a junior synonym of *Kuiperiana*) (Ayress 1992; Ayress & Drapala 1993; Ayress *et al.* 1994). Several *Kuiperiana* species other than the type species do not have flat anterior and posterior margins (Whatley & Maybury 1987; Maybury 1995), showing no external similarity to *Myrena* despite the fact that researchers tend to consider *Myrena* a junior synonym of *Kuiperiana* (Maybury 1990; Ayress 1992). Several quadrate but short and high species are known and have been assigned to *Palmoconcha*, *Kuiperiana* and *Loxoconcha* (Blaszyk 1987; Szczechura 2001; Yamaguchi & Kamiya 2007), but their true generic assignment is rather uncertain. Furthermore, many species similar to *Loxoconcha loculus* regarding their rounded, short and high outline and flat anterior and posterior margins with and without eye-tubercle development are known from Eocene and Paleocene strata from various places in the world (Murray 1938; Huff 1970; Neale & Singh 1985; Coles & Whatley 1989; Bassiouni & Luger 1990; McKenzie *et al.* 1991, 1993; Ayress 1995; Monostori 1998; Ceolin *et al.* 2015). Their genus-level taxonomic assignments remain uncertain, despite the fact that they are important with respect to the origin of this lineage of loxoconchids. Some of these species show very similar internal (hingement) details to *Myrena*, *Kuiperiana* and *Palmoconcha* (Murray 1938). Given these circumstances, detailed re-study of type or topotype specimens of these three genera is needed to resolve this taxonomic problem and also to understand better the taxonomy, evolution, phylogeny and palaeobiogeography of loxoconchids. In particular, internal details are imperfectly known in the type species of these genera.

Family **Paracytherideidae** Puri, 1957
Genus ***Paracytheridea*** Müller, 1894

Type species. *Paracytheridea depressa* Müller, 1894.

***Paracytheridea* sp. 1**
(Fig. 16A–G)

Remarks. Our specimens are poorly preserved. This species is very similar to *Paracytheridea anapetes* Ahmad, 1977 (Ahmad *et al.* 1991) and *Paracytheridea remanei orientalis* Warne, Whatley & Blagden, 2006, but it is distinguished by having vertically arranged primary reticulation and muri in the posterior third (Fig. 16C).

Family **Paradoxostomatidae** Brady & Norman, 1889
Genus ***Cytherois*** Müller, 1884

Type species. *Cytherois virens* Müller, 1884.

***Cytherois* sp. 1**
(Fig. 16H)

Family **Schizocytheridae** Howe in Moore, 1961
Genus ***Neomonoceratina*** Kingma, 1948

Type species. *Neomonoceratina columbiformis* Kingma, 1948.

Neomonoceratina afroangulosa sp. nov.
(Fig. 17A–I)

Derivation of name. From the type locality, Africa, and the similarity to *Neomonoceratina angulosa* (Siddiqui, 2006).

Material. Holotype: carapace, RGM.1349604 (LC2026) (Fig. 17A–C). Paratypes: LV, RGM.1349605 (LC2027)

Figure 15. Scanning electron microscope images of *Loxoconcha loculus* (Ahmad, Neale & Siddiqui, 1991). **A, B,** RGM.1349594 (LC2028), adult carapace; **C, D,** RGM.1349595 (LC2029), adult LV; **E, F,** RGM.1349596 (LC2052), adult carapace; **G, H,** RGM.1349597 (LC4023), adult RV; **I, J,** RGM.1349598 (LC4024), adult carapace. A, E, J: left lateral views of carapaces; B, F, I: right lateral views of carapaces; C, G: lateral views; D, H: internal views.

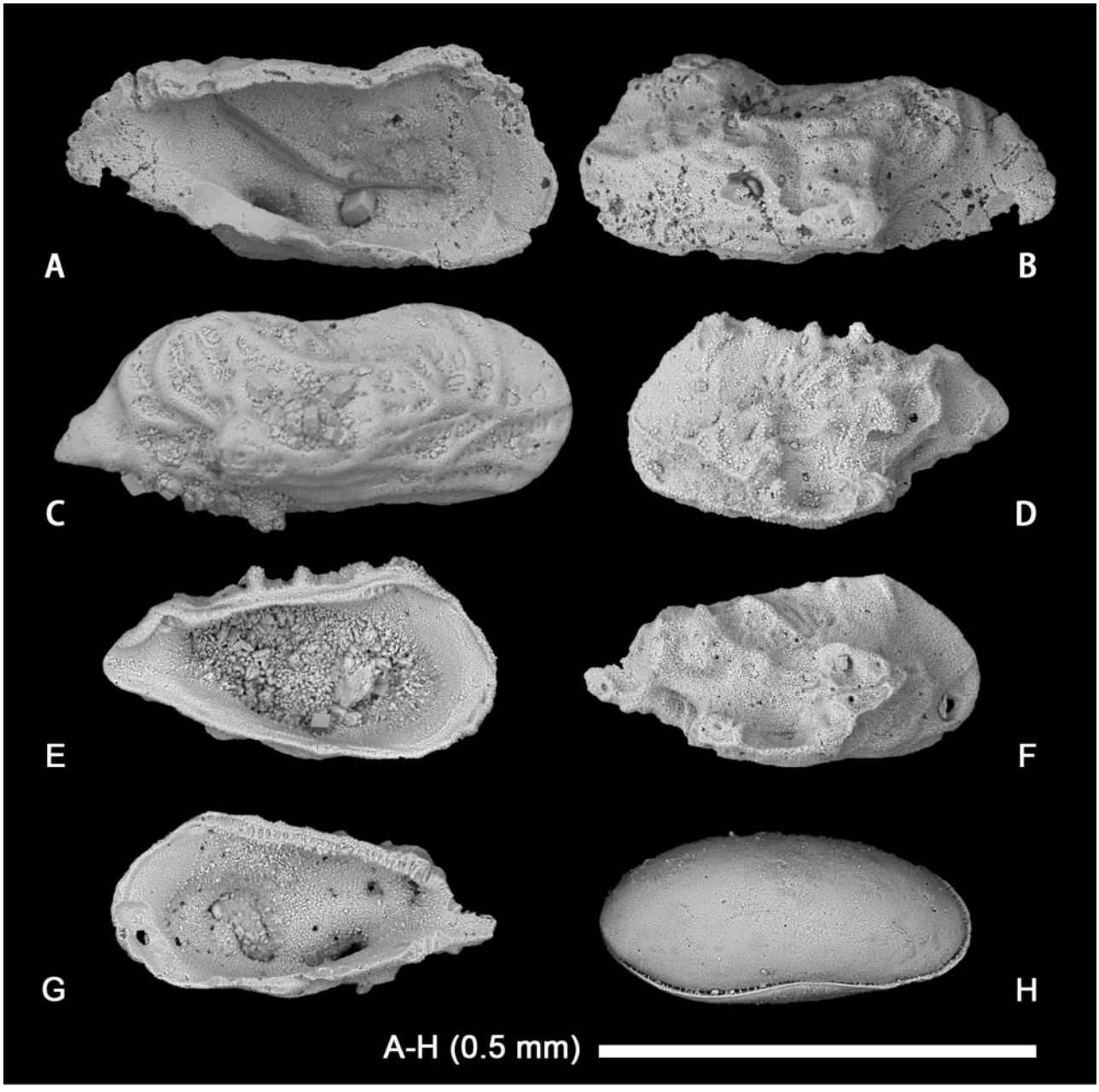


Figure 16. Scanning electron microscope images of *Paracytheridea* and *Cytherois* species. **A–G,** *Paracytheridea* sp. 1; **A, B,** RGM.1349599 (LC2A030), adult LV; **C,** RGM.1349600 (LC4022), adult carapace; **D, E,** RGM.1349601 (LC2A034), juvenile? LV; **F, G,** RGM.1349602 (LC2A035), juvenile? RV. **H,** *Cytherois* sp. 1, RGM.1349603 (LC2031), carapace. A, E, G: internal views; B, D, F: lateral views; C, H: right lateral views of carapaces.

(Fig. 17D, E); RV, RGM.1349606 (LC2051) (Fig. 17F, G); LV, RGM.1349607 (LC2060) (Fig. 17H, I).

Type locality and horizon. Southern Madagascar, Early–Middle Eocene.

Dimensions. RGM.1349604 (LC2026) (holotype): L = 0.463 mm; H = 0.248 mm. RGM.1349605 (LC2027) (paratype): L = 0.420 mm; H = 0.250 mm. RGM.1349607 (LC2060) (paratype): L = 0.430 mm; H = 0.242 mm.

Diagnosis. A *Neomonoceratina* species with well-developed ala, ridges constituting triangular loop on ala; well-developed, long, weakly sinuous, median lateral ridge; and almost smooth valve surface with very weak, fine punctation. The triangular loop is composed of an almost vertical ridge posteriorly, a semi-vertical anteriorly ridge

reaching to median lateral ridge at around dorsomedian sulcus, and a part of median lateral ridge.

Description. Carapace moderately calcified, small in size, highest at anterodorsal corner. Outline subrectangular-subtriangular in lateral view; anterior margin obliquely rounded, bearing marginal frill in the ventral half; caudal process prominent, upturned, pointed above mid-height; dorsal margin almost straight, dorsolateral ridge slightly extends above the dorsal margin; ventral margin curved; ala well developed, reaching to anterior margin and extended below ventral margin; ventral edge of ala sinuous. Anterodorsal and posterodorsal corners angular. Lateral surface partly ornamented with weak punctation. Median lateral ridge well developed, sinuous, once interrupted in the anterior part; dorsolateral ridge developed along the dorsal margin; a semi-vertical ridge starting from posterodorsal corner; two semi-vertical ridges starting from the apex of ala and constituting the triangular loop together with a part of median lateral ridge. Dorsomedian sulcus well developed. Internal details not well observable. Sexual dimorphism present.

Remarks. *Neomonoceratina afroangulosa* sp. nov. is very similar to *Neomonoceratina angulosa* Siddiqui, 2006, but is distinguished by having a better developed ala posteriorly, and a better developed median lateral ridge; lacking a semi-vertical ridge connecting median lateral and dorsolateral ridges in the central part; and having less developed surface punctation. This species is also similar to *Neomonoceratina gujaratensis* (Singh & Porwal, 1999), but it is distinguished by its better developed angular anterodorsal and posterodorsal corners; less sinuous median lateral ridge; and presence of ridges other than the median lateral ridge. The holotype and other specimens in the original description of *Neomonoceratina gujaratensis* are poorly preserved (Singh & Porwal 1999) and further detailed comparison is difficult. A species reported as *Paijenborchella narediensis* Guha, 1974 by Bhandari (1996) is more slender; lacks semi-vertical ridges; and has a sinuous horizontal ridge along the posteroventral margin. This species is also similar to *Neomonoceratina dambarholensis* (Bassiouni & Luger, 1996), but it is distinguished by having two well-developed semi-vertical ridges starting from the apex of the ala and reaching to the median lateral ridge, producing a triangular loop. In addition, the ala (= ventrolateral ridge) reaches the anterior margin in this species but ends distantly from the anterior margin in *Neomonoceratina dambarholensis*. *Cytheropteron* sp. S of Brouwers & Fatmi, 1992 is distinguished from the new species by its less developed ala posteriorly; less continuous and smoothly sinuous median lateral ridge; and lack of semi-vertical ridges.

The new species shows obvious similarities to the type species of *Neomonoceratina*, *Neomonoceratina columbiformis* Kingma, 1948, even though it is distinguished by the ala extended below the ventral margin, two semi-vertical ridges running into the apex of the ala, and dorsolateral ridge running much closer to the dorsal margin (Keij 1979; Zhao & Whatley 1988). Although species similar to this one tend to be assigned to *Paijenborchella* Kingma, 1948, *Paijenborchella* has a long caudal process pointed ventrally (Keij 1966). It is short, upturned and pointed dorsally in *Neomonoceratina* Kingma, 1948 (Zhao & Whatley 1988). Thus, *Neomonoceratina columbiformis* and closely related species including the new species, *Neomonoceratina angulosa*, *Neomonoceratina gujaratensis*, *Neomonoceratina dambarholensis* and *Cytheropteron* sp. S of Brouwers & Fatmi, 1992 are *Neomonoceratina*.

Genus ***Schizocythere*** Triebel, 1950

Type species. *Schizocythere hollandica* Triebel 1950.

