Bathyal molluscs from Upper Pleistocene methane seeps in Krishna-Godavari Basin, offshore eastern India

CRISPIN T.S. LITTLE, RAJENDAR KUMAR, JOEL E. JOHNSON, and LEON HOFFMAN

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Compared to other ocean basins there are few reported Recent methane seep communities from the Indian Ocean, with records from offshore Indonesia and Pakistan, and, more recently the east coast of India, in the Krishna-Godavari and Mannar Basins in bathyal water depths. Also from the former area, Upper Pleistocene aged fossil methane seep assemblages have been recovered from sediment cores. Here we describe systematically bivalves, gastropods and scaphopods from a methane seep assemblage penetrated by two sediment cores, drilled in 1045 m and 1050 m water depth, at horizons dated to between 40 and 52 kyrBP. The fossil molluscs comprise 29 taxa: 15 gastropods, 12 bivalves and two scaphopods. Of these, nine are new species: six gastropods (*Paralepetopsis bathyalus* Hoffman & Little sp. nov., *Mesopelex godavariensis* Hoffman & Little sp. nov., *Anatoma sahlingi* Hoffman & Little sp. nov., *Cirsonella aperta* Hoffman & Little sp. nov., *Dikoleps*? *magnarota* Hoffman & Little sp. nov., and *Alvania axistriata* Hoffman & Little sp. nov.) and three bivalves (*Ledella favus* Hoffman & Little sp. nov., *Yoldiella umbostriata* Hoffman & Little sp. nov., and *Vesicomya prashadi* Hoffman & Little sp. nov.). Six of the molluscan taxa likely had chemosymbionts: (*Acharax* sp., *Gigantidas* cf. *platifrons*, *Conchocele* sp., *Pliocardia* cf. *solidissima*, *Callogonia* cf. *leeana*, and *Archivesica* cf. *kawamurai*), representing 21% of the diversity in the seep assemblage. Apart from *Acharax* sp., all these putative chemosymbiotic taxa were likely obligate to seeps, as was probably the case for *Paralepetopsis bathyalus* Hoffman & Little sp. nov. and *Anatoma sahlingi* Hoffman & Little sp. nov. The other bivalve, gastropod and scaphopod species in the assemblage have living relatives common in bathyal habitats and can thus be considered as facultative or 'background' fauna. The fossil seep assemblage shares some taxa with recent seep communities in the east coast of India and elsewhere in the Indian Ocean, although additional systematic work is needed on the living taxa for a full comparison to be made.

Key words: Mollusca, Gastropoda, Bivalvia, Scaphopoda, taphonomy, hydrocabon seeps, Bay of Bengal, Indian Ocean.

Crispin T.S. Little [earctsl@leeds.ac.uk, ORCID 0000-0002-1917-4460], School of Earth and Environment, University of Leeds, Woodhouse Lane, Leeds LS2 9JT, UK; Life Sciences Department, Natural History Museum, London, Cromwell Road, London SW7 5BD, UK.
R. Rajendar Kumar [rrkumar@zsi.gov.in, ORCID 0000-0003-3711-4178], Zoological Survey of India, Marine Biology Regional Centre, 130 Santhome High Road, Chennai, Tamil Nadu, 600 028, India.
Joel E. Johnson [joel.johnson@unh.edu, ORCID 0000-0002-5671-7209], Department of Earth Sciences, University of New Hampshire, Durham, NH 03824, USA.
Leon Hoffman [Leon.Hoffman@senckenberg.de, ORCID 0000-0002-0205-186X], Marine Research Department, Senckenberg am Meer, Südstrand 40, 26382 Wilhelmshaven, Germany.

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Introduction

Marine hydrocarbon seeps are discrete sites where fluids rich in hydrocarbons, principally methane, flow onto the seafloor (e.g., Sibuet and Olu 1998; Levin 2005; Cordes et al. 2010; Joye 2020). They have subsequently proved to be common features of active and passive continental margins at bathymetric depths ranging from a few metres to more than seven kilometres (e.g., Fujikura et al. 1999; Leifer 2019). The abundance of reduced compounds at seeps (primarily methane and hydrogen sulphide) serve as the principal energy source for distinctive animal communities (e.g., Sibuet and Olu 1998; Levin 2005; Cordes et al. 2010). In water depths greater than about 400 m these communities are dominated in terms of biomass by larger animals that have symbiotic relationships with methanotrophic and/or sulphide-oxidizing bacteria, such as siboglinid tubeworms, and solemyid, bathymodiolin, vesicomyid, lucinid, and some thyasirid bivalves (e.g., Sibuet and Olu 1998; Sahling et al. 2003; Levin 2005; Dubilier et al. 2008; Cordes et al. 2010). However, there is more diversity amongst the smaller animals, such as provannid gastropods, some of which may be grazers of microbial mats (e.g., Levin 2005). In addition to these obligate animals, hydrocarbon seep communities comprise taxa that can also be found in surrounding deep-sea areas and are thus considered as "background" fauna. Examples amongst the bivalves are the solemyids, nuculanoids, pectinoids and small vesicomyids and thyasirids, and for the gastropods, the buccinoids (e.g., Levin 2005; Cordes et al. 2010). Because of the presence of methane derived authigenic carbonate (MDAC) and mollusc shells at seeps (exhumed from the subsurface in most cases) hard substrates are available for encrusting fauna, such as cirripede barnacles, serpulid polychaetes and corals (e.g., Pereira et al. 2021).

In contrast to the Pacific and Atlantic, relatively few hydrocarbon seeps have been discovered in the Indian Ocean. The Semeulue Seep (2°33.8' N, 96°45.4' E) is at 1134 m water depth in the Semeulue Basin, Sumatra Forearc, off northern Sumatra. The site has exposed MDAC and patches of microbial mats with a macrofauna comprising serpulid and probable siboglinid tubeworms, mytilid bivalves, and galatheoid squat lobsters (Wiedicke-Hombach et al. 2006; Siegert et al. 2011). Further South along the Sunda Arc is the Snail Hill Seep (7°57.5' S, 106°17.7' E) in 2900 m water depth in the Sunda Forearc Basin, off eastern Java (Wiedicke et al. 2002). Here is exposed MDAC, two genera of siboglinid tubeworms, probable vesicomyids, thyasirids, *Acharax* (confirmed genetically in Neulinger et al. 2006) and buccinoid gastropods (Wiedicke et al. 2002). Additional large vesicomyid specimens have been recovered from the seafloor in 2100 m water depth off eastern Java (7°24.6' S, 105°46.9' E) at what is likely to be one or more seep sites. A few of these specimens were studied genetically by Kojima et al. (2004) and others were described as *Calyptogena* (*Archivesica*) *garuda* Okutani & Soh, 2005. It is probable that these specimens are conspecific. Another seep site in the Java Trench is indicated by the presence of specimens of the siboglinid *Paraescarpia echinospica* Southward et al., 2002, dredged from 6°25.01' S, 104°49.53' E at a depth of approximately 1100–1550 m (Southward et al. 2002). From the western side of the Indian Ocean a large number of seeps have been found along the Makran accretionary margin, Pakistan, between 575 and 2870 m water depth (Bohrmann 2008; Römer et al. 2012; Wei et al. 2021). Below the Oxygen Minimum Zone at around 1000 m the seeps have exposed MDAC, microbial mats and are populated by siboglinid tubeworms, galatheoids, neolepadid barnacles, bathymodiolins, solemyids, and large vesicomyids (Bohrmann 2008; Wei et al. 2021). From this fauna *Calyptogena makranensis* Krylova & Sahling, 2006, has been described by Krylova and Sahling (2006), with a depth range of 2215–2336 m, and *Archarax* was genetically confirmed by Neulinger et al. (2006), from one of the seeps at 24°33.0' N, 64°15.6' E, in 2220 m water depth.

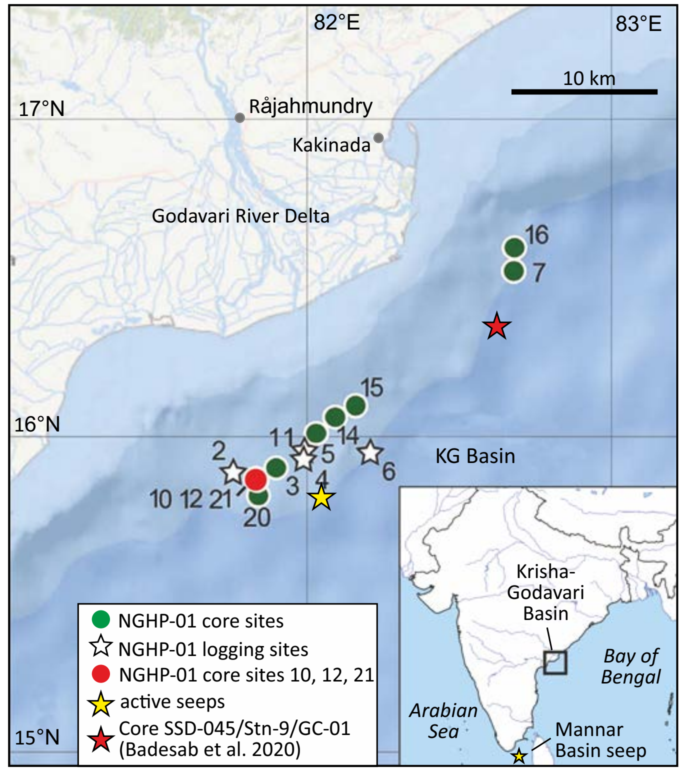

Fig. 1. Map showing NGHP-01 core sites (circles) and logging sites (stars) in the offshore Krishna-Godavari Basin (modified from Lorenson and Collett 2018). Site 12 is co-located with sites 10 and 21 (red circle). Yellow star indicates the position of the active seeps. Red star indicates the position of sediment core SSD-045/Stn-9/GC-01 of Badesab et al. (2020). Inset shows the study area in Krishna-Godavari Basin located on the eastern margin of peninsular India in the Bay of Bengal. Yellow star indicates the position of the active seep in the Mannar Basin, between Sri Lanka and Southern India.

More recently active seeps and associated animal communities have been found on the continental margin off eastern India in the Krishna-Godavari Basin and the Mannar Basin (Mazumdar et al. 2019, 2021; Dewangan et al. 2021; Sangodkar et al. 2022; Peketi et al. 2022) (Fig. 1). The Krishna-Godavari Basin seeps are located in a small area between 15°41.0' N, 82°2.0' 'E and 15°43.7' N, 82°4'48.7' E in 1752–1756 m water depth (Mazumdar et al. 2019). The living macrofauna comprises siboglinids and a diversity of other polychaetes, galatheoids (both galatheids and munidopsids), carid shrimps, neolepadids, ophiuroids, echinoids, and gastropod and bivalve molluscs (Mazumdar et al. 2019; Dewangan et al. 2021; Gonsalves et al. 2022; Sangodkar et al. 2022). The bivalves are bathymodiolins, large vesicomyids, thyasirids, soleymids, and pectinids; the gastropods are limpets, provannids, and nertitids. Apart from *Shinkaia crosnieri* Baba & Williams, 1998 (Gonsalves et al. 2022) and *Gigantidas niobengalensis* Oliver et al., 2024, none of the animals in these seep communities have been formally described. However, their trophic positions have been investigated using stable isotopes (Peketi et al. 2022). The Mannar Basin seep is located in a pockmark at 7°51.4' N, 78°36.46' E in a water depth of 1644 m (Mazumdar et al. 2021) (Fig. 1). The fauna here comprises living specimens of siboglinids, neolepadids, munidopsids, and buccinoid, and relict shells of large vesicomyids. The thyasirid *Ascetoaxinus ravichandrani* Ravinesh et al., 2024, is the only species to have been described from the Mannar Basin although a variety of lucinids is currently under study (Graham Oliver, personal communication 2024).

Prior to the discovery of active seeps in the Krishna-Godavari Basin, Upper Pleistocene aged bathyal fossil seepage in the same area was inferred by the presence of MDAC and associated bivalve shells from several sediment cores (Mazumdar et al. 2009; Teichert et al. 2014; Collett et al. 2014). Subsequently, a diverse fossil shell assemblage was recovered from two of these cores by CTSL, from which Gale et al. (2020) described the neolepadid cirripede *Ashinkailepas indica* Gale in Gale et al., 2020. In this paper we systematically describe the molluscan fauna (bivalves, gastropods, and scaphopods) from this material, and discuss it in terms of palaeoecology, and its relationship to the fossil and modern and seep communities off the eastern coast of India, and in other areas of the Indian Ocean.

Institutional abbreviations.—NHMUK, Natural History Museum, London, UK; SMF, Senckenberg Museum, Frankfurt am Main, Germany.

Other abbreviation.—MDAC, methane derived authigenic carbonate.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in ZooBank: LSIDurn:lsid:zoobank.org:pub:1A8C3C31-0761-41D1-925B-E7063975567.

