

# Early Miocene marine ostracodes from southwestern India: implications for their biogeography and the closure of the Tethyan Seaway

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**Abstract.**—Twenty-six genera and 34 species of early Miocene Indian shallow-marine ostracodes were examined for taxonomy and paleobiogeography. A new genus *Paractinocythereis* and new species *Costa ponticulocarinata* were described. Early Miocene Indian ostracode fauna shows strong affinity to Eocene–Miocene Eastern and Western Tethyan ostracode faunas and Miocene–Recent Indo-Pacific ostracode fauna, supporting the Hopping Hotspot Hypothesis that the Tethyan biodiversity hotspot has shifted eastward through Arabia to Indo-Australian Archipelago (IAA) together with concomitant biogeographic shifts of the Tethyan elements. The result also indicated an inverse westward distributional shift in a genus. It is important to note that Paleogene and Miocene shallow marine ostracodes from the IAA region remain poorly investigated, and more fossil ostracode data are needed to better test the Hopping Hotspot Hypothesis.

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## Introduction

The Hopping Hotspots Hypothesis (Renema et al., 2008) argues that the tropical hotspot of shallow-marine biodiversity has moved during the past 50 million years from the Western Tethys (>40 Ma), through the Arabian region (~30–20 Ma), to its present position in the Indo-Australian Archipelago (IAA: <20 Ma). The southern tip of India occupied a central position between the Arabian and IAA biodiversity hotspots during the early Miocene and is thus an important area to study the origins of the huge modern marine biodiversity in the IAA.

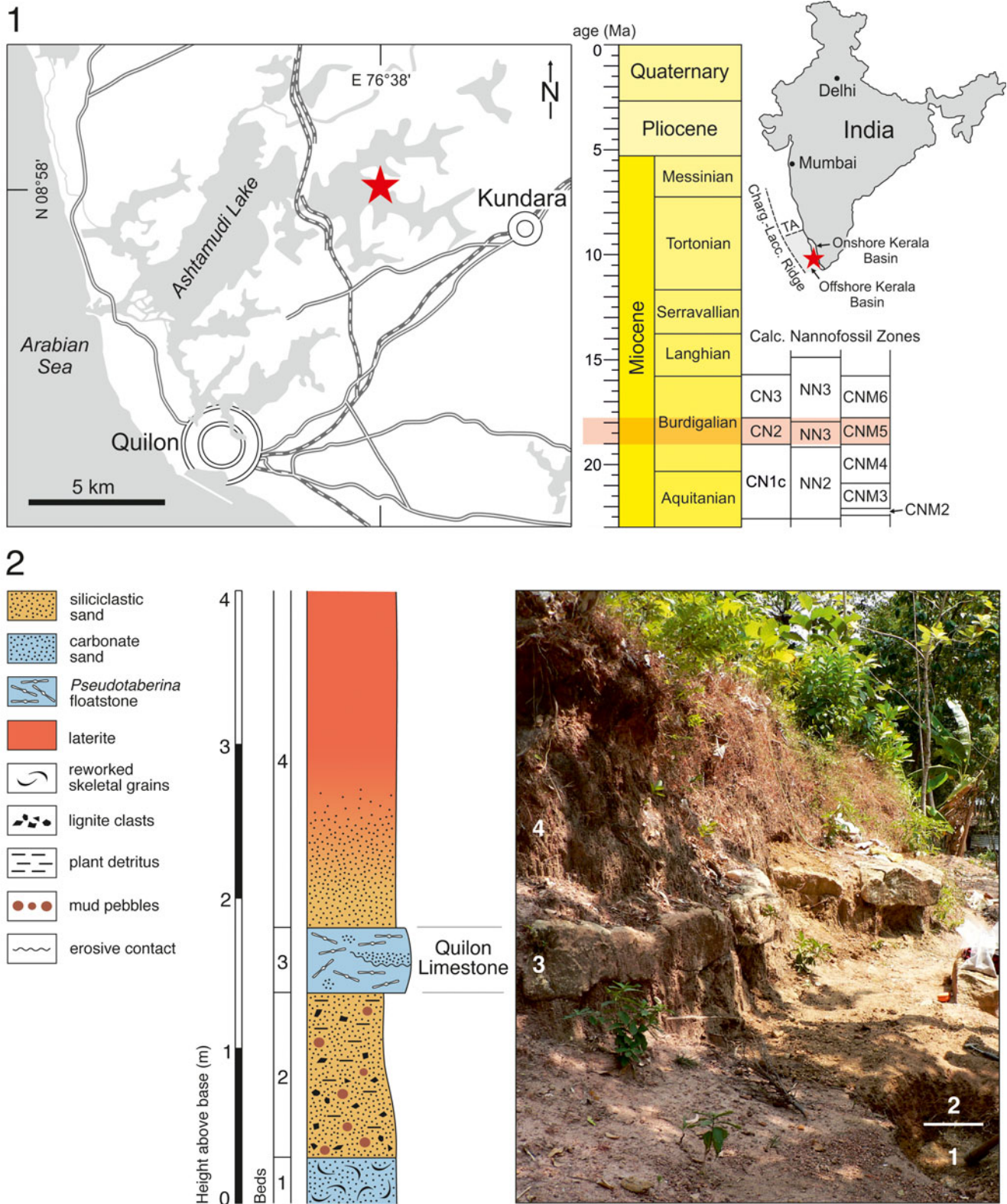
This study describes an early Miocene (Burdigalian) ostracode fauna from the shallow marine Quilon Formation in Kerala (southwestern India). Indian shallow marine ostracodes have well been investigated, especially since the 1960s, as summarized by the checklist in Jain (1981) and the atlases in 1990–2000s (Bhandari, 1996; Bhandari et al., 2001). In Indian ostracode papers, scanning electron microscopy (SEM) images appeared in 1980s. The atlases show SEM images, but detailed morphological characters are not always clear and internal views including muscle scars and hingement are seldom shown. Since the early 2000s, after publication of the atlases, comprehensive taxonomic update or re-evaluation has not been done for ~20 years. Herein, we re-evaluate the taxonomy of early Miocene ostracodes from southern India based on

high-resolution SEM images of external and internal views. We revised the generic assignments of several species and erected one new genus and one new species. We also discuss the paleobiogeographic affinities of the south Indian ostracode fauna with respect to the Hopping Hotspots Hypothesis of Renema et al. (2008).

## Geological setting

This study was carried out at “Channa Kodi” locality (8°58′36″N, 76°38′08″E) close to Padappakkara village in the southern onshore part of the Kerala Basin (Fig. 1). The Kerala Basin is the southernmost sedimentary basin on the Western Indian passive margin and extends ~600 km parallel to the coastline, bounded by the Tellicherry Arch in the north, the Chargos-Laccadive Ridge in the west, and the Central Indian Ocean Basin in the south. During the Cenozoic, the basin constituted a major depocenter for terrigenous clastic sediments that derived from denudation of the Western Ghats (Campanile et al., 2008). Channa Kodi is the type locality of the fossiliferous Quilon Limestone, which represents patchy carbonate occurrences in the Quilon Formation of the Neogene siliciclastic Warkalli Group (Menon, 1967; Vaidyanadhan and Ramakrishnan, 2008; Reuter et al., 2011). The Quilon Formation is underlain by the lower Miocene Mayyanad Formation and overlain by the Ambalapuzha Formation of Miocene to Pliocene age (Vaidyanadhan and Ramakrishnan, 2008). Palynofloras from the Warkalli Group document marginal marine brackish lagoonal

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**Figure 1.** (1) Locality maps and stratigraphic summary. Red star shows the location of the studied site CK-09-02, close to Padappakkara village. Light-red band indicates the biostratigraphic range and the age of the sample CK-09-02 (19.01–17.75 Ma). See main text for the details of calcareous nannofossil zones. TA: Telli-cherry Arch. Charg.-Lacc. Ridge: Chargos-Laccadive Ridge. (2) Columnar section and field photograph of the Channa Kodi type locality. The columnar section is divided into beds 1–4. The sample CK-09-02 is from bed 1. Modified after Reuter et al. (2011).

depositional environments as well as brackish and freshwater swamps similar to the present-day Kerala backwaters (Rao and Ramanujam, 1975; Ramanujan, 1987; Kern et al., 2013; Reuter et al., 2013). Facies analysis of the Quilon Limestone at Channa Kodi indicates a shallow marine seagrass environment that had likely developed temporarily during a sea-level rise (Reuter et al., 2011). In accordance with this paleoenvironmental interpretation, Harzhauser (2014) described a highly diverse seagrass-associated gastropod fauna from a weakly lithified, bioclastic carbonate sand of at least 0.3 m thickness, which is exposed ~1 m below the Quilon Limestone at the base of Channa Kodi section (bed 1: Reuter et al., 2011) (Fig. 1). The sediment sample used for this ostracode study (here we call the sample CK-09-02) derived also from bed 1 (Fig. 1). Based on the associated benthic foraminiferan fauna, which is characterized by mesophotic taxa (Brigulio and Rögl, 2018; Rögl and Brigulio, 2018), it has been recently suggested that the seagrass fauna was transported from seagrass beds, which grew in ~20–30 m water depth, down to 60–70 m water depth (Brigulio et al., 2018). This paleobathymetric reconstruction, however, has to be taken with caution because it does not consider the attenuation of light in seagrass canopies (e.g., Hedley et al., 2014) and turbid coastal waters along southern Kerala (Jyothibabu et al., 2018).

The presence of *Sphenolithus belemnus* Bramlette and Wilcoxon, 1967 in bed 1 (Fig. 1) of the Channa Kodi section (Reuter et al., 2011; Ćorić, 2019) allows correlation to the Calcareous Nannofossil Miocene Biozone (CNM) 5 of Backman et al. (2012), covering the time interval between 19.01 and 17.75 Ma. This age may be further constrained to 19.01–17.96 Ma because *Sphenolithus belemnus* shows a sharp decrease in abundance at the top of the biozone, occurring ca. 0.2 Ma prior to the appearance of *Sphenolithus heteromorphus* Deflandre, 1953, which defines the top of CNM5 (Backman et al., 2012). According to Backman et al. (2012), CNM5 corresponds to Zone CN2 of Okada and Bukry (1980) and encompasses most of Zone NN3 of Martini (1971).

## Materials and methods

The sample CK-09-02 was wet sieved through a 63 µm sieve and then oven-dried. Because the sample was ostracode-rich, the residue sample was 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 on a cardboard slide under a stereomicroscope, Leica S8 APO (Appendix 1). The number of specimens refers to valves and carapaces. Additional specimens were picked from the remaining splits and used for taxonomic purpose (note that these additional specimens are not included in the census count of Appendix 1). Full information about the sample and specimens used for this study is given in Table 1 and Appendices 1 and 2. Uncoated ostracode 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. High-resolution figures of ostracode SEM images (Figs. 2–19) are available at Dryad (<http://datadryad.org/>; <https://doi.org/10.5061/dryad>.

[Orxwdbrrww](#)). For the higher classification, we mainly referred to the World Ostracoda Database (Brandão et al., 2019), Whatley et al. (1993), and Horne et al. (2002). Abbreviations: LV, left valve; RV, right valve; A-1, last juvenile instar (adult minus one); L, length (mm); H, height (mm).

*Repository and institutional abbreviation.*—Figured specimens are deposited in the Natural History Museum Vienna (NHMW), under catalogue numbers 2019/0181/0001–2019/0181/0115. M.Y.'s personal catalogue numbers are also shown.

## Systematic paleontology

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, Lower Cretaceous, northern Germany. Designated by Ulrich (1894).

*Cytherella* sp. 1  
 Figure 2.1–2.4, 2.6

*Dimensions.*—See Table 1.

*Remarks.*—Juveniles of this species are very similar to *Cytherella mayyanadensis* Khosla and Nagori, 1989, but have slightly better-developed surface punctation.

Genus *Cytherelloidea* Alexander, 1929

*Type species.*—*Cytherella williamsoniana* Jones, 1849, Cretaceous, southeastern England.

*Cytherelloidea pandora* s.l. (Kornicker, 1963)  
 Figure 2.5, 2.7, 2.8

1963 *Cytherella pandora* Kornicker, p. 69, text-figs. 26–29, 43, 44.

1966 *Cytherella pandora*; Baker and Hulings, p. 114, pl. 1, fig. 15.

1966 *Cytherella* sp. aff. *C. pandora*; van den Bold, pl. 2, fig. 1.

2000 *Cytherella pandora*; Keyser and Schöning, p. 569, pl. 1, figs. 6, 7.

*Holotype.*—No. 107612 (National Museum of Natural History, Washington DC, USA) from Great Bahama Bank. Recent.

*Dimensions.*—See Table 1.

*Remarks.*—This species is very similar to *Cytherelloidea pandora* (Kornicker, 1963) described from Modern sediments from Bahama. However, given the large difference in type locality and age, we prefer to call our specimens *Cytherelloidea pandora* s.l.



**Table 1.** Dimensions of selected specimens.

NHMW	No.	Species	T	V/C	Instar	Sex	L (mm)	H (mm)	Figure
2019/0181/0003	CK-09-02-003	<i>Cytherella</i> sp. 1		L	J?		0.579	0.303	2.3, 2.4
2019/0181/0004	19B-ck-09-2-002	<i>Cytherella</i> sp. 1		R	A?		0.696	0.367	2.6
2019/0181/0005	CK-09-02-054	<i>Cytherelloidea pandora</i> s.l.		R	A?		0.635	0.346	2.5, 2.7, 2.8
2019/0181/0006	19A-ck-09-2-015	<i>Paranesidea</i> cf. <i>P. gajensis</i>		R	A		0.908	0.515	2.9
2019/0181/0010	CK-09-02-050	<i>Phlyctenophora meridionalis</i>		R	A		1.111	0.461	3.1–3.3
2019/0181/0013	CK-09-02-034	<i>Propontocypris</i> sp. 1		L	A		1.312	0.624	3.9–3.11
2019/0181/0014	CK-09-02-052	<i>Bythoceratina malaysiana</i>		R	A		0.538	0.269	3.12, 3.13
2019/0181/0115	19B-ck-09-2-005	<i>Flexus trifurcata</i>		R	A		0.657	0.311	4.1
2019/0181/0015	CK-09-02-007	<i>Flexus trifurcata</i>		R	A		0.627	0.296	4.2–4.4
2019/0181/0019	CK-09-02-065	<i>Paijenborchellina prona</i>		R	A		0.635	0.293	4.11–4.14
2019/0181/0020	CK-09-02-032	<i>Hemicyprideis kachharai</i>		R	A		0.641	0.323	4.15
2019/0181/0022	CK-09-02-037	<i>Neocyprideis murudensis</i>		L	A		0.566	0.31	5.1–5.4
2019/0181/0025	19A-ck-09-2-003	<i>Neocyprideis thirukkaruensis</i>		L	A		0.566	0.335	5.9
2019/0181/0030	CK-09-02-022	<i>Aurila singhi</i>		L	A		0.509	0.315	6.3–6.5
2019/0181/0061	19B-ck-09-2-022	<i>Pokornyella alata</i>		R	A		0.673	0.407	7.1–7.4
2019/0181/0068	CK-09-02-020	<i>Pokornyella chaasraensis</i>		L	A		0.659	0.429	8.4–8.6
2019/0181/0076	CK-09-02-010	<i>Tenedocythere keralaensis</i>		L	A		0.646	0.412	9.3–9.5
2019/0181/0035	19B-ck-09-2-014	<i>Krithe autochthona</i>		L	A	M	0.718	0.342	10.1–10.3
2019/0181/0043	CK-09-02-048	<i>Loxoconcha confinis</i>		R	A	F	0.472	0.323	11.5–11.8
2019/0181/0046	CK-09-02-055	<i>Loxoconcha keralaensis</i>		L	A		0.466	0.27	11.12–11.15
2019/0181/0050	CK-09-02-028	<i>Paracytheridea perspicua</i>		R	A		0.641	0.291	12.6, 12.7
2019/0181/0053	CK-09-02-029	<i>Neomonoceratina gajensis</i>		L	A		0.434	0.236	13.3–13.5
2019/0181/0054	CK-09-02-031	<i>Neomonoceratina kutchensis</i>		R	A		0.499	0.284	13.6, 13.7
2019/0181/0058	CK-09-02-056	<i>Neomonoceratina retispinata</i>		R	A		0.447	0.258	13.13–13.15
2019/0181/0083	19B-ck-09-2-030	<i>Acanthocythereis panti</i>		R	A	F	0.78	0.454	14.1, 14.2
2019/0181/0086	19A-ck-09-2-014	<i>Alococythere fossularis</i>		R	A		0.727	0.399	14.6–14.8
2019/0181/0089	CK-09-02-062	<i>Chrysocythere jaini</i>		R	A	F	0.608	0.296	14.11, 14.12
2019/0181/0090	19B-CK-09-036	<i>Costa ponticulocarinata</i> n. sp.	P	L	A		0.755	0.386	15.1, 15.2
2019/0181/0092	CK-09-02-061	<i>Costa ponticulocarinata</i> n. sp.	H	R	A		0.788	0.391	15.5–15.7
2019/0181/0060	CK-09-02-058	<i>Horrificiella?</i> sp. 1		L	J		0.448	0.286	16.1, 16.2
2019/0181/0099	CK-09-02-051	<i>Paractinocythereis gujaratensis</i>		R	A	M?	0.785	0.381	17.10–17.12
2019/0181/0101	CK-09-02-033	<i>Puricythereis reticulata</i>		L	A	M?	0.859	0.481	18.2–18.5
2019/0181/0103	CK-09-02-039	<i>Ruggieria guhai</i>		R	A		0.725	0.369	18.7–18.9
2019/0181/0108	CK-09-02-059	<i>Stigmatocythere interrupta</i>		R	A		0.621	0.366	19.3, 19.4
2019/0181/0111	CK-09-02-006b	<i>Stigmatocythere chaasraensis</i>		L	A		0.442	0.244	19.7–19.10
2019/0181/0112	19B-ck-09-2-039	<i>Stigmatocythere</i> cf. <i>S. arcuata</i>		L	A		0.625	0.348	19.11

All specimens are from the sample CK-09-02, southwestern India, early Miocene.

NHMW, catalog numbers of the Natural History Museum Vienna; 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; F, female; M, male; L, length; H, height.

Order Podocopida Sars, 1866  
 Suborder Bairdiocopina Gründel, 1967  
 Superfamily Bairdioidea Sars, 1866  
 Family Bairdiidae Sars, 1866

Genus *Paranesidea* Maddocks, 1969

*Type species.*—*Paranesidea fracticorallicola* Maddocks, 1969, Recent, Madagascar.

*Paranesidea* cf. *P. gajensis* Khosla, 1978  
 Figure 2.9–2.13

*Dimensions.*—See Table 1.

*Remarks.*—This species is similar to *Paranesidea gajensis* Khosla, 1978, but is distinguished by having a less-punctate valve.

Suborder Cypridocopina Jones, 1901  
 Superfamily Cypridoidea Baird, 1845  
 Family Candonidae Kaufmann, 1900

Genus *Phlyctenophora* Brady, 1880

*Type species.*—*Phlyctenophora zealandica* Brady, 1880, Recent; type locality not designated. Junior synonym of *Macrocypris orientalis* Brady, 1868, Recent; northern Java: see Whatley and Zhao (1987) and Wouters (1999).

*Phlyctenophora meridionalis* (Lubimova and Mohan in Lubimova et al., 1960)

Figure 3.1–3.8

1960 *Paracypris meridionalis* Lubimova and Mohan in Lubimova et al., p. 23, pl. 2, fig. 3.