Schizocythere cf. ***prolata*** Siddiqui, 1981
(Fig. 18A, B)

Remarks. Our specimen is similar to *Schizocythere prolata* Siddiqui, 1981, reported from the Late Paleocene of Pakistan and Late Paleocene–Early Eocene of India (Bhandari 1996; Siddiqui 1981), because they share the same primary reticulation pattern; have coarse primary reticulation and a well-developed dorsolateral ridge posteriorly; and lack any horizontal ridge other than ventrolateral and dorsolateral ridges. We note that our specimens have a better developed dorsolateral ridge extending above the dorsal margin; straighter ventrolateral ridge; more elongated, subrectangular outline; and better developed primary reticulation, compared to the type specimens (Siddiqui 1981). We prefer to call our specimen *Schizocythere* cf. *prolata*. We need more specimens from both Madagascar and Pakistan for a definite taxonomic assignment.

Family **Thaerocytheridae** Hazel, 1967
Genus ***Muellerina*** Bassiouni, 1965

Type species. *Cythere latimarginata* Speyer, 1863.

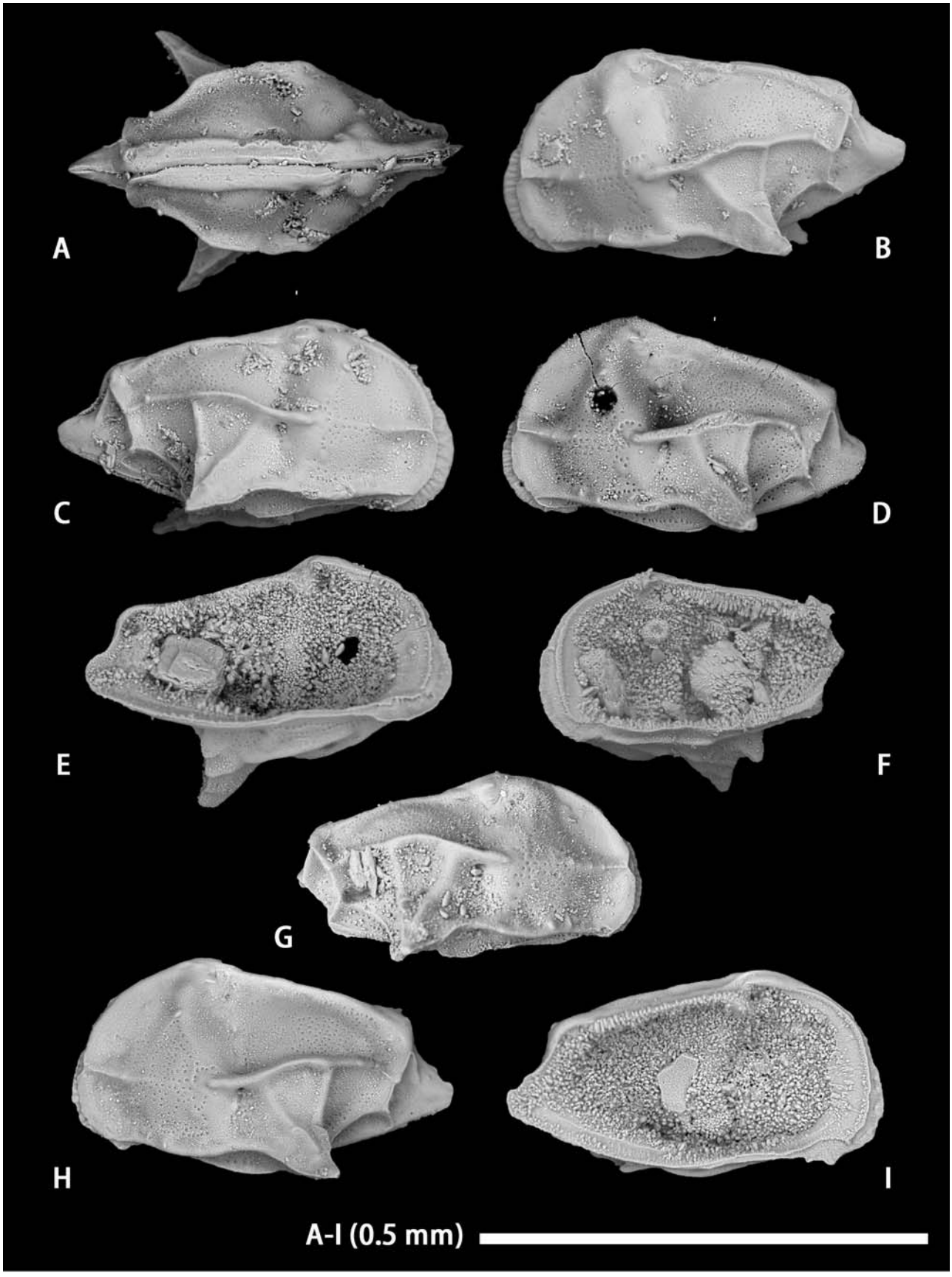
Muellerina eocenica sp. nov.
(Fig. 18C–G)

Derivation of name. From the type horizon, Eocene.

Material. Holotype: carapace, RGM.1349609 (LC2019) (Fig. 18C, D). Paratypes: carapace, RGM.1349610 (LC2046) (Fig. 18E); carapace, RGM.1349611 (LC2047) (Fig. 18F, G).

Type locality and horizon. Southern Madagascar, Early–Middle Eocene.

Dimensions. RGM.1349609 (LC2019) (holotype): L = 0.891 mm; H = 0.451 mm. RGM.1349610 (LC2046)


A
B
C
D
E
F
G
H
I
A-I (0.5 mm)

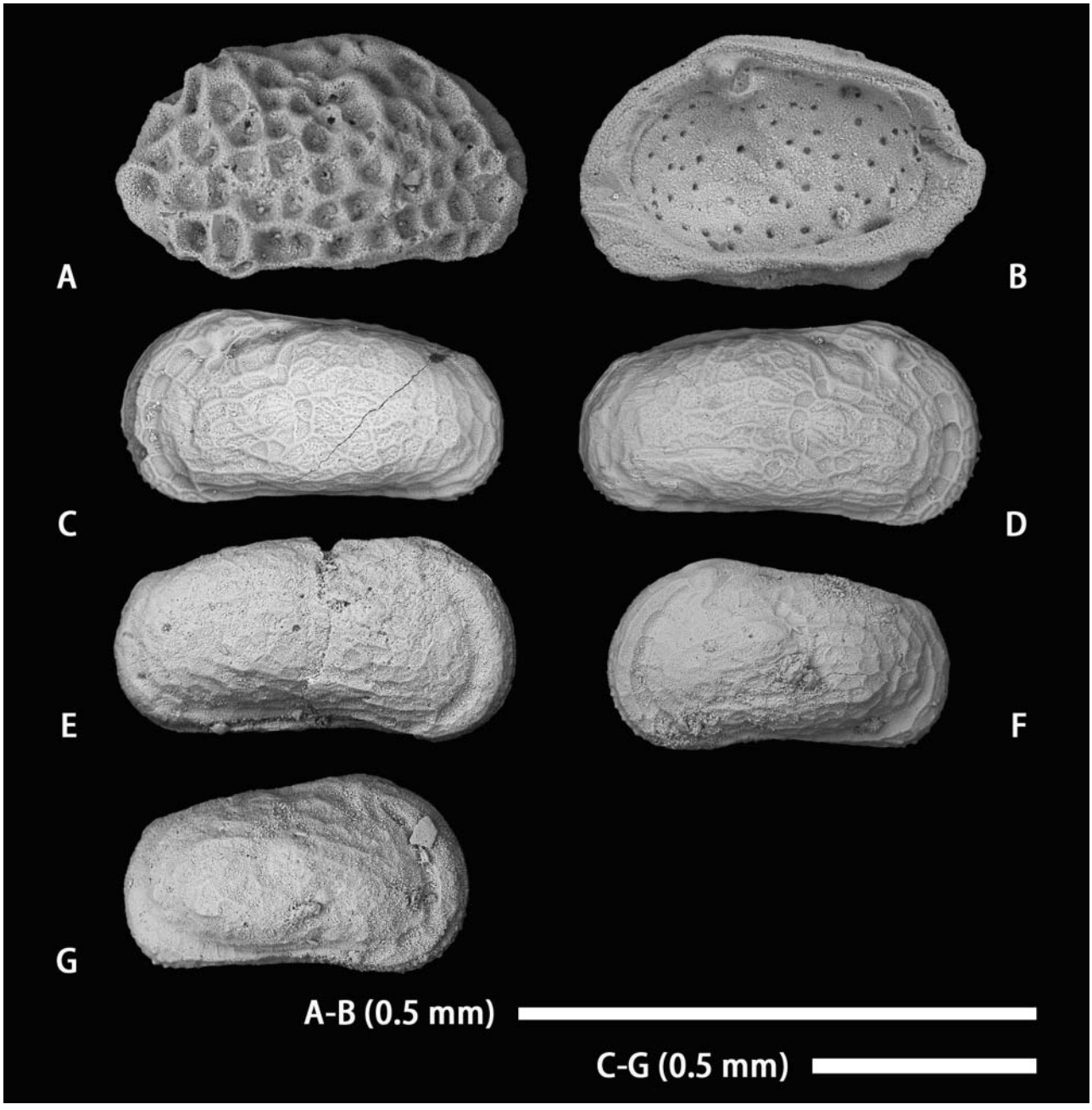
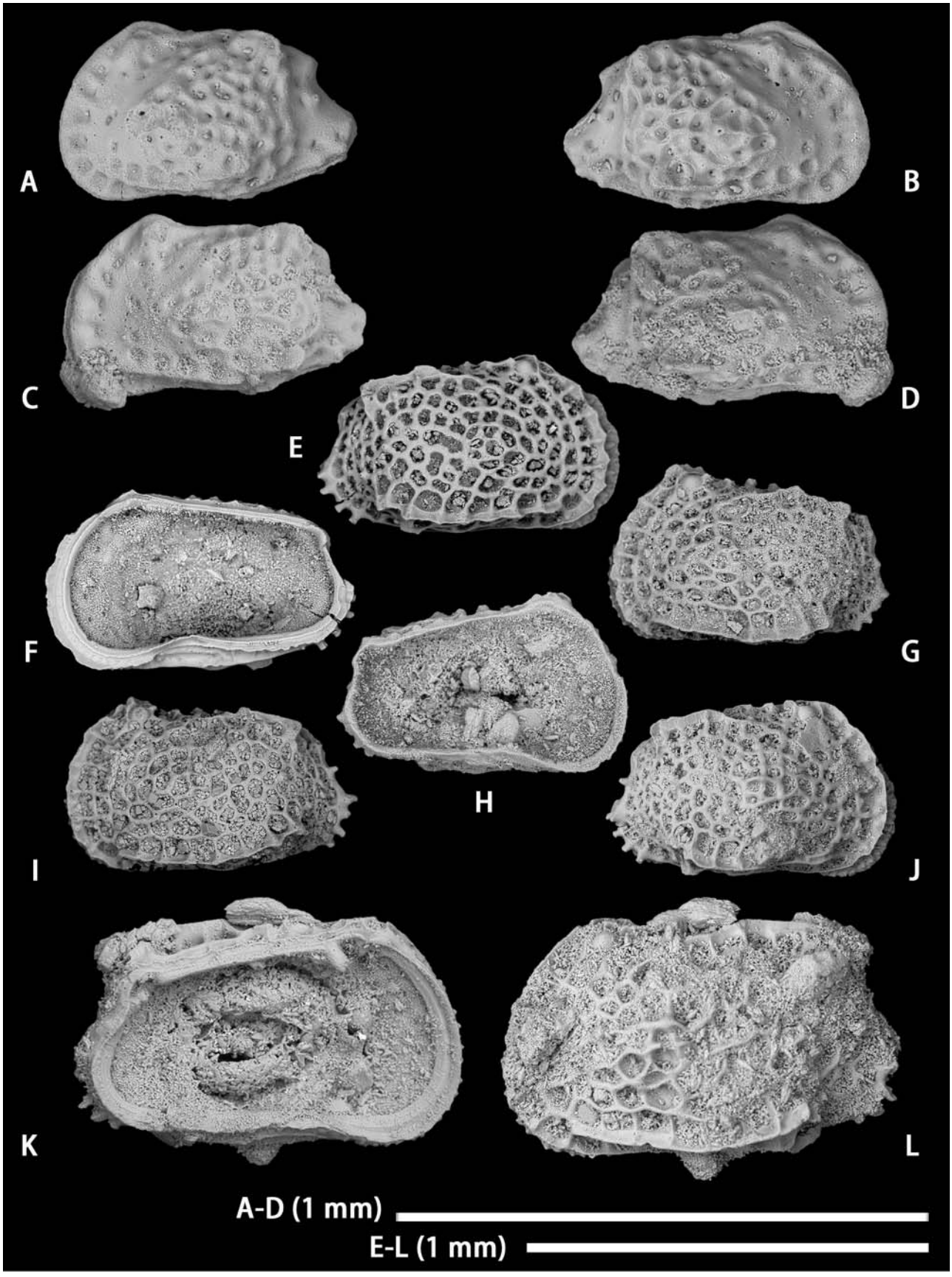


Figure 18. Scanning electron microscope images of *Schizocythere* and *Muellerina* species. **A, B,** *Schizocythere* cf. *prolata* Siddiqui, 1981, RGM.1349608 (LC2A031), adult RV. **C–G,** *Muellerina eocenica* sp. nov.; **C, D,** RGM.1349609 (LC2019), adult male carapace; **E,** RGM.1349610 (LC2046), adult male carapace; **F, G,** RGM.1349611 (LC2047), adult female carapace. A: lateral view; B: internal view; C, F: left lateral views of carapaces; D, E, G: right lateral views of carapaces.