Material and methods

The studied specimens come from two sediment cores drilled in 2006 by the D/V JOIDES Resolution during the Indian National Gas Hydrate Program Expedition 01 (NGHP-01) in the Krishna-Godavari Basin, Bay of Bengal, offshore eastern India (Collett et al. 2014, 2015). Core NGHP-01-12A was drilled in 1045.8 m of water at 15°51.6335' N, 81°50.2274' E; core NGHP-01-10D was drilled approximately 500 m to the northeast in 1050.4 m water depth at 15°51.8647' N, 81°50.0709' E (Fig. 1). The sediment in the cores and throughout the offshore Krishna-Godavari Basin consists of variably coloured hemipelagic clay containing greater or lesser quantities of organic carbon (Collett et al. 2015; Phillips et al. 2014). Slumping, debris flows, and turbidites are also common (Johnson et al. 2014, 2021; Flores et al. 2014). The sediment subsamples used in this study were taken from the two cores at depths below seafloor of 16–17 mbsf in core NGHP-01-12A, 15–17 mbsf, 41–42 mbsf, and at 61 mbsf in core NGHP-01-10D. Carbon-14 (^{14}C) ages obtained from foraminiferan and mollusc shells at 16.35 mbsf from core NGHP-01-12A have an age of 40 100 ± 360 and 50 300 ± 790 a (BP 1950), respectively (Teichert et al. 2014). Mollusc shells at 16.99 mbsf have a ^{14}C age of 51 600 ± 910 a (BP 1950). These dates correlate to the Upper Pleistocene. No radiocarbon dates have been obtained from concretions or shells from deeper in either of the cores as they are likely to fall outside the range of applicability for this dating method (Teichert et al. 2014).

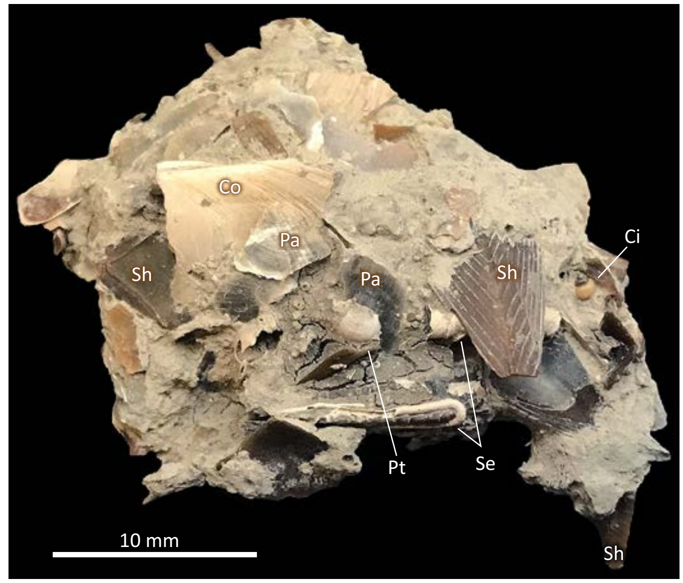

Fig. 2. Upper Pleistocene cemented mudstone concretion from core NGHP-01-12A, sample SMF373061 from Krishna-Godavari Basin, offshore eastern India, with shells of *Conchocele* sp. (Co), *Parvamussium*? aff. *scitulum* (Smith, 1885) (Pa), *Cirsonella aperta* Hoffman & Little sp. nov. (Ci), *Ashinkailepas indica* Gale in Gale et al., 2020 (Sh), and serpulid tubes (Se).

Variable sediment thickness of sediment (2–10 cm; Table 1) was sampled from the working halves of the cores and this was later sieved (1.7 mm, 300 µm and 125 µm mesh sizes) at the University of Leeds to remove the fine grains. The residual material comprised variably preserved macrofossils and microfossils, mineral grains, and variably cemented mudstone concretions of varying sizes, most of which had a shelly component (Fig. 2). The planktonic elements present in the sieved residues included fish otoliths and the shells of foraminifera, as well as pteropod and heteropod gastropods. The benthic elements comprised foraminifera, serpulid tubes, scleractinian corals, ostracod valves, isolated neolepadid plates, isolated echinoid plates and spines, and mollusc shells (chitons, bivalves, gastropods, and scaphopods). The bivalve, gastropod, and scaphopod shells were removed from the residues for identification under a low magnification binocular microscope. Subsequently, some of the larger specimens were then coated with ammonium chloride for photographic documentation using a digital camera at the University of Leeds. Some of smaller specimens were imaged using Scanning Electron Microscopes (SEM) at the University of Leeds, UK and Senckenberg am Meer, Wilhelmshaven, Germany, with gold coating to enhance image quality. The electron incident energy was 20 keV at the University of Leeds and

Table 1. Occurrence of bivalves, gastropods, and scaphopods, and selected other benthic taxa from cores NGHP-01-12A and NGHP-01-10D. p, present. Counts include both type and non-type material. CSV version of this table is available in SOM 2.

Sample	Average (mbsf)	*Paralepetopsis bathyalus* sp. nov.	*Mesopelex godavariensis* sp. nov.	Fissurellidae sp. indet.	*Anatoma sahlingi* sp. nov.	Seguenzioidea sp. indet.	*Cirsonella aperta* sp. nov.	*Dikoleps*? *magnarota* sp. nov.	*Alvania axistriatus* sp. nov.	*Benthonellania* sp.	Columbellidae sp. indet.	Conoidea sp. indet.	*Eulimella* sp. 1	*Eulimella* sp. 2	*Odostomia* sp.	Cylichnidae? sp. indet.	*Acharax* sp.	*Ledella favus* sp. nov.	*Yoldiella umbostriatus* sp. nov.	*Gigantidas* cf. *platifrons*	*Parvamussium*? aff. *scitulum*	Propeamussiidae? sp. indet.	*Conchocele* sp.	*Vesicomya prashadi* sp. nov.	*Pliocardia* cf. *solidissima*	*Callogonia* cf. *leeana*	*Archivesica* cf. *kawamurai*	Cuspidariidae? sp. indet.	Dentaliidae? sp. indet.	*Cadulus chuni*	Bathymodiolinae shell fragments	Propeamussiidae shell fragments	Vesicomyidae shell fragments	Chitons	*Caryophyllia* sp.	Serpulids	*Ashinkailepas indica*	Echinoid test plates	*Radulichnus* sp.
Core NGHP-01-10D																																							
CLM 3H2 20-22 cm	15.3																																p						
CLM 3H2 42-46 cm	15.52																																p						
CLM 3H2 44-46 cm	15.54																1																				p		
CLM 3H2 60-62 cm	15.7																																p						p
CLM 3H2 62-64 cm	15.72																																p						
CLM 3H2 63-65 cm	15.73																									1													
CLM 7x1 44-46 cm	41.54																																p						p
CLM 7x1 82-83 cm	41.92																																p						p
CLM 7x1 91-93 cm	42.01																			1												p							
CLM 7x1 117-119 cm	42.27																																p						p
CLM 10x2 1-1 cm	61.03																																p						
Abundance																	**1**			**1**						**1**													
Core NGHP-01-12A																																							
CLM 3H2 30-40 cm	16.18	12			6	1	8	2	4		1								13	13	8	3	1				2				p	p	p	p		p		p	p
CLM 3H2 40-50 cm	16.28	16	2		19		2	3	5			1						1	1	13	6	5					3				p	p	p	p		p	p		p
CSD 3H2 52-54.5 cm	16.36				7		2	2	8										2	2	1										p	p	p			p	p		p
FOS 3H2 52-54 cm	16.36																																		p				
CLM 3H2 50-60 cm	16.38	10	1		23	1	4	1	11										7	4		4		1			3				p	p	p	p			p		p
CSD 3H2 52-57 cm	16.38	2	1	1	4	2		4	7					1	1				2	2	1	3									p	p	p	p		p	p		
CLM 3H2 60-70 cm	16.48	7	1		6	1	2	1	10		1							1	4	1		1		2			2							p		p	p		
CLM 3H2 80-90 cm	16.68	8			3	1	2		11	1	1		1					2	1	1	3	2	2	5	1		2					p	p			p	p	p	p
CSD 3H2 84-86 cm	16.68								7												1	1										p	p	p			p		p
CLM 3H2 90-100 cm	16.78	5							18									6	1	2	1	3					3		6	4		p	p			p	p		
CLM 3H2 100-110 cm	16.88	3					2		10							1	1	4	1	1		3	1	1			4	1		1		p	p	p		p	p		p
CSD 3H2 116-117 cm	17																																p						
CSD 3H2 116-118 cm	17																																				p		
Abundance		**63**	**5**	**1**	**68**	**6**	**22**	**13**	**91**	**1**	**3**	**1**	**1**	**1**	**1**	**1**	**1**	**14**	**32**	**39**	**21**	**25**	**4**	**9**	**1**		**19**	**1**	**6**	**5**									

10 keV at Senckenberg am Meer. Imaging was performed using direct and back-scatter electrons. The SEM provided calibrated measurements for shell sizes for the smaller specimens. Counts of specimens were limited to those that were complete enough for reliable identification, both in the sieved material and on the surfaces of the concretions. Single gastropod and scaphopod shells were counted as one individual. Articulated bivalve shells were counted as one individual, as were left and right valves from the same sediment sample that obviously belonged to the same specimen; single left and right valves were counted as one individual. Many of the bivalve shell fragments were identifiable only to higher taxonomic level; these were recorded as "present" in the respective samples, but not counted. This was also done for other benthic taxa (chitons, serpulid tubes, corals, cirripedes, echinoids, and ichnofossils) for palaeoecological analysis (Table 1). Species identifications were done to the lowest taxonomic level possible using existing literature. The holotypes and subsets of paratypes (including all those figured) for the new species were deposited in the collection of the Senckenburg Museum, Frankfurt am Main, Germany (SMF). A representative suite of non-type specimens has been accessioned in the collections of the Palaeozoology Division, Zoological Survey of India, Kolkata (for details, see SOM 1, Supplementary Online Material available at http://app.pan.pl/SOM/app70-Little_etal_SOM.pdf).

Systematic palaeontology

Class Gastropoda Cuvier, 1795

Subclass Patellogastropoda Lindberg, 1986

Family Neolepetopsidae McLean, 1990

Genus *Paralepetopsis* McLean, 1990

Type species: *Paralepetopsis floridensis* McLean, 1990, by original designation; Recent, USA, off Florida, in cold seeps.

Paralepetopsis bathyalus Hoffman & Little sp. nov.

Fig. 3.

Zoobank LCID: urn:lsid:zoobank.org:act:411077AB-6C98-422E-A455-17BFE8841F10.

Etymology: After the habitat in a bathyal (palaeo-) depth range.

Type material: Holotype, SMF373134. Paratypes, 11 shells, SMF373131; seven shells, SMF373132; one shell, SMF373135; five shells, SMF 373136; four shells, SMF373137; one shell, SMF373133. All from the type locality and horizon.

Type locality: Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335' N, 81°50.2274' E, 1046 m water depth.

Type horizon: 16.18–16.88 mbsf level, core NGHP-01-12A; Upper Pleistocene.

Material.—Type material and several specimens from core NGHP-01-12A (for details see Table 1).