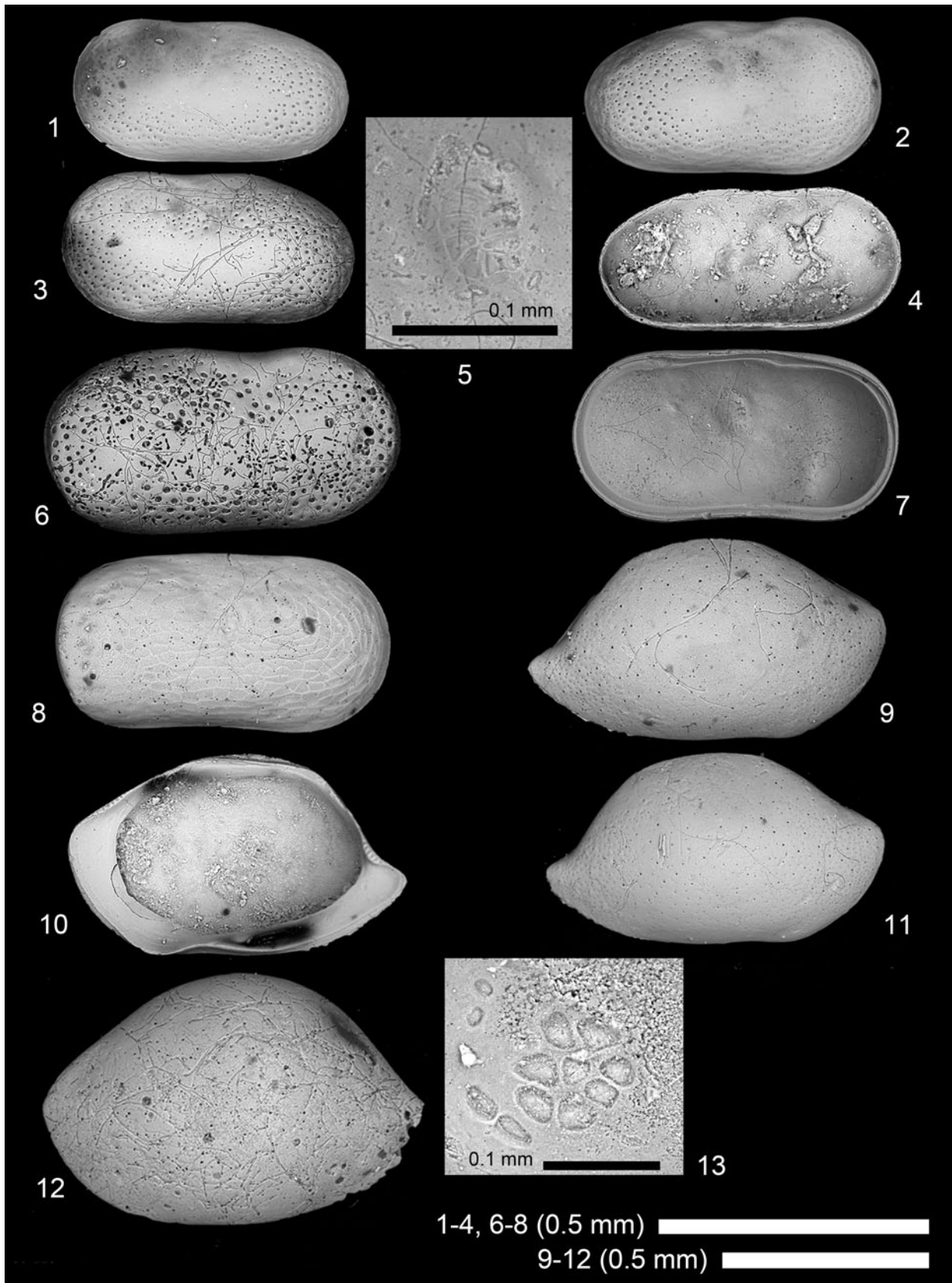
1960 *Paracypris gajensis* Tewari and Tandon, p. 151, text-fig. 2, fig. 3a, b.

1978 *Phlyctenophora meridionalis*; Khosla, p. 261, pl. 2, fig. 7, pl. 6, fig. 1.

1990b *Phlyctenophora meridionalis*; Khosla and Nagori, p. 91, pl. 3, fig. 15.

2001 *Phlyctenophora meridionalis*; Bhandari et al., p. 132, pl. 113, figs. 1, 2.

*Holotype.*—No. II-6 (Palaeontology Laboratory, Oil and Natural Gas Commission, Dehra Dun, India) from Kutch, India. Early Miocene.



**Figure 2.** Scanning electron microscope images of ostracode species. (1–4, 6) *Cytherella* sp. 1: (1), juvenile? LV, 2019/0181/0001 (19A-ck-09-2-001); (2) juvenile? RV, 2019/0181/0002 (19B-ck-09-2-001); (3, 4) juvenile? LV, 2019/0181/0003 (CK-09-02-003); (6) adult? RV, 2019/0181/0004 (19B-ck-09-2-002); (5, 7, 8) *Cytherelloidea pandora* s.l. (Kornicker, 1963), adult? RV, 2019/0181/0005 (CK-09-02-054); (9–13) *Paranesidea* cf. *P. gajensis* Khosla, 1978: (9), adult RV, 2019/0181/0006 (19A-ck-09-2-015); (10) adult RV, 2019/0181/0007 (CK-09-02-001); (11, 13) adult RV, 2019/0181/0008 (19B-ck-09-2-003); (12) adult LV, 2019/0181/0009 (19B-ck-09-2-004). (1–3, 6, 8, 9, 11, 12) Lateral views; (4, 5, 7, 10, 13) internal views; (5, 13) close-up of subcentral muscle scars.

*Dimensions.*—See [Table 1](#).

*Remarks.*—Internal details of this species have rarely been shown. Our high-resolution SEM images clearly showed six subcentral muscle scars, supplementing Khosla (1978) who drew five scars only. The distinct arrangement of subcentral muscle scars clearly supports the affiliation of this species to *Phlyctenophora* (van Morkhoven, 1963).

Superfamily Pontocypridoidea Müller, 1894  
Family Pontocyprididae Müller, 1894

Genus *Propontocypris* Sylvester-Bradley, 1947

*Type species.*—*Pontocypris trigonella* Sars, 1866, Recent, off the northwest coast of Norway.

*Propontocypris* sp. 1  
[Figure 3.9–3.11](#)

*Dimensions.*—See [Table 1](#).

*Remarks.*—This species is distinguished from *Propontocypris* (*Propontocypris*) sp. cf. *P. (P.) herdmani* (Scott) of Bhandari et al. (2001) by having a more slender shape in lateral view.

Suborder Cytherocopina Gründel, 1967  
Superfamily Cytheroidea Baird, 1850b  
Family Bythocytheridae Sars, 1866

Genus *Bythoceratina* Hornibrook, 1952

*Type species.*—*Bythoceratina mestayerae* Hornibrook, 1952, Recent, New Zealand.

*Bythoceratina malaysiana* Whatley and Zhao, 1987  
[Figure 3.12, 3.13](#)

- 1987 *Bythoceratina malaysiana* Whatley and Zhao, p. 341, pl. 3, figs. 3–5.  
non *Bythoceratina malaysiana*; Mostafawi, p. 69, fig. 41A, B.  
1989 *Bythoceratina nealei* Khosla and Nagori, p. 51, pl. 12, figs. 8, 9.  
2001 *Bythoceratina nealei*; Bhandari et al., p. 40, pl. 21, figs. 1, 2.

*Holotype.*—No. 1986.124 (Natural History Museum, London, UK) from Malacca Straits. Recent.

*Dimensions.*—See [Table 1](#).

*Remarks.*—The specimen shown here is much better preserved than the type specimens. Delicate reticulation is visible in our specimen ([Fig. 3.12](#)). Mostafawi (2003) considered *Bythoceratina nealei* Khosla and Nagori, 1989 a junior synonym of *Bythoceratina malaysiana* Whatley and Zhao, 1987. We agree with this, but the Persian Gulf specimens reported as *Bythoceratina malaysiana* by Mostafawi (2003)

are not conspecific to *Bythoceratina malaysiana* in our opinion. Mostafawi's (2003) specimens have less-rectangular outline, less-developed subcentral sulcus, and downward ala compared to *Bythoceratina malaysiana*.

Family Cytherettidae Triebel, 1952

Genus *Flexus* Neviani, 1928

*Type species.*—*Cythere plicata* Münster, 1830, “Tertiary,” northwestern Germany (see Weiss, 1983 for SEM images).

*Flexus trifurcata* (Lubimova and Guha in Lubimova et al., 1960)  
[Figure 4.1–4.10](#)

- 1960 *Cytheretta trifurcata* Lubimova and Guha in Lubimova et al., p. 45, pl. 4 fig. 3.  
1960 *Cytherelloidea kathiawarensis* Tewari and Tandon, p. 160, text-fig. 5, fig. 5.  
1978 *Cytheretta (Flexus) trifurcata*; Khosla, p. 271, pl. 3, figs. 3, 4.  
1990b *Cytheretta (Flexus) trifurcata*; Khosla and Nagori, p. 89, pl. 3, fig. 4.  
2001 *Cytheretta (Flexus) trifurcata*; Bhandari et al., p. 62, pl. 44, figs. 1, 2.  
non *Flexus trifurcata*; Aziz and Al-Shumam, p. 167, pl. 3, fig. 3.  
2013 *Flexus trifurcata*; Hawramy and Khalaf, p. 56, pl. 2, fig. 21.

*Holotype.*—No. II-24 (Palaeontology Laboratory, Oil and Natural Gas Commission, Dehra Dun, India) from Kutch, India. Early Miocene.

*Dimensions.*—See [Table 1](#).

*Remarks.*—There is a certain morphological variation in this species. Posterior loop connecting median lateral and ventrolateral ridges can be angular (our specimens; Khosla, 1978; Lubimova et al., 1960) or rounded (Bhandari et al., 2001). Very broad inner lamella ([Fig. 4.6](#)) is a typical character of this family.

Family Cytheridae Baird, 1850b

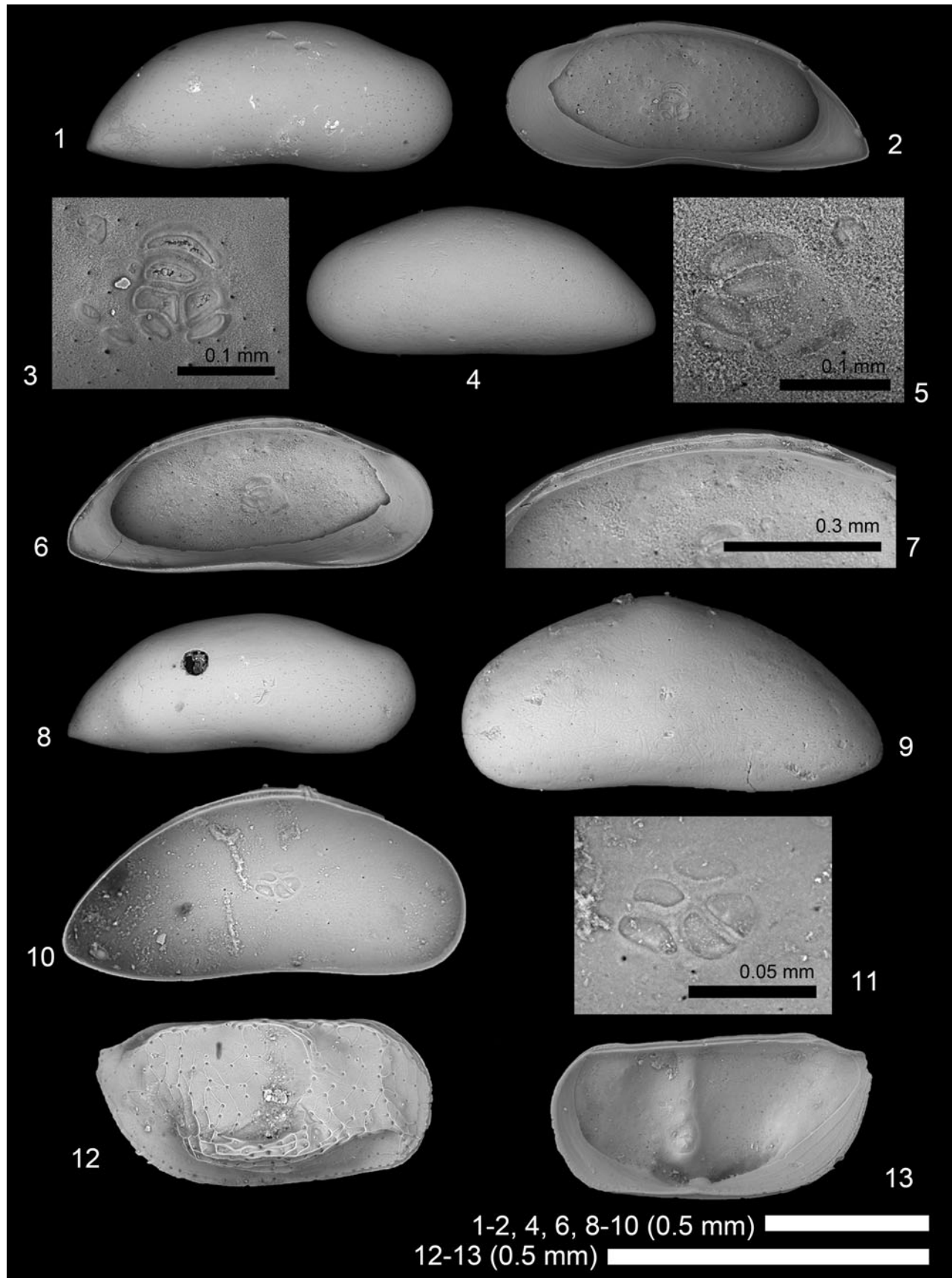
Genus *Paijenborchellina* Kusnetzova in Mandelstam et al., 1957

*Type species.*—*Paijenborchellina excelens* Kusnetzova in Mandelstam et al., 1957, Lower Cretaceous (Barremian), Caspian coast of Azerbaijan.

*Paijenborchellina prona* (Lubimova and Guha in Lubimova et al., 1960)  
[Figure 4.11–4.14](#)

- 1960 *Paijenborchella prona* Lubimova and Guha in Lubimova et al., p. 43, pl. 4 fig. 1a, b.





**Figure 3.** Scanning electron microscope images of ostracode species. (1–8) *Phlyctenophora meridionalis* (Lubimova and Mohan in Lubimova et al., 1960): (1–3) adult RV, 2019/0181/0010 (CK-09-02-050); (4–7) adult LV, 2019/0181/0011 (CK-09-02-049); (8) juvenile RV, 2019/0181/0012 (CK-09-02-002). (9–11) *Proponocypris* sp. 1, juvenile LV, 2019/0181/0013 (CK-09-02-034). (12, 13) *Bythoceratina malaysiana* Whatley and Zhao, 1987, adult RV, 2019/0181/0014 (CK-09-02-052). (1, 4, 8, 9, 12) Lateral views; (2, 3, 5–7, 10, 11, 13) internal views; (3, 5, 11) close-up of subcentral muscle scars; (7), close-up of hinge.

- 1960 *Paijenborchella boldi* Tewari and Tandon, p. 159, text-fig. 5, fig. 2a, b.  
 1968 *Paijenborchella prona*; Guha, p. 213, fig. 4.  
 1978 *Paijenborchella (Eupaijenborchella) prona*; Khosla, p. 274, pl. 5, fig. 8.  
 1989 *Paijenborchellina prona*; Khosla and Nagori, p. 49, pl. 12, fig. 1.  
 2001 *Paijenborchellina prona*; Bhandari et al., p. 118, pl. 100, figs. 1, 2.

*Holotype*.—No. II-22 (Palaeontology Laboratory, Oil and Natural Gas Commission, Dehra Dun, India) from Kutch, India. Early Miocene.

*Dimensions*.—See Table 1.

*Remarks*.—We found well-preserved specimens of *Paijenborchellina prona* (Lubimova and Guha in Lubimova et al., 1960). High-resolution SEM images clearly showed that this species has not only primary but also secondary reticulation.

Family Cytherideidae Sars, 1925

Genus *Hemicyprideis* Malz and Triebel, 1970

*Type species*.—*Hemicyprideis aucta* Malz and Triebel, 1970, early Miocene, Germany.

*Hemicyprideis kachharai* Khosla, 1978  
 Figure 4.15–4.17

- 1978 *Hemicyprideis kachharai* Khosla, p. 272, pl. 3, figs. 1, 2, pl. 6, fig. 5.  
 1990b *Hemicyprideis kachharai*; Khosla and Nagori, p. 89, pl. 1, fig. 12.  
 2001 *Hemicyprideis kachharai*; Bhandari et al., p. 74, pl. 55, figs. 1, 2.

*Holotype*.—RUGDMF no. 80 (Department of Geology, University of Rajasthan, Udaipur, India) from Gujarat, India. Early Miocene.

*Dimensions*.—See Table 1.

*Remarks*.—This species is known only from early Miocene of India.

Genus *Neocyprideis* Apostolescu, 1956

*Type species*.—*Cyprideis (Neocyprideis) durocortoriensis* Apostolescu, 1956, lower Eocene, northeastern France.

*Neocyprideis murudensis* (Bhandari, Khosla, and Nagori, 2001)  
 Figure 5.1–5.8

- 2001 *Miocyprideis murudensis* Bhandari, Khosla, and Nagori, p. 92, pl. 73 figs. 1, 2.

*Holotype*.—IPE/H02/04/8037 (Paleontology Laboratory, Keshava Deva Malaviya Institute of Petroleum Exploration, Oil and Natural Gas Corporation Limited, Dehra Dun, India) from off Bombay, India. Middle Miocene.

*Dimensions*.—See Table 1.

*Remarks*.—Following Titterton and Whatley (Titterton and Whatley, 1988, 2006; Titterton et al., 2001) and Yasuhara et al. (2018), we abstain from separating *Neocyprideis* Apostolescu, 1956 and *Miocyprideis* Kollmann, 1960, at least for now, although we believe their generic status merits further consideration, as discussed in Yasuhara et al. (2018). *Neocyprideis murudensis* (Bhandari, Khosla, and Nagori, 2001) was known only as right lateral views of the holotype and a paratype (Bhandari et al., 2001). Here we showed lateral and internal details of left valves.

*Neocyprideis thirukkaruvensis* (Guha and Rao, 1976)  
 Figure 5.9–5.14

- 1976 *Miocyprideis thirukkaruvensis* Guha and Rao, p. 94, pl. 1, figs. 2–4.  
 1988 *Miocyprideis thirukkaruvensis*; Khosla, p. 102, pl. 2, figs. 5–8.  
 2001 *Miocyprideis thirukkaruvensis*; Bhandari et al., p. 94, pl. 76, figs. 1–4.

*Holotype*.—Repository uncertain.

*Dimensions*.—See Table 1.

*Remarks*.—*Neocyprideis thirukkaruvensis* (Guha and Rao, 1976) is similar to *Neocyprideis murudensis* (Bhandari, Khosla, and Nagori, 2001), but distinguished by having better-developed posteroventral marginal spines and by a lack of secondary reticulation (fine punctation) in ventral, dorsal, and posterior margins.

Family Hemicytheridae Puri, 1953

Genus *Aurila* Pokorný, 1955

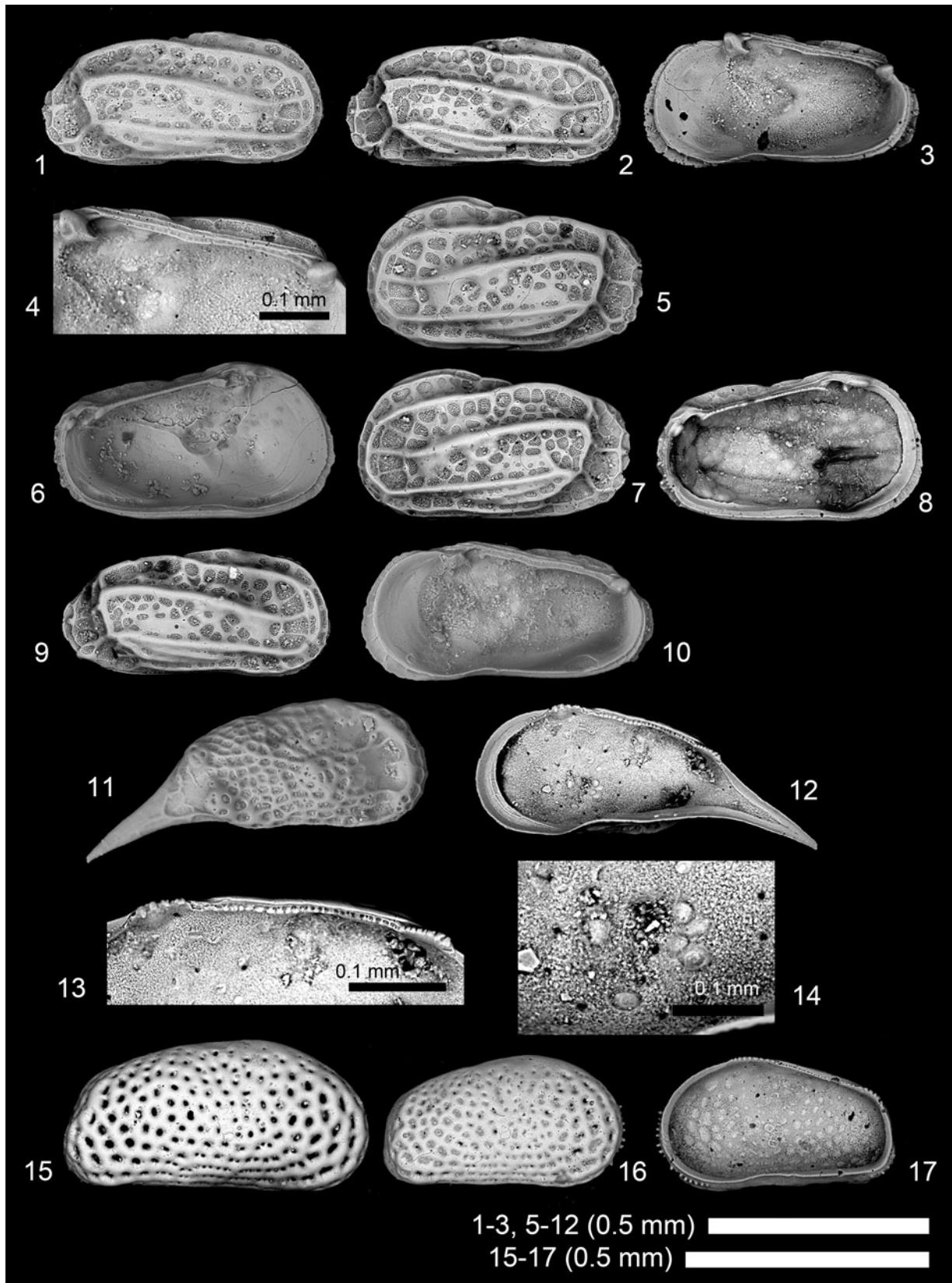
*Type species*.—*Cythere convexa* Baird, 1850b, Recent, UK.