Figure 17. Scanning electron microscope images of *Neomonoceratina afroangulosa* sp. nov. **A–C,** RGM.1349604 (LC2026), adult male? Carapace; **D, E,** RGM.1349605 (LC2027), adult female? LV; **F, G,** RGM.1349606 (LC2051), adult male? RV (caudal process broken); **H, I,** RGM.1349607 (LC2060), adult male? LV. A: dorsal view; B: left lateral view of a carapace; C: right lateral view of a carapace; D, G, H: lateral views; E, F, I: internal views.


A
B
C
D
E
F
G
H
I
J
K
L
A-D (1 mm)
E-L (1 mm)

(paratype): L = 0.924 mm; H = 0.474 mm. RGM.1349611 (LC2047) (paratype): L = 0.771 mm; H = 0.442 mm.

Diagnosis. A *Muellerina* species with weakly developed primary and secondary reticulation and inconspicuous prominence of posterior margin. A single row of fossae concentrically arranged around the subcentral tubercle.

Description. Carapace moderately calcified, highest at anterodorsal corner. Outline elongated, subrectangular; anterior margin rounded, bearing denticulation in its ventral half; posterior margin blunt and only very weakly caudate, bearing denticulation in its ventral half; dorsal margin almost straight; ventral margin slightly concave; ventrolateral ridge inconspicuous; subcentral tubercle inconspicuous; anterior marginal sulcus well developed, posterior marginal sulcus weakly developed. Anterodorsal corner weakly angular; posterodorsal corner angular. Lateral surface ornamented with weak primary and secondary reticulation. Internal features not well observable.

Remarks. This discovery of an Eocene *Muellerina* represents the oldest record of a genus previously known from the Oligocene but mostly recorded in the Neogene–Recent (Wood & Whatley 1997; Yasuhara *et al.* 2015). Morphological characteristics of the new species are consistent with the emended diagnosis of the genus given by Wood & Whatley (1997), the only slight deviation being the weakly developed caudal process. This species shows some superficial similarity to *Neocytheromorpha* Guan in Guan *et al.* 1978 but *Neocytheromorpha* has a rounded posterior margin and a different primary reticulation pattern, and lacks marginal sulci [e.g. see *Neocytheromorpha regalis* Guan] *et al.* 1978 (Hou & Gou 2007) and *Neocytheromorpha indoarabica* (Khosla, 1989)].

The new species is similar to *Muellerina abyssicola* (Sars, 1866) (see Yasuhara *et al.* 2015) in its weakly developed reticulation and general appearance, but it is distinguished by the deticulate anterior marginal rim, less developed caudal process, less developed marginal sulci, less angular anterodorsal and posterodorsal corners, less developed ventrolateral ridge, and lack of a posterodorsal tubercle.

Genus ***Pokornyella*** Oertli, 1956

Type species. *Cythere limbata* Bosquet, 1852.

Remarks. Compared to *Quadracythere* Hornibrook, 1952, *Tenedocythere* Sissingh, 1972, and *Hornibrookella* Moos, 1966, *Pokornyella* Oertli, 1956 is characterized by weakly developed ridges; almond-shaped/rounded outline; posterodorsal tubercle; and often very well-developed and prominent caudal process (Bonaduce *et al.* 1984; Ducasse & Coustillas 1981; Ruggieri *et al.* 1977). *Quadracythere* has a higher, shorter, and quadrate outline; caudal process pointed at mid-height; and better developed ventrolateral, median lateral, and dorsolateral ridges (Bonaduce *et al.* 1984; Swanson 1979). Compared to *Pokornyella*, *Tenedocythere* has a subrectangular outline and predominant horizontal ridges. Compared to *Quadracythere*, *Tenedocythere* has a lower carapace; posterior margin pointed below mid-height; less developed, but two ventrolateral ridges (one continuing into anteromarginal ridge between the A and B fossae and the other shorter often ended at mid-length); predominant horizontal ridges; and a very well developed dorsolateral ridge often continuing into the posterior margin [Bonaduce *et al.* 1984; see also Titterton & Whatley (2008) for Indo-Pacific species that show considerable difference from the European species]. Compared to *Pokornyella*, *Hornibrookella* has a less inflated carapace; more slender (i.e. comparatively elongated and low) and trapezoidal outline; well-developed ventrolateral and dorsolateral ridges; and less developed caudal process.

Pokorniella, especially its type species *Pokornyella limbata* (Bosquet, 1852) (see Keij 1957; Ducasse & Coustillas 1981), is similar to *Aurila* Pokorný, 1955 (Harrison *et al.* 2000) but is distinguished externally by the posterodorsal tubercle situated very close to the margin and better developed caudal process that tends to lack reticulation. *Pokorniella* tends to have a more inflated valve and subrectangular outline compared to *Aurila*, although the type species of *Pokorniella* lacks these tendencies (Ruggieri *et al.* 1977; Ducasse & Coustillas 1981; Bonaduce *et al.* 1984).

Internal details are not observable in our specimens or in many of the Palaeogene ostracods. Thus, our comparisons are restricted to external characters.

Pokornyella lamarckiana s. l. (Bosquet, 1852) (Fig. 19A–D)

1852 *Cythere lamarckiana* Bosquet: 71, pl. 3, figs a–d.
?1951 *Hemicythere lienosa* Howe: 13, pl. 3, figs 5–7.

Figure 19. Scanning electron microscope images of *Pokornyella* and *Reticuloquadracythere* species. **A–D,** *Pokornyella lamarckiana* sensu lato (Bosquet, 1852); **A, B,** RGM.1349612 (LC2044), adult? carapace; **C, D,** RGM.1349613 (LC2045), adult? carapace. **E–L,** *Reticuloquadracythere apostolescui* sensu lato Ducasse, 1963; **E, F,** RGM.1349614 (LC2014), A-1 juvenile RV; **G, H,** RGM.1349615 (LC2015), A-1 juvenile LV; **I,** RGM.1349616 (LC4019), A-1 juvenile LV; **J,** RGM.1349617 (LC2036), A-1 juvenile RV; **K, L,** RGM.1349618 (LC2037), adult LV. A, C: left lateral views of carapaces; B, D: right lateral views of carapaces; E, G, I, J, L: lateral views; F, H, K: internal views.

1955 *Cythereis deshayesiana* (Bosquet); Apostolescu: 269, pl. 7, figs 109–113.
1957 *Quadracythere lamarckiana* (Bosquet); Keij: 105, pl. 19, fig. 6, pl. 20, figs 9, 10.
1960 *Cythereis arcanus* Lubimova & Guha in Lubimova, Guha, & Mohan: 33, pl. 3, fig. 1a, b.
1971 *Quadracythere* (*Hornibrookella*) *arcana* (Lubimova & Guha); Siddiqui: 67, pl. 34, figs 3–5.
1977 *Quadracythere vahrenkampi* Moos; Monostori: pl. 4, figs 12, 13.
1987 *Quadracythere vahrenkampi* Moos; Monostori: pl. 6, figs 8–10.
1991 *Quadracythere arcana cornigera* Ahmad, Neale & Siddiqui: 231, pl. 25, figs 4–8.
1994 *Hornibrookella arcana* (Lubimova & Guha); Khosla: pl. 2, fig. 7.
1996 ?*Quadracythere karkarensis* Bassiouni & Luger: 44, pl. 13, figs 2–9.
1998 *Hornibrookella lamarckiana* (Bosquet); Monostori: 55, pl. 9, figs 5–10.
2009 *Jugosocythereis nishii* Yamaguchi & Kamiya: 230 (part), fig. 6.8 (non figs 6.2–6.7).
2012 *Quadracythere*? *lamarckiana* (Bosquet); Guernet, Huyghe, Lartaud, Merle, Emmanuel, Gély, Michel, & Pilet: 942, fig. 7M.

Remarks. This species has often been included in *Quadracythere* or *Hornibrookella* but is better placed in *Pokornyella* which has an almond-shaped outline, posterodorsal tubercle, and well-developed caudal process (e.g. as seen in Ducasse *et al.* 1985). We consider *Pokornyella lamarckiana* (Bosquet, 1852), *Pokornyella arcana* (Lubimova & Guha in Lubimova *et al.* 1960), and *Pokornyella karkarensis* (Bassiouni & Luger, 1996) conspecific. Although there is some variation in development of the posterodorsal tubercle, ridges, and primary reticulation, such variation exists even within each study or local population. A specimen reported as *Jugosocythereis nishii* Yamaguchi & Kamiya, 2009 (fig. 6.8) is also this species. *Pokornyella arcana cornigera* (Ahmad, Neale & Siddiqui, 1991) is included in this species in a broad sense, although it has better developed horizontal ridges and posterodorsal tubercle.

This species is similar to *Pokornyella vanga* (Ahmad, Neale & Siddiqui, 1991) but it is distinguished by the much coarser primary reticulation and more distinct subcentral tubercle. *Pokornyella pseudotriangularis* Morsi & Scheibner, 2009, *Pokornyella* sp. 2 of Morsi & Scheibner (2009), and a species reported as *Hornibrookella* sp. A by El Sogher (1996) are distinguished from this species by the less inflated posterior part of the carapace and finer reticulation. *Pokornyella brevis* Ducasse, 1963 is distinguished from this species by the less prominent anterodorsal corner, less developed posterodorsal tubercle, and more slender outline.

Pokornyella lamarckiana sensu lato (Bosquet, 1852) has a distinct morphology and has been very widely reported from Eocene strata over most of the Tethyan region in a broad sense (including Europe, Indo-Pakistan, Africa, Japan, and perhaps North America). Thus, this species is a good biostratigraphical marker for the Eocene.

Genus ***Reticuloquadracythere*** Monostori, 1998

Type species. *Quadracythere apostolescui* Ducasse, 1963.

Remarks. Some species of *Gyrocythere* Siddiqui, 1971 [e.g. *Gyrocythere mudhensis* (Khosla, 1972) and *Gyrocythere memorans* (Lubimova & Guha, 1960)] are very similar to *Reticuloquadracythere* Monostori, 1998 but differ in the less inflated posterior part; smaller height at the posterior cardinal angle; finer primary reticulation in the posterior fourth; and oblique ventrolateral ridge situated well above the ventral margin. Khosla (1972) included these species in *Anticythereis* van den Bold, 1946. However, based on the lectotype specimen of the type species of *Anticythereis* shown by van den Bold (1964), *Anticythereis* is very similar to *Alocopocythere* Siddiqui, 1971 in general external features, ovate outline, and inconspicuous caudal process and ventrolateral ridge, and is not similar to *Reticuloquadracythere* or any other genera related to *Quadracythere*. *Isalocopocythere* Carbonnel, Alzouma & Dikouma, 1990 (type species *Alocopocythere immodica* Al-Furaih, 1980) is similar to *Reticuloquadracythere* but is distinguished by its more rounded (instead of quadrate) and inflated carapace, smooth and less developed ventrolateral and dorsolateral ridges, ventrolateral ridge distant from the ventral margin, regularly rounded fossae, and smooth muri; and in lacking an anterior marginal rim.