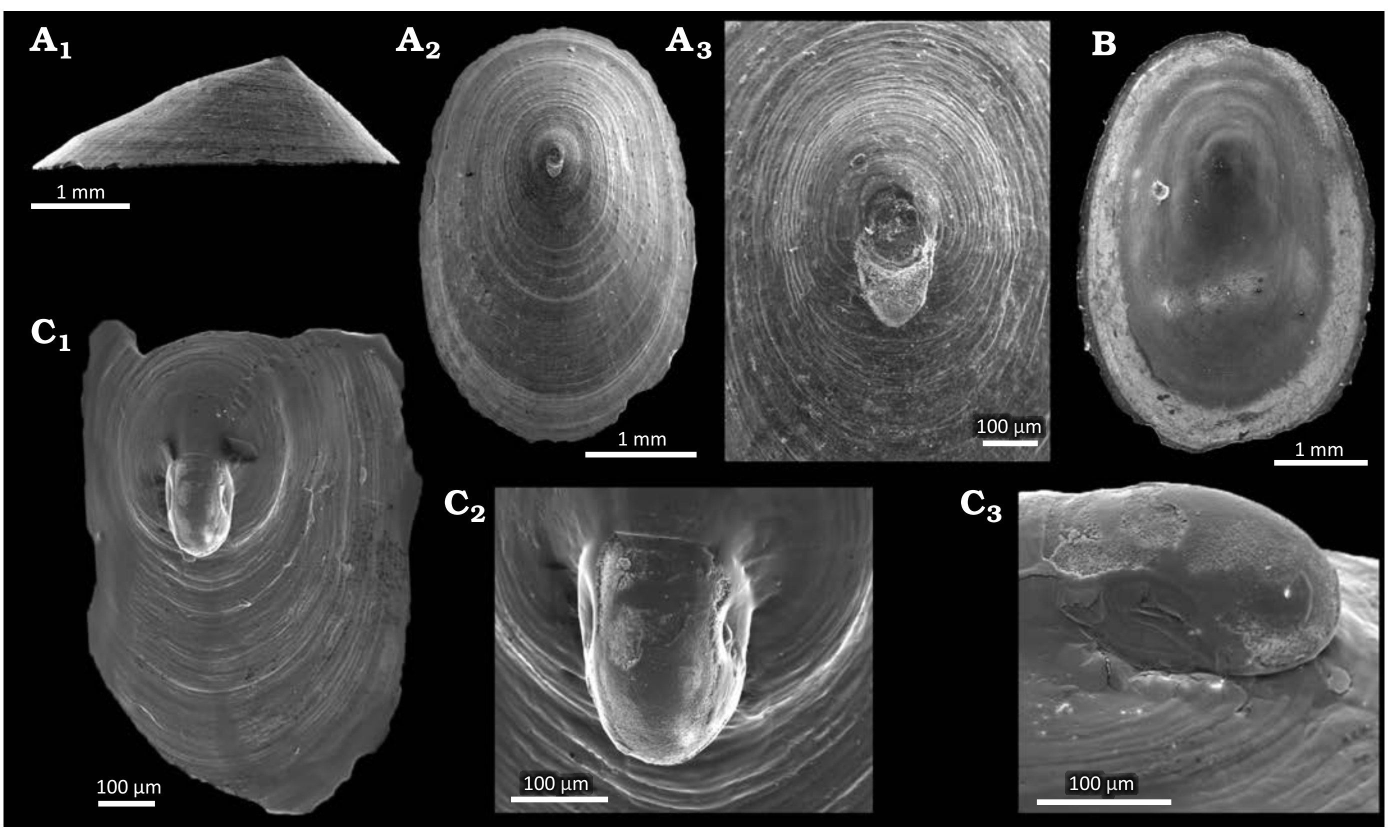

Fig. 3. The neolepetopsid gastropod *Paralepetopsis bathyalus* Hoffman & Little sp. nov. from Upper Pleistocene seep deposits from core NGHP-01-12A, Krishna-Godavari Basin, offshore eastern India. **A**. SMF373134, holotype, lateral (A_1) and external (A_2) views, apical detail with protoconch scar (A_3). **B**. SMF373135, paratype, internal view. **C**. SMF373133, paratype, partial specimen with protoconch, external view (C_1), protoconch details (C_2, C_3).

Diagnosis.—Small, thin, solid, limpet shell, oval apertural outline, apex anterior of midline. Protoconch simple exposed whorl, smooth sculpture, often eroded in adult specimens.

Dimensions.—Holotype height 2.5 mm, length 3.8 mm, width 1.2 mm. Shells in type set maximum length 5 mm, height 3 mm, width 1.6 mm.

Description.—Protoconch single stage only, only present on juvenile shells, smooth, planispiral aligned along major height and length axes, 30% from anterior margin, shell leaning posteriorly, fused with teleoconch. Transition to teleoconch clear by change in sculpture, margin sharp. Length 200 μm. Teleoconch convex outline on all margins in dorsal view, anterior margin highest convexity, shell broader posteriorly. Apical angle in side view 120°; anterior outline short, straightened; several convex stages posteriorly. Apex in adult shells with oblong scar and imprint of lost protoconch posteriorly; often worn apex. Sculpture with fine irregular growth lines, fine radial ridges, frequently with nodules at interfaces with major growth stages. Margin smooth, sharp. Internally smooth, glossy, with inconspicuous imprint of muscle. Deep smooth pit at apex.

Remarks.—Eight species in the genus *Paralepetopsis* have been described from hydrothermal vent and seep habitats in the Atlantic and the Pacific Ocean (McLean 1990, 2008; Beck 1996; Warén and Bouchet 2001, 2009; Chen et al. 2023). *Paralepetopsis floridensis* McLean, 1990, has a near identical protoconch compared to *Paralepetopsis bathyalus* Hoffman & Little sp. nov., but the outline is more oval and it has a stronger radial sculpture (McLean 1990). Beck (1996: 89–90, pl. 1) described *Paralepetopsis rosemariae* Beck, 1996, based on a single specimen from a seamount in the western Pacific; the decapitated shell has a raised outline with little sculpture apart from a few major growth stages. The eastern Pacific *Paralepetopsis tunnicliffae* McLean, 2008, has a similar morphology compared to *Paralepetopsis bathyalus* Hoffman & Little sp. nov., but it has a strong radial sculpture (McLean 2008: 18–19, fig. 2A). The Mid-Atlantic Ridge hydrothermal vent species *Paralepetopsis ferrugivora* Warén & Bouchet, 2001, has a strong radial as well as concentric sculpture (Warén and Bouchet 2001: 123–124, fig. 2e–f). The northwestern Pacific seep species *Paralepetopsis lepichoni* Warén & Bouchet, 2001, is most similar to *Paralepetopsis bathyalus* Hoffman & Little sp. nov., but has a coarse as well as fine radial sculpture (Warén and Bouchet 2001: 125, figs. 2c, 5a–f). The eastern Atlantic seep species *Paralepetopsis sasakii* Warén & Bouchet, 2009, has a coarse radial sculpture and a similar protoconch (Warén and Bouchet 2009: 2331–2332, fig. 3). *Paralepetopsis polita* Chen et al., 2023, from the South China Sea has a polished shell and all known specimens lack a protoconch. *Paralepetopsis bathyalus* Hoffman & Little sp. nov. has co-marginal ridges with a few growth stages and juveniles show a protoconch. Chen et al. (2023) found a mitochondrial molecular sequence (COI) of *Paralepetopsis polita* similar to that of Lepetidae, but radular characteristics similar to those in Neolepetopsidae.

Stratigraphic and geographic range.—Type locality and horizon only.

Subclass Vetigastropoda Salvini-Plawen, 1989
Family Pseudococculinidae Hickman, 1983
Genus *Mesopelex* Marshall, 1986

Type species: *Mesopelex zelandica* Marshall, 1986; Recent, New Zealand.

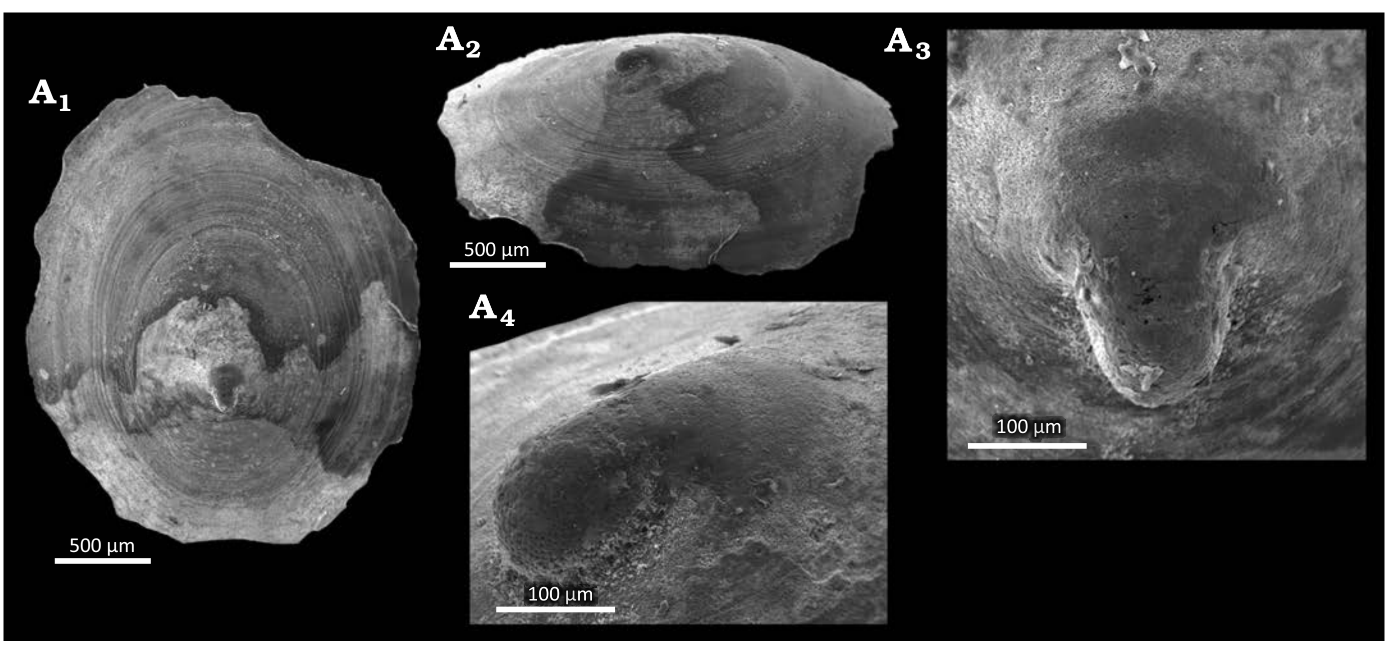

Fig. 4. The pseudococculinid gastropod *Mesopelex godavariensis* Hoffman & Little sp. nov. from Upper Pleistocene seep deposits from core NGHP-01-12A, Krishna-Godavari Basin, offshore eastern India. **A**. SMF373138, holotype, external (A_1) and oblique lateral (A_2) views, protoconch details (A_3, A_4).

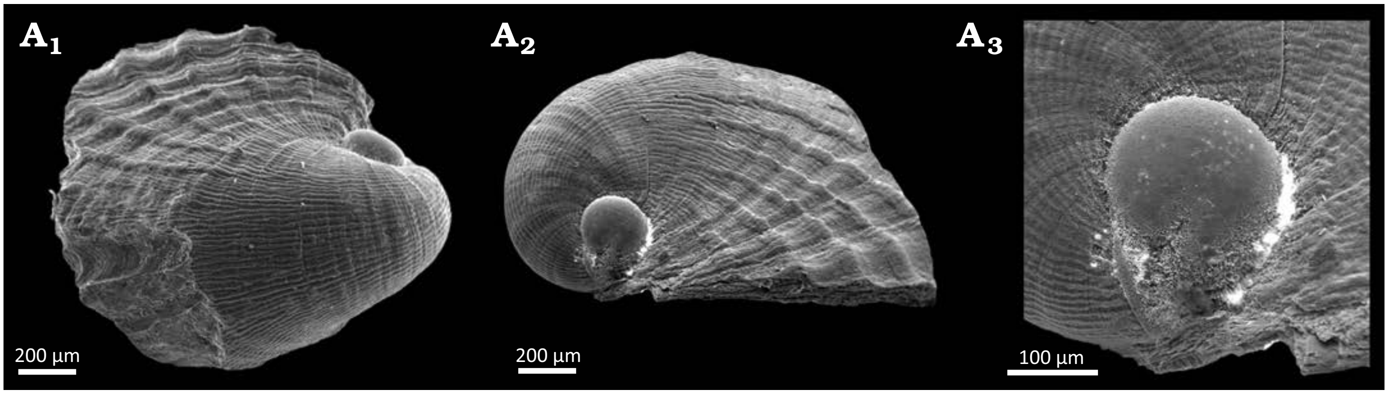

Fig. 5. Fissurellid gastropod Fissurellidae gen. et sp. indet. from Upper Pleistocene seep deposits from core NGHP-01-12A, Krishna-Godavari Basin, offshore eastern India. **A**. SMF373112, external (A_1) and lateral (A_2) views, protoconch detail (A_3).

Mesopelex godavariensis Hoffman & Little sp. nov.

Fig. 4.

Zoobank LCID: urn:lsid:zoobank.org:act:13902726-1A3C-49F9-864E-98E4D1E3C46B.

Etymology: After the type locality in the Krishna-Godavari Basin.

Type material: Holotype, SMF373138, relatively well preserved limpet shell with protoconch. Paratype, SMF373139, relatively well preserved limpet shell with protoconch.

Type locality: Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335' N, 81°50.2274' E, 1046 m water depth.

Type horizon: 16.28–16.48 mbsf level, core NGHP-01-12A; Upper Pleistocene.

Material.—Type material and several additional specimens from core NGHP-01-12A (for details see Table 1).

Diagnosis.—Small, thin, fragile, patelliform shell, oval apertural outline, apex posterior of midline. Protoconch simple exposed whorl with pitted sculpture.

Dimensions.—Holotype height 2.0 mm, length 2.4 mm, width 0.8 mm.

Description.—Protoconch single stage only, network of spirally and axial line segments, spirally aligned pitted sculpture, planispiral aligned along major height and length axes, 40% from posterior margin, shell leaning posteriorly, fused with teleoconch. Transition to teleoconch clear by change in sculpture, margin indistinct. Length 150 µm. Teleoconch convex sub-elliptical in dorsal view; anterior margin highest convexity. In side view, weakly convex anterior and posterior margins; apical angle high (approximately 160°). Sculpture smooth with fine irregular growth lines. Margin smooth, sharp. Internally smooth, glossy.