*Aurila singhi* Khosla and Nagori, 1989  
 Figure 6

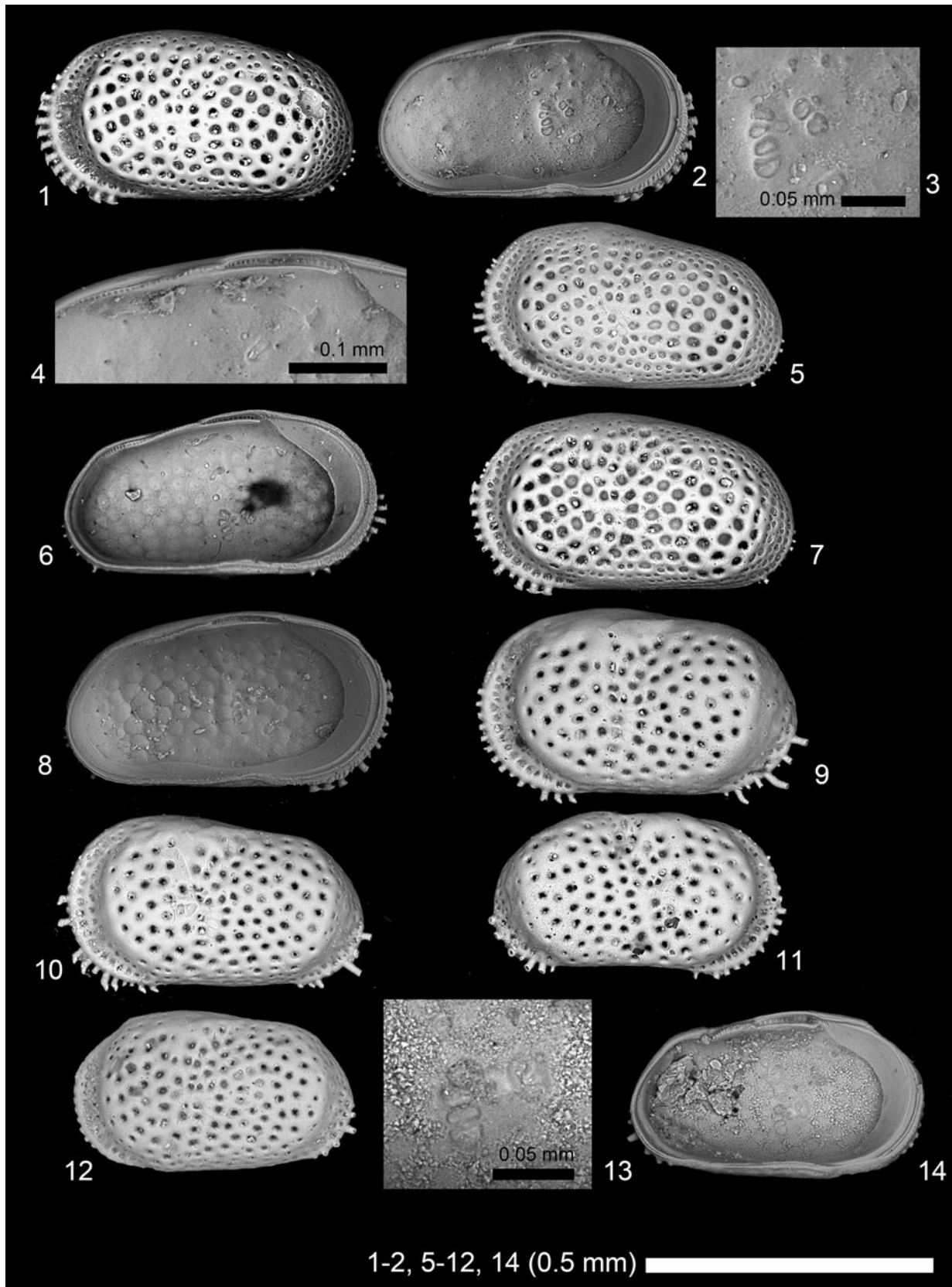
- 1978 *Aurila* sp. cf. *A. amygdala* Khosla, p. 262, pl. 3, fig. 5.  
 1989 *Aurila singhi* Khosla and Nagori, p. 36, pl. 7, figs. 1–3.  
 2001 *Aurila singhi*; Bhandari et al., p. 34, pl. 16, figs. 1–4.  
 non 2013 *Aurila singhi*; Aziz and Al-Shumam, p. 166, pl. 2, fig. 5.

*Holotype*.—SU371 (Department of Geology, Moban Lal Sukbadia University, Udaipur, India) from Quilon beds, Padappakkara, Kerala, India. Early Miocene.



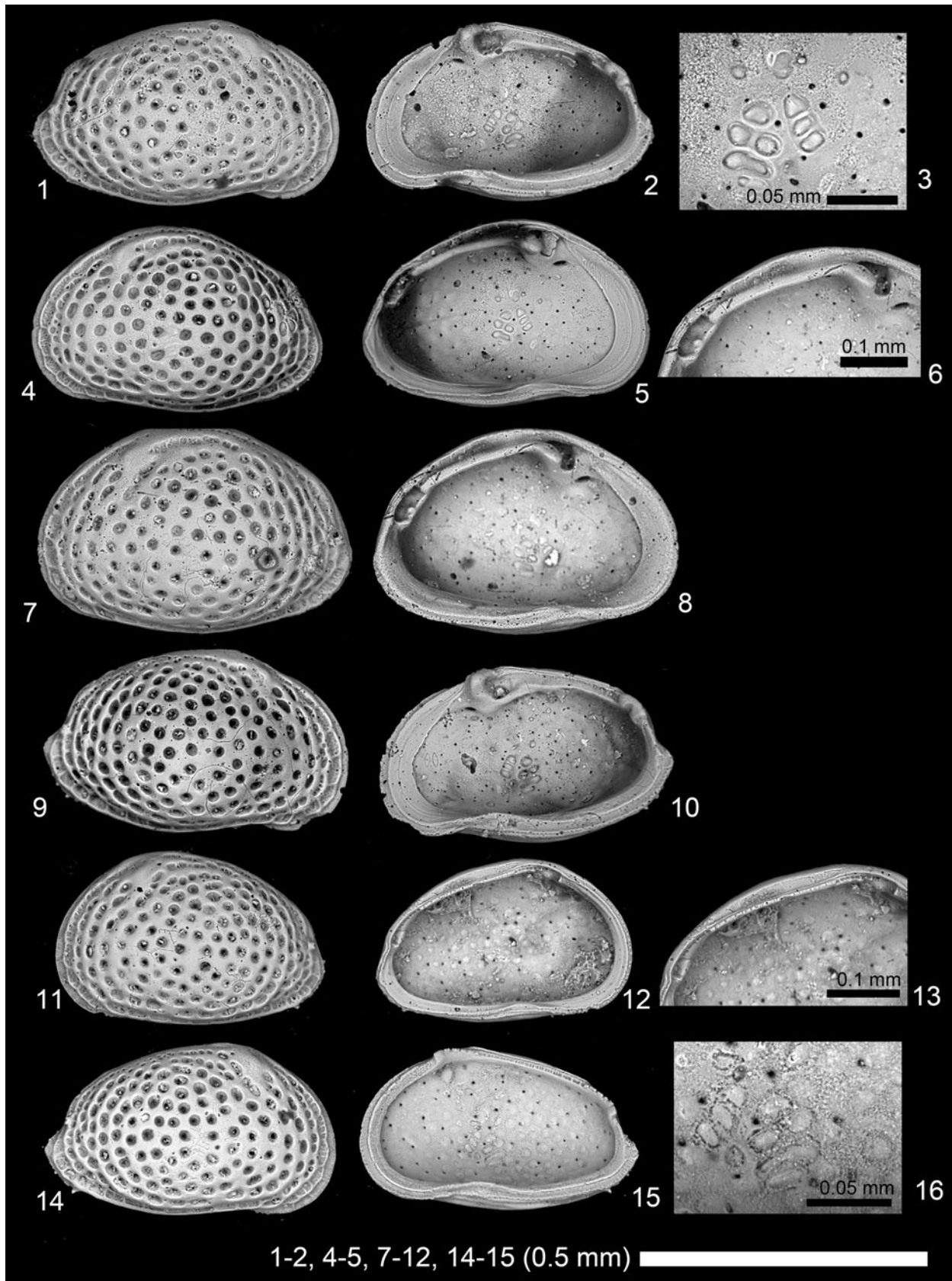


**Figure 4.** Scanning electron microscope images of ostracode species. (1–10) *Flexus trifurcata* (Lubimova and Guha in Lubimova et al., 1960): (1) adult RV, 2019/0181/0115 (19B-ck-09-2-005); (2–4) adult RV, 2019/0181/0015 (CK-09-02-007); (5, 6) adult LV, 2019/0181/0016 (CK-09-02-064); (7, 8) adult LV, 2019/0181/0017 (CK-09-02-008); (9, 10) adult RV, 2019/0181/0018 (CK-09-02-063). (11–14) *Paijenborchellina prona* (Lubimova and Guha in Lubimova et al., 1960), adult RV, 2019/0181/0019 (CK-09-02-065). (15–17) *Hemicyprideis kachharai* Khosla, 1978: (15) adult RV, 2019/0181/0020 (CK-09-02-032); (16, 17) juvenile? RV, 2019/0181/0021 (19B-ck-09-2-007). (1, 2, 5, 7, 9, 11, 15, 16) lateral views; (3, 4, 6, 8, 10, 12–14, 17) internal views; (14) close-up of subcentral muscle scars; (4, 13) close-up of hingement.



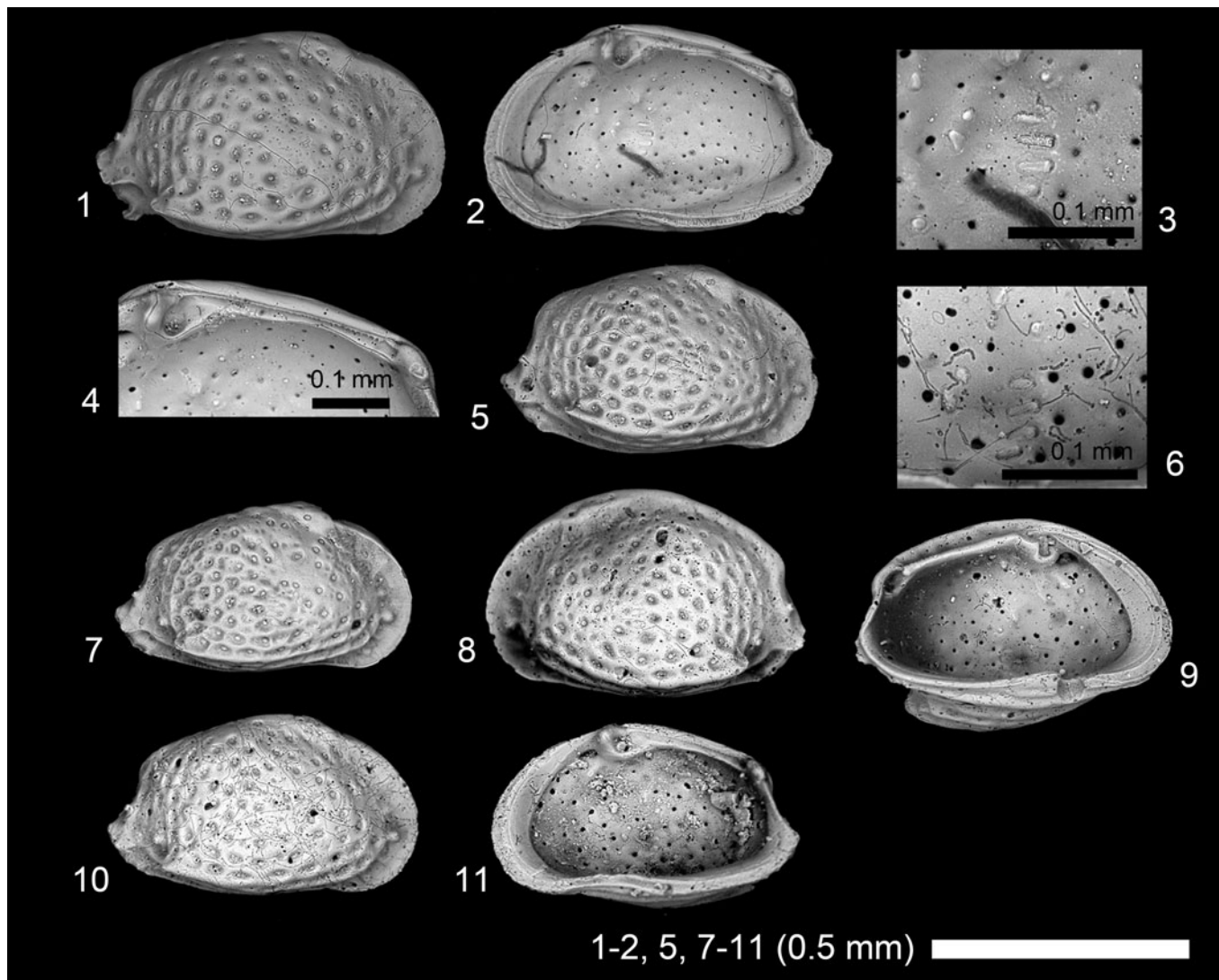
**Figure 5.** Scanning electron microscope images of ostracode species. (1–8) *Neocyprideis murudensis* (Bhandari, Khosla, and Nagori, 2001): (1–4) adult LV, 2019/0181/0022 (CK-09-02-037); (5, 6) adult LV, 2019/0181/0023 (19B-ck-09-2-006); (7, 8) adult LV, 2019/0181/0024 (CK-09-02-035). (9–14) *Neocyprideis thirukkaruvensis* (Guha and Rao, 1976): (9) adult LV, 2019/0181/0025 (19A-ck-09-2-003); (10) adult LV, 2019/0181/0026 (19B-ck-09-2-008); (11) adult RV, 2019/0181/0027 (19B-ck-09-2-009); (12–14) adult LV, 2019/0181/0028 (19B-CK-09-043). (1, 5, 7, 9–12) Lateral views; (2–4, 6, 8, 13, 14) internal views; (3, 13) close-up of subcentral muscle scars; (4) close-up of hingement.





**Figure 6.** Scanning electron microscope images of *Aurila singhi* Khosla and Nagori, 1989. (1, 2) Adult RV, 2019/0181/0029 (19A-ck-09-2-006); (3–5) adult LV, 2019/0181/0030 (CK-09-02-022); (6–8) adult LV, 2019/0181/0031 (19A-ck-09-2-05); (9, 10) adult RV, 2019/0181/0032 (CK-09-02-024); (11–13) A-1 LV, 2019/0181/0033 (19A-ck-09-2-07); (14–16) A-1 RV, 2019/0181/0034 (19B-ck-09-2-013). (1, 4, 7, 9, 11, 14) Lateral views; (2, 3, 5, 6, 8, 10, 12, 13, 15, 16) internal views; (3, 16) close-up of subcentral muscle scars; (6, 13) close-up of hingement.





**Figure 7.** Scanning electron microscope images of *Pokornyyella alata* Khosla, 1978. (1–4) Adult RV, 2019/0181/0061 (19B-ck-09-2-022); (5, 6) adult RV, 2019/0181/0062 (19B-ck-09-2-023); (7) A-1 RV, 2019/0181/0063 (19B-ck-09-2-024c); (8, 9) adult LV, 2019/0181/0064 (CK-09-02-025); (10, 11) A-1 RV, 2019/0181/0065 (19B-ck-09-2-026). (1, 5, 7, 8, 10) lateral views; (2–4, 6, 9, 11) interval views; (3, 6) close-up of subcentral muscle scars; (4) close-up of hingement.

*Dimensions.*—See Table 1.

*Remarks.*—While hingement is different between adult (holamphidont) and A-1 specimens (antimerodont), subcentral muscle scars are the same between adult and A-1 specimens, showing three frontal scars and a divided dorsomedian adductor scar. It suggests that subcentral muscle scars are more conservative and useful for taxonomy (e.g., defining genus) compared to hingement, which may be more affected by developmental stage, calcification degree, etc., especially in Hemicytheridae, given that we see a similar expression in *Pokornyyella* and *Tenedocythere* (see below).

Genus *Pokornyyella* Oertli, 1956

*Type species.*—*Cythere limbata* Bosquet, 1852, type horizon not designated (reported from the middle Oligocene and late Eocene in the original paper), north-central France.

*Pokornyyella alata* Khosla, 1978

Figure 7

1978 *Pokornyyella alata* Khosla, p. 264, pl. 3, figs. 7, 8.

1990b *Pokornyyella alata*; Khosla and Nagori, p. 91, pl. 2, fig. 10.

2001 *Pokornyyella alata*; Bhandari et al., p. 132, pl. 114, figs. 1, 2.

*Holotype.*—RUGDMF no. 38 (Department of Geology, University of Rajasthan, Udaipur, India) from Gujarat, India. Early Miocene.

*Dimensions.*—See Table 1.

*Remarks.*—*Pokornyyella* is similar to *Aurila*, but distinguished by two (instead of three) frontal scars and undivided dorsomedian scar, which are found both in adults and A-1

juveniles (see *Pokornyella chaasraensis*; Fig. 8.2, 8.14, 8.18). As discussed above for *Aurila singhi*, subcentral muscle scars seem to be useful for genus-level taxonomy in Hemicytheridae.

*Pokornyella chaasraensis* (Lubimova and Guha in  
Lubimova et al., 1960)  
Figure 8

- 1960 *Trachyleberis chaasraensis* Lubimova and Guha in Lubimova et al., p. 39, pl. 3, fig. 6a, b.  
1960 *Hemicythere* aff. *amygdala* Tewari and Tandon, p. 157, text-fig. 4, fig. 2a, b  
1961 *Aurila chaasraensis*; Guha, p. 3, text-figs. 2, 4, 6.  
1978 *Pokornyella chaasraensis*; Khosla, p. 265, pl. 3, fig. 6, pl. 6, fig. 11.  
1990b *Pokornyella chaasraensis*; Khosla and Nagori, p. 91, pl. 2, fig. 13.  
2001 *Pokornyella chaasraensis*; Bhandari et al., p. 134, pl. 115, figs. 1, 2.

*Holotype*.—No. II-20 (Palaeontology Laboratory, Oil and Natural Gas Commission, Dehra Dun, India) from Kutch, India. Early Miocene.

*Dimensions*.—See Table 1.

*Remarks*.—*Pokornyella chaasraensis* (Lubimova and Guha in Lubimova et al., 1960) is similar to *Pokornyella alata* Khosla, 1978 in overall appearance, but distinguished by lacking a distinct ventrolateral ridge, especially in adult specimens.

Genus *Tenedocythere* Sissingh, 1972

*Type species*.—*Cythereis prava* Baird, 1850a, Recent, Greece.

*Tenedocythere keralaensis* Khosla and Nagori, 1989  
Figure 9

- 1989 *Tenedocythere keralaensis* Khosla and Nagori, p. 43, pl. 9, figs. 6–10.  
2001 *Tenedocythere keralaensis*; Bhandari et al., p. 160, pl. 142, figs. 1–4.

*Holotype*.—No. 394 (Department of Geology, University of Rajasthan, Udaipur, India) from Quilon beds, Padappakkara, Kerala, India. Early Miocene.

*Dimensions*.—See Table 1.

*Remarks*.—Subcentral muscle scars of *Tenedocythere* are the same as those of *Pokornyella*, consisting of two frontal scars and undivided dorsomedian scar both in adult and A-1 specimens (Fig. 9.2, 9.16, 9.19), suggesting a very close relationship between *Tenedocythere* and *Pokornyella*, especially given the high overall similarity between A-1 juveniles of these genera.

Family Krithidae Mandelstam in Bubikyan, 1958

Genus *Krithe* Brady, Crosskey, and Robertson, 1874

*Type species*.—*Ilyobates praetexta* Sars, 1866, Recent, off the northwest coast of Norway.

*Krithe autochthona* Lubimova and Guha in Lubimova et al.,  
1960  
Figure 10

- 1960 *Krithe autochthona* Lubimova and Guha in Lubimova et al., p. 25, pl. 2, fig. 4.  
1960 *Krithe indica* var. *kutchensis* Tewari and Tandon, p. 153, text-fig. 6, fig. 2a, b.  
1968 *Krithe autochthona*; Guha, p. 213, pl. 2, fig. 2.  
1978 *Krithe autochthona*; Khosla, p. 272, pl. 2, figs. 18–20, pl. 6, fig. 10.  
1980 *Dentokrithe autochthona*; Khosla and Haskins, p. 211, pl. 1, figs. 1–6.  
1990b *Dentokrithe autochthona*; Khosla and Nagori, p. 89, pl. 1, fig. 13.  
2001 *Dentokrithe autochthona*; Bhandari et al., p. 64, pl. 46, figs. 1, 2.

*Holotype*.—No. II-7 (Palaeontology Laboratory, Oil and Natural Gas Commission, Dehra Dun, India) from Kutch, India. Early Miocene.

*Dimensions*.—See Table 1.