Quadracythere sensu stricto and related genera to *Quadracythere* show certain similarity, but are not very similar, to *Reticuloquadracythere*. *Quadracythere* sensu stricto according to the type species (Swanson 1979; Bonaduce et al. 1984) [also including *Quadracythere* biruga Hornibrook, (Moos 1965); Note that *Quadracythere* sensu stricto may be endemic to New Zealand] has a well-developed median lateral and a few other lateral ridges; straight ventrolateral and dorsolateral ridges constituting entire ventral and dorsal margins; caudal process pointed at (instead of below) mid-height; and less regular primary reticulation pattern. *Tenedocythere* Sissingh, 1972 is distinguished from *Reticuloquadracythere* by having well-developed horizontal ridges; more rectangular outline, characterized by angular corners and straighter margins; continuous ventrolateral-posteromarginal-dorsolateral ridge; two parallel ventrolateral ridges, one continuing into the anterior margin between the A and B fossae (Liebau 1975, 1991) and the other shorter; and also two median lateral ridges (Bonaduce *et al.* 1984; Swanson 1979). As seen in

detailed studies of the type species (Al-Furaih 1975; Liebau 1991), *Hornibrookella* Moos, 1966 has much less inflated carapace; more slender (i.e. comparatively elongated and low) outline; smooth appearance, with evenly rounded fossae, smooth muri, and lacking lateral spines; less developed ventrolateral and dorsolateral ridges; and trapezoidal outline (rather than quadrate), compared to *Reticuloquadracythere*. The outline and general appearance of *Reticuloquadracythere* is also similar to *Mutilus* Neviani, 1928. *Mutilus* is similar to *Reticuloquadracythere* in general appearance, but the primary reticulation is much coarser and its primary pattern is substantially different. *Mutilus* also has a more rounded outline (Bonaduce *et al.* 1987). *Martinicythere* Bassiouni, 1969, *Oertliella* Pokorný, 1964, and *Aysegulina* Özdikmen, 2010 (= *Limburgina* Deroo, 1966) differ from *Reticuloquadracythere* by having a more slender outline and better developed subcentral tubercle. *Martinicythere* and *Oertliella* are more spinose, while *Aysegulina* has a better developed subcentral tubercle.

Although future discovery of species with intermediate features and revision of type and other species of related genera discussed above may lead us to conclude that *Reticuloquadracythere* should be placed in synonymy with another genus, for now we prefer to consider it to be a valid genus.

Reticuloquadracythere apostolescui s. l. Ducasse, 1963
(Fig. 19E–L)

1963 *Quadracythere apostolescui* Ducasse: 240, pl. 3, figs 32–33.
1969 *Mutilus apostolescui* (Ducasse); Bassiouni: 205, pl. 18, figs 4, 5.
1985. *Quadracythere apostolescui* Ducasse; Ducasse, Guernet, & Tambareau: pl. 84, figs 4, 5.
?1996 *Isalocopocythere carbonneli* Bassiouni & Luger: 46, pl. 14, figs 1–4, pl. 27, fig. 17.
1998 *Reticuloquadracythere apostolescui* (Ducasse); Monostori: 58, pl. 11, figs 6–10, pl. 12, fig. 1.

Remarks. Our specimens are very similar to the type species of *Reticuloquadracythere*, *Reticuloquadracythere apostolescui* (Ducasse, 1963). They share all of the major diagnostic characters of regularly and evenly developed primary reticulation covering the entire lateral surface with high and narrow muri, inflated carapace, short and high outline, caudal process pointed below mid-height, lack of ridges other than ventrolateral and dorsolateral ridges, and long ventrolateral ridge almost continuing into the anterior margin. Thus, they are obviously congeneric and, in our opinion, conspecific in a broad sense. A comprehensive synonymy of this species can be found in Monostori (1998). *Reticuloquadracythere carbonneli* (Bassiouni & Luger, 1996) is probably a junior synonym of this species. Although Bassiouni & Luger (1996) indicated that *Reticuloquadracythere carbonneli* has a different reticulation pattern, this is not clear to us.

Investigating not only adult but also juvenile specimens will probably give better insight for solving the problem of the generic status of this genus and related genera. For example, our A-1 juveniles (Fig. 19E, G, I, J) show much better the irregular-shaped fossae and spinous muri than the adult specimen (Fig. 19L), that contrast with some similar genera such as *Isalocopocythere* and *Hornibrookella* having regularly rounded fossae and smooth muri. Investigating juveniles of *Isalocopocythere* and *Hornibrookella* species should better clarify these differences.

Genus ***Stigmatobradleya*** gen. nov.

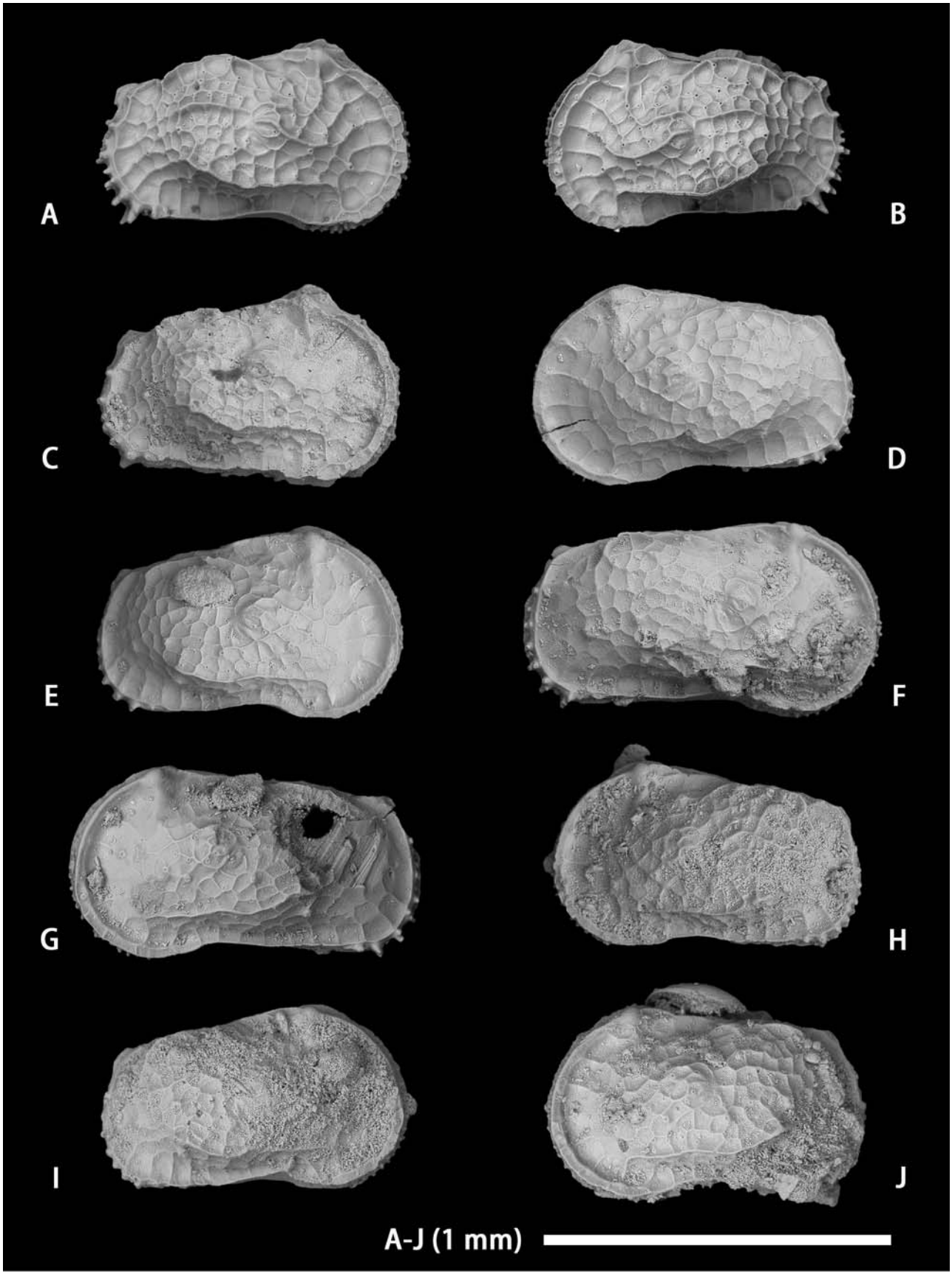
Type species. *Stigmatobradleya hunti* gen. et sp. nov.

Derivation of name. From the affinity to *Bradleya* Hornibrook, 1952, and superficial similarity to *Stigmatocythere* Siddiqui, 1971.

Diagnosis. A thaerocytherid genus with very broad flat areas along the anterior and posterior margins. Outline *Bradleya*-like. Ventrolateral ridge oblique and curved. Dorsolateral ridge curved. Lateral surface covered by shallow primary reticulation. Posterior margin denticulate.

Remarks. *Stigmatobradleya* gen. nov. is superficially similar to *Stigmatocythere* Siddiqui, 1971 and *Moosina* Bassiouni & Luger, 1990 (note that *Moosina* Bassiouni & Luger, 1990 may be a junior synonym of *Stigmatocythere*; the type species, *Moosina barisensis* Bassiouni & Luger, 1990, and *Stigmatocythere obliqua* Siddiqui, 1971 are very similar in external morphology), especially in the ridge arrangement, reticulation pattern, and very wide flat areas along the anterior and posterior margins. However, the general appearance, trapezoidal outline, posterior margin pointed ventrally, and marginal spines in the ventral half of the posterior margin clearly indicate that this genus belongs to Thaerocytheridae. *Phyrocythere* Al-Furaih, 1980 shows certain similarities to *Stigmatobradleya* but is nodose and has the caudal process better developed and upturned.

Although several European Eocene species show certain similarities to this genus, including *Quadracythere angusticostata* (Bosquet, 1852) (Guernet *et al.* 2012; Keij 1957; Monostori 1998), *Bradleya thiliensis* Apostolescu 1956 (Ducasse *et al.* 1985) and a species reported as '*Quadracythere* (*Hornibrookella*) *glyptica* Tambareau, 1972' in a thesis cited by Ducasse *et al.* (1985), we prefer to consider *Stigmatobradleya* to be currently monospecific. Benson (1972) clearly defined the genus *Bradleya* Hornibrook, 1952 but the *Bradleya* problem in a broad sense remains. Tethyan '*Bradleya*-like' thaerocytherid species (currently assigned to, for example, *Bradleya*,


A
B
C
D
E
F
G
H
I
J
A-J (1 mm)

Quadracythere, and *Hornibrookella*) require fundamental taxonomic revision at the genus level.

Stigmatobradleya hunti sp. nov.
(Fig. 20A–J)

Derivation of name. In honour of Gene Hunt, Smithsonian Institution (Washington DC) for his work on thaerocytherid ostracods.

Material. Holotype: carapace, RGM.1349619 (LC2A026) (Fig. 20A, B). Paratypes: carapace, RGM.1349620 (LC4020) (Fig. 20C); carapace, RGM.1349621 (LC2018) (Fig. 20D, E); carapace, RGM.1349622 (LC2038) (Fig. 20F, G); carapace, RGM.1349623 (LC2039) (Fig. 20H, I; carapace, RGM.1349624 (LC2040) (Fig. 20J).

Type locality and horizon. Southern Madagascar, Early–Middle Eocene.

Dimensions. RGM.1349619 (LC2A026) (holotype): L = 0.904 mm; H = 0.562 mm. RGM.1349621 (LC2018) (paratype): L = 0.892 mm; H = 0.560 mm. RGM.1349622 (LC2038) (paratype): L = 1.054 mm; H = 0.582 mm.

Diagnosis. A *Stigmatobradleya* species with shallow primary reticulation and dorsolateral ridge extended above the dorsal margin.

Description. Carapace moderately calcified, highest at anterodorsal corner. Outline trapezoidal; anterior margin obliquely rounded and weakly denticulate; posterior margin blunt and weakly caudate, bearing spines especially in its ventral half; dorsal margin almost straight; ventral margin slightly concave; ventrolateral ridge oblique and curved; dorsolateral ridge curved and extended above the dorsal margin; subcentral tubercle present; anterior and posterior margins retain very broad flat areas. Well-ornamented specimens have sinuous median lateral ridge. Anterodorsal corner strongly angular; posterodorsal corner angular. Lateral surface ornamented with shallow primary reticulation. Internal features not observable. Sexual dimorphism distinct.

Remarks. This species is distinguished from *Moosina barisensis* Bassiouni & Luger, 1990 by its posteromarginal spines especially in the ventral half of the posterior margin and downturned caudal process.

We found two morphological forms: a 'robust' form, in which muri, ridges and spines are much better developed (Fig. 20A–C); and a 'delicate' form, in which muri, ridges, and spines are subdued (Fig. 20D–J). We treat these as intraspecific variations because they are otherwise identical.