Remarks.—A single species has been described in *Mesopelex* Marshall, 1986 (MolluscaBase 2024). The type species *Mesopelex zelandica* Marshall, 1986, was found off New Zealand on muddy sediment (Marshall 1986: 535–536, fig. 10a–d). Its apex is more raised and its protoconch is less elongated than in *Mesopelex godavariensis* Hoffman & Little sp. nov. The dorsal outline, protoconch shape and sculpture are very similar to *Mesopelex godavariensis* Hoffman & Little sp. nov. Pseudococculinid species in other genera have a strong sculpture (for example in the genera *Copulabyssia* Haszprunar, 1988, *Kaikarapelta* Marshall, 1986, *Notocrater* Finley, 1926), a raised shell (for example in the genera *Pseudococculina* Schepman, 1908, *Pterodacna* Herbert, 2024, *Tentaoculus* Marshall, 1986) or a pointed conical outline (*Punctabyssia* McLean, 1991).

Stratigraphic and geographic range.—Type locality and horizon only.

Family Fissurellidae Fleming, 1822

Fissurellidae gen. et sp. indet.

Fig. 5.

Material.—One shell (SMF373112) from Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335' N, 81°50.2274' E, 1046 m water depth, 16.38 mbsf level, core NGHP-01-12A; Upper Pleistocene.

Description.—Small cap-shaped shell, planispiral coiling. Protoconch paucispiral, three-quarters whorl, smooth, large nucleus, diameter 200 µm. Teleoconch in two stages. First stage half whorl, without selenizone, sculpture with fine radial bifurcating riblets, diameter about 600 µm. Second stage with about 15 radial ribs and commarginal somewhat regular growth margins, weak blunt nodules are formed at the crossings. Shell fragment length about 1 mm, width about 1 mm, thickness about 600 µm.

Remarks.—The shell is too fragmentary to identify below family level.

Family Anatomidae McLean, 1989

Genus *Anatoma* Woodward, 1859

Type species: *Scissurella crispata* J. Fleming, 1828, by monotypy; Recent, NE Atlantic and Mediterranean.

Anatoma sahlingi Hoffman & Little sp. nov.

Fig. 6.

Zoobank LCID: urn:lsid:zoobank.org:act:C51A4420-6F20-4CF1-9748-8C5B3489F090.

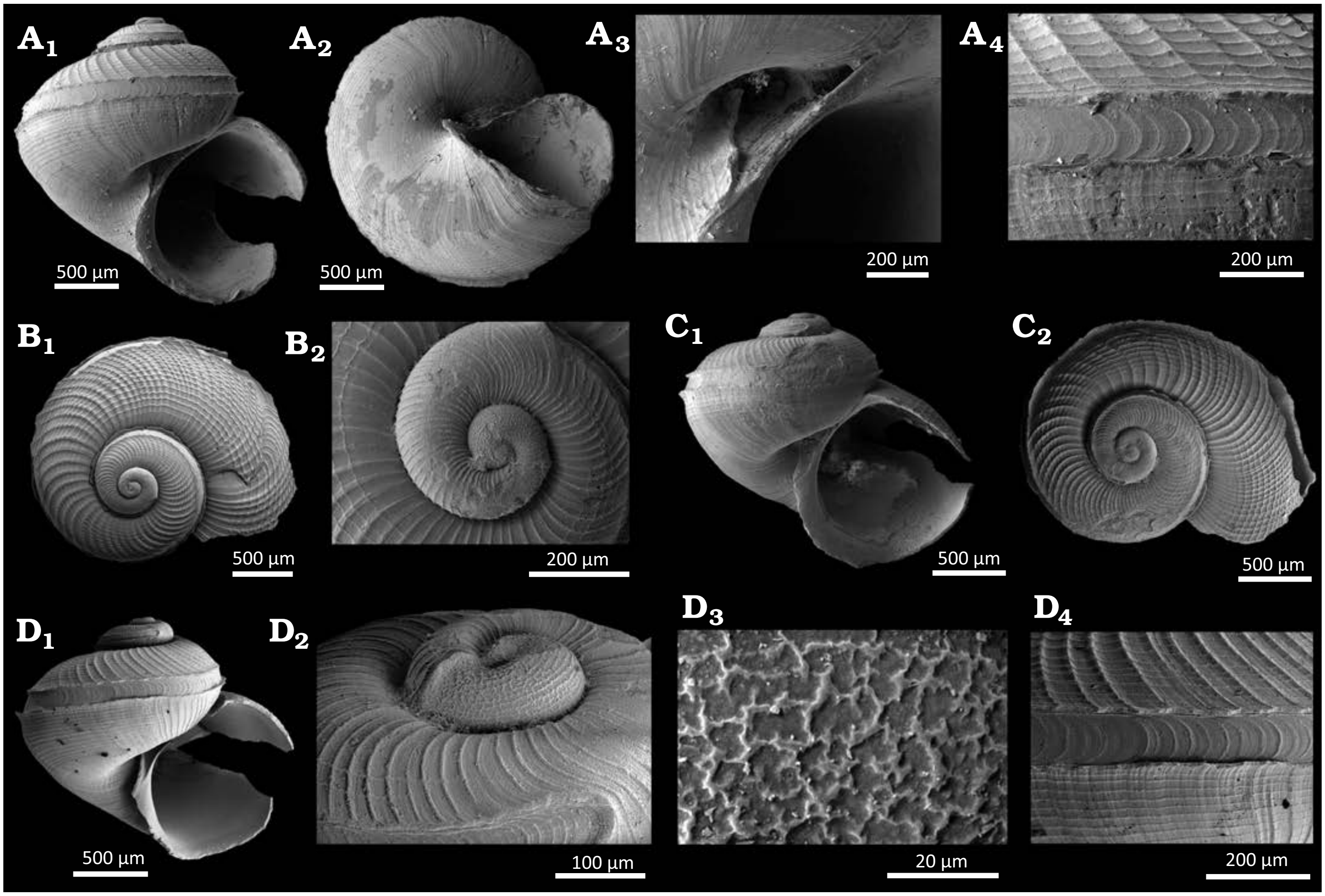

Fig. 6. The anatomid gastropod *Anatoma sahlingi* Hoffman & Little sp. nov. from Upper Pleistocene seep deposits from core NGHP-01-12A, Krishna-Godavari Basin, offshore eastern India. **A**. SMF373130, holotype, lateral (A_1) and adapical (A_2) views, detail of umbilicus (A_3), detail of selenizone (A_4). **B**. SMF373126, paratype, apical view (B_1), detail of protoconch (B_2). **C**. SMF373125, paratype, lateral (C_1) and apical (C_2) views. **D**. SMF373127, paratype, lateral view (D_1), oblique detail of protoconch (D_2), detail of protoconch microsculpture (D_3), detail of selenizone (D_4).

Etymology: After Heiko Sahling (1969–2018), to celebrate his pioneering work on hydrocarbon seep community ecology.

Type material: Holotype, SMF373130. Paratypes, five shells, SMF 373124; one shell, SMF373125; one shell, SMF373126; one shell, SMF373127; 12 shells, SMF373128; four shells, SMF373129.

Type locality: Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335’ N, 81°50.2274’ E, 1046 m water depth.

Type horizon: 16.18–16.68 mbsf level, core NGHP-01-12A; Upper Pleistocene.

Material.—Type material and several additional specimens from core NGHP-01-12A (for details see Table 1).

Diagnosis.—Small, thin, fragile, globose elevated shell, apertural wide anal slit, strong sculpture with spirals and ribs on shoulder, weak spiral sculpture below selenizone, selenizone sculpture weak.

Dimensions.—Maximum length 2.5 mm, height 2.3 mm.

Description.—Protoconch single stage only, three quarters flattened whorl. Sculpture rough, grooved network of dominating spirals and short axial line segments. Transition to protoconch clear by terminating smooth rim and change in sculpture. Length 200 µm. Teleoconch with two stages. First stage without selenizone three quarters whorl, convex, sculpture worn; suture to protoconch deep. Second stage one and three quarters globose whorls, spirals and dominating raised prosocline ribs above selenizone; 50 ribs, 15 spirals on body whorl; ribs extending on margin above selenizone, rib frequency increased near lip. Outline raised with early development of area below selenizone and suture. Very broad selenizone at periphery; sculpture reverse-arched ribs, frequency twice of axial ribs above; extended margins above and below eroded. Lower half whorl evenly convex; sculpture fine spiral lines and fine growth lines, flexuous near base. Deep open umbilicus with spiral lines, near vertical umbilical keel ending on columellar callus. Aperture circular, smooth internally with sharp lip; peripheral slit one fifth whorl deep. Union of parietal lip and shoulder area at 90°. Parietal and columellar lip united, concave, ending in pointed extended lip area.

Remarks.—Anatomids in the Indian Ocean were reviewed by Geiger (2012) and Hoffman et al. (2022). Hoffman et al. (2022) identified 17 species in the Indian Ocean of which six species were found alive in the lower (>2000 m) bathyal

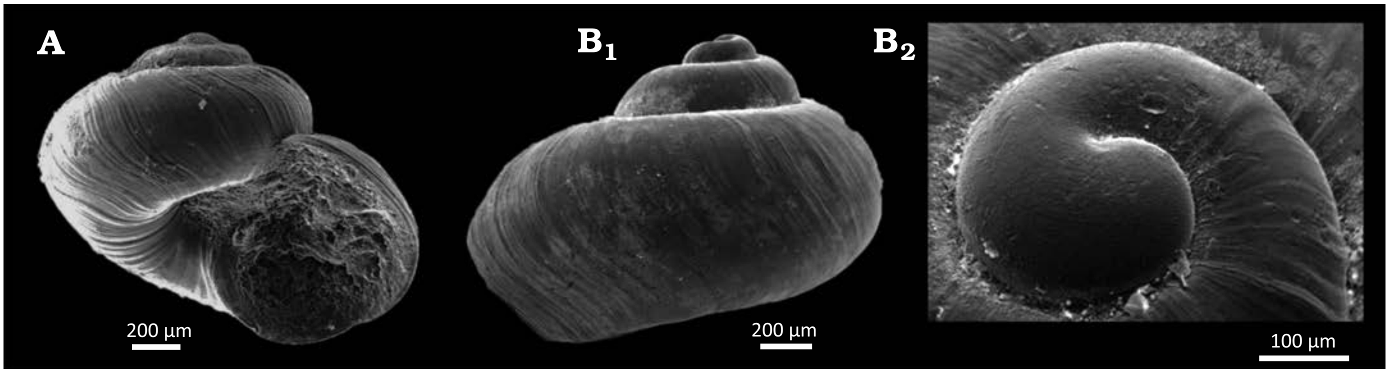

Fig. 7. Seguenzioid gastropod Seguenzioidea gen. et sp. indet. from Upper Pleistocene seep deposits from core NGHP-01-12A, Krishna-Godavari Basin, offshore eastern India. **A**. SMF373111, lateral view. **B**. Shell lost in processing, lateral view (B_1), detail of protoconch (B_2).

depth range; four species were associated with hydrothermal vents on the Central Indian Ridge and the SE Indian Ridge. The combination of strong ribs and spirals on the shoulder, weak spirals on the lower whorl and very wide selenizone in the specimens here is different from all known species in the Indian Ocean. The strong sculpture on the shoulder is common in anatomids, but this is commonly combined with ribs and occasionally spirals at the base. The lack of basal ribs is unique. For example, *Anatoma paucisculpta* Hoffman et al., 2022, has a weak basal rib and spiral sculpture but lacks the rib sculpture on the shoulder (Hoffman et al. 2022: 155–156, fig. 11). *Anatoma sagamiana* (Okutani, 1964) from the Western Pacific has a similar outline and wide selenizone with thin margins like *Anatoma sahlingi* Hoffman & Little sp. nov., but it has a weak reticulated sculpture above and below the selenizone and its umbilicus is closed (Geiger 2012: 1075–1081, figs. 875–880); *Anatoma sahlingi* Hoffman & Little sp. nov. has a stronger sculpture on the shoulder and a weak spiral sculpture below, and its umbilicus is open. The similar *Anatoma soyoae* (Habe, 1951) is found off NW Honshu, Japan. It has a similar wide selenizone with thin margins and its umbilicus is open, but its upper sculpture is finer and the outline is more compressed (Geiger 2012: 1095–1097, figs. 895–896).

Stratigraphic and geographic range.—Type locality and horizon only.

Superfamily Seguenzioidea Verrill, 1884

Seguenzioidea gen. et sp. indet.

Fig. 7.

Material.—Two shells, SMF373111 and one lost in processing. Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335’ N, 81°50.2274’ E, 1046 m water depth, 16.18–16.38 mbsf level, core NGHP-01-12A; Upper Pleistocene.

Description.—Small shell with broad spire, umbilicate. Protoconch paucispiral, three quarters whorl, small nucleus, sculpture with weak tiny dimples, terminal smooth straight rim, diameter about 300 µm. Teleoconch with two convex whorls with slightly cyrtoconoid outline, sculpture with numerous flexuous growth lines, suture deep, umbilicus filled but probably wide and deep. Aperture broad piriform, outer lip thin, prosocline, columellar lip sharp.