*Remarks*.—This species has recently been assigned to *Dentokrithe* Khosla and Haskins, 1980 (Bhandari et al., 2001), which is a junior synonym of *Thracella* Sönmez, 1963 (Guernet et al., 2012). *Thracella* (= *Dentokrithe*) and *Krithe* are almost identical, except a slight difference in hingement (adont versus pseudadont). We agree with Mazzini's (2005) opinion that this hingement difference is an intra-generic variation.

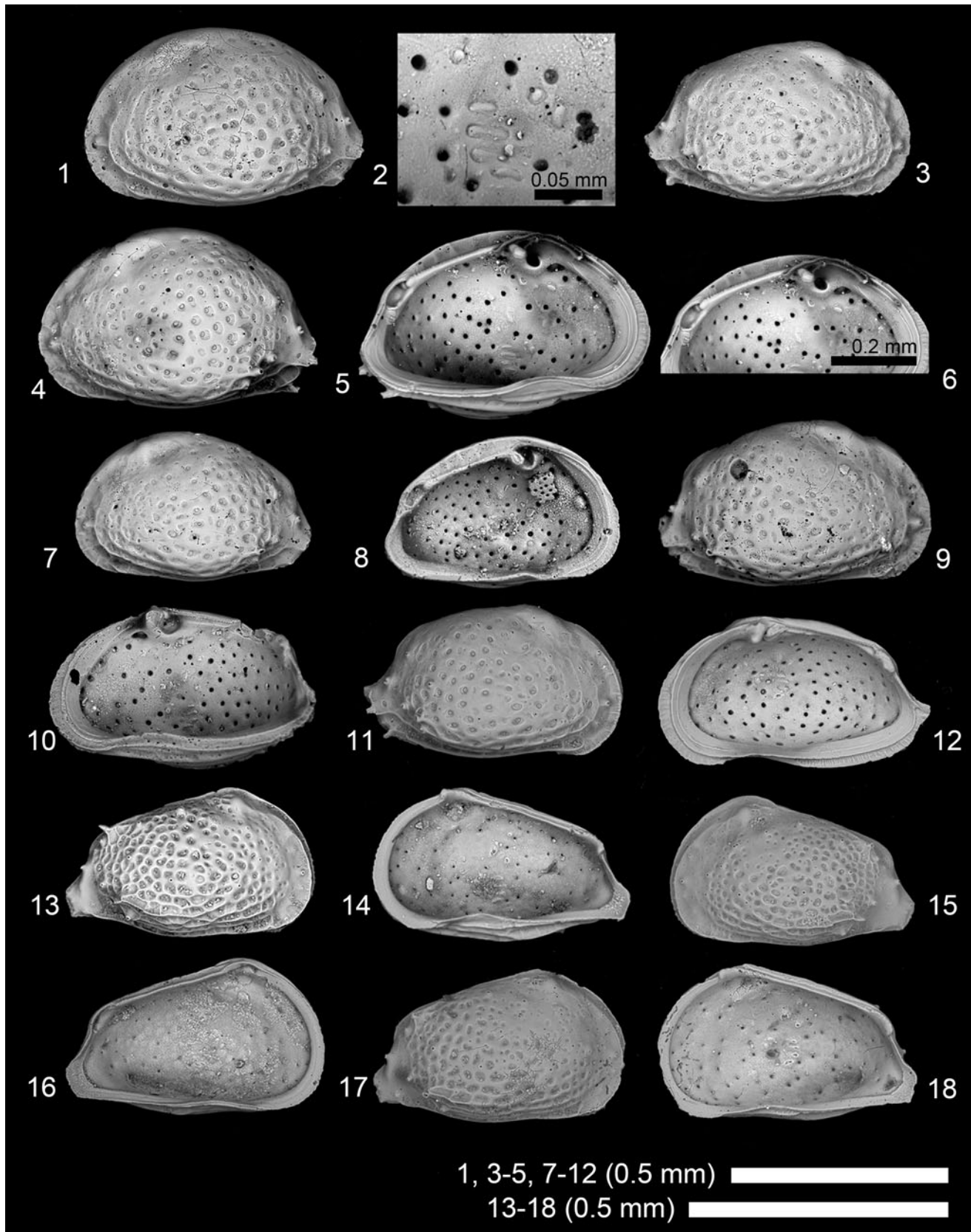
Family Loxoconchidae Sars, 1925

Genus *Loxoconcha* Sars, 1866

*Type species*.—*Cythere rhomboidea* Fischer, 1855, Recent, Baltic Sea and Kattegat.

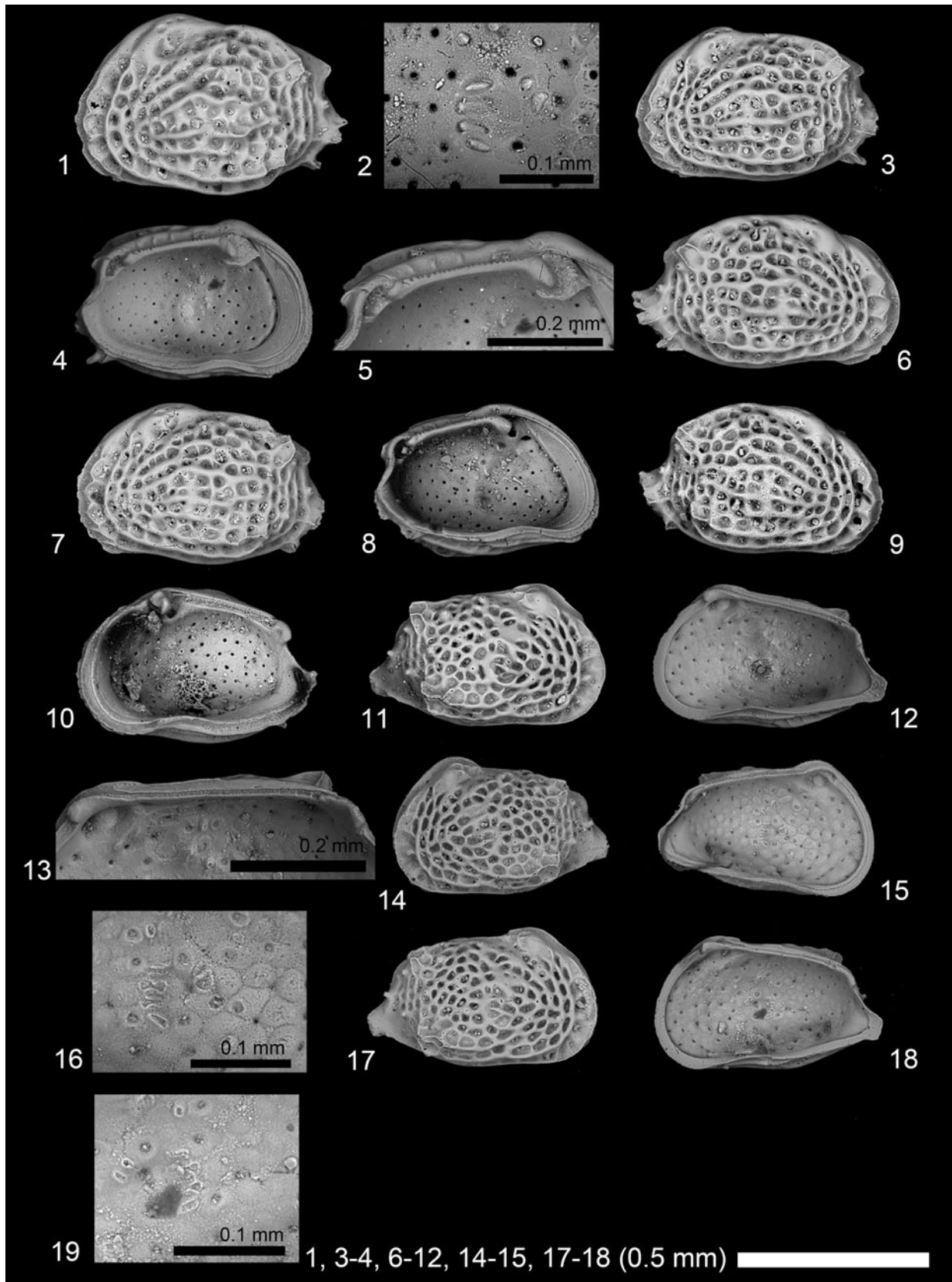
*Loxoconcha confinis* (Lubimova and Guha in Lubimova  
et al., 1960)  
Figure 11.1–11.10

- 1960 *Cytheropteron confinis* Lubimova and Guha in Lubimova et al., p. 52, pl. 4, fig. 10.  
1968 *Cytheropteron confinis*; Guha, p. 213, pl. 1, fig. 3.  
1974 *Loxoconcha confinis*; Guha, p. 171.  
1978 *Loxoconcha confinis*; Khosla, p. 275, pl. 5, fig. 11.  
1990b *Loxoconcha (Loxoconcha) confinis*; Khosla and Nagori, p. 91, pl. 3, fig. 5.  
2001 *Loxoconcha (Loxoconcha) confinis*; Bhandari et al., p. 82, pl. 64, figs. 1, 2.

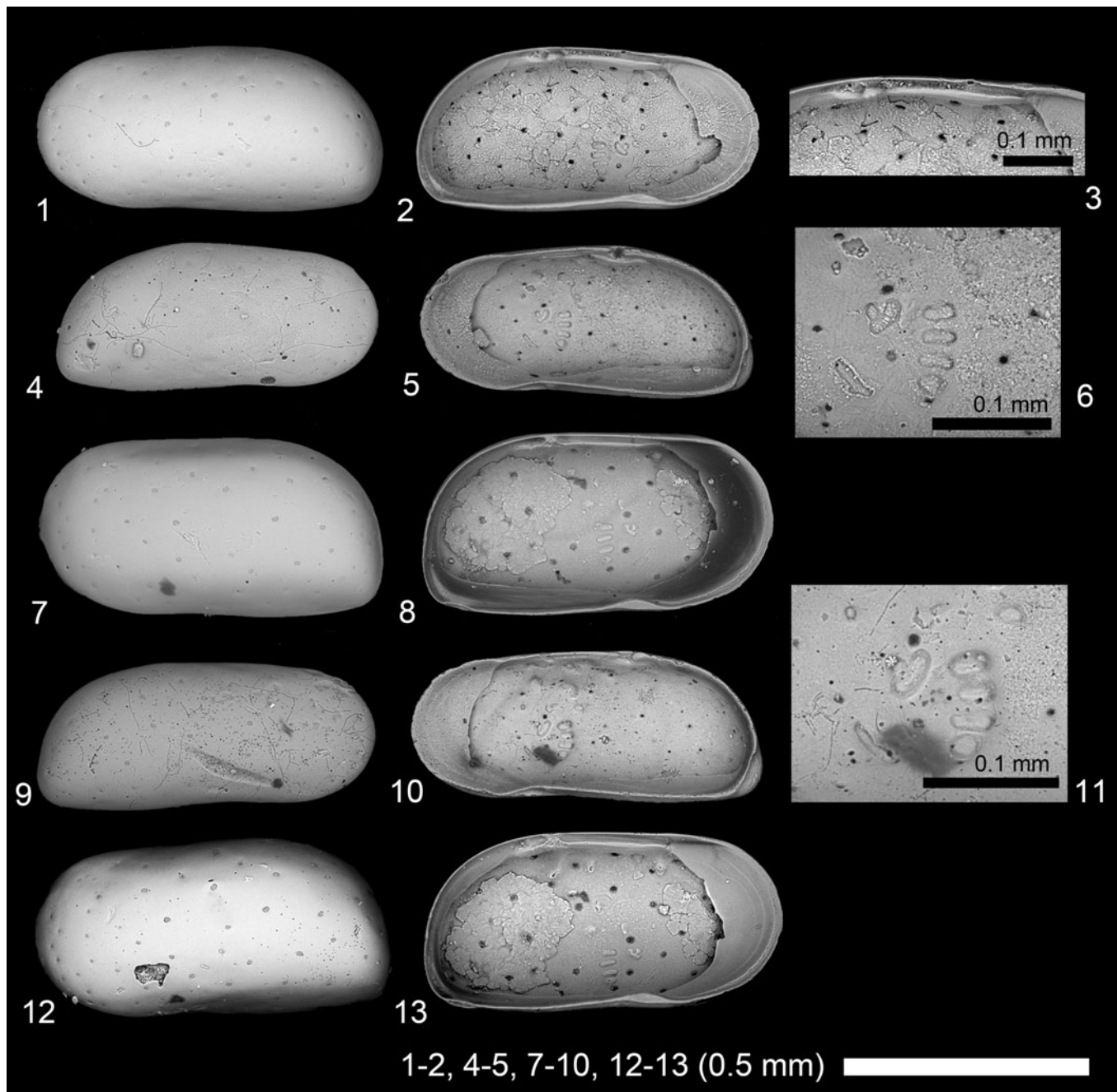


**Figure 8.** Scanning electron microscope images of *Pokornyyella chaasraensis* (Lubimova and Guha in Lubimova et al., 1960). (1, 2) Adult LV, 2019/0181/0066 (19B-ck-09-2-027); (3) adult RV, 2019/0181/0067 (19B-ck-09-2-025); (4–6) adult LV, 2019/0181/0068 (CK-09-02-020); (7, 8) subadult? LV, 2019/0181/0069 (CK-09-02-021); (9, 10) adult RV, 2019/0181/0070 (CK-09-02-023); (11, 12) adult RV, 2019/0181/0071 (19B-CK-09-050); (13, 14) juvenile RV, 2019/0181/0072 (CK-09-02-017); (15, 16) A-1 LV, 2019/0181/0073 (19B-CK-09-047); (17, 18) A-1 RV, 2019/0181/0074 (19B-CK-09-048). (1, 3, 4, 7, 9, 11, 13, 15, 17) Lateral views; (2, 5, 6, 8, 10, 12, 14, 16, 18) internal views; (2) close-up of subcentral muscle scars; (6) close-up of hingement.





**Figure 9.** Scanning electron microscope images of *Tenedocythere keralaensis* Khosla and Nagori, 1989. (1, 2) Adult LV, 2019/0181/0075 (19B-ck-09-2-028); (3–5) adult LV, 2019/0181/0076 (CK-09-02-010); (6) adult RV, 2019/0181/0077 (19B-ck-09-2-029); (7, 8) adult LV, 2019/0181/0078 (CK-09-02-013); (9, 10) adult RV, 2019/0181/0079 (CK-09-02-019); (11–13) A-1 RV, 2019/0181/0080 (CK-09-02-011); (14–16) A-1 LV, 2019/0181/0081 (19B-CK-09-051); (17–19) A-1 RV, 2019/0181/0082 (19B-CK-09-053). (1, 3, 6, 7, 9, 11, 14, 17) Lateral views; (2, 4, 5, 8, 10, 12, 13, 15, 16, 18, 19) internal views; (2, 16, 19) close-up of subcentral muscle scars; (5, 13) close-up of hingement.



**Figure 10.** Scanning electron microscope images of *Krithe autochthona* Lubimova and Guha in Lubimova et al., 1960. (1–3) Adult male LV, 2019/0181/0035 (19B-ck-09-2-014); (4–6) adult male RV, 2019/0181/0036 (19B-CK-09-044); (7, 8) adult female LV, 2019/0181/0037 (CK-09-02-005); (9–11) adult male RV, 2019/0181/0038 (CK-09-02-045a); (12) adult female LV, 2019/0181/0039 (CK-09-02-004); (13) adult female LV, 2019/0181/0040 (CK-09-02-006a). (1, 4, 7, 9, 12) Lateral views; (2, 3, 5, 6, 8, 10, 11, 13) internal views; (6, 11) close-up of subcentral muscle scars; (3) close-up of hingement.

*Holotype*.—No. II-27 (Palaeontology Laboratory, Oil and Natural Gas Commission, Dehra Dun, India) from Kutch, India. Miocene.

*Dimensions*.—See Table 1.

*Remarks*.—External and internal views of male and female specimens are shown (Fig. 11).

*Loxococoncha keralaensis* Khosla and Nagori, 1990a  
Figure 11.11–11.15

1978 *Loxococoncha* sp. cf. *L. alata* Khosla, p. 275, pl. 5, figs. 12, 13.

1989 *Loxococoncha (Loxococoncha) subalata* Khosla and Nagori, p. 46, pl. 11, figs. 1–4.

- 1990a *Loxococoncha (Loxococoncha) keralaensis* Khosla and Nagori, p. 314.  
 2001 *Loxococoncha (Loxococoncha) keralaensis*; Bhandari et al., p. 84, pl. 65, figs. 1–4.

*Holotype*.—SU407 (Department of Geology, Moban Lal Sukbadia University, Udaipur, India) from Quilon beds, Padappakkara, Kerala, India. Early Miocene.

*Dimensions*.—See Table 1.

*Remarks*.—Internal details are shown in Figure 11.13–11.15.

Family Paracytherideidae Puri, 1957

Genus *Paracytheridea* Müller, 1894

*Type species*.—*Paracytheridea depressa* Müller, 1894, Recent, Bay of Naples, Italy.

*Paracytheridea perspicua* Lubimova and Guha in  
 Lubimova et al., 1960  
 Figure 12

- 1960 *Paracytheridea perspicua* Lubimova and Guha in Lubimova et al., p. 50, pl. 4, fig. 8a, b.  
 1960 *Paracytheridea misrai* Tewari and Tandon, p. 153, text-fig. 2, fig. 4a–c.  
 1978 *Paracytheridea perspicua*; Khosla, p. 275, pl. 5, fig. 6.  
 1990b *Paracytheridea perspicua*; Khosla and Nagori, p. 91, pl. 3, fig. 6.  
 2001 *Paracytheridea perspicua*; Bhandari et al., p. 126, pl. 108, figs. 1, 2.

*Holotype*.—No. II-25 (Palaeontology Laboratory, Oil and Natural Gas Commission, Dehra Dun, India) from Kutch, India. Early Miocene.

*Dimensions*.—See Table 1.

*Remarks*.—Left valves shown here (Fig. 12.1, 12.3) are identical to the original drawing (Lubimova et al., 1960, pl. 4, fig. 8a).

Family Schizocytheridae Howe in Moore, 1961

Genus *Neomonoceratina* Kingma, 1948

*Type species*.—*Neomonoceratina columbiformis* Kingma, 1948, type horizon not designated (reported from the Pliocene and Recent in the original paper), type locality not designated (reported from north Sumatra and Java Sea in the original paper).

*Neomonoceratina gajensis* Guha, 1974  
 Figure 13.1–13.5

- 1974 *Neomonoceratina gajensis* Guha, p. 169, pl. 1, figs. 16–19, pl. 2, fig. 15.  
 1978 *Neomonoceratina gajensis*; Khosla, p. 273, pl. 5, figs. 16, 17.

- 1990b *Neomonoceratina gajensis*; Khosla and Nagori, p. 91, pl. 1, fig. 9.  
 2001 *Neomonoceratina gajensis*; Bhandari et al., p. 100, pl. 82, figs. 1, 2.

*Holotype*.—No. III-23 (Palaeontology Laboratory, Oil and Natural Gas Commission, Baroda, India) from Kutch, India. Early Miocene.

*Dimensions*.—See Table 1.

*Remarks*.—Our specimens have a better-developed keel and less-developed reticulation and calcification compared to the specimens shown in Khosla (1978) and Bhandari et al. (2001). The original description (Guha, 1974) is not clear enough to compare in this regard.

*Neomonoceratina kutchensis* Guha, 1961  
 Figure 13.6–13.10

- 1961 *Neomonoceratina kutchensis* Guha, p. 3, figs. 12, 14, 18.  
 1968 *Neomonoceratina kutchensis*; Guha, p. 213, pl. 2, fig. 1.  
 1978 *Neomonoceratina kutchensis*; Khosla, p. 274, pl. 5, fig. 15.  
 1990b *Neomonoceratina kutchensis*; Khosla and Nagori, p. 91, pl. 1, fig. 10.  
 2001 *Neomonoceratina kutchensis*; Bhandari et al., p. 102, pl. 83, figs. 1, 2.

*Holotype*.—No. II-29 (Palaeontology Laboratory, Oil and Natural Gas Commission, Dehra Dun, India) from Kutch, India. Early Miocene.

*Dimensions*.—See Table 1.

*Remarks*.—Internal details are shown in Figure 13.7, 13.9, and 13.10.

*Neomonoceratina retispinata* Khosla and Nagori, 1989  
 Figure 13.11–13.17

- 1989 *Neomonoceratina retispinata* Khosla and Nagori, p. 23, pl. 2, figs. 8–10.  
 2001 *Neomonoceratina retispinata*; Bhandari et al., p. 108, pl. 89, figs. 1–4.

*Holotype*.—No. 333 (Department of Geology, University of Rajasthan, Udaipur, India) from Quilon beds, Padappakkara, Kerala, India. Early Miocene.

*Dimensions*.—See Table 1.