Family **Trachyleberididae** Sylvester-Bradley, 1948
Genus ***Echinocythereis*** Puri, 1954

Type species. *Cythere margaritifera* Brady, 1870 [= *Cythereis garretti* Howe & McGuirt in Howe, Chambers, Brown, McGuirt,Neill, Hough, Ellis, Stephenson, Spurgeon, Pyeatt, Dorm, Hadley, Taylor, & Johnson, 1935; see Hazel 1967].

Remarks. In our opinion, many *Echinocythereis* species have been erroneously assigned to other genera in various Palaeogene and Cretaceous studies. *Togoina orientalis* Bassiouni & Luger, 1996, *Nucleolina zihorica* Honigstein & Rosenfeld, 1985, and a species reported as *Megahemicythere oertlii* Witt, 1967 by Monostori (2004) are probably *Echinocythereis*, although subcentral muscle scars that are an important character to define *Echinocythereis* are not known in these species. *Scelidocythereis* Siddiqui, 1971 [type species *Echinocythereis* (*Scelidocythereis*) *multibullata* Siddiqui, 1971] is a junior synonym of *Echinocythereis* Puri, 1954. Siddiqui (1971) erected *Scelidocythereis* as a subgenus of *Echinocythereis* for species with a ventrolateral ridge. But even in the type species *Echinocythereis multibullata* (Siddiqui, 1971), the ventrolateral ridge is not very distinct (Siddiqui 1971; Bhandari 1996), and *Echinocythereis* species in general have an inconspicuous ventrolateral ridge (e.g. Yasuhara *et al.* 2015). In addition, Siddiqui (1971) seems to have misunderstood the generic concept of *Echinocythereis* sensu stricto and to have assigned several species of *Henryhowella* (or a closely related genus) (see Yasuhara *et al.* 2015) to *Echinocythereis* sensu stricto [his '*Echinocythereis* (*Echinocythereis*) *contexta'* and *Echinocythereis* (*Echinocythereis*) *elongata*]. Given these circumstances, we think a better developed ventrolateral ridge insufficient by itself to separate (sub)genera.

Echinocythereis sahnii (Tewari & Tandon, 1960)
(Fig. 21A, B)

1960 *Hemicythere sahnii* Tewari & Tandon: 157, text-fig. 4, fig. 1a–d.
1967 *Echinocythereis septentrionalis* Ducasse: 66, pl. 4, fig. 72.
1968 *Hemicythere sahnii* Tewari & Tandon; Tewari & Bhargava: 29, pl. 11, fig. 2a, b.

Figure 20. Scanning electron microscope images of *Stigmatobradleya hunti* sp. nov. **A, B,** RGM.1349619 (LC2A026), adult female carapace; **C,** RGM.1349620 (LC4020), adult female carapace; **D, E,** RGM.1349621 (LC2018), adult female carapace; **F, G,** RGM.1349622 (LC2038), adult male carapace; **H, I,** RGM.1349623 (LC2039), adult female carapace; **J,** RGM.1349624 (LC2040), adult female carapace. A–C: robust forms; D–J: delicate forms; A, C, E, F, I: right lateral views of carapaces; B, D, G, H, J: left lateral views of carapaces.

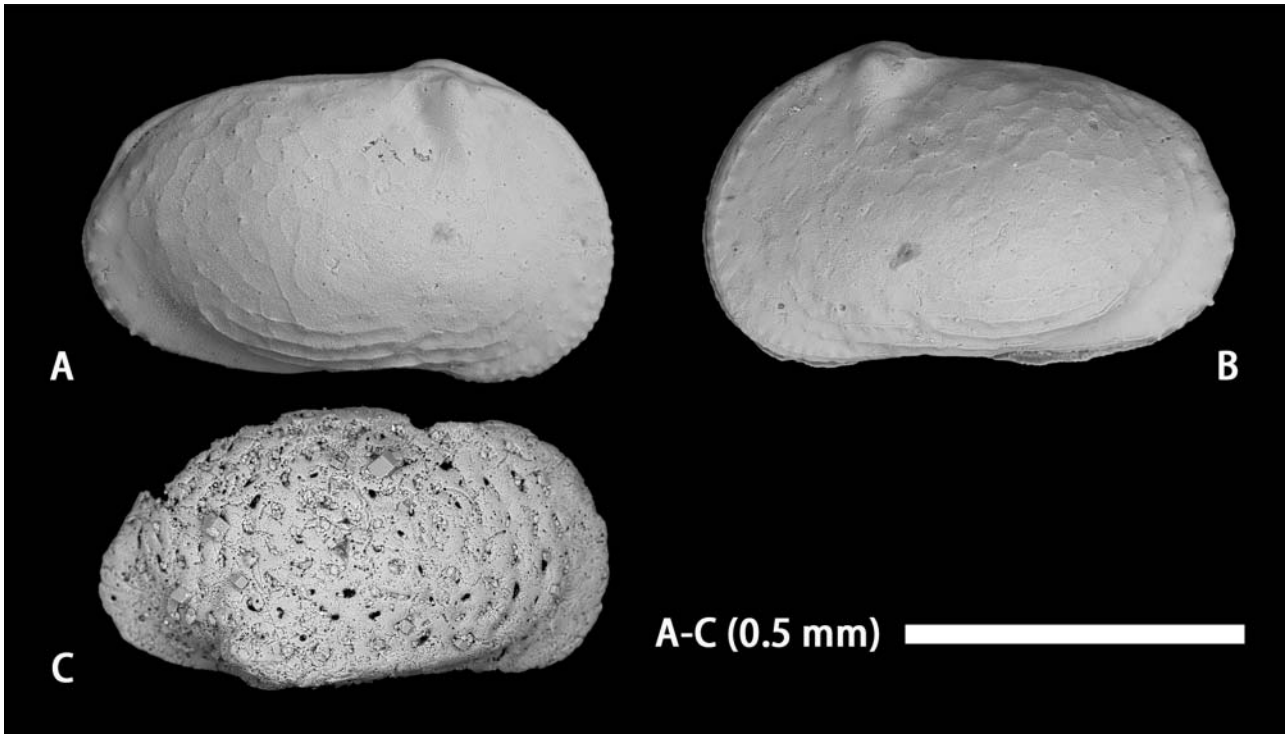


Figure 21. Scanning electron microscope images of *Echinocythereis* and *Kingmaina*? species. **A, B,** *Echinocythereis sahnii* (Tewari & Tandon, 1960), RGM.1349625 (LC2020), adult? carapace. **C,** *Kingmaina*? sp. 1, RGM.1349626 (LC4018), adult? RV (dorsal part partially broken). A: right lateral view of a carapace; B: left lateral view of a carapace; C: lateral view.

1971 *Echinocythereis* (*Scelidocythereis*) *rasilis* Siddiqui: 36, pl. 17, figs 5, 6, 10, pl. 18, figs 1–3, 5, 7.
1972 *Hemicythere sahnii* Tewari & Tandon; Khosla: 493, pl. 2, fig. 26.
1985 *Echinocythereis septentrionalis* Ducasse; Ducasse, Guernet, & Tambareau: pl. 80, fig. 9.
1991 *Echinocythereis* (*Scelidocythereis*) *sahnii* (Tewari & Tandon); Bhandari: 46, pl. 1, fig. 9.
1996 *Echinocythereis* (*Scelidocythereis*) *sahnii* (Tewari & Tandon); Bhandari: 76, pl. 52, figs 1, 2.
2013 *Echinocythereis* (*Scelidocythereis*) *sahnii* (Tewari & Tandon); Nagori, Khosla, & Jakhar: pl. 2, fig. 3.

Remarks. This species is similar to *Echinocythereis echinata* (Sars, 1866) (Barra & Bonaduce 2000; Yasuhara *et al.* 2015) in general appearance and very weak primary reticulation, but it is distinguished by having subdued spines and a less inflated carapace. It is also similar to a species reported as *Megahemicythere oertlii* Witt, 1967 by Monostori (2004), but is distinguished by the flatter posterior margin, less inflated carapace, and more prominent anterodorsal corner. Our specimen shows an intermediate morphology between Indo-Pakistan and European populations. The Indo-Pakistan population has a more prominent anterodorsal corner and better developed ventrolateral ridge compared to the European population (i.e. *Echinocythereis septentrionalis* Ducasse, 1967). Our specimen has a more prominent anterodorsal corner and less developed ventrolateral ridge. This species is widely known from the Middle Eocene of Indo-Pakistan (Khosla 1994; Bhandari 1996) and the Eocene of France (Ducasse *et al.* 1985).

Genus ***Kingmaina*** Keij, 1957

Type species. *Cythere forbesiana* Bosquet, 1852.

***Kingmaina*? sp. 1**
(Fig. 21C)

Remarks. We tentatively include our specimen in *Kingmaina* Keij, 1957 because of its elongated outline; well-developed, long ventrolateral ridge extended below the ventral margin posteriorly; and irregular-shaped fossae. The dorsal part of the specimen is partly broken.

Family **Xestoleberididae** Sars, 1928
Genus ***Uroleberis*** Triebel, 1958

Type species. *Cytheropteron* (*Eocytheropteron*) *parnensis* Apostolescu, 1955.

Remarks. The taxonomic status of *Uroleberis* Triebel, 1958 and *Foveoleberis* Malz, 1980 has been a matter of serious debate in ostracod taxonomy. Malz (1980) erected *Foveoleberis* based on crenate median hinge element to separate it from *Uroleberis*. However, hingement details

of the type species of *Uroleberis* have never been shown (hingement details are not always preserved in fossil specimens; Neale & Singh 1988), and the development of crenation of the median hinge element varies even within a xestoleberidid genus (Athersuch 1976). By comparing the type species of *Foveoleberis* and *Uroleberis*, *Xestoleberis foveolata* Brady, 1880 and *Cytheropteron* (*Eocytheropteron*) *parnensis* Apostolescu, 1955 (SEM images are shown in several studies: Malz 1980; Neale & Singh 1988; Whatley & Zhao 1988; Guernet *et al.* 2012), major differences are: (1) punctation (presence or absence); (2) eye tubercle (presence or absence); (3) outline (rounded or trapezoidal); (4) caudal process (inconspicuous or prominent); (5) anterodorsal and posterodorsal margins (arched or concave); and (6) ventral margin (comparatively rounded or flat). But many species showing intermediate states exist, and subsequent studies following the erection of *Foveoleberis* (Malz 1980) did not find useful diagnostic character(s) to separate these genera clearly (Ducasse *et al.* 1985; Neale & Singh 1988; Neale & Huang 1993). Some (Ducasse *et al.* 1985; Neale & Singh 1988; Neale & Huang 1993) considered that *Foveoleberis* is practically indistinguishable from *Uroleberis* (or just did not use *Foveoleberis*), while others preferred to use *Foveoleberis* as a separate genus (Al-Furaih 1984; Whatley & Zhao 1988; Zhao & Whatley 1989a; McKenzie *et al.* 1991; Bassiouni & Elewa 1999; Jellinek & Swanson 2003; Warne *et al.* 2006). By following Neale (Neale & Huang 1993; Neale & Singh 1988), we prefer to not separate *Foveoleberis* from *Uroleberis* for now. Details of the type species of *Uroleberis* are needed to resolve the *Uroleberis* problem. Also, there is some uncertainty whether *Xestoleberis foveolata* Brady, 1880 is a junior synonym of *Cythere cypraeoides* Brady, 1868 (Neale & Singh 1988; Whatley & Zhao 1988; Zhao & Whatley 1989a; Neale & Huang 1993).

Uroleberis paranuda sp. nov.
(Fig. 22A–I)

Derivation of name. From the similarity to *Uroleberis nuda* Ducasse, 1967.

Material. Holotype: RV, RGM.1349628 (LC2009) (Fig. 22C–E). Paratypes: LV, RGM.1349627 (LC2055) (Fig. 22A, B); RV, RGM.1349629 (LC2035) (Fig. 22F, G); LV, RGM.1349630 (LC4012) (Fig. 22H, I).

Type locality and horizon. Southern Madagascar, Early–Middle Eocene.

Dimensions. RGM.1349628 (LC2009) (holotype): L = 0.639 mm; H = 0.459 mm. RGM.1349627 (LC2055) (paratype): L = 0.620 mm; H = 0.463 mm. RGM.1349630 (LC4012) (paratype): L = 0.589 mm; H = 0.414 mm.

Diagnosis. A robust *Uroleberis* species with very weakly developed caudal process in RV and weak punctation.

Description. Carapace strongly calcified, highest in the middle. Outline high, short, and ovate in lateral view; anterior margin obliquely rounded; posterior margin very weakly caudate in RV and evenly rounded in LV; dorsal margin strongly and evenly arched; ventral margin slightly convex. Anterodorsal corner straight; posterodorsal corner weakly angular. Lateral surface weakly punctate. Hingement as for genus. Subcentral muscle scars are not observable.