Remarks.—Specific characters are the flexuous growth lines and prosocline lip. The general outline and protoconch are clearly skeneimorph, but the small number of collected specimens precludes us identifying them at a lower taxonomic level. The shells are very similar to *Akritogyra curvilineata* Warén, 1992, from the NE Atlantic. This genus has not yet been assigned to a family in the Seguenzioidea.

Family Skeneidae Clark, 1851

Genus *Cirsonella* Angas, 1877

Type species: *Cirsonella australis* Angas, 1877, junior synonym of *Cirsonella weldii* (Tenison Woods, 1877), by monotypy; Recent, New South Wales, Australia.

Cirsonella aperta Hoffman & Little sp. nov.

Fig. 8.

Zoobank LCID: LSIDurn:lsid:zoobank.org:act:60068CBB-196B-4C4E-82E5-8F4CD3D84E52.

Etymology: With reference to the partly open umbilicus.

Type material: Holotype, shell, SMF373123. Paratypes, one shell, SMF 373118; one shell, SMF373119; one shell, SMF373120; one shell, SMF373121; two shells, SMF373122, from the type locality and horizon.

Type locality: Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335’ N, 81°50.2274’ E, 1046 m water depth.

Type horizon: 16.18–16.88 mbsf level, core NGHP-01-12A; Upper Pleistocene.

Material.—Type material and several specimens from core NGHP-01-12A (for details see Table 1).

Diagnosis.—Small shell with moderately raised spire, solid, smooth, narrow open umbilicus, umbilical chink with two broad spiral cords, suture shallow impressed.

Dimensions.—Holotype height 1.7 mm, length 2.0 mm. Shells in type set maximum height 2.1 mm, length 2.3 mm.

Description.—Protoconch single stage only, half whorl, flattened, smooth, curved sharp lip. Transition to disso-

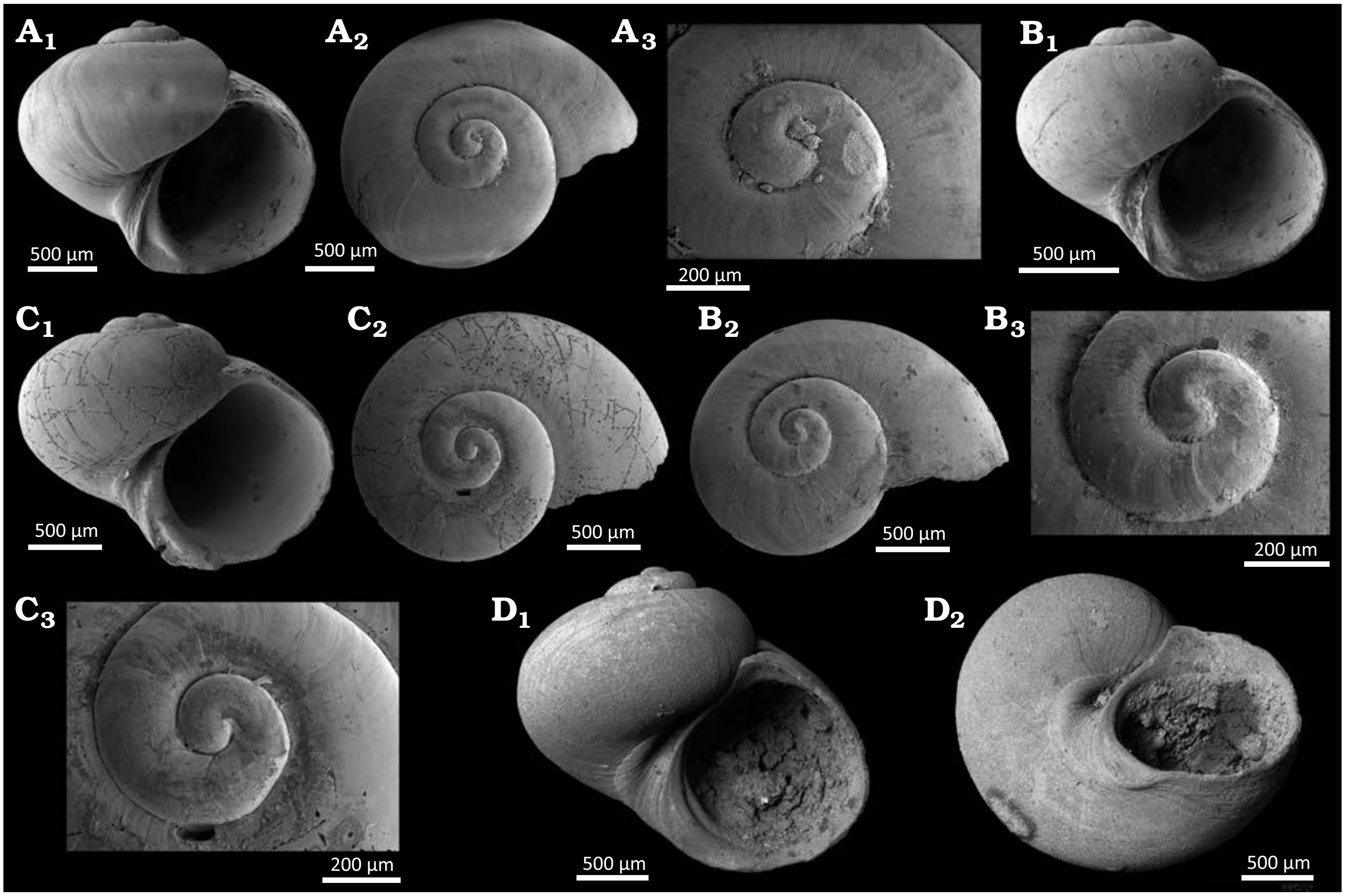

Fig. 8. The skeneid gastropod *Cirsonella aperta* Hoffman & Little sp. nov. from Upper Pleistocene seep deposits from core NGHP-01-12A, Krishna-Godavari Basin, offshore eastern India. **A**. SMF373123, holotype, lateral (A_1) and apical (A_2) views, detail of protoconch (A_3). **B**. SMF373119, paratype, lateral (B_1) and apical (B_2) views, detail of protoconch (B_3). **C**. SMF373120, paratype, lateral (C_1) and apical (C_2) views, detail of protoconch (C_3). **D**. SMF373121, paratype, lateral (D_1) and apical (D_2) views.

conch clear by labial margin. Length 330 µm. Teleoconch raised with flat apex, two convex whorls. Smooth, slightly flexuous growth lines. Umbilical area demarcated with rim, few axial, curved ridges with variable strength fill area to columella, narrow open umbilical slit. Aperture subcircular, internally smooth with (operculum?) edge near external margin, external lip blunt.

Remarks.—We place the species in *Cirsonella* (Skeneidae) on the basis of the morphology of the protoconch, teleoconch and the partly closed umbilicus. Alternatively, it could be placed in the genus *Skenea* Fleming, 1825. Species in *Cirsonella* are widely distributed, e.g., the Northern Atlantic, the SW Pacific (off Australia and New Zealand), South Africa and the Kerguelen Islands (MolluscaBase 2024). This is the first species from the Northern Indian Ocean. An open umbilicus is typical in young specimens and a narrow umbilical slit is common in for example the NE Atlantic *Cirsonella ateles* (Dautzenberg & Fischer, 1896) and *Cirsonella gaudryi* (Dautzenberg & Fischer, 1896) (Hoffman et al. 2020: 55–59, figs. 48–49). Known species show a well-defined chink in the umbilical area; the open umbilicus is often covered by smooth columellar callus in adult specimens. The umbilical grooves and ridges distinguish *Cirsonella aperta* Hoffman & Little sp. nov. from other described species.

Stratigraphic and geographic range.—Type locality and horizon only.

Genus *Dikoleps* Høisaeter, 1968

Type species: *Margarita pusilla* Jeffreys, 1847, junior synonym of *Dikoleps nitens* (Philippi, 1844), by original designation; Recent, NE Atlantic.

Dikoleps? *magnarota* Hoffman & Little sp. nov.

Fig. 9.

Zoobank LCID: urn:lsid:zoobank.org:act:2B99F77B-E09E-4802-8D26-DDE333A81C5F.

Etymology: From the resemblance of the species to a big wheel, *magna rota* in Latin.

Type material: Holotype, SMF376542, well preserved shell with protoconch. Paratypes, two shells, SMF 376541; one shell, SMF376543; one shell, SMF376544, from the type locality and horizon.

Type locality: Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335’ N, 81°50.2274’ E, 1046 m water depth.

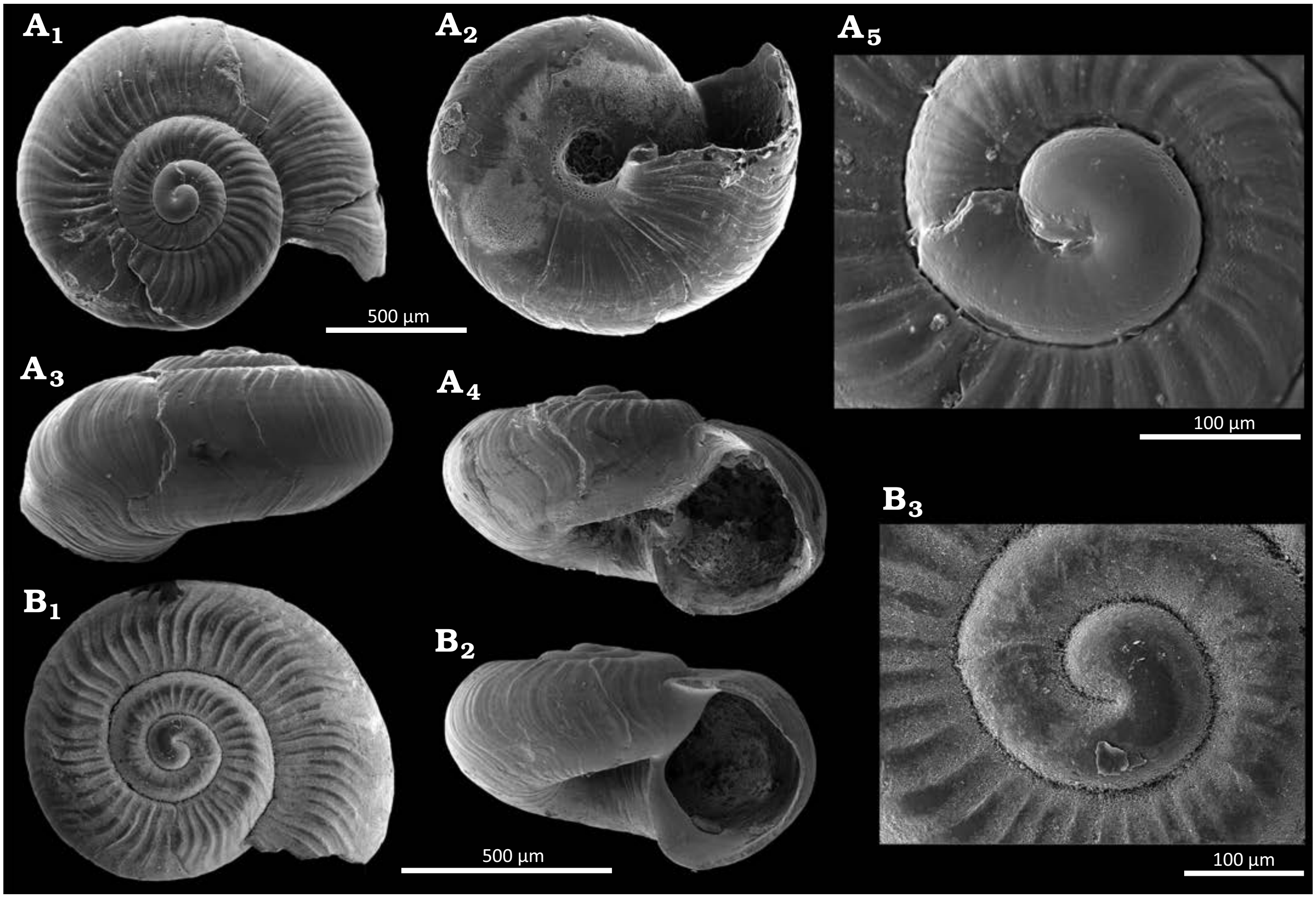

Fig. 9. The skeneid gastropod *Dikoleps*? *magnarota* Hoffman & Little sp. nov. from Upper Pleistocene seep deposits from core NGHP-01-12A, Krishna-Godavari Basin, offshore eastern India. **A**. SMF376542, holotype, apical (A_1), adapical (A_2), and lateral (A_3, A_4) views, detail of protoconch (A_5). **B**. SMF376543, paratype, apical (B_1) and lateral (B_2) views, detail of protoconch (B_3).

Type horizon: 16.18–16.48 mbsf level, core NGHP-01-12A; Upper Pleistocene.