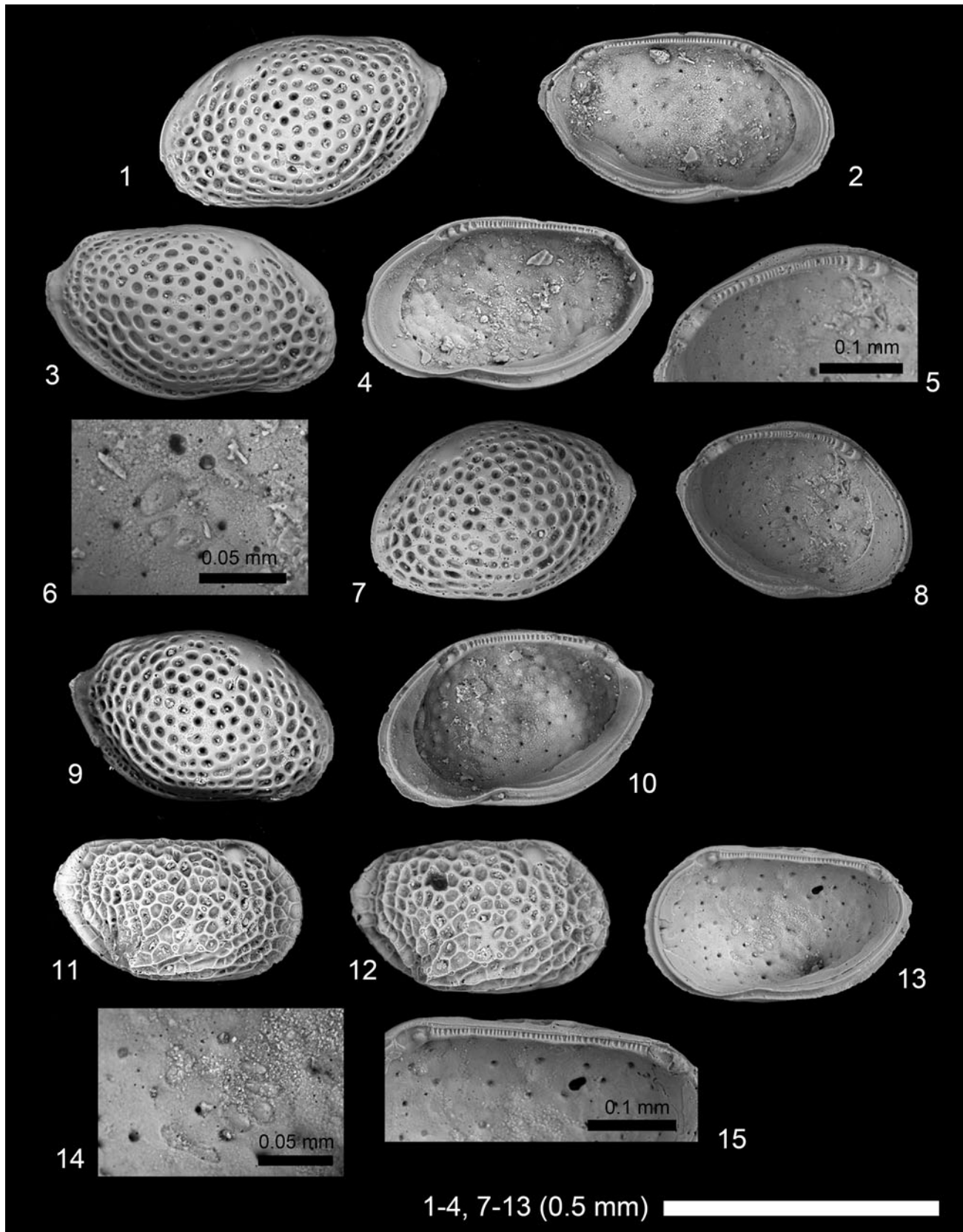
*Remarks*.—*Neomonoceratina retispinata* Khosla and Nagori, 1989 is similar to *Neomonoceratina kutchensis* Guha, 1961 in outline, but distinguished by having better-developed spines and primary reticulation on lateral surface.

Family Trachyleberididae Sylvester-Bradley, 1948

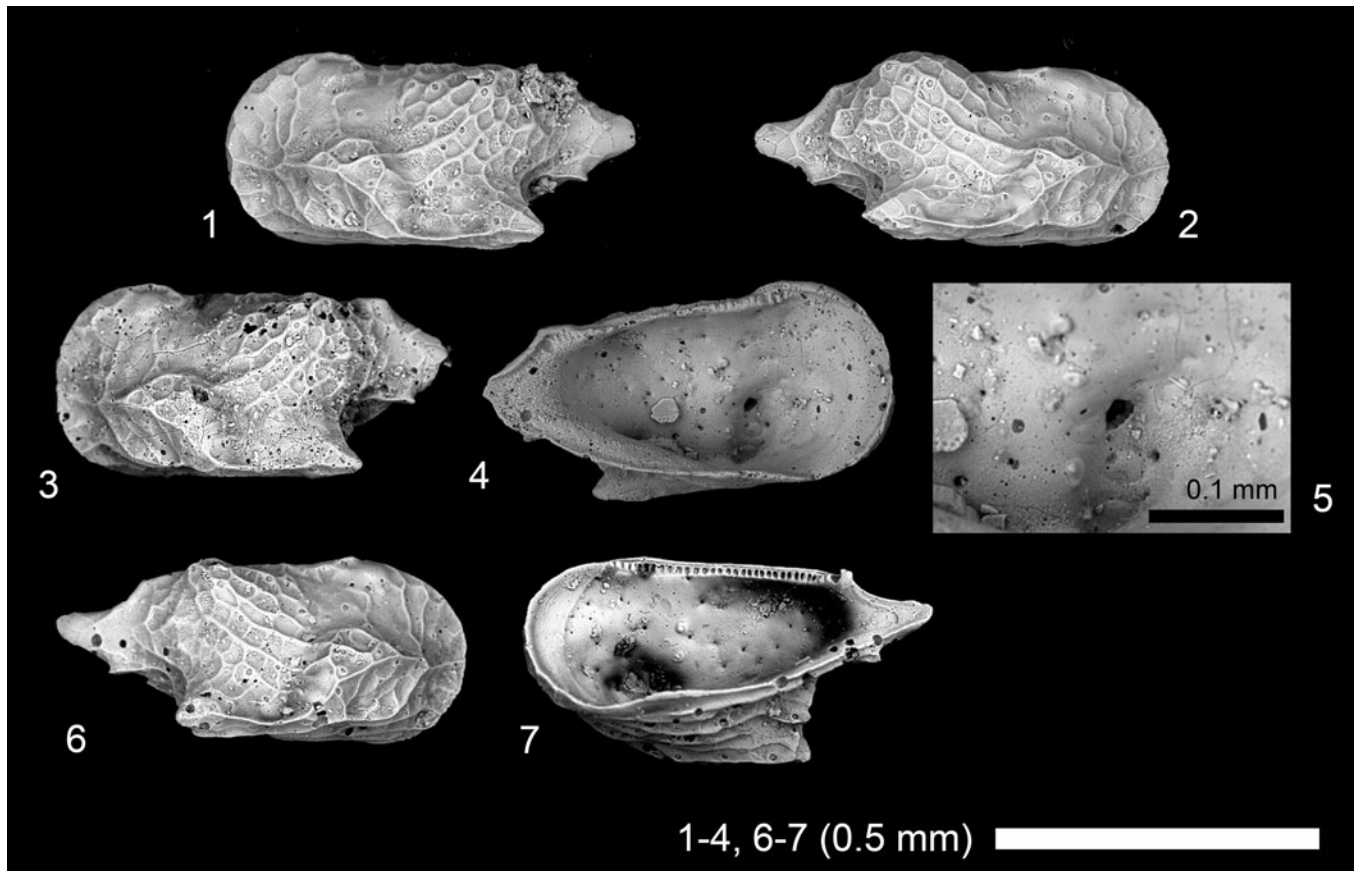
Genus *Acanthocythereis* Howe, 1963

*Type species*.—*Acanthocythereis araneosa* Howe, 1963, middle Eocene, Louisiana, USA.





**Figure 11.** Scanning electron microscope images of *Loxoconcha* species. (1–10) *Loxoconcha confinis* (Lubimova and Guha in Lubimova et al., 1960): (1, 2) adult male LV, 2019/0181/0041 (19B-ck-09-2-015); (3, 4) adult male RV, 2019/0181/0042 (CK-09-02-047); (5–8) adult female LV, 2019/0181/0043 (CK-09-02-048); (9, 10) adult female RV, 2019/0181/0044 (CK-09-02-046). (11–15) *Loxoconcha keralaensis* Khosla and Nagori, 1990a: (11) adult? RV, 2019/0181/0045 (19B-ck-09-2-016); (12–15) adult RV, 2019/0181/0046 (CK-09-02-055). (1, 3, 7, 9, 11, 12) Lateral views; (2, 4–6, 8, 10, 13–15) internal views; (6, 14) close-up of subcentral muscle scars; (5, 15) close-up of hingement.



**Figure 12.** Scanning electron microscope images of *Paracytheridea perspicua* Lubimova and Guha in Lubimova et al., 1960. (1) Adult LV, 2019/0181/0047 (19B-ck-09-2-017); (2) adult RV, 2019/0181/0048 (19B-ck-09-2-018); (3-5) adult LV, 2019/0181/0049 (19A-ck-09-2-016 = CK-09-02-027); (6, 7) adult RV, 2019/0181/0050 (CK-09-02-028). (1-3, 6) Lateral views; (4, 5, 7) internal views; (5) close-up of subcentral muscle scars.

*Acanthocythereis panti* Khosla and Nagori, 1989  
Figure 14.1-14.5

1989 *Acanthocythereis panti* Khosla and Nagori, p. 28, pl. 4, figs. 1-4.

2001 *Acanthocythereis panti*; Bhandari et al., p. 20, pl. 1, figs. 1-4.

*Holotype*.—No. 343 (Department of Geology, University of Rajasthan, Udaipur, India) from Quilon beds, Padappakkara, Kerala, India. Early Miocene.

*Dimensions*.—See Table 1.

*Remarks*.—Both female and male specimens are shown.

Genus *Alocopocythere* Siddiqui, 1971

*Type species*.—*Alocopocythere transcendens* Siddiqui, 1971, middle Eocene, Pakistan.

*Alocopocythere fossularis* (Lubimova and Guha in Lubimova et al., 1960)  
Figure 14.6-14.8

1960 *Trachyleberis fossularis* Lubimova and Guha in Lubimova et al., p. 40, pl. 3, fig. 7.

1961 *Echinocythereis fossularis*; Guha, p. 4, figs. 5, 9.

1989 *Alocopocythere fossularis*; Khosla and Nagori, p. 33, pl. 5, fig. 6.

*Holotype*.—No. II-17 (Palaeontology Laboratory, Oil and Natural Gas Commission, Dehra Dun, India) from Kutch, India. Early Miocene.

*Dimensions*.—See Table 1.

*Remarks*.—Only one broken valve was found in this study.

Genus *Chrysocythere* Ruggieri, 1962

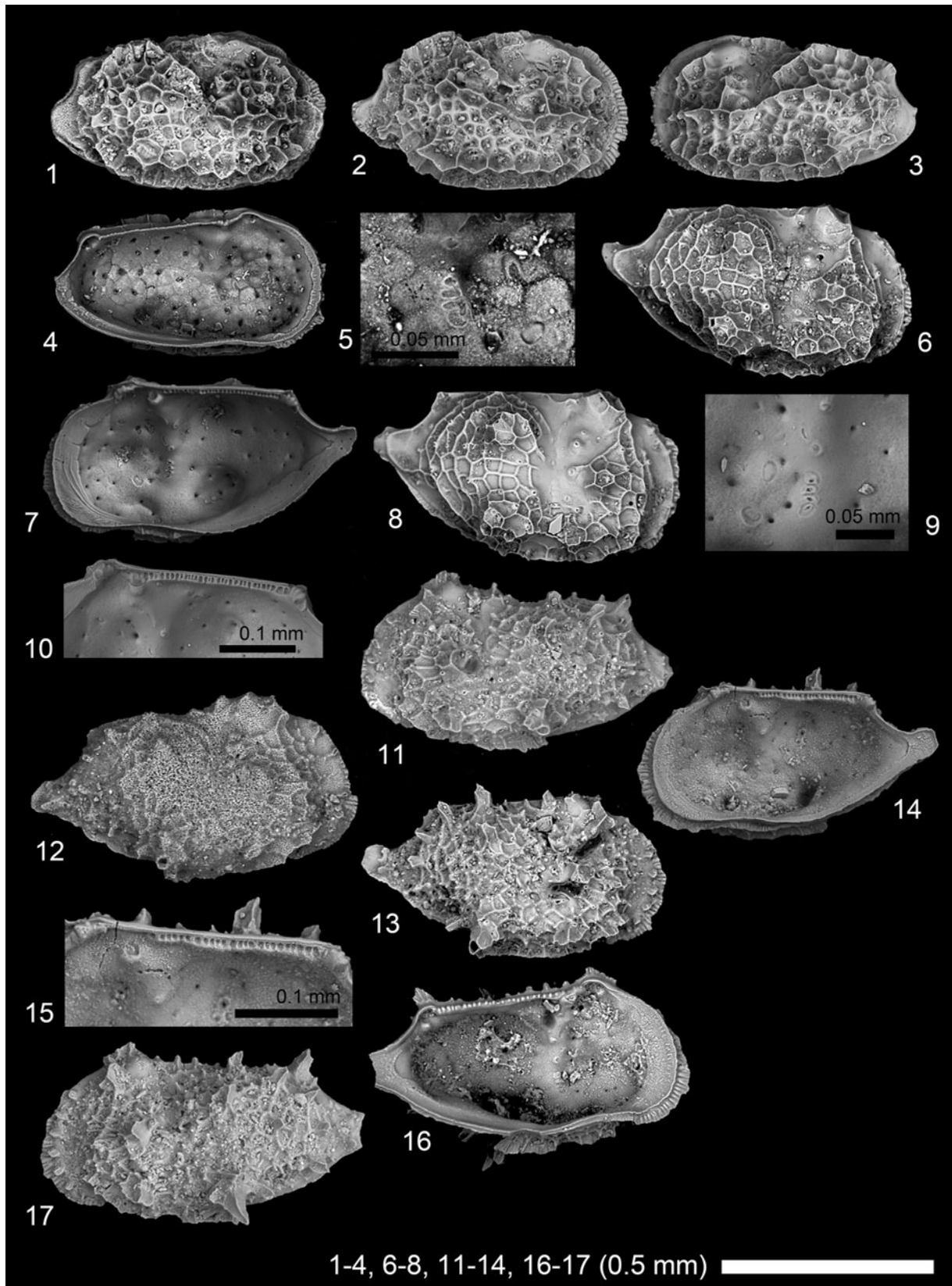
*Type species*.—*Chrysocythere cataphracta* Ruggieri, 1962, Miocene, Sicily, Italy.

*Chrysocythere jaini* Khosla and Nagori, 1989  
Figure 14.9-14.12

1978 *Hiltermanicythere* sp. Khosla, p. 269, pl. 4, figs. 12, 13.

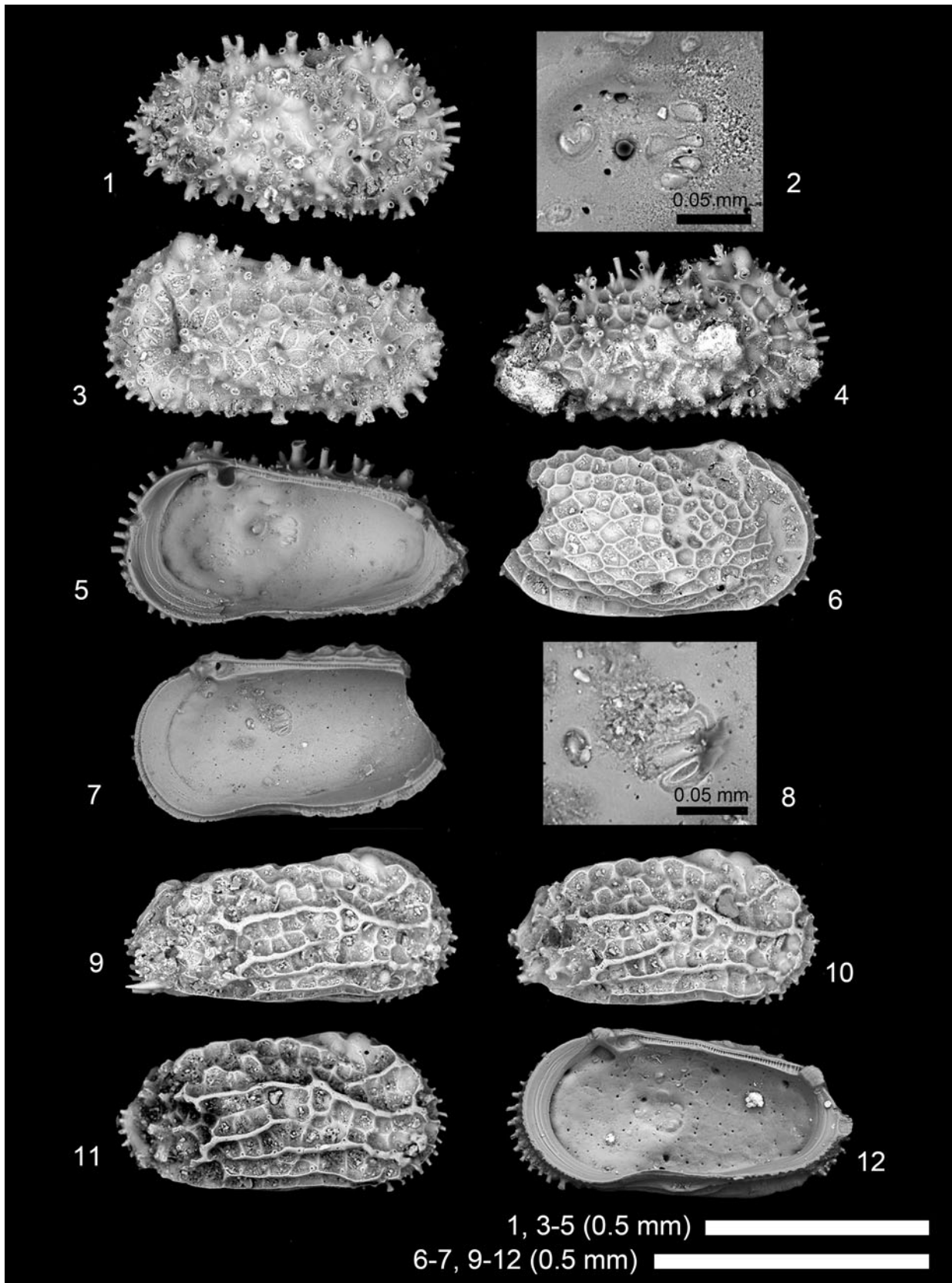
1989 *Chrysocythere jaini* Khosla and Nagori, p. 29, pl. 4, figs. 9, 10.



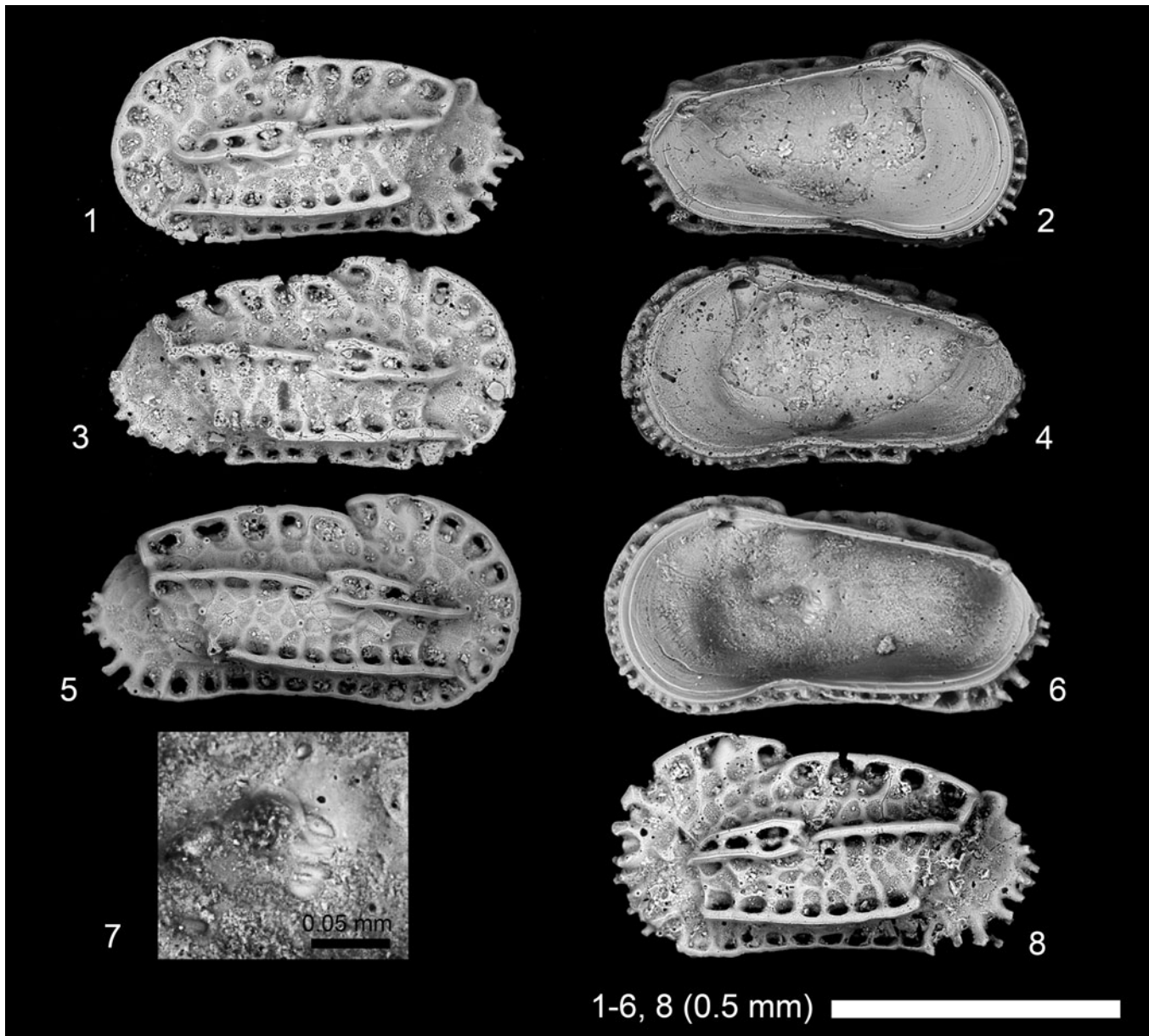


**Figure 13.** Scanning electron microscope images of *Neomonoceratina* species. (1–5) *Neomonoceratina gajensis* Guha, 1974: (1) adult RV, 2019/0181/0051 (19A-ck-09-2-009); (2) adult RV, 2019/0181/0052 (19B-ck-09-2-021); (3–5) adult LV, 2019/0181/0053 (CK-09-02-029). (6–10) *Neomonoceratina kutchensis* Guha, 1961: (6, 7) adult RV, 2019/0181/0054 (CK-09-02-031); (8–10) adult RV, 2019/0181/0055 (CK-09-02-057). (11–17) *Neomonoceratina retispinata* Khosla and Nagori, 1989: (11) adult LV, 2019/0181/0056 (19B-ck-09-2-019); (12) adult RV, 2019/0181/0057 (19B-ck-09-2-020); (13–15) adult RV, 2019/0181/0058 (CK-09-02-056); (16, 17) adult LV, 2019/0181/0059 (CK-09-02-030). (1–3, 6, 8, 11–13, 17) Lateral views; (4, 5, 7, 9, 10, 14–16) internal views; (5, 9) close-up of subcentral muscle scars; (10, 15) close-up of hingement.