Remarks. This species is very similar to *Uroleberis nuda* Ducasse, 1967 [= '*Uroleberis' nudus* (*sic*)] (Ducasse 1967; Ducasse *et al.* 1985; Neale & Singh 1988), but it is distinguished by its reverse asymmetry between left and right valves. In *Uroleberis paranuda* sp. nov., the caudal process is better developed in the RV, and the outline is higher and slightly more angular in the RV. The same is true for the LV in *Uroleberis nuda*. In addition, the punctation is probably better developed in this species. The published photographic and SEM images of *Uroleberis nuda* are not clear enough to confirm this (Ducasse 1967; Ducasse *et al.* 1985; Neale & Singh 1988), but Ducasse *et al.* (1985) wrote that the valve surface is smooth and the SEM image shown in their paper seems to support their description. This species is similar to *Uroleberis foveolata* (Brady, 1880) in the outline and inconspicuous caudal process, but is distinguished by its much weaker punctation and less pointed anterior margin and caudal process.

Genus ***Xestoleberis*** Sars, 1866

Type species. *Cythere aurantia* Baird, 1838.

Xestoleberis renemai sp. nov.
(Fig. 23B–G)

1996 *Xestoleberis subglobosa* (Bosquet); Bhandari: 146, pl. 122, figs 1, 2.
?1996 *Xestoleberis* cf. *complanata* Deltel; Bassiouni & Luger: 74, pl. 24, figs 19–21.
2012 *Xestoleberis subglobosa* (Bosquet); Guernet, Huyghe, Lartaud, Merle, Emmanuel, Gély, Michel, & Pilet: p. 951, fig. 8V.

Derivation of name. In honour of Willem Renema, Naturalis Biodiversity Center (Netherlands), for his work on Cenozoic palaeobiogeography.

Material. Holotype: carapace, RGM.1349633 (LC2050) (Fig. 23D, E). Paratypes: carapace, RGM.1349632 (LC2012) (Fig. 23B, C); LV, RGM.1349634 (LC2056) (Fig. 23F, G).

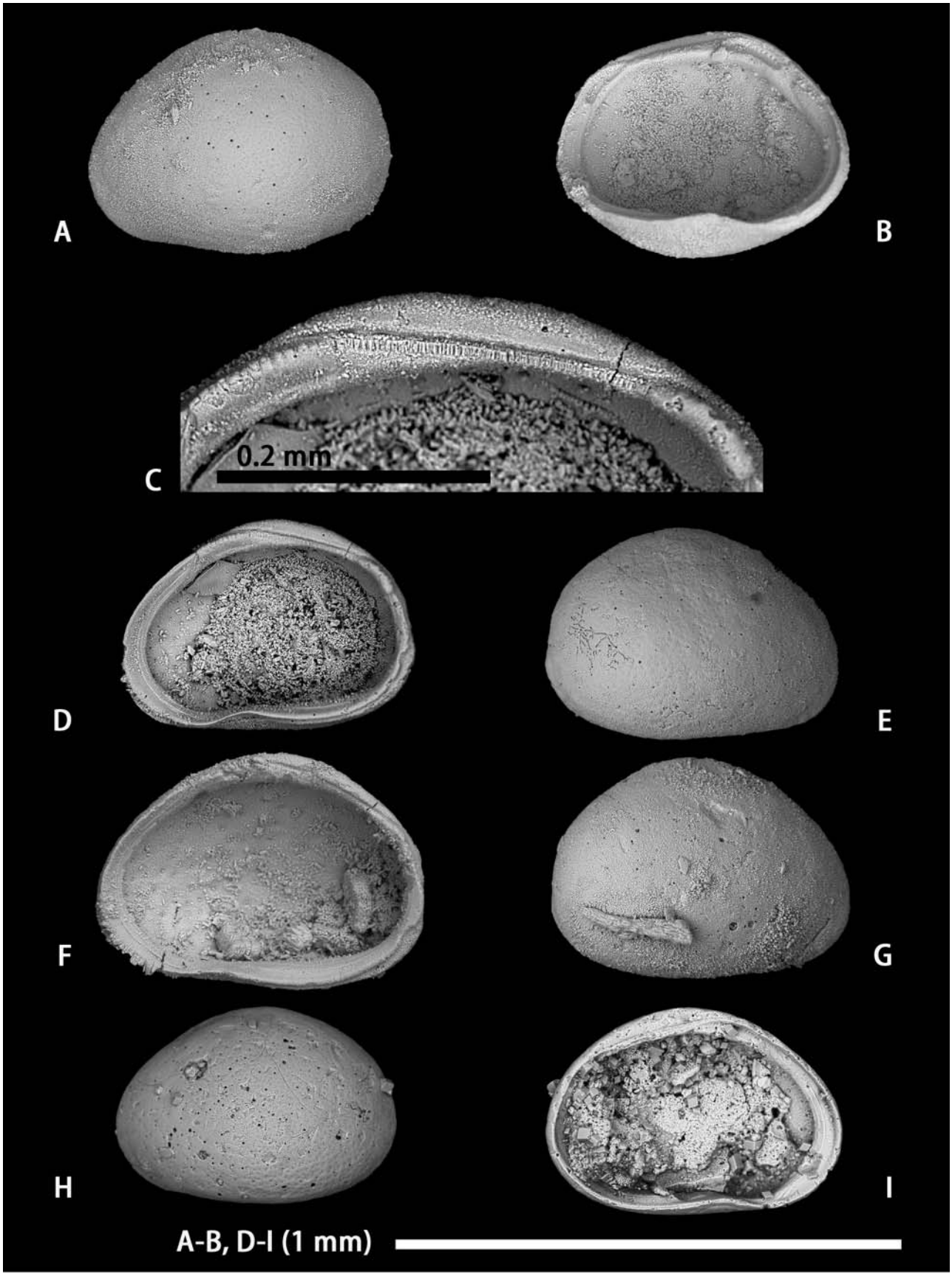


Figure 22. Scanning electron microscope images of *Uroleberis paranuda* sp. nov. **A, B,** RGM.1349627 (LC2055), adult female? LV; **C–E,** RGM.1349628 (LC2009), adult female? RV; **F, G,** RGM.1349629 (LC2035), adult female? RV; **H, I,** RGM.1349630 (LC4012), adult male? LV. A, E, G–H: lateral views; B–D, F, I: internal views; C: hingement close-up.

Type locality and horizon. Southern Madagascar, Early–Middle Eocene.

Dimensions. RGM.1349633 (LC2050) (holotype): L = 0.656 mm; H = 0.368 mm. RGM.1349632 (LC2012) (paratype): L = 0.695 mm; H = 0.438 mm. RGM.1349634 (LC2056) (paratype): L = 0.591 mm; H = 0.375 mm.

Diagnosis. A *Xestoleberis* species with elongated outline and upturned posterior part.

Description. Carapace delicately calcified, highest in the middle. Outline elongated; anterior margin obliquely rounded; posterior margin truncated and weakly rounded; dorsal margin weakly arched; ventral margin slightly curved. Anterodorsal corner straight; posterodorsal corner angular. The posterior third shows upturned appearance. Lateral surface smooth. Internal features not observable. Sexual dimorphism distinct; male smaller and more elongated.

Remarks. *Xestoleberis renemai* sp. nov. is similar to *Xestoleberis* cf. *complanata* Deltel of Bassiouni & Luger (1996) in outline and general appearance, but it is distinguished by having a more slender outline. The specimens reported as *Xestoleberis subglobosa* (Bosquet, 1852) by Bhandari (1996) from the Eocene of India and by Guernet *et al.* (2012) from the Eocene of France are conspecific with this species in our opinion. Keij (1957) wrote in his redescription of *Xestoleberis subglobosa* (Bosquet, 1852) that "the immature valves have an upward swing posteriorly." We suspect that Keij misunderstood a different species (our *Xestoleberis renemai* sp. nov.) as the juvenile of *Xestoleberis subglobosa*. The lectotype specimen of *Xestoleberis subglobosa* designated by Keij (1957) is clearly distinct from *Xestoleberis renemai* sp. nov. in having a much higher outline and lacking an upturned appearance of the posterior part.

***Xestoleberis* sp. 1**
(Fig. 23A)

Discussion

Depositional environment

The ostracod fauna described here from the south-western Madagascan sections indicates a very shallow, hypersaline and unstable environment, e.g. a hypersaline lagoon. As discussed in the Systematic palaeontology section, the occurrence of *Paijenborchellina madagascarensis* sp. nov. indicates a very shallow and hypersaline environment of salinity > 40. In addition, the morphological variations of this species indicate an unstable and varying environment, such as a lagoon. These interpretations are based on the habitat of a very similar extant species, *Paijenborchellina venosa* (Bate 1971; Al-Abdul-Razzaq *et al.* 1982; Mostafawi 2003). The dominance of *Neocyprideis armata* sensu lato is also considered to indicate a shallow-marine hypersaline environment (Bassiouni & Luger 1996). The large intraspecific variation of *Neocyprideis* also suggests an unstable and varying environment. Monospecific dominance is common in either brackish or hypersaline environments (Keen 1977b, 1990; Keen & Racey 1991), and our Madagascar fauna does not include any obvious brackish-water taxa. In sum, it is likely that the depositional environment was similar to that of the present-day Abu Dhabi lagoon, Persian Gulf (Bate 1971; Al-Abdul-Razzaq *et al.* 1982; Mostafawi 2003). A similar environment might have been distributed broadly along Arabia, Indo-Pakistan, and the eastern coast of Africa during the Early–Middle Eocene (Siddiqui 1971; Keen & Racey 1991).

Palaeobiogeography: southern end of the Tethys?

Dingle (1976) for South Africa and Ahmad *et al.* (1991) for Tanzania showed strong affinities of their Eocene ostracod faunas to those from Pakistan. Our comprehensive taxonomic survey of species in the Early–Middle Eocene of Madagascar, in conjunction with many taxonomy papers published since Ahmad *et al.* (1991), allows us to place the Eocene south-eastern African ostracods in a global biogeographical context. We summarize the palaeobiogeographical distribution of the species found in this study below.

Cytherella cf. *kimensis* is similar to Early–Middle Eocene Indian [*Cytherella kimensis* and *Cytherella hastata* (Bhandari *et al.* 2005; Neale & Singh 1985)] and Somalian species [*Cytherella ahlmadoensis* (Bassiouni & Luger 1996)]. *Bairdoppilata ilaroensis* sensu lato is widely known from the Paleocene of Nigeria (Reyment & Reyment 1959; Reyment 1981), Maastrichtian of Ghana (Reyment 1981), Maastrichtian–Early Eocene of Egypt (Bassiouni & Luger 1990), Late Eocene–Oligocene of Tanzania (Ahmad *et al.* 1991), Middle Eocene of Somalia (Bassiouni & Luger 1996), Early Eocene of Egypt (Morsi *et al.* 2008), and other African countries. *Phlyctenophora* cf. *chauhani* is very similar to an Early Miocene Indian species, *Phlyctenophora chauhani* (Khosla, 1978). Similar species are also known from the Middle Eocene of Somalia (*Paracypris darrorensis* Bassiouni & Luger, 1996) and the Maastrichtian–Paleocene of Libya (*Bythocypris* sp. A and *Paracypris* aff. *Paracypris* sp. A of El Sogher 1996). A very similar species to *Paijenborchellina madagascarensis* sp. nov., *Paijenborchellina venosa*, is known from the Recent of the Persian Gulf (Gurney 1979; Mostafawi 2003) and India (Jain 1981a; Mostafawi 2003). *Neocyprideis armata* sensu lato, the almost monospecifically dominant species in our samples, is known from the


A
B
C
D
E
F
G
A-G (1 mm)

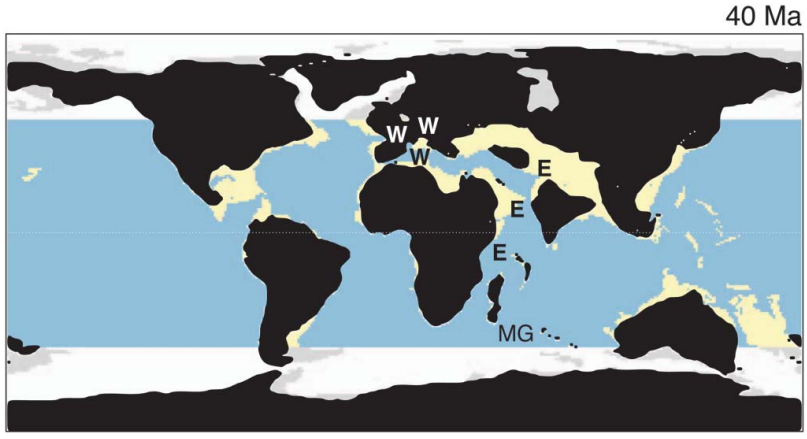


Figure 24. Middle Eocene (40 Ma) palaeogeographical map from Leprieur *et al.* (2016). Light blue, deep tropical ocean; yellow, tropical shallow reefs; white and light grey, deep ocean and shallow waters outside the tropical boundary, respectively. MG, Madagascar. Ws and Es are indicative of general areas of Western Tethys and Eastern Tethys palaeobiogeographical sub-realms, respectively. Our results strongly indicate that Madagascar was a part of the Eastern Tethys palaeobiogeographical sub-realm during the Eocene.