Material.—Type material and several specimens from core NGHP-01-12A (for details see Table 1).

Diagnosis.—Very small shell with flattened spire, fragile, sculpture with broadly undulating ribs on shoulder, suture narrow and deep.

Dimensions.—Holotype height 0.8 mm, length 1.3 mm. Maximum dimensions of shells in type set as in holotype.

Description.—Protoconch single stage only, three quarters flattened smooth whorl, curved broken lip. Transition to protoconch clear by change in sculpture. Length 220 μm Teleoconch slightly raised, two and a half rounded whorls. Sculpture smooth with fine growth lines and flexuous undulations on shoulder, undulations disappearing near periphery; base smooth with fine flexuous growth lines. Umbilicus open, deep. Aperture well rounded convex, flexuous, sharp external and columellar lip; parietal side concave; callus very thin.

Remarks.—We are somewhat uncertain about the generic assignment of the species, but place it in the genus *Dikoleps* (Skeneidae) on the basis of the morphology of the protoconch, teleoconch and the flexuous base of the lip and the growth lines. Currently, nine *Dikoleps* species are known; eight species in the NE Atlantic and Mediterranean Sea, mostly living subtidally down to an upper bathyal depth range, and one species is known from South Africa (MolluscaBase 2024). This is the first species from the northern Indian Ocean.

Stratigraphic and geographic range.—Type locality and horizon only.

Subclass Caenogastropoda Cox, 1960

Family Rissoidae Gray, 1847

Genus *Alvania* Risso, 1826

Type species: *Alvania europea* Risso, 1826, junior synonym of *Alvania cimex* (Linnaeus, 1758), by subsequent designation; Recent, NE Atlantic.

Alvania axistriata Hoffman & Little sp. nov.

Fig. 10.

Zoobank LCID: urn:lsid:zoobank.org:act:63375D11-3BF0-4D60- B958-B7D3A0901AC5.

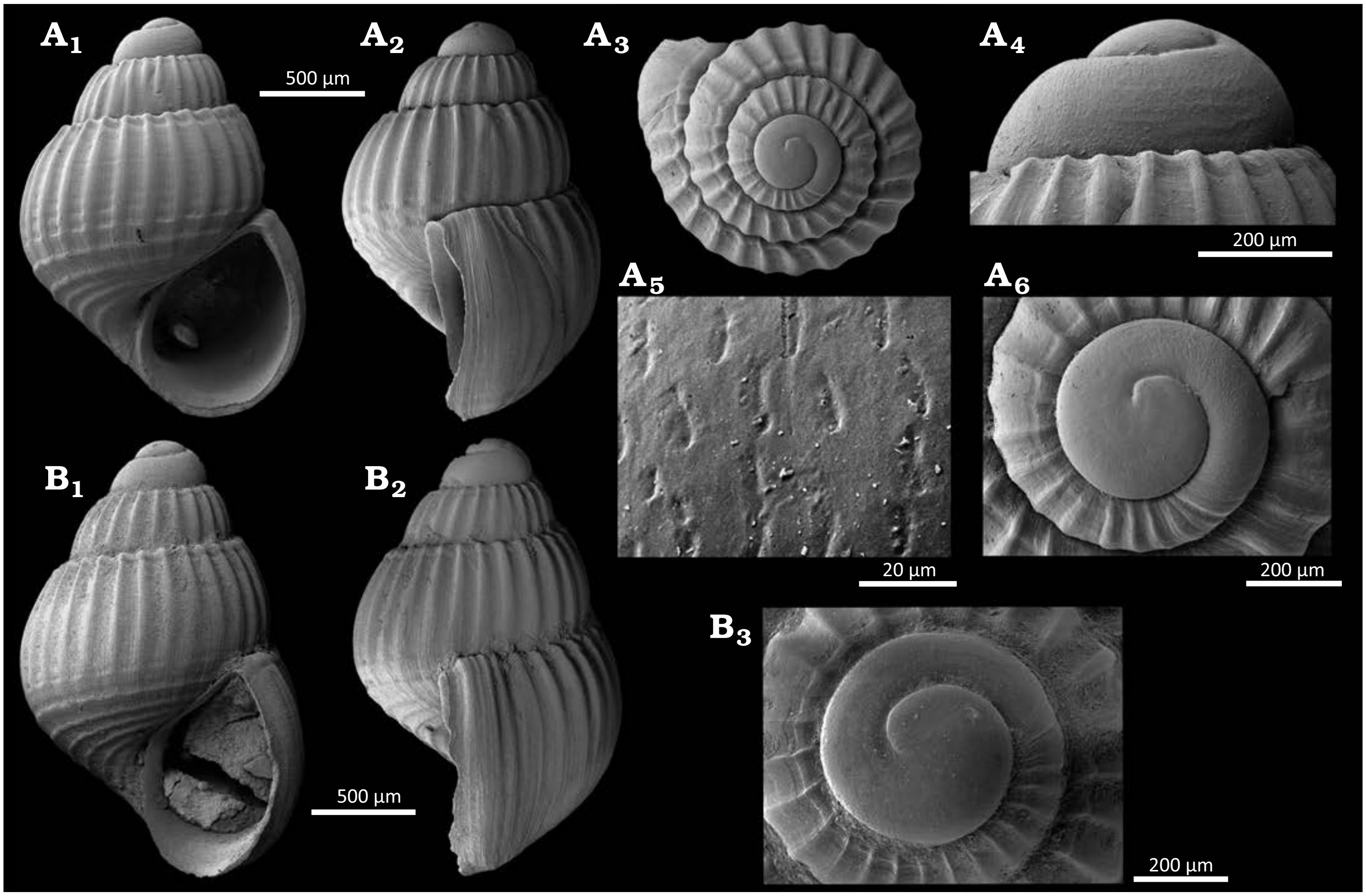

Fig. 10. The rissoid gastropod *Alvania axistriata* Hoffman & Little sp. nov. from Upper Pleistocene seep deposits from core NGHP-01-12A, Krishna-Godavari Basin, offshore eastern India. **A**. SMF373064, paratype, lateral (A_1, A_2) and apical (A_3) views, detail of protoconch, lateral view (A_4), detail of protoconch microsculpture (A_5), detail of protoconch, apical view (A_6). **B**. SMF373067, holotype, lateral view (B_1, B_2), detail of protoconch, apical view (B_3).

Etymology: After the axial ribs that are aligned with the spire axis.

Type material: Holotype, SMF373067, well preserved shell with protoconch.. Paratypes, three shells, SMF 373063; five shells, SMF373065; two shells, SMF373068; one shell, SMF373064; six shells, SMF373066, from the type locality and horizon.

Type locality: Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335' N, 81°50.2274' E, 1046 m water depth.

Type horizon: 16.18–16.88 mbsf level, core NGHP-01-12A; Upper Pleistocene.

Material.—Type material and several specimens from core NGHP-01-12A (for details see Table 1).

Diagnosis.—Small shell with raised rounded outline with pointed apex, fragile, broad ribs and weaker broad spiral cords on shell face, suture deeply impressed.

Dimensions.—Holotype height 2.2 mm, length 1.4 mm. Maximum dimensions of shells in type set as in holotype.

Description.—Protoconch single stage only; raised, slightly over one whorl; embryonic shell smooth; last half whorl with shallow vertical line segments, somewhat spirally aligned, length 10–20 µm, width 2 µm; thin sharp margin. Transition to protoconch clear by change in sculpture. Maximum diameter 470 µm. Teleoconch conical, apical angle 50–60°, two and half convex whorls. Sculpture wide axial ribs, interspaces of comparable width, about 30 ribs on each whorl; fine spiral threads overrunning the ribs; one broad spiral channel high on the shoulder. Base whorl with 6–7 strong spiral cords, fading near periphery. Thickened rim near lip. Aperture orthocline, pyriform, bevelled external lip, thick callus, peristome complete.

Remarks.—We place the specimens in the genus *Alvania* on the basis of the combination of morphological features, for example size, outline, aperture, sculpture and protoconch. The genus is cosmopolitan, but most diverse in the NE Atlantic and Mediterranean Sea. *Alvania stigmata* Frauenfeld, 1867, is a similar species described from the Nicobar Islands. However, that species has 16–18 vertical ribs and 3–4 basal cords and a few subsutural lines; our species has 30 ribs, 6–7 basal cords and one subsutural channel (Frauenfeld 1867: 12). The Indian Ocean *Alvania versoverana* (Melvill, 1893) has a similar outline and size, but its axial ribs are curved and the spiral cords cover the full shell face (Mellvill 1893: 61, pl. 1: 15). *Alvania mahimensis* (Melvill, 1893) has a similar outline and size, but its suprasutural sculpture has 3–4 rows of broad nodules (Mellvill 1893: 61, pl. 1: 17). The NE Atlantic *Alvania electa*

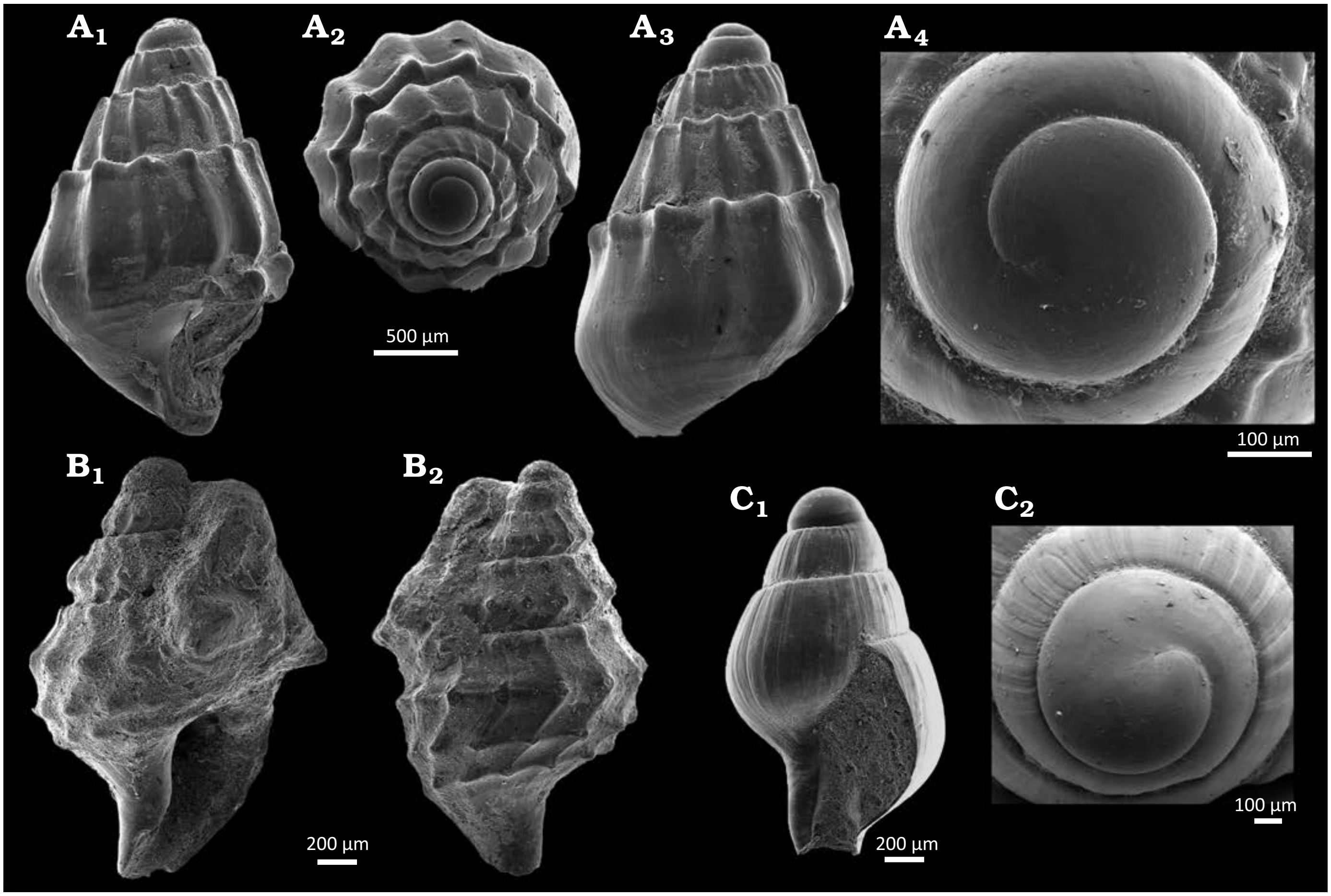

Fig. 11. Gastropods from Upper Pleistocene seep deposits from core NGHP-01-12A, Krishna-Godavari Basin, offshore eastern India. **A**. Rissoid *Benthonellania* sp., SMF373110, lateral (A_1, A_3) and apical (A_2) views, detail of protoconch (A_4). **B**. Conoidea gen. et sp. indet., SMF373107, lateral view (B_1, B_2). **C**. Columbellidae gen. et sp. indet., SMF373108, lateral view (C_1), detail of protoconch (C_2).