**Figure 14.** Scanning electron microscope images of ostracode species. (1–5) *Acanthocythereis panti* Khosla and Nagori, 1989: (1, 2) adult female RV, 2019/0181/0083 (19B-ck-09-2-030); (3) adult male LV, 2019/0181/0084 (19B-ck-09-2-032); (4, 5) adult male RV, 2019/0181/0085 (CK-09-02-045b). (6–8) *Alococythere fossularis* (Lyubimova and Guha, 1960), adult RV, 2019/0181/0086 (19A-ck-09-2-014). (9–12) *Chrysocythere jaini* Khosla and Nagori, 1989: (9) adult male RV, 2019/0181/0087 (19B-ck-09-2-035); (10) adult female RV, 2019/0181/0088 (19B-ck-09-2-034); (11, 12) adult female RV, 2019/0181/0089 (CK-09-02-062). (1, 3, 4, 6, 9–11) lateral views; (2, 5, 7, 8, 12) internal views; (2, 8) close-up of subcentral muscle scars.



**Figure 15.** Scanning electron microscope images of *Costa ponticulocarinata* n. sp. (1, 2) adult LV, 2019/0181/0090 (19B-CK-09-036); (3, 4) adult RV, 2019/0181/0091 (19B-CK-09-037); (5–7) adult RV, 2019/0181/0092 (CK-09-02-061; holotype); (8) adult LV, 2019/0181/0093 (CK-09-02-042). (1, 3, 5, 8) lateral views; (2, 4, 6, 7) internal views; (7) close-up of subcentral muscle scars.

2001 *Chrysocythere jaini*; Bhandari et al., p. 42, pl. 24, figs. 1–4.

*Holotype*.—No. 348 (Department of Geology, University of Rajasthan, Udaipur, India) from Quilon beds, Padappakkara, Kerala, India. Early Miocene.

*Dimensions*.—See Table 1.

*Remarks*.—Both female and male specimens are shown.

Genus *Costa* Neviani, 1928

*Type species*.—*Cytherina edwardsii* Roemer, 1838, “Tertiary,” Sicily, Italy. Designated by Howe (1955).

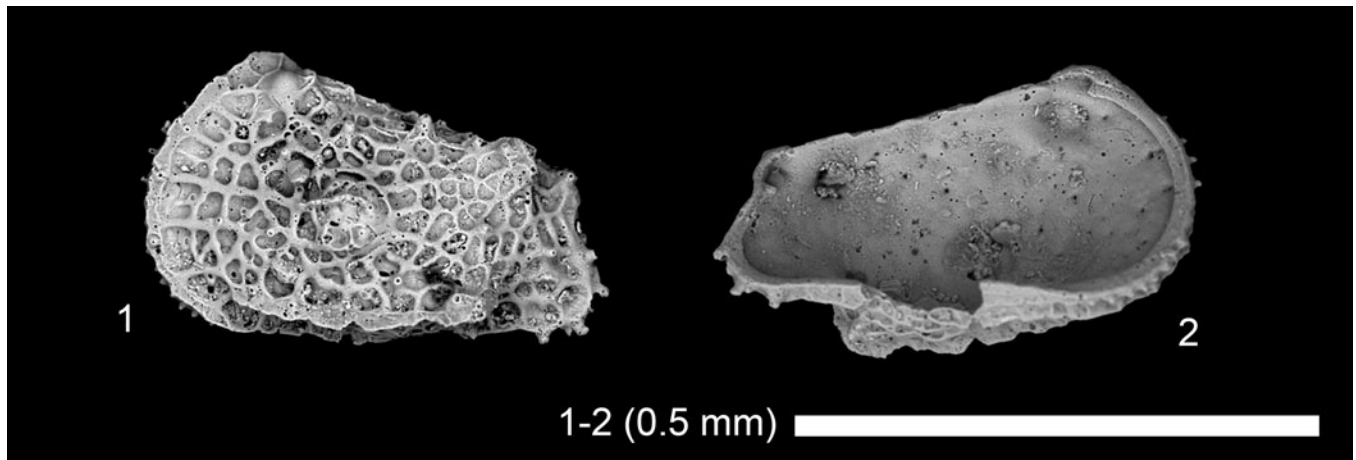
*Costa ponticulocarinata* new species

Figure 15

*Holotype*.—Adult RV, 2019/0181/0092 (CK-09-02-061) (Fig. 15.5–15.7). The type locality and horizon: CK-09-02, Channa Kodi, Quilon Formation, southwestern India, early Miocene (Fig. 1).

*Paratypes*.—2019/0181/0090 (19B-CK-09-036) (Fig. 15.1, 15.2), 2019/0181/0091 (19B-CK-09-037) (Fig. 15.3, 15.4), 2019/0181/0093 (CK-09-02-042) (Fig. 15.8).

*Diagnosis*.—A *Costa* species with very well-developed ponticulate carinae and very broad inner lamella.



**Figure 16.** Scanning electron microscope images of *Horrificiella?* sp. 1. (1, 2) Juvenile LV, 2019/0181/0060 (CK-09-02-058). (1) Lateral view; (2) internal view.

**Occurrence.**—CK-09-02, Channa Kodi, Quilon Formation, southwestern India, early Miocene.

**Description.**—Carapace moderately calcified, highest at the anterodorsal corner. Outline elongate and subrectangular; anterior margin rounded, bearing spines (visible from internal view), especially in ventral two-thirds; posterior margin bluntly acuminate and upturned, bearing long spines, especially in ventral half; dorsal margin curved at anterior one-third, bearing well-developed dorsolateral ridge (ponticulate carina); ventral margin slightly concave; ventrolateral ridge well developed as ponticulate carina, almost straight, relatively short without reaching anterior or posterior margin; median lateral ridge well developed as ponticulate carina, straight, composed of two parallel ridges in anterior half and single ridge in posterior half. Anterodorsal corner prominent; posterodorsal corner angular. Lateral surface ornamented with primary reticulation and ponticulate carinae. Hingement amphidont. Frontal muscle scar V-shaped. Adductor muscle scars consist of a vertical row of four elongate scars; ventral and ventromedian scars close to each other, dorsomedian scar curved. Anterior marginal frill well developed in internal view.

**Etymology.**—From the Latin *ponticulata* + *carinata* (adjective in the nominative singular, feminine), with reference to very well-developed ponticulate carinae of this species.

**Dimensions.**—See Table 1.

**Remarks.**—Species of *Costa* Neviani, 1928 usually have moderately broad inner lamella (Moore, 1961; van Morkhoven, 1963; Doruk, 1973), but this species has a very broad inner lamella. Also, hingement of this genus is reported to be holamphidont (Moore, 1961; van Morkhoven, 1963; Doruk, 1973), but some of our specimens show crenulation on anterior and posterior hinge teeth, indicating a paramphidont hinge. However, the taxonomic importance of width of inner lamella is uncertain at genus level, and the minor difference of amphidont-type hingement may be related to calcification degree rather than taxonomic difference because we see

similar hingement difference between adult and A-1 in single species in *Aurila* and *Pokornyella* in this study. Otherwise, this species shows considerable similarity to the type species of *Costa edwardsii* (Roemer, 1838) (Doruk, 1973). Thus, we prefer to put this species in *Costa*.

#### Genus *Horrificiella* Liebau, 1975

**Type species.**—*Cythere horridula* Bosquet, 1854, Upper Cretaceous, type locality not designated (reported from southwestern Netherlands and west-central Belgium in the original paper).

#### *Horrificiella?* sp. 1 Figure 16

**Dimensions.**—See Table 1.

**Remarks.**—This species is also similar to *Jugosocythereis* Puri, 1957 (type species *Cythereis bicarinata* Swain, 1946). It is difficult to assure the generic assignment of this species because only one juvenile specimen occurred in our material.

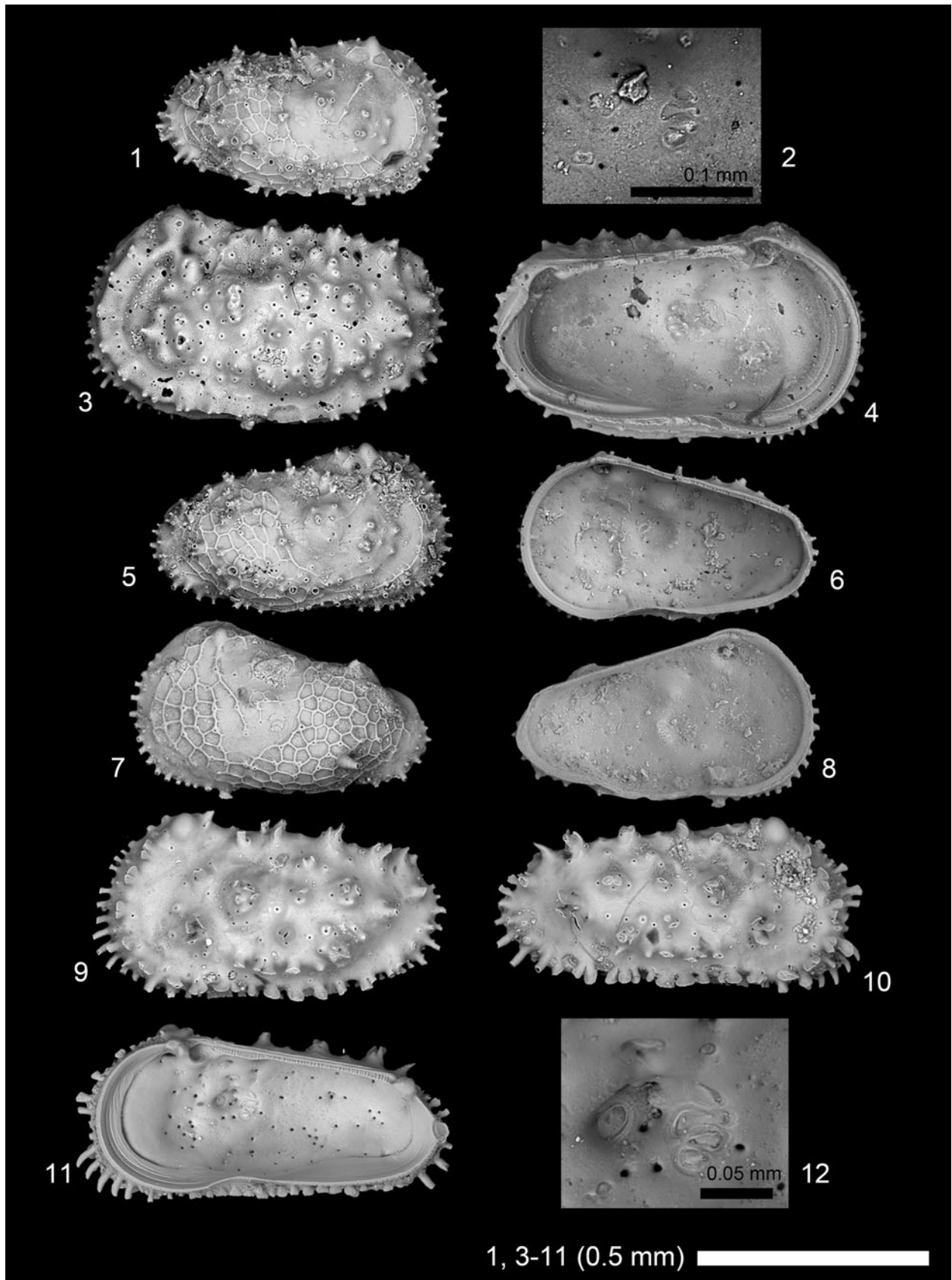
#### Genus *Paractinocythereis* new genus

**Type species.**—*Actinocythereis gujaratensis* Tewari and Tandon, 1960, early Miocene, southwestern Kutch, India.

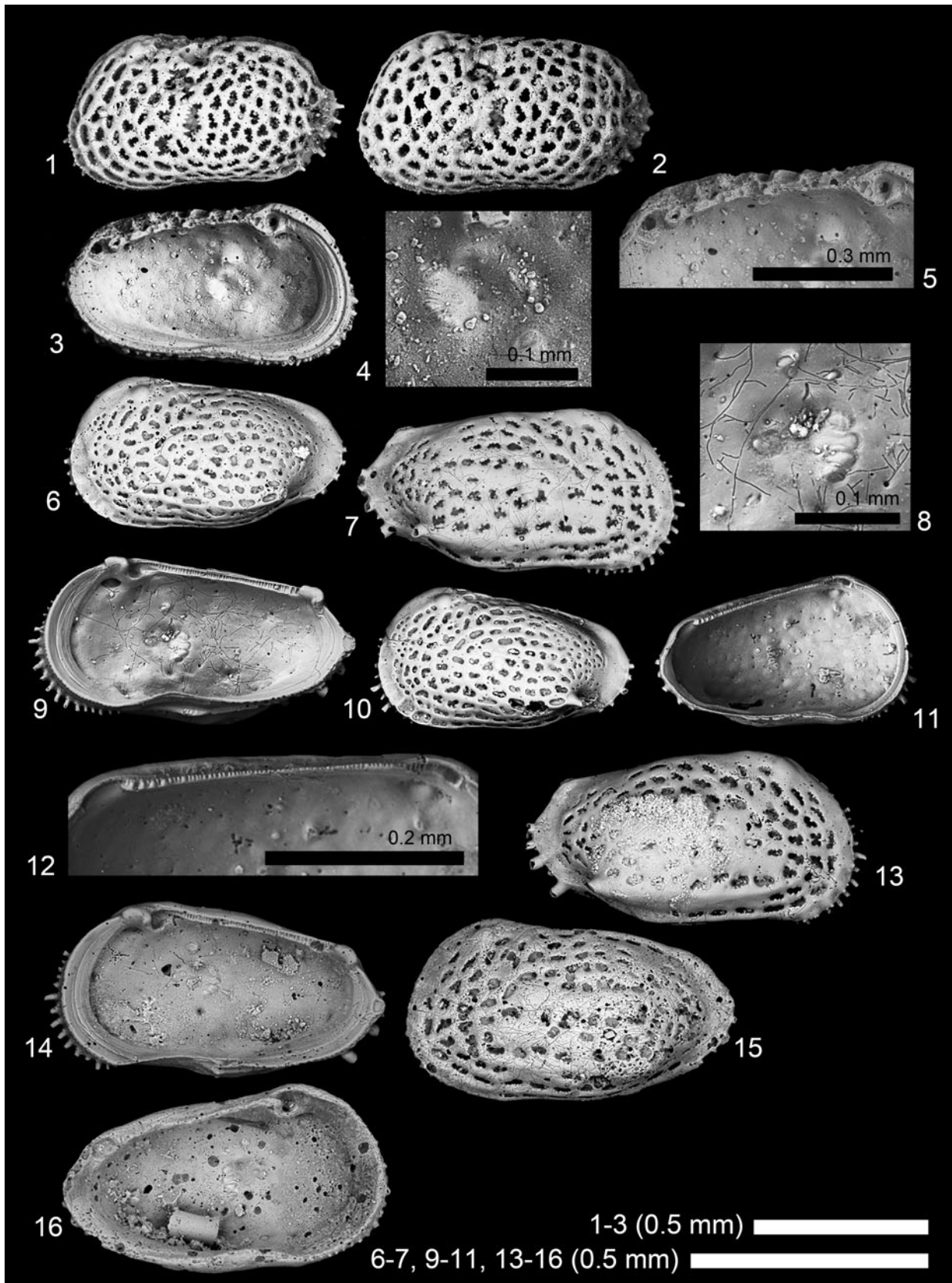
**Diagnosis.**—Trachyleberidid genus characterized by three horizontal rows of spines and a lack of ocular ridge. Carapace subrectangular and/or subovate (male elongate). Anterior margin rounded, strongly denticulate with clavate spines. Posterior margin blunt and upturned, with dense spines in its ventral half. Primary reticulation weak or absent. Frontal scar V-shaped; adductor muscle scars consisting of an oblique row of four scars, with the second scar from the top elongate and largest. Hingement holamphidont with denticulate median hinge element. Internal snap-knob structure present.

**Etymology.**—Referring to similarity and affinity of this genus to *Actinocythereis*.





**Figure 17.** Scanning electron microscope images of *Paractinocythereis gujaratensis* (Tewari and Tandon, 1960). (1, 2) A-1 RV, 2019/0181/0094 (19B-ck-09-2-033); (3, 4) adult female? LV, 2019/0181/0095 (CK-09-02-043); (5, 6) A-1 RV, 2019/0181/0096 (CK-09-02-044); (7, 8) A-1 LV, 2019/0181/0097 (CK-09-02-053); (9) adult male? LV, 2019/0181/0098 (19B-ck-09-2-031); (10–12) adult male? RV, 2019/0181/0099 (CK-09-02-051). (1, 3, 5, 7, 9, 10) lateral views; (2, 4, 6, 8, 11, 12) internal views; (2, 12) close-up of subcentral muscle scars.



**Figure 18.** Scanning electron microscope images of ostracode species. (1–5) *Puricythereis reticulata* (Khosla and Nagori, 1989): (1) adult female? LV, 2019/0181/0100 (19A-ck-09-2-010); (2–5) adult male? LV, 2019/0181/0101 (CK-09-02-033). (6–16) *Ruggieria guhai* Khosla, 1978: (6) A-1 LV, 2019/0181/0102 (19A-ck-09-2-012); (7–9) adult RV, 2019/0181/0103 (CK-09-02-039); (10–12) A-1 LV, 2019/0181/0104 (CK-09-02-041); (13, 14) adult RV, 2019/0181/0105 (CK-09-02-038); (15, 16) adult LV, 2019/0181/0106 (CK-09-02-040). (1, 2, 6, 7, 10, 13, 15) lateral views; (3–5, 8, 9, 11, 12, 14, 16) internal views; (4, 8) close-up of subcentral muscle scars; (5, 12) close-up of hingement.



*Remarks.*—This genus is similar to *Actinocythereis*, but distinguished by lacking an ocular ridge and having a higher carapace in lateral view, resulting in subrectangular and/or suboval outline. This genus was distributed in Africa (Apostolescu, 1961; El Sogher, 1996), India (Khosla and Pant, 1988), and USA (Huff, 1970; Yasuhara et al., 2015) during the Paleogene; and in Arab-Africa (El-Waer, 1988; Khalaf, 1989; Hawramy and Khalaf, 2013; Ied and Ismail, 2016), India (Bhandari et al., 2001), IAA (Shin et al., 2019), and South China Sea (Gou et al., 1981) during the Neogene. Given their absence in Cenozoic Europe (Western Tethys) (e.g., Ducasse et al., 1985; Guernet, 2005; Lord et al., 2009; Wood et al., 2009; Guernet et al., 2012) and Paleogene Pacific (e.g., Yamaguchi, 2006; Yamaguchi and Kamiya, 2007a, b, 2009) fossil records, the relationship between American and Eastern Tethys Paleogene *Paractinocythereis* n. gen. remains uncertain, but we speculate on a possible dispersal from the Eastern Tethys through the African coast to the Atlantic coast of the USA (or the opposite direction). *Actinocythereis* probably evolved from and took over *Paractinocythereis* in the USA in the Miocene.