Middle Eocene of Somalia (Bassiouni & Luger 1996). Two very similar species, *Neocyprideis chaudhuryi* and *Neocyprideis formosa*, are known from the Early Miocene of India (Lubimova *et al.* 1960) and Late Eocene of Pakistan (Siddiqui 2000). Other similar species are known from the Early Miocene of India, i.e. *Neocyprideis okhaensis* and *Neocyprideis paravurensis* (Khosla 1988). *Alciella irizukii* sp. nov. in our study is very similar to *Alciella parisiensis* (Guernet, 1984) known from the Middle Eocene of France (Guernet 1984), and to *Alciella bicostata* (Monostori, 1998) known from the Middle–Late Eocene of Hungary (Monostori 1998). *Alciella* was previously known exclusively from the Eocene–Oligocene of Europe (Guernet 1984; Guernet *et al.* 2012; Liebau 1991; Monostori 1998), with *A. irizukii* being the first record outside Europe. Similar species to *Hermanites* cf. *percultus* are known from the Late Eocene of Tanzania (*Hermanites percultus* (Ahmad *et al.* 1991)) and the Eocene of Europe [*Hermanites orbignyana*, *Hermanites vahrenkampi dudarensis*, *Hermanites vermiculata* (Bosquet 1852; Keij 1957; Ducasse *et al.* 1985; Monostori 1998)]. *Loxoconcha loculus* seems to be a regional species of south-eastern Africa and is known from the Late Eocene of Tanzania (Ahmad *et al.* 1991). *Neomonoceratina angulosa*, very similar to *Neomonoceratina afroangulosa* sp. nov., is well known from the Early Eocene of Indo-Pakistan (Bhandari 1996; Siddiqui 2006). Another very similar species, *Neomonoceratina dambarholensis*, is known from the Middle Eocene of Somalia (Bassiouni & Luger 1996). *Schizocythere* cf. *prolata* is very similar to *Schizocythere prolata* from the Late Paleocene of Pakistan and Late Paleocene–Early Eocene of India (Bhandari 1996; Siddiqui 1981). *Pokornyella lamarckiana* sensu lato has a very wide geographical distribution and is known from the Eocene of Europe (Keij 1957; Ducasse 1963; Monostori 1998; Guernet *et al.* 2012), Indo-Pakistan (Siddiqui 1971; Khosla 1994), Arab-Africa (Ahmad *et al.* 1991; Bassiouni & Luger 1996), Japan (Yamaguchi & Kamiya 2009) and perhaps North America (Howe 1951). *Reticuloquadracythere apostolescui* sensu lato Ducasse, 1963 is known from the Middle Eocene–Early Oligocene of Europe (Monostori 1998). *Stigmatobradleya hunti* sp. nov. may be a Madagascan endemic. *Echinocythereis sahnii* was originally reported from the Middle Eocene of India and is widely known from the Middle Eocene of Indo-Pakistan (Tewari & Tandon 1960; Siddiqui 1971; Bhandari 1996), as well as the Eocene of Europe (Ducasse 1967; Ducasse *et al.* 1985). *Muellerina eocenica* sp. nov. is the oldest record of this well-known European genus. *Uroleberis paranuda* sp. nov. is very similar to a Middle–Late Eocene European species, *Uroleberis nuda* (Ducasse *et al.* 1985). *Xestoleberis renemai* sp. nov. and its close relative are known from the Middle Eocene of Europe (Guernet *et al.* 2012), Middle Eocene of India (Bhandari 1996), and Middle Eocene of Somalia (Bassiouni & Luger 1996).

Figure 23. Scanning electron microscope images of *Xestoleberis* species. **A,** *Xestoleberis* sp. 1, RGM.1349631 (LC2010), LV. **B–G,** *Xestoleberis renemai* sp. nov.; **B, C,** RGM.1349632 (LC2012), adult carapace; **D, E,** RGM.1349633 (LC2050), adult carapace; **F, G,** RGM.1349634 (LC2056), adult? LV. A, F: lateral views; B, D: right lateral views of carapaces; C, E: left lateral views of carapaces; G: internal view.

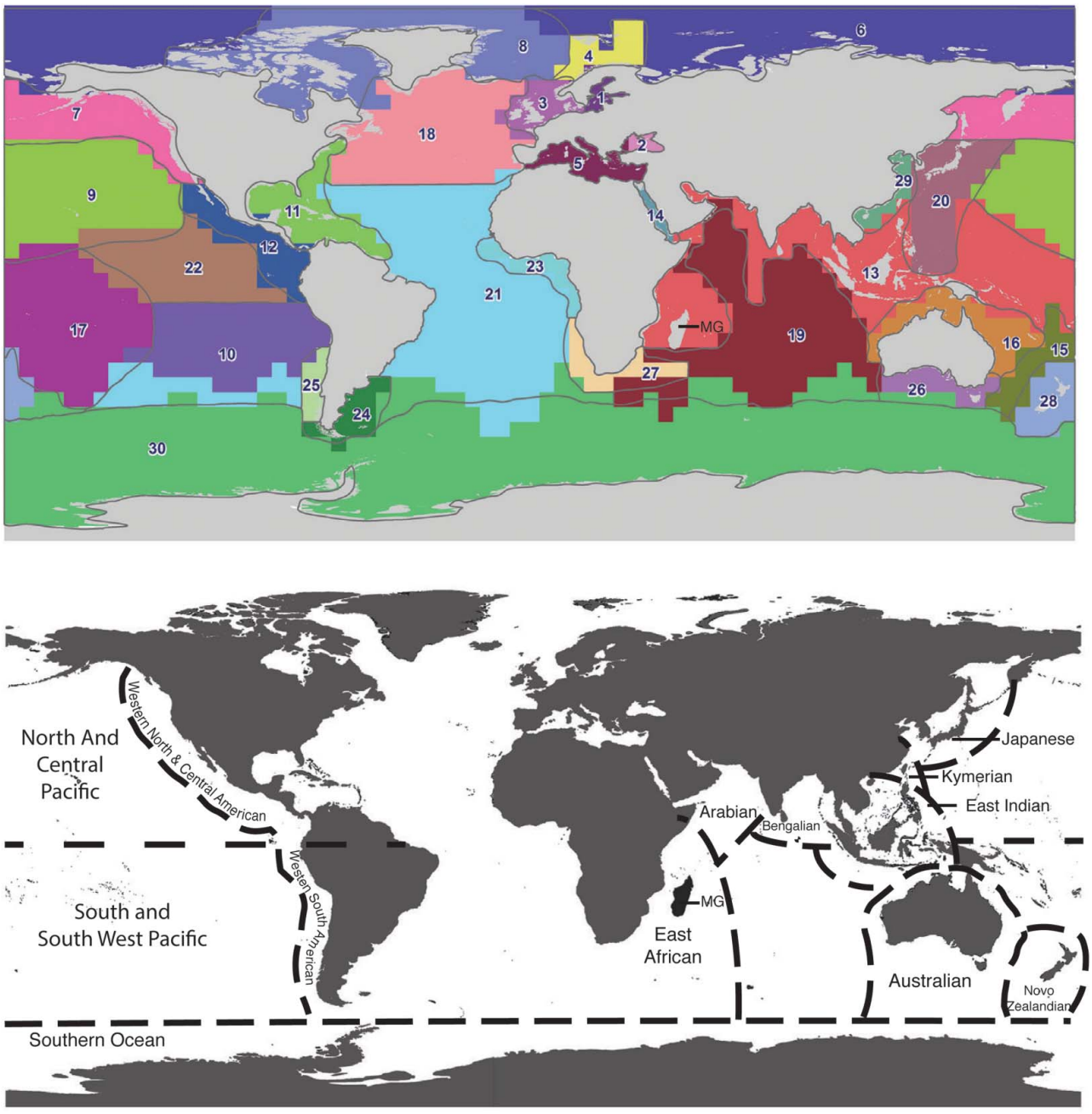


Figure 25. Comparison of global biogeographical divisions. Top panel: latest global biogeographical division of marine organisms (from Costello *et al.* 2017). Bottom panel: the shallow-marine ostracod specific division (Whatley 1987; Titterton & Whatley 1988). MG, Madagascar. In the top panel, biogeographical realms are numbered: 1, inner Baltic Sea; 2, Black Sea; 3, NE Atlantic; 4, Arctic Europe; 5, Mediterranean; 6, Arctic; 7, N Pacific; 8, N Atlantic Boreal; 9, mid-tropical North Pacific Ocean; 10, South-east Pacific; 11, tropical W Atlantic; 12, tropical E Pacific; 13, tropical Indo-Pacific (East Indies) and coastal Indian Ocean; 14, Red Sea; 15, Tasman Sea to SW Pacific; 16, tropical Australia and Coral Sea; 17, mid S tropical Pacific; 18, offshore and NW North Atlantic; 19, offshore Indian Ocean; 20, offshore W Pacific; 21, offshore S Atlantic; 22, offshore mid-E Pacific; 23, tropical E Atlantic; 24, Argentina; 25, Chile; 26, S Australia; 27, S Africa; 28, New Zealand; 29, NW Pacific; 30, Southern Ocean. Madagascar is included in the Indo-Pacific seas and coastal Indian Ocean biogeographical realm (Realm 13) together with the Arabian, Indian, and Indo-Pacific coasts in the latest global marine biogeographical division scheme (top panel). Our results fit better with this biogeographical scheme than with the ostracod-specific scheme proposed ~30 years ago (bottom panel), suggesting the need for an update of the global ostracod biogeographical division scheme.

In summary, the Eocene Madagascan ostracod fauna is characterized as follows.

1. There is considerable similarity to the adjacent Tanzanian fauna. The faunal difference between the Madagascan and Tanzanian faunas is probably because of different environments (hypersaline lagoon vs normal shallow marine environment: Ahmad *et al.* 1991) and ages (Early–Middle Eocene vs Late Eocene: Ahmad *et al.* 1991). There is not much similarity to the South African fauna (Dingle 1976), probably due to the deeper depositional environment of the South African fauna, as evidenced by the continuous occurrence of the deep-water genus *Krithe* (Dingle 1976).
2. A strong connection between the Madagascan and Indo-Pakistan faunas as indicated by previous studies (Dingle 1976; Ahmad *et al.* 1991) is strongly supported at the species level. We also found a strong palaeobiogeographical connection with the Arab-African region (Bassiouni & Luger 1996). The East African, Arabian, and Indo-Pakistan regions seem to constitute an East Tethyan palaeobiogeographical sub-realm with strong faunal similarity during the Eocene (Fig. 24). The region might also have shared a similar depositional environment of high salinity, probably due to an arid climate like the present-day Persian Gulf.
3. We discovered a strong faunal affinity between south-eastern Africa and Europe, not clearly recognized previously (Dingle 1976; Ahmad *et al.* 1991), indicating a strong connection between East and West Tethyan faunas (Fig. 24). The south-eastern African region clearly belongs to the Tethys palaeobiogeographical realm. Furthermore, some species found in the Eocene of Madagascar show very wide distributions beyond Europe and Indo-Pakistan. Notably, *Pokornyella lamarckiana* sensu lato is known from the Eocene of Europe, Indo-Pakistan, Arab-Africa, Japan, and perhaps North America, clearly characterizing the spatial extent of the Tethys palaeobiogeographical realm from Asia-Oceania to eastern America (e.g. Keij 1976; McKenzie 1982).
4. Madagascar is situated in the East African ostracod biogeographical realm defined on the basis of Recent and Cenozoic shallow-marine ostracods (Whatley 1987; Titterton & Whatley 1988) (Fig. 25). The East African ostracod realm shows strongest affinity with the Southern-South-western Pacific and Australian ostracod realms (Titterton & Whatley 1988). However, East African ostracod distribution remained poorly understood (especially at the time of Whatley's and Titterton's papers) and our Eocene Madagascan findings do not show much similarity to South and South-West Pacific and Australian ostracods. Furthermore, a recent global marine biogeographical study (Costello *et al.* 2017) using 65,000 species of marine animals and plants included Madagascar as a part of the Indo-Pacific seas and coastal Indian Ocean biogeographical realm (Realm 13 of Costello *et al.* 2017) together with the Arabian, Indian, and Indo-Pacific coasts (Fig. 25). Our results showing an Eocene East Tethyan palaeobiogeographical sub-realm fit better with this biogeographical scheme than with the ostracod-specific scheme of the 1980s (Whatley 1987; Titterton & Whatley 1988) (Fig. 25). An update of global ostracod biogeographical division is needed.