(Monterosato, 1874) is very similar to our species, but has a strong spiral sculpture on the shell face and it lacks the spiral channel on the shoulder (Bouchet and Warén 1993: 633–634, figs. 1410–1420). *Alvania porcupinae* Gofas & Warén, 1982, is also very similar but has a larger protoconch with two whorls (Bouchet and Warén 1993: 636–638, figs. 1379, 1421–1429).

Stratigraphic and geographic range.—Type locality and horizon only.

Genus *Benthonellania* Lozouet, 1990

Type species: *Benthonellania gofasi* Lozouet, 1990, by original designation; Recent, NE Atlantic.

Benthonellania sp.

Fig. 11A.

Material.—One shell, SMF373110. Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335’ N, 81°50.2274’ E, 1046 m water depth, 16.68 mbsf level, core NGHP-01-12A; Upper Pleistocene.

Description.—Elevated, conical, strong rissoid shell. Protoconch paucispiral with large nucleus, one and a quarter whorls, smooth, diameter about 350 µm. Teleoconch with three flattened whorls, sculpture with about 14 broadly undulating axial ribs with protruding pointed nodules on the shoulder, very fine growth lines, narrow undulating shoulder area, deeply impressed suture. Abapically pointed. Ultimate whorl shows fading axial ribs and few weak chords below periphery. Lip broken. Estimated height 2.5 mm.

Remarks.—The single shell is well preserved, apart from a broken lip. The shell is morphologically very similar to the East Atlantic type species. As several congeneric species are similar we refrain from a species determination based on only one specimen.

Order Neogastropoda Wenz, 1938

Superfamily Buccinoidea Rafinesque, 1815

Family Columbellidae Swainson, 1840

Columbellidae gen. et sp. indet.

Fig. 11C.

Material.—Two shells, SMF373108 and SMF373109, Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335’ N, 81°50.2274’ E, 1046 m water depth, 16.18–16.68 mbsf level, core NGHP-01-12A; Upper Pleistocene. For additional material see Table 1.

Description.—Elevated, small, smooth collumbellid shell with blunt apex. Protoconch paucispiral, one whorl with large nucleus, smooth, diameter about 600 µm. Teleoconch juvenile only, two whorls, smooth with very fine growth lines, impressed suture, very narrow shoulder. Outline straightened suprasutural whorl face, widely convex periphery, concave below, columellar area straightened. Aperture piriform with open straight siphonal channel, outer lip orthocline, thin.

Remarks.—All three shells are juveniles, so identification below family level is not possible.

Superfamily Conoidea Fleming, 1822

Conoidea gen. et sp. indet.

Fig. 11B.

Material.—One shell (SMF373107) from Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335’ N, 81°50.2274’ E, 1046 m water depth, 16.28 mbsf level, core NGHP-01-12A; Upper Pleistocene.

Description.—Elevated conical shell, raphitomiform, strongly sculptured with blunt apex. Protoconch paucispiral, about one whorl with large nucleus, smooth, diameter about 350 µm. Teleoconch juvenile only, three whorls with flexuous growth lines. Sculpture with three spiral cords, one shoulder cord, one at the suture and one below the suture, about 16 flexuous axial ribs with pointed nodules at crossings with cords. Aperture piriform.

Remarks.—The apex and part of the teleoconch is obscured, so the material is inadequate for a determination or a complete description. However, it is possible the shells belongs to the genus *Taranis* Jeffreys, 1870 (Raphitomidae Bellardi, 1875).

Subclass Heterobranchia Burmeister, 1837

Superfamily Pyramidelloidea Gray, 1840

Family Pyramidellidae Gray, 1840

Genus *Eulimella* Forbes & M’Andrew, 1846

Type species: *Eulima macandrei* Forbes, 1844; original designation, junior synonym of *Eulimella scillae* (Scacchi, 1835); Recent, NE Atlantic.

Eulimella sp. 1

Fig. 12A.

Material.—One shell (SMF373103) from Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335’ N, 81°50.2274’ E, 1046 m wa-

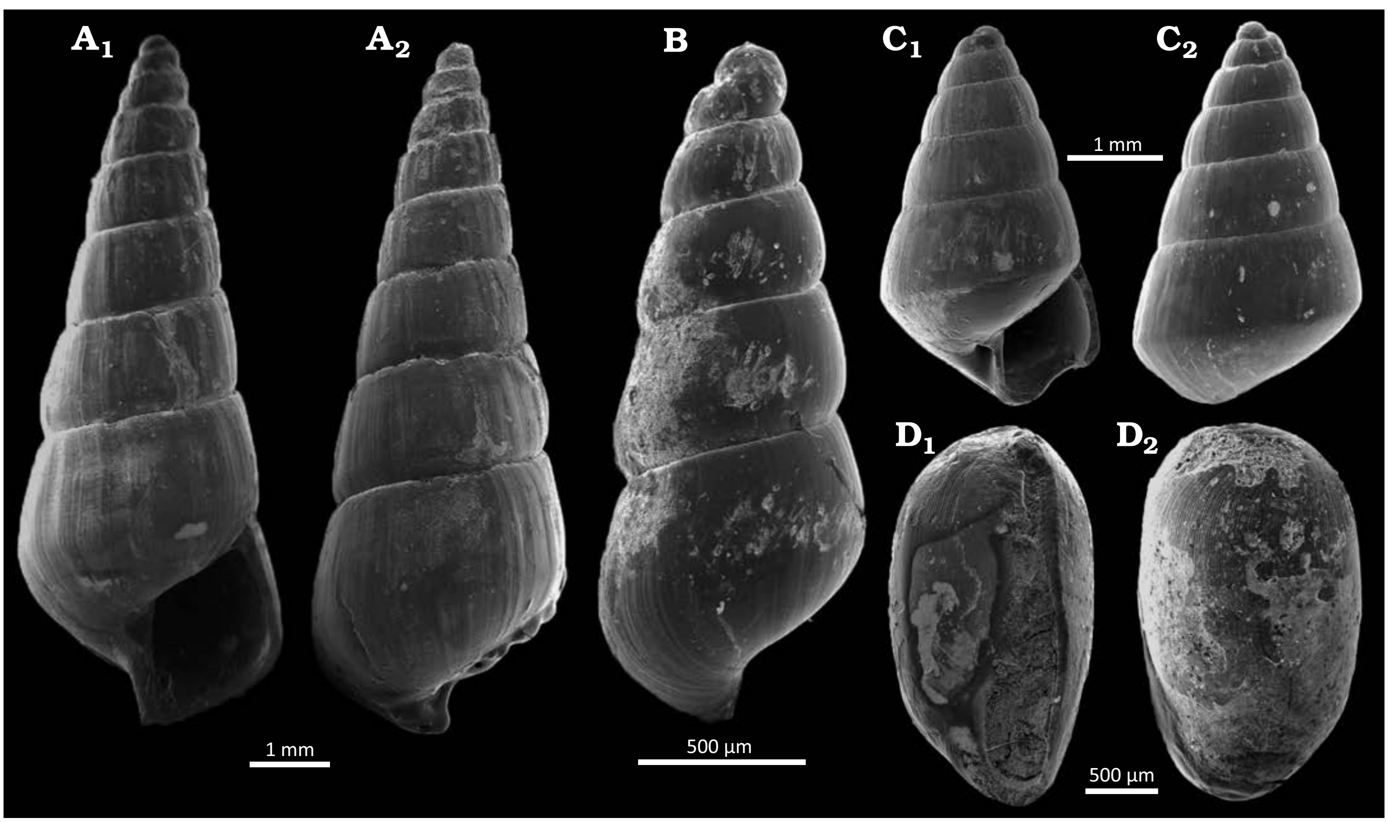

Fig. 12. Heterobranch gastropods from Upper Pleistocene seep deposits from core NGHP-01-12A, Krishna-Godavari Basin, offshore eastern India. **A**. SMF373103, *Eulimella* sp. 1, lateral view (A_1, A_2). **B**. SMF373104, *Eulimella* sp. 2, lateral view. **C**. SMF373105, *Odostomia* sp., lateral view (C_1, C_2). **D**. SMF373106 Cylichnidae? gen. et sp. indet, lateral view (D_1, D_2). H, height.

ter depth, 16.68 mbsf level, core NGHP-01-12A; Upper Pleistocene.

Description.—Highly elevated shell, eullimelliform, smooth with fine apex. Protoconch sinistral, axis rotated about 120° from spire axis, one whorl, smooth, diameter about 300 µm. Teleoconch dextral, smooth, with fine orthocline growth lines, seven whorls, slightly convex above deeply impressed suture, ultimate whorl below suture with straightened columella. Aperture trapezoidal.

Remarks.—Placement in *Eulimella* is based on the smooth elevated shell and the rotated heterotrophic protoconch. However, the single shell is considered as inadequate for a description.

Eulimella sp. 2

Fig. 12B.

Material.—One shell (SMF373104) from Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335' N, 81°50.2274' E, 1046 m water depth, 16.38 mbsf level, core NGHP-01-12A; Upper Pleistocene.

Description.—Highly elevated shell, eullimelliform, smooth, with large apex. Protoconch sinistral, axis rotated about 100° from spire axis, one whorl, smooth, diameter about 300 µm. Teleoconch smooth with fine orthocline growth lines, four and half whorls, maximum convexity at periphery, deeply impressed suture, ultimate whorl below suture with straightened columella. Aperture trapezoidal.

Remarks.—Placement in *Eulimella* is based on the smooth elevated shell and the rotated heterotrophic protoconch. However, the single shell is considered as inadequate for a description.

Genus *Odostomia* Fleming, 1813

Type species: *Turbo plicatus* Montagu, 1803, accepted as *Odostomia plicata* (Montagu, 1803), type by subsequent designation.

Odostomia sp.

Fig. 12C.

Material.—One shell (SMF373105) from Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335' N, 81°50.2274' E, 1046 m water depth, 16.38 mbsf level, core NGHP-01-12A; Upper Pleistocene.

Description.—Highly elevated shell, eullimellid shape, smooth with large apex. Protoconch sinistral, axis rotated about 100 degrees from spire axis, one whorl, smooth, diameter about 300 µm. Teleoconch smooth with fine orthocline growth lines, four and half whorls, maximum convexity at periphery, deeply impressed suture, ultimate whorl below suture straightened columella. Aperture trapezoidal.

Remarks.—Placement in *Odostomia* is based on the protoconch and on the smooth conical shell with flattened whorls. The single shell is too poorly preserved for a more detailed description.

Order Cephalaspidea Fischer, 1883
Superfamily Cylichnoidea Adams & Adams, 1854
Family Cylichnidae Adams & Adams, 1854
Cylichnidae? gen. et sp. indet.

Fig. 12D.

Material.—One shell (SMF373106) from Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335' N, 81°50.2274' E, 1046 m water depth, 16.88 mbsf level, core NGHP-01-12A; Upper Pleistocene.

Description.—Small elongated, convolved shell, cylichnid shape. Protoconch not seen, intorted. Teleoconch, ultimate whorl only, smooth with fine curved growth lines. Outline ovate, slightly angular, maximum convexity apically, periphery weakly convex. Aperture elongated ovate, widening abapically, narrow adapically.

Remarks.—The single shell is poorly preserved for a detailed description and consequently the family-level placement is uncertain.

Class Bivalvia Linnaeus, 1758
Subclass Protobranchia Pelseneer, 1889
Order Solemyida Dall, 1889b
Family Solemyidae Gray, 1840
Genus *Acharax* Dall, 1908a

Type species: *Solemya johnsoni* Dall, 1891, by original designation; Recent, Baja California.

Acharax sp.

Fig. 13A.

Material.—One shell (SMF373102) from Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India; 15°51.8647' N, 81°50.0709' E, 1050 m water depth, 15.54 mbsf level, core NGHP-01-10D; Upper Pleistocene. For additional material see Table 1.

Description.—Large elongated, oblong, thick solemyid shell. Prodissoconch inconspicuous. Dissoconch flattened, oblong with coarse irregular growth lines, irregular radial lines from umbo towards antero-ventral margin. Outline blunt marginally protruding umbo, straight antero-dorsal margin, postero-dorsal marging slightly concave. Anterior and posterior ends most convex, ventral margin weakly convex. External ligament groove present. Maximum length of fragmented shell 34 mm.

Remarks.—Our material is too poorly preserved to conclusively compare with a described species or describe it as new. It is placed in *Acharax* because of presence of an external ligament pit, but no sign of any internal ligament scars.