Species included: *Paractinocythereis purii* (Huff, 1970) n. comb., *P. texana* (Stadnichenko, 1927) n. comb., *P. scutigera* (Brady, 1868) n. comb., *P. sinensis* (Gou in Gou et al., 1981) n. comb., *P. iraqensis* (Khalaf, 1981) n. comb., *P. costata* (Khalaf, 1989) n. comb., *P. cornuocula* (Khalaf, 1989) n. comb., *P. dextraspina* (Khalaf, 1989) n. comb., *P. spinosa* (Khalaf, 1989) n. comb., *P. modesta* (Apostolescu, 1961) n. comb., *P. spinosa* (El-Waer, 1988) n. comb., which is a junior homonym of *P. spinosa* (Khalaf, 1989), *P. khariensis* (Khosla and Pant, 1988) n. comb., *P. gujaratensis* (Tewari and Tandon, 1960) n. comb., *P. tumefacientis* (Lubimova and Guha in Lubimova et al., 1960) n. comb., *P. vinjhanensis* (Tewari and Tandon, 1960) n. comb. (male of *Actinocythereis gujaratensis*, in our opinion).

*Paractinocythereis gujaratensis* (Tewari and Tandon, 1960)  
new combination

Figure 17

- 1960 *Actinocythereis gujaratensis* Tewari and Tandon, p. 154, text-fig. 3, fig. la, b.  
 1960 *Trachyleberis vinjhanensis* Tewari and Tandon, p. 155, text-fig. 3, fig. 4a, b.  
 1978 “*Archicythereis*” sp. A Khosla, p. 267, pl. 4, fig. 8, pl. 6, fig. 12.  
 1989 “*Archicythereis*” *vermai* Khosla and Nagori, p. 24, pl. 3, figs. 1–3.  
 1990b *Actinocythereis gujaratensis*; Khosla and Nagori, p. 89, pl. 2, fig. 2.  
 1990b *Trachyleberis vinjhanensis*; Khosla and Nagori, p. 89, pl. 2, fig. 3.  
 2001 *Actinocythereis gujaratensis*; Bhandari et al., p. 20, pl. 2, figs. 1–4.  
 2001 “*Archicythereis*” *vermai*; Bhandari et al., p. 30, pl. 12, figs. 1–4.  
 2001 *Actinocythereis vinjhanensis*; Bhandari et al., p. 22, pl. 4, figs. 1, 2.

*Holotype.*—No. 138 (probably Geology Department, Lucknow University, Lucknow, India) from Kutch, India. Early Miocene.

*Dimensions.*—See Table 1.

*Remarks.*—“*Archicythereis*” *vermai* Khosla and Nagori, 1989 is a juvenile of *Actinocythereis gujaratensis* Tewari and Tandon, 1960 n. comb., in our opinion. In addition, *Actinocythereis vinjhanensis* (Tewari and Tandon, 1960) n. comb. is probably male of and, thus, conspecific with (and thus junior synonym of) *Actinocythereis gujaratensis* Tewari and Tandon, 1960 n. comb. (considering alphabetical order of species name), in our opinion.

Genus *Puricythereis* Bonaduce, Masoli, and Pugliese, 1976

*Type species.*—*Puricythereis papilio* Bonaduce, Masoli, and Pugliese, 1976, Recent, Gulf of Aqaba, Red Sea.

*Remarks.*—*Quadraleberis* Bate and Sheppard, 1980 and *Crenaleya* Ahmad et al., 1991 are junior synonyms of *Puricythereis*. *Spongicythere* Howe, 1951 (type species *Spongicythere spissa* Howe, 1951) is very similar to *Puricythereis* in outline and reticulation (Howe, 1951) and may be the senior synonym. However, the original 1950s micrographic images do not allow detailed comparisons (Howe, 1951) and the type or topotype specimens of *Spongicythere spissa* need to be restudied to determine if *Puricythereis* is a junior synonym of *Spongicythere*.

*Puricythereis reticulata* (Khosla and Nagori, 1989)

Figure 18.1–18.5

- 1989 *Lankacythere reticulata* Khosla and Nagori, p. 35, pl. 6, figs. 8–10.  
 2001 *Lankacythere reticulata*; Bhandari et al., p. 82, pl. 63, figs. 1–4.

*Holotype.*—No. 365 (Department of Geology, University of Rajasthan, Udaipur, India) from Quilon beds, Padappakkara, Kerala, India. Early Miocene.

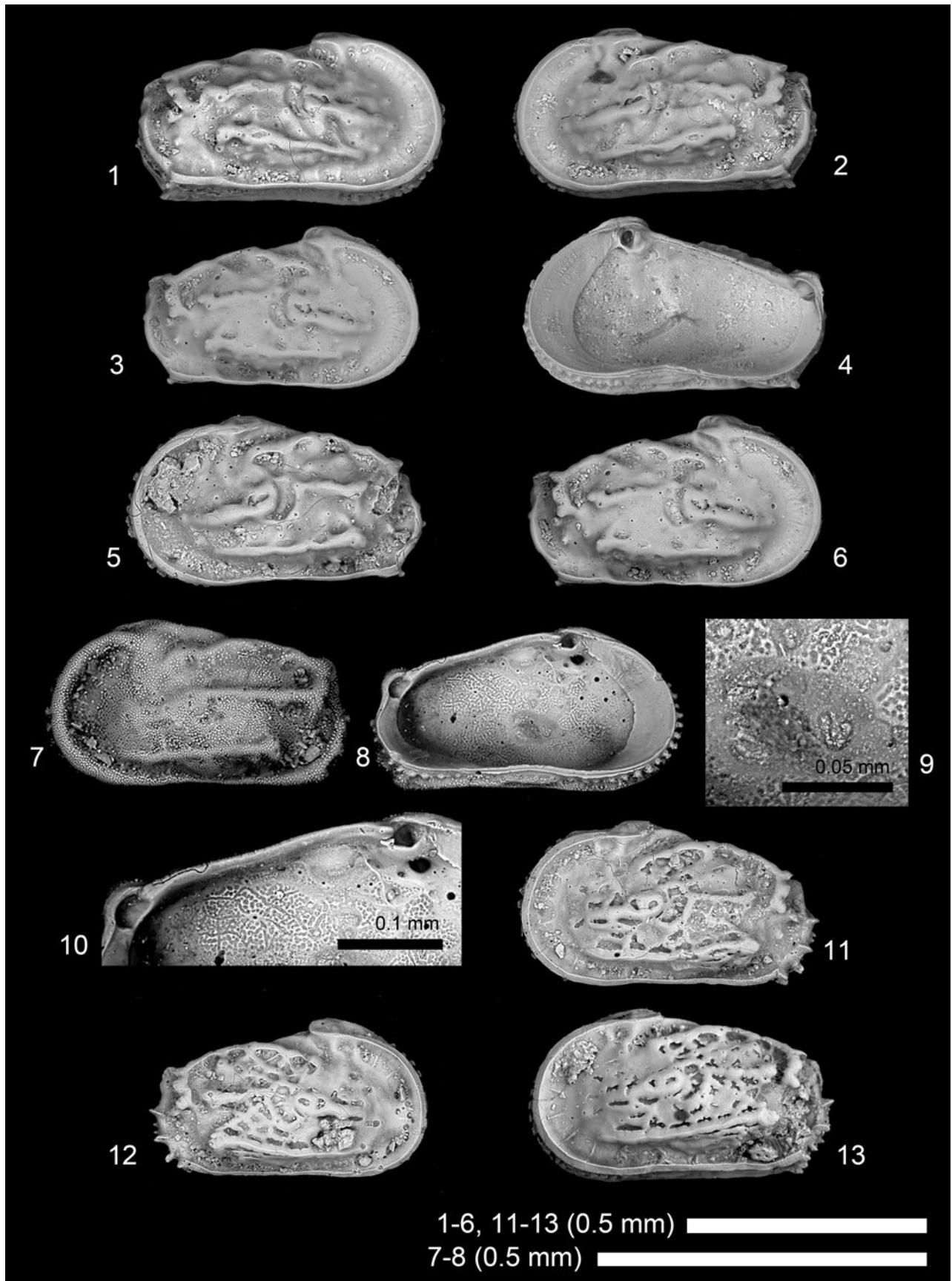
*Dimensions.*—See Table 1.



*Remarks.*—This species is better placed in *Puricythereis* rather than *Lankacythere* Bhatia and Kumar, 1979, in our opinion. The type species of *Lankacythere*, *Cythere coralloides* Brady, 1886 (Mostafawi, 1992; Jellinek, 1993), is clearly distinct from *Puricythereis*, and this species is very similar to the type species of *Puricythereis* (Bonaduce et al., 1976) in having irregular-shaped fossae with ingrowing spines and posteroventral margin bearing spines.

Genus *Ruggieria* Keij, 1957

*Type species.*—*Cythere micheliniana* Bosquet, 1852, Miocene, southwestern France.





1-6, 11-13 (0.5 mm)   
7-8 (0.5 mm) 

**Figure 19.** Scanning electron microscope images of *Stigmatocythere* species. (1–6) *Stigmatocythere interrupta* Khosla and Nagori, 1988: (1, 2) adult carapace, 2019/0181/0107 (19B-ck-09-2-038); (3, 4) adult RV, 2019/0181/0108 (ck-09-02-059); (5) adult LV, 2019/0181/0109 (19B-ck-09-2-040a); (6) adult RV, 2019/0181/0110 (CK-09-02-060). (7–10) *Stigmatocythere chaasraensis* (Guha, 1961), adult LV, 2019/0181/0111 (CK-09-02-006b). (11–13) *Stigmatocythere* cf. *S. arcuata*: (11) adult LV, 2019/0181/0112 (19B-ck-09-2-039); (12) adult RV, 2019/0181/0113 (19B-ck-09-2-041); (13) adult carapace, 2019/0181/0114 (CK-09-02-009). (1) right lateral view of carapace; (2, 13) left lateral views of carapaces; (3, 5–7, 11, 12) lateral views; (4, 8–10) internal views; (9) close-up of subcentral muscle scars; (10) close-up of hingement.

*Ruggieria guhai* Khosla, 1978  
Figure 18.6–18.16

- 1961 *Ruggieria* aff. *micheliniana* (Bosquet); Guha, p. 4, fig. 15.  
1978 *Ruggieria guhai* Khosla, p. 270, pl. 4, figs. 18, 19, pl. 6, fig. 19.  
2001 *Ruggieria guhai*; Bhandari et al., p. 144, pl. 126, figs. 1, 2.

*Holotype*.—RUGDMF no. 64 (Department of Geology, University of Rajasthan, Udaipur, India) from Gujarat, India. Early Miocene.

*Dimensions*.—See Table 1.

*Remarks*.—Lateral and internal views of adult and juvenile specimens are shown.

Genus *Stigmatocythere* Siddiqui, 1971

*Type species*.—*Stigmatocythere obliqua* Siddiqui, 1971, early Eocene, Pakistan.

*Stigmatocythere* cf. *S. arcuata* Khosla and Nagori, 1988  
Figure 19.11–19.13

*Dimensions*.—See Table 1.

*Remarks*.—This species is very similar to *Stigmatocythere arcuata* Khosla and Nagori, 1988, but has stronger primary reticulation and irregular-shaped fossae.

*Stigmatocythere chaasraensis* (Guha, 1961)  
Figure 19.7–19.10

- 1961 *Occultocythereis chaasraensis* Guha, p.4, figs. 8, 10, 13.  
1976 *Stigmatocythere chaasraensis*; Khosla, p. 136, pl. 1, figs. 7–9.  
1978 *Stigmatocythere chaasraensis*; Khosla, p. 271, pl. 5, fig. 2, pl. 6, fig. 16.  
1988 *Stigmatocythere (Stigmatocythere) chaasraensis*; Khosla and Nagori, p.110, pl. 1, fig. 1.  
1990b *Stigmatocythere (Stigmatocythere) chaasraensis*; Khosla and Nagori, p. 91, pl. 3, fig. 1.  
2001 *Stigmatocythere (Stigmatocythere) chaasraensis*; Bhandari et al., p. 154, pl. 135, figs. 1, 2.  
2004 *Stigmatocythere (Stigmatocythere) chaasraensis*; Bhandari, p. 187, fig. 8.2.

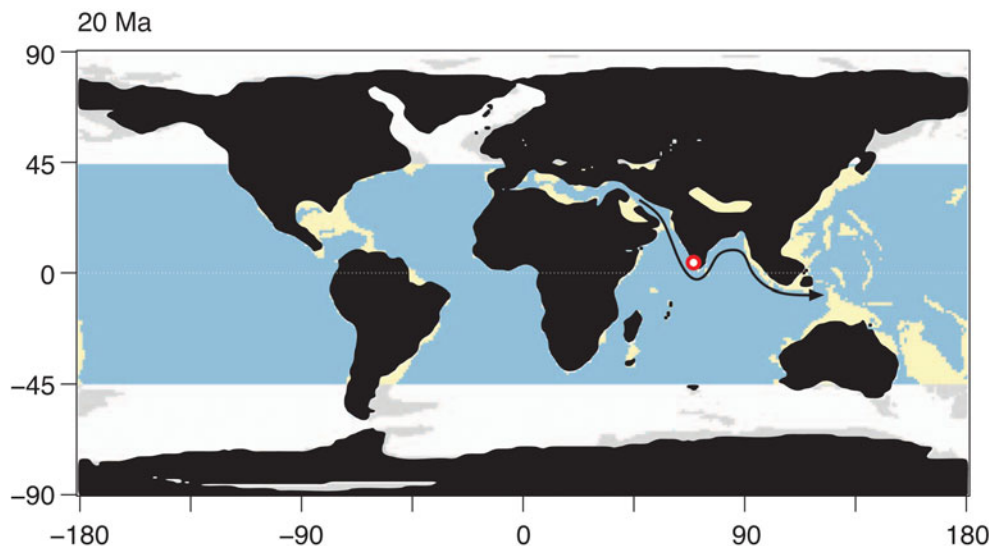
*Holotype*.—No. II-30 (Palaeontology Laboratory, Oil and Natural Gas Commission, Dehra Dun, India) from Kutch, India. Early Miocene.

*Dimensions*.—See Table 1.

*Remarks*.—Only one left valve was found in this study.

*Stigmatocythere interrupta* Khosla and Nagori, 1988  
Figure 19.1–19.6

- 1988 *Stigmatocythere (Bhatiacythere) interrupta* Khosla and Nagori, p. 115, pl. 2, figs. 1–4.



**Figure 20.** Early Miocene paleogeographic map (20 Ma), from Leprieur et al. (2016). Red circle indicates the studied site CK-09-02. Light blue, deep tropical ocean; yellow, tropical shallow reefs; white and light gray, deep ocean and shallow waters outside the tropical boundary, respectively. Arrow indicates hypothetical route of biogeographic shift of Tethyan elements from Tethys to IAA.

2001 *Stigmatocythere* (*Bhatiacythere*) *interrupta*; Bhandari et al., p. 150, pl. 131, figs. 1–4.

2004 *Stigmatocythere* (*Bhatiacythere*) *interrupta*; Bhandari, p. 193, fig. 9.4.

*Holotype*.—RUGDMF no. 284 (Department of Geology, University of Rajasthan, Udaipur, India) from Quilon beds, Kerala, India. Early Miocene.

*Dimensions*.—See Table 1.

*Remarks*.—*Stigmatocythere interrupta* Khosla and Nagori, 1988 is similar to *Stigmatocythere rete* Khosla and Nagori, 1988, but distinguished by the lack of primary reticulation. *Stigmatocythere arcuata* Khosla and Nagori, 1988 has finer ridges and slightly different ridge arrangement compared to *Stigmatocythere interrupta*.

## Discussion

*Paleoenvironmental interpretation*.—Abundant genera in the sample CK-09-02 include *Pokornyella*, *Loxoconcha*, *Tenedocythere*, and *Aurila*. All of these genera are known to be indicative of shallow (upper shelf or neritic), fully marine, and warm water environments (Bonaduce et al., 1984; Whatley and Jones, 1999; Zorn, 2003; Whatley et al., 2004; Szczechura, 2006; Titterton and Whatley, 2008; Hajek-Tadesse and Prtoljan, 2011; Seko et al., 2012). *Kriithe* is the only typical deep-sea genus from this sample (Zhou and Ikeya, 1992; Coles et al., 1994; Zhao and Whatley, 1997; Rodriguez-Lazaro and Cronin, 1999; Huang et al., 2018). Although shallow-marine *Kriithe* occurrences and species are known (Ishizaki, 1971; Whatley and Zhao, 1993; Zhao and Whatley, 1997), *Kriithe* is indicative of comparatively deeper waters, even in shallow marine environments, and suggests deeper waters than those suggested from the abundant genera mentioned above (Yasuhara et al., 2002a, 2005; Yasuhara and Seto, 2006). No other typical deep-water genera, such as *Cytheropteron* and *Argilloecia*, occurred in this sample, even though these genera are known to be abundant in upper bathyal depths in the Indo-Pacific region (Iwatani et al., 2018). In addition to the above-mentioned abundant genera, many other warm (often tropical) water indicator genera occurred in this sample (e.g., *Cytherelloidea*, *Neomonoceratina*, *Paijenborchellina*, *Ruggieria*, *Phlyctenophora*, and *Stigmatocythere*) (Wood and Whatley, 1994; Yasuhara et al., 2018; Hong et al., 2019; Shin et al., 2019). *Loxoconcha* and *Aurila* are typical phytal genera, although they include sediment-dwelling species (Kamiya, 1988; Yasuhara et al., 2002b, 2005; Szczechura, 2006; Yasuhara and Seto, 2006; Reich et al., 2015). In sum, the depositional environment interpreted based on ostracodes for the sample CK-09-02 is shallow (upper–middle shelf or neritic), full marine, and warm water environment, with some phytal environment nearby. This is generally consistent with the paleoenvironment interpreted based on other fossil groups (see the geological setting section above).

*Paleobiogeographic remarks*.—Compared to relatively well-investigated Paleogene global shallow-marine ostracode

paleobiogeography (Yamaguchi, 2006; Yamaguchi and Kamiya, 2009; Yasuhara et al., 2018), Miocene shallow-marine Indian ostracodes have seldom been discussed in a global paleobiogeography context (Szczechura, 1980; Siddiqui, 1983).