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Supplemental data

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Supplementary Table 1. Detailed information of the specimens used for the present study.

NBC	No.	Species	T	V/C	Instar	Sex	Sample	Figure
RGM.1349541	LC4010	*Cytherella* cf. *kimensis*		R	?		TOL4-LC4	2A–B
RGM.1349542	LC2033	*Cytherelloidea* sp. 1		C	?		TOL4-LC2	2C
RGM.1349543	LC4009	*Cytherelloidea* sp. 2		R	?		TOL4-LC4	2D–E
RGM.1349544	LC2007	*Bairdoppilata ilaroensis* s.l.		L	A-1		TOL4-LC2	2F
RGM.1349545	LC2008	*Bairdoppilata ilaroensis* s.l.		R	A		TOL4-LC2	2G–H
RGM.1349546	LC2013	*Phlyctenophora* cf. *chauhani*		C	?		TOL4-LC2	3A
RGM.1349547	LC4028	*Phlyctenophora* cf. *chauhani*		L	A		TOL4-LC4	3B–C
RGM.1349548	LC4011	*Phlyctenophora* cf. *chauhani*		L	A		TOL4-LC4	3D–F
RGM.1349549	LC4030	*Phlyctenophora* cf. *chauhani*		L	A		TOL4-LC4	3G–H
RGM.1349550	LC4031	*Phlyctenophora* cf. *chauhani*		R	A		TOL4-LC4	3I–J
RGM.1349551	LC2030	*Argilloecia?* sp. 1		C	?		TOL4-LC2	4A
RGM.1349552	LC2032	*Pontocythere* sp. 1		R	A?		TOL4-LC2	4B–C
RGM.1349553	LC2022	*Paijenborchellina madagascarensis*	P	L	A	M	TOL4-LC2	5A
RGM.1349554	LC2023	*Paijenborchellina madagascarensis*	P	L	A	F?	TOL4-LC2	5B–C
RGM.1349555	LC2024	*Paijenborchellina madagascarensis*	P	R	A	M	TOL4-LC2	5D–E
RGM.1349556	LC2025	*Paijenborchellina madagascarensis*	P	R	A	F	TOL4-LC2	5F–G
RGM.1349557	LC2048	*Paijenborchellina madagascarensis*	P	R	A	F	TOL4-LC2	5H–I
RGM.1349558	LC2049	*Paijenborchellina madagascarensis*	P	L	A	M	TOL4-LC2	5J–K
RGM.1349559	LC4014	*Paijenborchellina madagascarensis*	P	L	A	M	TOL4-LC4	6A–B
RGM.1349560	LC4015	*Paijenborchellina madagascarensis*	P	L	A	F	TOL4-LC4	6C–D
RGM.1349561	LC4016	*Paijenborchellina madagascarensis*	H	R	A	F	TOL4-LC4	6E–F
RGM.1349562	LC4017	*Paijenborchellina madagascarensis*	P	R	A-1		TOL4-LC4	6G–H
RGM.1349563	LC2001	*Neocyprideis polygonoreticulata*	H	R	A		TOL4-LC2	7A–B, E–G
RGM.1349564	LC2053	*Neocyprideis polygonoreticulata*	P	C	A		TOL4-LC2	7C–D
RGM.1349565	LC2003	*Neocyprideis armata* s.l.		L	A	F	TOL4-LC2	7H–J
RGM.1349566	LC2004	*Neocyprideis armata* s.l.		L	A	M	TOL4-LC2	8A
RGM.1349567	LC2006	*Neocyprideis armata* s.l.		R	A	M	TOL4-LC2	8B–C
RGM.1349568	LC2005	*Neocyprideis armata* s.l.		L	A	F	TOL4-LC2	8D–F
RGM.1349569	LC4001	*Neocyprideis armata* s.l.		L	A	F?	TOL4-LC4	8G–I
RGM.1349570	LC4002	*Neocyprideis armata* s.l.		L	A	M	TOL4-LC4	8J, 9A–C
RGM.1349571	LC4003	*Neocyprideis armata* s.l.		R	A	F	TOL4-LC4	9D–E
RGM.1349572	LC4004	*Neocyprideis armata* s.l.		L	A	M	TOL4-LC4	9F
RGM.1349573	LC2A036	*Neocyprideis armata* s.l.		R	A	F	TOL2-LC2A	9G–H
RGM.1349574	LC2054	*Neocyprideis* sp. 1		L	A	F?	TOL4-LC2	9I–J
RGM.1349575	LC2A037	*Neocyprideis armata* s.l.		R	A	F	TOL2-LC2A	10A–B
RGM.1349576	LC4032	*Neocyprideis armata* s.l.		R	A	M	TOL4-LC4	10C–F
RGM.1349577	LC4027	*Neocyprideis armata* s.l.		R	A	M	TOL4-LC4	10G–H
RGM.1349578	LC4005	*Neocyprideis armata* s.l.		L	A-1		TOL4-LC4	11A–C
RGM.1349579	LC4006	*Neocyprideis armata* s.l.		R	A-1		TOL4-LC4	11D–E
RGM.1349580	LC4007	*Neocyprideis armata* s.l.		L	A-2		TOL4-LC4	11F
RGM.1349581	LC4008	*Neocyprideis armata* s.l.		R	A-2		TOL4-LC4	11G–H

RGM.1349582	LC2021	*Alciella irizukii*	H	C	A?		TOL4-LC2	12A–B
RGM.1349583	LC2058	*Alciella irizukii*	P	C	J?		TOL4-LC2	12C
RGM.1349584	LC4021	*Semicytherura* sp. 1		R	A?		TOL4-LC4	12D–E
RGM.1349585	LC2016	*Hermanites* sp. 1		R	J?		TOL4-LC2	13A–B
RGM.1349586	LC2017	*Hermanites* cf. *percultus*		C	A		TOL4-LC2	13C
RGM.1349587	LC2041	*Hermanites* cf. *percultus*		C	A		TOL4-LC2	13D–E
RGM.1349588	LC2042	*Hermanites* cf. *percultus*		C	A		TOL4-LC2	13F–G
RGM.1349589	LC2057	*Hermanites* cf. *percultus*		L	A		TOL4-LC2	13H–I
RGM.1349590	LC2043	*Hermanites* cf. *percultus*		C	A		TOL4-LC2	14A–B
RGM.1349591	LC4029	*Hermanites* cf. *percultus*		C	A		TOL4-LC4	14C–D
RGM.1349592	LC4025	*Urocythereis?* sp. 1		C	?		TOL4-LC4	14E–F
RGM.1349593	LC2059	*Urocythereis?* sp. 1		R	A?		TOL4-LC2	14G–H
RGM.1349594	LC2028	*Loxoconcha loculus*		C	A		TOL4-LC2	15A–B
RGM.1349595	LC2029	*Loxoconcha loculus*		L	A		TOL4-LC2	15C–D
RGM.1349596	LC2052	*Loxoconcha loculus*		C	A		TOL4-LC2	15E–F
RGM.1349597	LC4023	*Loxoconcha loculus*		R	A		TOL4-LC4	15G–H
RGM.1349598	LC4024	*Loxoconcha loculus*		C	A		TOL4-LC4	15I–J
RGM.1349599	LC2A030	*Paracytheridea* sp. 1		L	A		TOL2-LC2A	16A–B
RGM.1349600	LC4022	*Paracytheridea* sp. 1		C	A		TOL4-LC4	16C
RGM.1349601	LC2A034	*Paracytheridea* sp. 1		L	J?		TOL2-LC2A	16D–E
RGM.1349602	LC2A035	*Paracytheridea* sp. 1		R	J?		TOL2-LC2A	16F–G
RGM.1349603	LC2031	*Cytherois* sp. 1		C	?		TOL4-LC2	16H
RGM.1349604	LC2026	*Neomonoceratina afroangulosa*	H	C	A	M?	TOL4-LC2	17A–C
RGM.1349605	LC2027	*Neomonoceratina afroangulosa*	P	L	A	F?	TOL4-LC2	17D–E
RGM.1349606	LC2051	*Neomonoceratina afroangulosa*	P	R	A	M?	TOL4-LC2	17F–G
RGM.1349607	LC2060	*Neomonoceratina afroangulosa*	P	L	A	M?	TOL4-LC2	17H–I
RGM.1349608	LC2A031	*Schizocythere* cf. *prolata*		R	A		TOL2-LC2A	18A–B
RGM.1349609	LC2019	*Muellerina eocenica*	H	C	A	M	TOL4-LC2	18C–D
RGM.1349610	LC2046	*Muellerina eocenica*	P	C	A	M	TOL4-LC2	18E
RGM.1349611	LC2047	*Muellerina eocenica*	P	C	A	F	TOL4-LC2	18F–G
RGM.1349612	LC2044	*Pokornyella lamarckiana* s.l.		C	A?		TOL4-LC2	19A–B
RGM.1349613	LC2045	*Pokornyella lamarckiana* s.l.		C	A?		TOL4-LC2	19C–D
RGM.1349614	LC2014	*Reticuloquadracythere apostolescui* s.l.		R	A-1		TOL4-LC2	19E–F
RGM.1349615	LC2015	*Reticuloquadracythere apostolescui* s.l.		L	A-1		TOL4-LC2	19G–H
RGM.1349616	LC4019	*Reticuloquadracythere apostolescui* s.l.		L	A-1		TOL4-LC4	19I
RGM.1349617	LC2036	*Reticuloquadracythere apostolescui* s.l.		R	A-1		TOL4-LC2	19J
RGM.1349618	LC2037	*Reticuloquadracythere apostolescui* s.l.		L	A		TOL4-LC2	19K–L
RGM.1349619	LC2A026	*Stigmatobradleya hunti*	H	C	A	F	TOL2-LC2A	20A–B
RGM.1349620	LC4020	*Stigmatobradleya hunti*	P	C	A	F	TOL4-LC4	20C
RGM.1349621	LC2018	*Stigmatobradleya hunti*	P	C	A	F	TOL4-LC2	20D–E
RGM.1349622	LC2038	*Stigmatobradleya hunti*	P	C	A	M	TOL4-LC2	20F–G
RGM.1349623	LC2039	*Stigmatobradleya hunti*	P	C	A	F	TOL4-LC2	20H–I
RGM.1349624	LC2040	*Stigmatobradleya hunti*	P	C	A	F	TOL4-LC2	20J

RGM.1349625	LC2020	*Echinocythereis sahnii*		C	A?		TOL4-LC2	21A–B
RGM.1349626	LC4018	*Kingmaina?* sp. 1		R	A?		TOL4-LC4	21C
RGM.1349627	LC2055	*Uroleberis paranuda*	P	L	A	F?	TOL4-LC2	22A–B
RGM.1349628	LC2009	*Uroleberis paranuda*	H	R	A	F?	TOL4-LC2	22C–E
RGM.1349629	LC2035	*Uroleberis paranuda*	P	R	A	F?	TOL4-LC2	22F–G
RGM.1349630	LC4012	*Uroleberis paranuda*	P	L	A	M?	TOL4-LC4	22H–I
RGM.1349631	LC2010	*Xestoleberis* sp. 1		L	J?		TOL4-LC2	23A
RGM.1349632	LC2012	*Xestoleberis renemai*	P	C	A		TOL4-LC2	23B–C
RGM.1349633	LC2050	*Xestoleberis renemai*	H	C	A		TOL4-LC2	23D–E
RGM.1349634	LC2056	*Xestoleberis renemai*	P	L	A?		TOL4-LC2	23F–G

All specimens are from Early–Middle Eocene Madagascar.
NBC, Naturalis Biodiversity Center catalog number; No., M.Y.'s personal catalog number. T, type (P, paratype; H, holotype); V/C, valve or carapace (L, left valve; R, right valve; C, carapace); A, adult; J, juvenile (A-1, adult minus one juvenile; A-2. adult minus two juvenile); F, female; M, male.