Many genera that we found here and reported from Miocene India (Khosla, 1978; Khosla and Nagori, 1989; Bhandari et al., 2001) are well known and widely distributed in the Tethyan region (see Fig. 20 for early Miocene paleogeographic map). *Phlyctenophora* is widely known from Tethyan Paleogene (see Yasuhara et al., 2018) and Paratethyan Miocene (Aiello and Szczechura, 2004; Gross and Piller, 2006). *Flexus* is widely known from the Oligocene–Miocene of Europe (Moore, 1961; Weiss, 1983; Ducasse and Cahuzac, 1997; Gross and Piller, 2006; Szczechura, 2006; Faranda et al., 2008; Hajek-Tadesse and Prtoljan, 2011; Seko et al., 2012) and from the Eocene–Miocene of Arabia (Al-Furaih, 1980; Aziz and Al-Shumam, 2013). *Paijenborchellina* is also a Tethyan genus, known from the Cretaceous to Recent circum-Mediterranean region, including Africa, Russia, Arabia, and West Asia (Szczechura, 1980; Brouwers and Fatmi, 1992a, b [as *Paijenborchella*]; Bassiouni and Luger, 1996; Bhandari, 1996; Hawramy and Khalaf, 2013; Yasuhara et al., 2018). *Costa* is also a typical Tethyan genus (Yamaguchi and Kamiya, 2009). *Hemicyprideis* is basically an European genus known from the Oligocene to the Miocene (Malz and Triebel, 1970; Ducasse et al., 1985; Monostori, 2004; Tóth, 2008), and known from the Arabian Miocene (Hawramy and Khalaf, 2013). *Neocyprideis* (sensu Yasuhara et al., 2018) was widely distributed in the Tethyan Region during the Paleogene including Europe, Arabia, Africa, and West Asia (Keen and Racey, 1991; Siddiqui, 2000; Yasuhara et al., 2018). The center of distribution of these Tethyan genera has shifted eastward to the Indo-Pacific region in the Neogene, and they have been widely reported from the Miocene Indian and IAA regions (Khosla, 1988; Bhandari et al., 2001; Yasuhara et al., 2018; Shin et al., 2019). *Kriithe* with pseudadont hinge has been reported as *Thracella* and *Dentokriithe* from the European Eocene (Lord et al., 2009; Guernet et al., 2012) and the Indian Eocene and Miocene (Bhandari, 1996; Bhandari et al., 2001), respectively. *Aurila* and *Loxoconcha* are globally distributed Cenozoic genera (van Morkhoven, 1963; Athersuch and Horne, 1984), but they are diverse in the European Miocene and thereafter (Ruggieri, 1975; Athersuch and Horne, 1984; Harrison et al., 2000; Guernet, 2005; Gross and Piller, 2006; Zorn, 2010). In addition, there is a similar species to *Loxoconcha confinis* known in Europe—*Loxoconcha punctatella* (Reuss, 1850) (see Gross and Piller, 2006). *Paracytheridea* is globally known, but *Paracytheridea perspicua* is very similar to the Tanzanian Eocene species *Paracytheridea anapetes* Ahmad 1977 (Ahmad, 1977; Ahmad et al., 1991). Although *Neomonoceratina* is most diverse in the tropical Indo-West Pacific (Zhao and Whatley, 1988), oldest records of the genus are known from the Eastern Tethys of Indo-Pakistan and Arab-Africa (Bassiouni and Luger, 1996; Bhandari, 1996; Siddiqui, 2006; Yasuhara et al., 2018). *Pokornyella* is obviously a Tethyan genus, well known from the Paleogene and Miocene of Europe (Ducasse and Coustillas, 1981; Ducasse et al., 1985; Gross and Piller, 2006; Zorn, 2010; Guernet et al., 2012), as well as its adjacent regions (Holden, 1976; Yasuhara



et al., 2018). *Pokornyella chaasraensis* is very similar to a European species *Pokornyella deformis* (Reuss, 1850) (Gross and Piller, 2006; Zorn, 2010). *Ruggieria* is a Miocene–Recent European genus (Moore, 1961) that is also known from the early Miocene of Africa (Ahmad et al., 1991) and India (Bhandari et al., 2001) and Recent Indo-Pacific (Whatley and Zhao, 1988; Dewi, 1997). The trachyleberidid genera *Chrysocythere* and *Costa* are globally distributed, but are also typical European genera (Ruggieri, 1961; Guernet, 2005; Bossio et al., 2006). *Puricythereis* is known from the Oligocene–Miocene of Africa as *Crenaleya* (Ahmad et al., 1991), the Eocene of Europe as *Leguminocythereis heistensis* (Keij, 1957) in Ducasse et al. (1985, pl. 81, fig. 9, not others; we do not think this specimen is conspecific with *Leguminocythereis heistensis*), the Miocene of India as *Quadrableberis* and *Lankacythere* (Khosla and Nagori, 1989), and the Recent Red Sea, Persian Gulf, and East African coast as *Puricythereis* and *Quadrableberis* (Bate and Sheppard, 1980; Jellinek, 1993; Mostafawi, 2003). *Stigmatocythere* is known from the Eocene–Miocene of Indo-Pakistan (Siddiqui, 1971, 1983; Bhandari, 2004), Paleocene–Miocene Arab-Africa (Reyment, 1963; Okosun, 1987; Ahmad et al., 1991; Guernet et al., 1991; Keen and Racey, 1991; Bassiouni and Luger, 1996; Hawramy and Khalaf, 2013), and Recent Indo-Pacific (Whatley and Zhao, 1988; Dewi, 1997). In summary, our early Miocene Indian ostracode fauna shows strong affinity both to Eocene–Miocene Eastern and Western Tethyan ostracode faunas and to Miocene–Recent Indo-Pacific ostracode faunas, supporting the Hopping Hotspot Hypothesis that the Tethyan biodiversity hotspot has shifted eastward through Arabia to IAA, together with concomitant biogeographic shifts of the Tethyan elements (Renema et al., 2008) (Fig. 20).

*Tenedocythere* is well known from the middle–late Miocene of Europe (Bonaduce et al., 1984; Gross and Piller, 2006; Szczechura, 2006; Hajek-Tadesse and Prtoljan, 2011), but older (Eocene–early Miocene) records are known only from the Central Pacific (Holden, 1976) and the Eastern Tethys of Africa and India (Ahmad et al., 1991; Bhandari et al., 2001). *Quadracythere subquadra* Siddiqui, 1971 sensu Ahmad et al. (1991) (note that, in our opinion, Ahmad’s specimens are not conspecific or congeneric to *Quadracythere subquadra*) and *Quadracythere vanga* Ahmad et al., 1991 are *Tenedocythere*, in our opinion, and are from Oligocene of Africa, the oldest records of the genus (Ahmad et al., 1991). Especially *Tenedocythere keralaensis* is very similar to *Tenedocythere subquadra* (Siddiqui, 1971) sensu Ahmad et al. (1991). Thus, inverse westward shift had also existed.

It is important to note that Paleogene and Miocene ostracodes from the IAA region remain poorly investigated, although Shin et al. (2019) recently reported a middle–late Miocene ostracode fauna from Java, Indonesia. *Neomonoceratina gajensis*, *Neomonoceratina kutchensis*, and *Neomonoceratina retispinata* that occurred in our early Miocene sample have very similar Recent species *Neomonoceratina koenigswaldi* Keij, 1954, *Neomonoceratina entomon* (Brady, 1890), and *Neomonoceratina spinosa* Zhao and Whatley, 1988, respectively, from the IAA region (see Zhao and Whatley, 1988; Mostafawi, 1992). This similarity most likely reflects the eastward hopping global hotspot of marine biodiversity, but, given the paucity of Paleogene and early Miocene records in the IAA region, we may have

missed opposite, westward ostracode migration from the IAA to the Eastern Tethyan region. More fossil shallow-marine ostracode data are needed from the Paleogene and Miocene IAA region to better test the Hopping Hotspot Hypothesis (Renema et al., 2008; Yasuhara et al., 2017).

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## Accessibility of supplemental data

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## Appendix 1. Miocene Indian ostracode data summary.

	CK-09-02
<i>Acanthocythereis panti</i>	1
<i>Alocopocythere fossularis</i>	1
<i>Aurila singhi</i>	25
<i>Bythoceratina malaysiana</i>	3
<i>Chrysocythere jaini</i>	2
<i>Costa ponticulocarinata</i> n. sp.	4
<i>Cytherella</i> sp. 1	6
<i>Cytherelloidea pandora</i> s.l.	1
<i>Flexus trifurcata</i>	14
<i>Hemicyprideis kachharai</i>	8
<i>Horrificiella?</i> sp. 1	1
<i>Krithe autochthona</i>	19
<i>Loxoconcha confinis</i>	65
<i>Loxoconcha keralaensis</i>	1
<i>Neocyprideis murudensis</i>	9
<i>Neocyprideis thirukkaruvensis</i>	2
<i>Neomonoceratina gajensis</i>	2
<i>Neomonoceratina kutchensis</i>	2
<i>Neomonoceratina retispinata</i>	5
<i>Paijenborchellina prona</i>	1
<i>Paractinocythereis gujaratensis</i>	16
<i>Paracytheridea perspicua</i>	11
<i>Paranesidea</i> cf. <i>P. gajensis</i>	11
<i>Phlyctenophora meridionalis</i>	8
<i>Pokornyella alata</i>	33
<i>Pokornyella chaasraensis</i>	72
<i>Propontocypris</i> sp. 1	1
<i>Puricythereis reticulata</i>	2
<i>Ruggieria guhai</i>	11
<i>Stigmatocythere</i> cf. <i>S. arcuata</i>	1
<i>Stigmatocythere chaasraensis</i>	1
<i>Stigmatocythere interrupta</i>	5
<i>Tenedocythere keralaensis</i>	63
<i>Xestoleberis</i> sp. 1	1
Total	408
Number of species	34

## Appendix 2. Detailed information of the specimens used for the present study.

NHMW	No.	species	T	V/C	Instar	Sex	Figure
2019/0181/0001	19A-ck-09-2-001	<i>Cytherella</i> sp. 1		L	J?		2.1
2019/0181/0002	19B-ck-09-2-001	<i>Cytherella</i> sp. 1		R	J?		2.2
2019/0181/0003	CK-09-02-003	<i>Cytherella</i> sp. 1		L	J?		2.3, 2.4
2019/0181/0004	19B-ck-09-2-002	<i>Cytherella</i> sp. 1		R	A?		2.6
2019/0181/0005	CK-09-02-054	<i>Cytherelloidea pandora</i> s.l.		R	A?		2.5, 2.7, 2.8
2019/0181/0006	19A-ck-09-2-015	<i>Paranesidea</i> cf. <i>P. gajensis</i>		R	A		2.9
2019/0181/0007	CK-09-02-001	<i>Paranesidea</i> cf. <i>P. gajensis</i>		R	A		2.10
2019/0181/0008	19B-ck-09-2-003	<i>Paranesidea</i> cf. <i>P. gajensis</i>		R	A		2.11, 2.13
2019/0181/0009	19B-ck-09-2-004	<i>Paranesidea</i> cf. <i>P. gajensis</i>		L	A		2.12
2019/0181/0010	CK-09-02-050	<i>Phlyctenophora meridionalis</i>		R	A		3.1–3.3
2019/0181/0011	CK-09-02-049	<i>Phlyctenophora meridionalis</i>		L	A		3.4–3.7
2019/0181/0012	CK-09-02-002	<i>Phlyctenophora meridionalis</i>		R	J		3.8
2019/0181/0013	CK-09-02-034	<i>Propontocypris</i> sp. 1		L	A		3.9–3.11
2019/0181/0014	CK-09-02-052	<i>Bythoceratina malaysiana</i>		R	A		3.12, 3.13
2019/0181/0115	19B-ck-09-2-005	<i>Flexus trifurcata</i>		R	A		4.1
2019/0181/0015	CK-09-02-007	<i>Flexus trifurcata</i>		R	A		4.2–4.4
2019/0181/0016	CK-09-02-064	<i>Flexus trifurcata</i>		L	A		4.5, 4.6
2019/0181/0017	CK-09-02-008	<i>Flexus trifurcata</i>		L	A		4.7, 4.8
2019/0181/0018	CK-09-02-063	<i>Flexus trifurcata</i>		R	A		4.9, 4.10
2019/0181/0019	CK-09-02-065	<i>Paijenborchellina prona</i>		R	A		4.11–4.14
2019/0181/0020	CK-09-02-032	<i>Hemicyprideis kachharai</i>		R	A		4.15
2019/0181/0021	19B-ck-09-2-007	<i>Hemicyprideis kachharai</i>		R	J?		4.16, 4.17
2019/0181/0022	CK-09-02-037	<i>Neocyprideis murudensis</i>		L	A		5.1–5.4
2019/0181/0023	19B-ck-09-2-006	<i>Neocyprideis murudensis</i>		L	A		5.5, 5.6
2019/0181/0024	CK-09-02-035	<i>Neocyprideis murudensis</i>		L	A		5.7, 5.8
2019/0181/0025	19A-ck-09-2-003	<i>Neocyprideis thirukkaruensis</i>		L	A		5.9
2019/0181/0026	19B-ck-09-2-008	<i>Neocyprideis thirukkaruensis</i>		L	A		5.10
2019/0181/0027	19B-ck-09-2-009	<i>Neocyprideis thirukkaruensis</i>		R	A		5.11
2019/0181/0028	19B-CK-09-043	<i>Neocyprideis thirukkaruensis</i>		L	A		5.12–5.14
2019/0181/0029	19A-ck-09-2-006	<i>Aurila singhi</i>		R	A		6.1, 6.2
2019/0181/0030	CK-09-02-022	<i>Aurila singhi</i>		L	A		6.3–6.5
2019/0181/0031	19A-ck-09-2-05	<i>Aurila singhi</i>		L	A		6.6–6.8
2019/0181/0032	CK-09-02-024	<i>Aurila singhi</i>		R	A		6.9, 6.10
2019/0181/0033	19A-ck-09-2-07	<i>Aurila singhi</i>		L	A-1		6.11–6.13
2019/0181/0034	19B-ck-09-2-013	<i>Aurila singhi</i>		R	A-1		6.14–6.16
2019/0181/0061	19B-ck-09-2-022	<i>Pokornyella alata</i>		R	A		7.1–7.4
2019/0181/0062	19B-ck-09-2-023	<i>Pokornyella alata</i>		R	A		7.5, 7.6
2019/0181/0063	19B-ck-09-2-024c	<i>Pokornyella alata</i>		R	J		7.7
2019/0181/0064	CK-09-02-025	<i>Pokornyella alata</i>		L	A		7.8, 7.9
2019/0181/0065	19B-ck-09-2-026	<i>Pokornyella alata</i>		R	A-1		7.10, 7.11
2019/0181/0066	19B-ck-09-2-027	<i>Pokornyella chaasraensis</i>		L	A		8.1, 8.2
2019/0181/0067	19B-ck-09-2-025	<i>Pokornyella chaasraensis</i>		R	A		8.3
2019/0181/0068	CK-09-02-020	<i>Pokornyella chaasraensis</i>		L	A		8.4–8.6
2019/0181/0069	CK-09-02-021	<i>Pokornyella chaasraensis</i>		L	A		8.7, 8.8
2019/0181/0070	CK-09-02-023	<i>Pokornyella chaasraensis</i>		R	A		8.9, 8.10
2019/0181/0071	19B-CK-09-050	<i>Pokornyella chaasraensis</i>		R	A		8.11, 8.12
2019/0181/0072	CK-09-02-017	<i>Pokornyella chaasraensis</i>		R	J		8.13, 8.14
2019/0181/0073	19B-CK-09-047	<i>Pokornyella chaasraensis</i>		L	A-1		8.15, 8.16
2019/0181/0074	19B-CK-09-048	<i>Pokornyella chaasraensis</i>		R	A-1		8.17, 8.18
2019/0181/0075	19B-ck-09-2-028	<i>Tenedocythere keralaensis</i>		L	A		9.1, 9.2
2019/0181/0076	CK-09-02-010	<i>Tenedocythere keralaensis</i>		L	A		9.3–9.5
2019/0181/0077	19B-ck-09-2-029	<i>Tenedocythere keralaensis</i>		R	A		9.6
2019/0181/0078	CK-09-02-013	<i>Tenedocythere keralaensis</i>		L	A		9.7, 9.8
2019/0181/0079	CK-09-02-019	<i>Tenedocythere keralaensis</i>		R	A		9.9, 9.10
2019/0181/0080	CK-09-02-011	<i>Tenedocythere keralaensis</i>		R	A-1		9.11–9.13
2019/0181/0081	19B-CK-09-051	<i>Tenedocythere keralaensis</i>		L	A-1		9.14–9.16
2019/0181/0082	19B-CK-09-053	<i>Tenedocythere keralaensis</i>		R	A-1		9.17–9.19
2019/0181/0035	19B-ck-09-2-014	<i>Kritho autochthona</i>		L	A	M	10.1–10.3
2019/0181/0036	19B-CK-09-044	<i>Kritho autochthona</i>		R	A	M	10.4–10.6
2019/0181/0037	CK-09-02-005	<i>Kritho autochthona</i>		L	A	F	10.7, 10.8
2019/0181/0038	CK-09-02-045a	<i>Kritho autochthona</i>		R	A	M	10.9–10.11
2019/0181/0039	CK-09-02-004	<i>Kritho autochthona</i>		L	A	F	10.12
2019/0181/0040	CK-09-02-006a	<i>Kritho autochthona</i>		L	A	F	10.13
2019/0181/0041	19B-ck-09-2-015	<i>Loxoconcha confinis</i>		L	A	M	11.1, 11.2
2019/0181/0042	CK-09-02-047	<i>Loxoconcha confinis</i>		R	A	M	11.3, 11.4
2019/0181/0043	CK-09-02-048	<i>Loxoconcha confinis</i>		L	A	F	11.5–11.8
2019/0181/0044	CK-09-02-046	<i>Loxoconcha confinis</i>		R	A	F	11.9, 11.10
2019/0181/0045	19B-ck-09-2-016	<i>Loxoconcha keralaensis</i>		R	A?		11.11



Continued.

NHMW	No.	species	T	V/C	Instar	Sex	Figure
2019/0181/0046	CK-09-02-055	<i>Loxoconcha keralaensis</i>		R	A		11.12–11.15
2019/0181/0047	19B-ck-09-2-017	<i>Paracytheridea perspicua</i>		L	A		12.1
2019/0181/0048	19B-ck-09-2-018	<i>Paracytheridea perspicua</i>		R	A		12.2
2019/0181/0049	19A-ck-09-2-016/CK-09-02-027	<i>Paracytheridea perspicua</i>		L	A		12.3–12.5
2019/0181/0050	CK-09-02-028	<i>Paracytheridea perspicua</i>		R	A		12.6, 12.7
2019/0181/0051	19A-ck-09-2-009	<i>Neomonoceratina gajensis</i>		R	A		13.1
2019/0181/0052	19B-ck-09-2-021	<i>Neomonoceratina gajensis</i>		R	A		13.2
2019/0181/0053	CK-09-02-029	<i>Neomonoceratina gajensis</i>		L	A		13.3–13.5
2019/0181/0054	CK-09-02-031	<i>Neomonoceratina kutchensis</i>		R	A		13.6, 13.7
2019/0181/0055	CK-09-02-057	<i>Neomonoceratina kutchensis</i>		R	A		13.8–13.10
2019/0181/0056	19B-ck-09-2-019	<i>Neomonoceratina retispinata</i>		L	A		13.11
2019/0181/0057	19B-ck-09-2-020	<i>Neomonoceratina retispinata</i>		R	A		13.12
2019/0181/0058	CK-09-02-056	<i>Neomonoceratina retispinata</i>		R	A		13.13–13.15
2019/0181/0059	CK-09-02-030	<i>Neomonoceratina retispinata</i>		L	A		13.16, 13.17
2019/0181/0083	19B-ck-09-2-030	<i>Acanthocythereis panti</i>		R	A	F	14.1, 14.2
2019/0181/0084	19B-ck-09-2-032	<i>Acanthocythereis panti</i>		L	A	M	14.3
2019/0181/0085	CK-09-02-045b	<i>Acanthocythereis panti</i>		R	A	M	14.4, 14.5
2019/0181/0086	19A-ck-09-2-014	<i>Alocopocythere fossularis</i>		R	A		14.6–14.8
2019/0181/0087	19B-ck-09-2-035	<i>Chrysocythere jaini</i>		R	A	M	14.9
2019/0181/0088	19B-ck-09-2-034	<i>Chrysocythere jaini</i>		R	A	F	14.10
2019/0181/0089	CK-09-02-062	<i>Chrysocythere jaini</i>		R	A	F	14.11–14.12
2019/0181/0090	19B-CK-09-036	<i>Costa ponticulocarinata</i> n. sp.	P	L	A		15.1, 15.2
2019/0181/0091	19B-CK-09-037	<i>Costa ponticulocarinata</i> n. sp.	P	R	A		15.3, 15.4
2019/0181/0092	CK-09-02-061	<i>Costa ponticulocarinata</i> n. sp.	H	R	A		15.5–15.7
2019/0181/0093	CK-09-02-042	<i>Costa ponticulocarinata</i> n. sp.	P	L	A		15.8
2019/0181/0060	CK-09-02-058	<i>Horrificiella?</i> sp. 1		L	J		16.1, 16.2
2019/0181/0094	19B-ck-09-2-033	<i>Paractinocythereis gujaratensis</i>		R	A-1		17.1, 17.2
2019/0181/0097	CK-09-02-043	<i>Paractinocythereis gujaratensis</i>		L	A	F?	17.3, 17.4
2019/0181/0096	CK-09-02-044	<i>Paractinocythereis gujaratensis</i>		R	A-1		17.5, 17.6
2019/0181/0097	CK-09-02-053	<i>Paractinocythereis gujaratensis</i>		L	A-1		17.7, 17.8
2019/0181/0098	19B-ck-09-2-031	<i>Paractinocythereis gujaratensis</i>		L	A	M?	17.9
2019/0181/0099	CK-09-02-051	<i>Paractinocythereis gujaratensis</i>		R	A	M?	17.10–17.12
2019/0181/0100	19A-ck-09-2-010	<i>Puricythereis reticulata</i>		L	A	F?	18.1
2019/0181/0101	CK-09-02-033	<i>Puricythereis reticulata</i>		L	A	M?	18.2–18.5
2019/0181/0102	19A-ck-09-2-012	<i>Ruggieria guhai</i>		L	A-1		18.6
2019/0181/0103	CK-09-02-039	<i>Ruggieria guhai</i>		R	A		18.7–18.9
2019/0181/0104	CK-09-02-041	<i>Ruggieria guhai</i>		L	A-1		18.10–18.12
2019/0181/0105	CK-09-02-038	<i>Ruggieria guhai</i>		R	A		18.13, 18.14
2019/0181/0106	CK-09-02-040	<i>Ruggieria guhai</i>		L	A		18.15, 18.16
2019/0181/0107	19B-ck-09-2-038	<i>Stigmatocythere interrupta</i>		C	A		19.1, 19.2
2019/0181/0108	ck-09-02-059	<i>Stigmatocythere interrupta</i>		R	A		19.3, 19.4
2019/0181/0109	19B-ck-09-2-040a	<i>Stigmatocythere interrupta</i>		L	A		19.5
2019/0181/0110	CK-09-02-060	<i>Stigmatocythere interrupta</i>		R	A		19.6
2019/0181/0111	CK-09-02-006b	<i>Stigmatocythere chaasraensis</i>		L	A		19.7–19.10
2019/0181/0112	19B-ck-09-2-039	<i>Stigmatocythere</i> cf. <i>S. arcuata</i>		L	A		19.11
2019/0181/0113	19B-ck-09-2-041	<i>Stigmatocythere</i> cf. <i>S. arcuata</i>		R	A		19.12
2019/0181/0114	CK-09-02-009	<i>Stigmatocythere</i> cf. <i>S. arcuata</i>		C	A		19.13

All specimens are from the sample CK-09-02, southwestern India, early Miocene.

NHMW, catalog numbers of the Natural History Museum Vienna; 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); F, female; M, male.

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