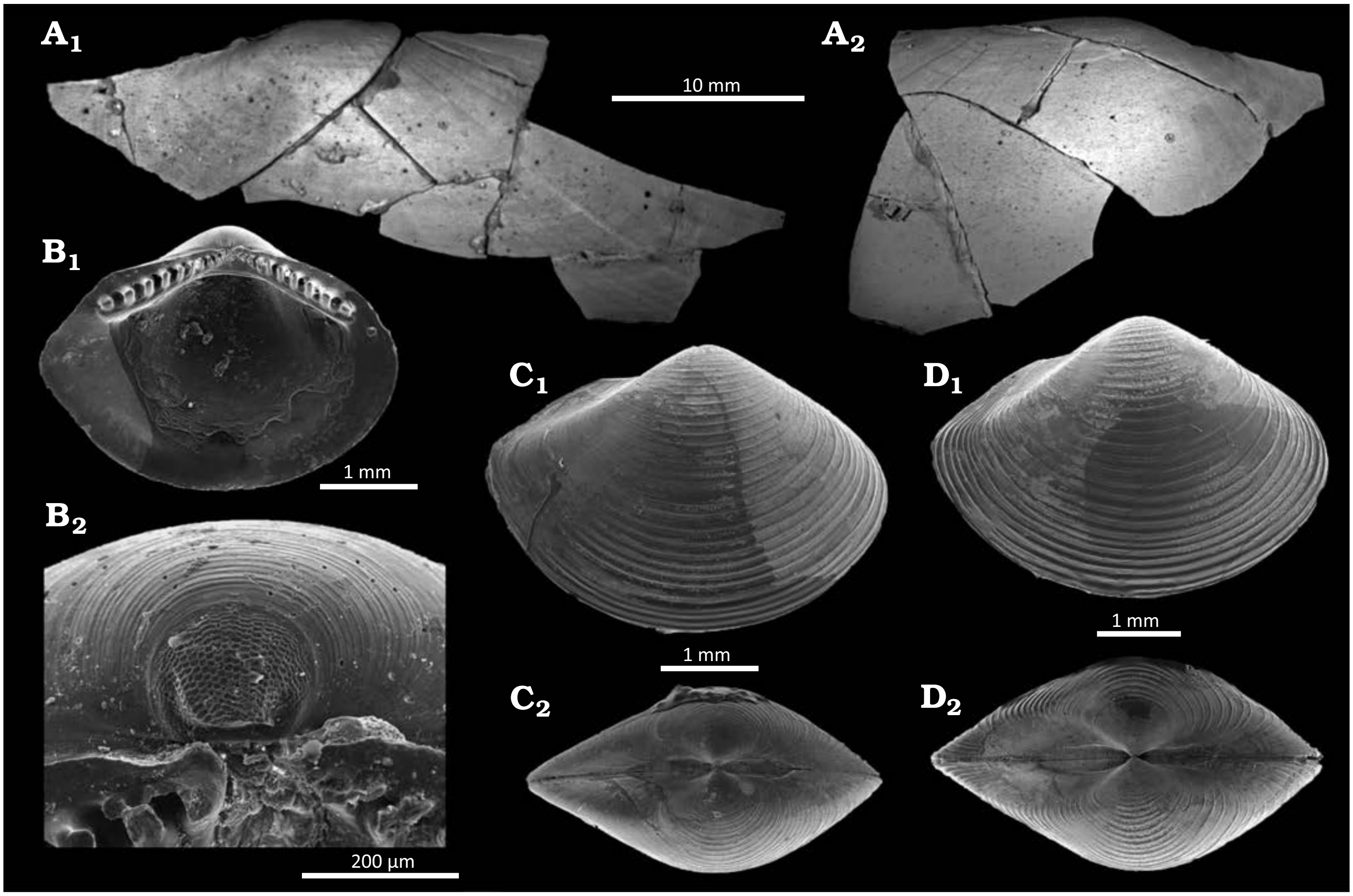

Fig. 13. Solemyid and nuculanid bivalves from Upper Pleistocene seep deposits from cores NGHP-01-12A and NGHP-01-10D, Krishna-Godavari Basin, offshore eastern India. **A**. *Acharax* sp. SMF373102, external views of partial right (A_1) and left (A_2) valves. **B**–**D**. *Ledella favus* Hoffman & Little sp. nov. **B**. SMF373071, paratype 2, internal view of left valve (B_1), and detail of prodissoconch (B_2). **C**. SMF373070, paratype 1, external view of right valve (C_1), and dorsal view (C_2). **D**. SMF373069, holotype, external view of right valve (D_1), and dorsal view (D_2).

Order Nuculanida Carter et al., 2000

Superfamily Nuculanoidea Adams & Adams, 1858 (1854)

Family Nuculanidae Adams & Adams, 1858 (1854)

Genus *Ledella* Verrill & Bush, 1897

Type species: *Ledella bushae* Warén, 1978, junior synonym of *Ledella ultima* (Smith, 1885), by subsequent designation; Recent, Atlantic.

Ledella favus Hoffman & Little sp. nov.

Fig. 13B–D.

Zoobank LCID: urn:lsid:zoobank.org:act:C0663527-E813-4D74-B94B-B85AAE34D9F6.

Etymology: After the honeycomb (*favus* in Latin) sculpture on the prodissoconch.

Type material: Holotype, one shell, SMF373069. Paratypes, one valve, SMF373071; one shell, SMF373070, from the type locality and horizon.

Type locality: Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335’ N, 81°50.2274’ E, 1046 m water depth.

Type horizon: 16.28–16.88 mbsf level, core NGHP-01-12A; Upper Pleistocene.

Material.—Type material and several specimens from core NGHP-01-12A (for details see Table 1).

Diagnosis.—Solid shell, oval outline, posteriorly truncated obliquely: strong co-marginal growth margins; length up to 6 mm. Internally smooth, broad hinge plates and heavy dentation.

Dimensions.—Holotype height 4.2 mm, length 5.8 mm, tumidity 3.2 mm. Maximum dimensions of shells in type set as in holotype.

Description.—Prodissoconch single stage evident only, oblong, truncated dorsally, flattened, raised ridge on dorsal side with pointed end; sculpture with central hexagonal network (honeycomb-like), smooth at margins. Transition to dissoconch clear by change in sculpture. Length 200 µm. Dissoconch with straightened dorsal outline posteriorly; ventral and anterior margins convex; posterior with obliquely truncated cusp at end of ridge; shell moderately inflated. Lunule and escutcheon long and lanceolate, escutcheon somewhat inconspicuous, both with fine growth lines. Margins sharp and smooth. Sculpture with regular co-marginal growth stages, width growth lines equal to inter-spaces. Internal surface and margin smooth; muscle scars and pallial line inconspicuous. Pallial line without sinus. Hinge only known from right valve; wide hinge plates at 120°; nine sharp teeth on either side (in right valve with length 4 mm), rectangular in cross-section, central teeth in either row most pronounced. Triangular resilifer placed centrally below umbo.

Remarks.—Placement in *Ledella* is based on the truncated-oval outline with a cusp, the solid shell, the wide hinge plates each with few teeth and the clear resilifer. The bathyal *Ledella procumbens* (Prashad, 1932) is known from the Bay of Bengal in 450–1820 m (Huber 2010). This species has a long pointed rostrum, unlike our specimens (Prashad 1932: 20, pl. 1: 21–22). The cosmopolitan type species *Ledella ultima* (Smith, 1885) has a more globose shell, convex dorsal outline posteriorly, and has thickened (box-shaped) margins when adult (Knudsen 1970). Tan (2021) reported a similarly shaped species, *Nuculana* cf. *corbuloides* (Smith, 1885), from deep water off Java but this species has a more pointed rostrum and coarser co-marginal ribs. The prodissoconch sculpture on *Ledella favus* Hoffman & Little sp. nov. resembles that of other modern and fossil nuculanids, for example *Nuculana grasslei* Allen, 1993 (Allen 1993: figs. 2, 3; Kiel 2006).

Stratigraphic and geographic range.—Type locality and horizon only.

Family Yoldiidae Dall, 1908b

Genus *Yoldiella* Verrill & Bush, 1897

Type species: *Yoldia lucida* Lovén, 1846, by original designation; Recent, NE Atlantic.

Yoldiella umbostriata Hoffman & Little sp. nov.

Fig. 14.

Zoobank LCID: urn:lsid:zoobank.org:act:40B9B90E-1FB5-42F7-811D-4EFEAB577ED6.

Etymology: After the striated sculpture on the prodissoconch.

Type material: Holotype, one shell, SMF373114. Paratypes, six shells, SMF373113; one shell, SMF373116; one valve, SMF373117; two shells, SMF373115, from the type locality and horizon.

Type locality: Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335’ N, 81°50.2274’ E, 1046 m water depth.

Type horizon: 16.18–16.88 mbsf level, core NGHP-01-12A; Upper Pleistocene.

Material.—Type material and several specimens from core NGHP-01-12A (for details see Table 1).

Diagnosis.—Small protobranch, solid, equivalve, inequilateral shell oblong outline, beaks anteriorly, smooth. Sculpture prodissoconch with parallel lines.

Dimensions.—Holotype height 1.6 mm, length 2.5 mm, tumidity 1.0 mm. Maximum dimensions of shells in type set height 2.2 mm, length 3.3 mm, tumidity 1.3 mm.

Description.—Prodissoconch single stage evident only, oblong, truncated dorsally, flattened; sculpture with central irregular fine ridges, aligned parallel, occasionally connected by thin ridge segments, smooth at margins. Transition to dissoconch clear by change in sculpture. Length 200 µm. Dissoconch with straightened dorsal outline posteriorly; ventral, posterior and anterior margins convex; anterior most convex; shell rather flattened. Lunule and escutcheon ab-

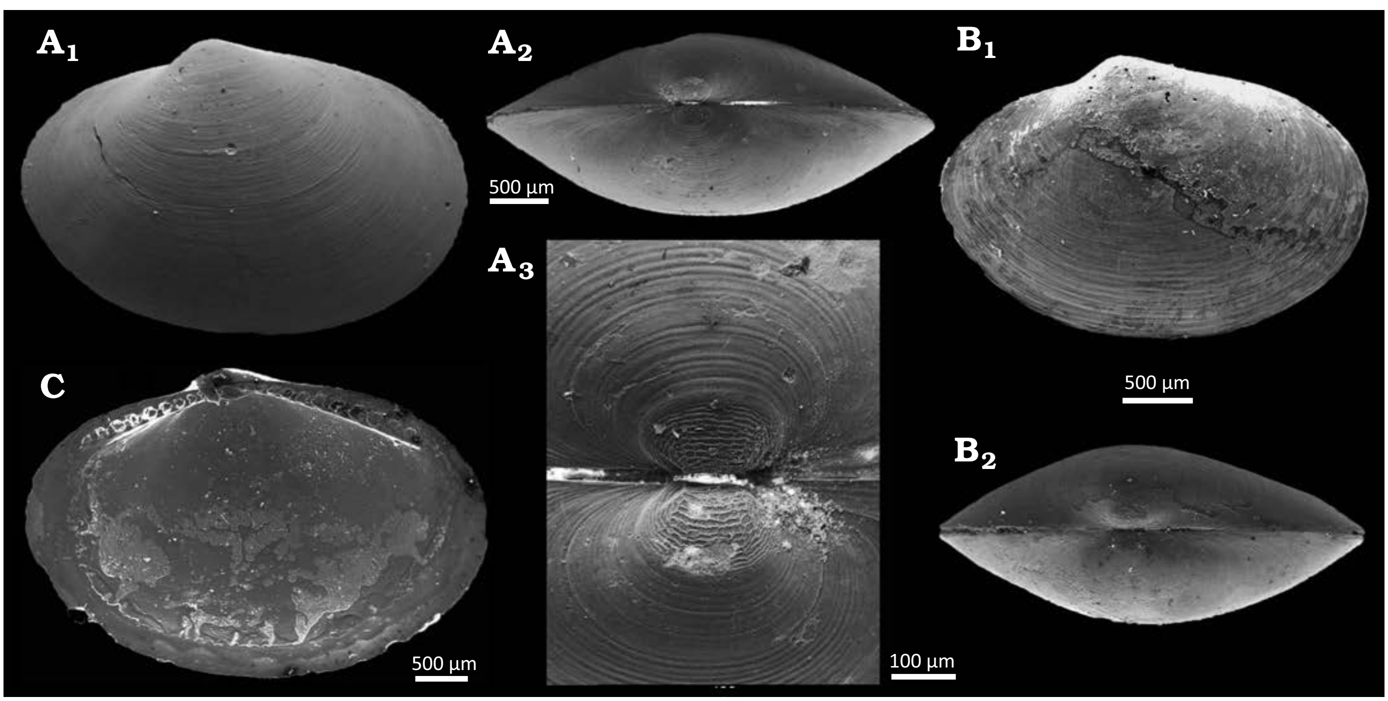

Fig. 14. The yoldiid bivalve *Yoldiella umbostriata* Hoffman & Little sp. nov. from Upper Pleistocene seep deposits from core NGHP-01-12A, Krishna-Godavari Basin, offshore eastern India. **A**. SMF373114, holotype, external view of right valve (A_1), dorsal view (A_2), detail of prodissoconch (A_3). **B**. SMF373116, paratype 1, external view of right valve (B_1), dorsal view (B_2). **C**. SMF373117, paratype 2, internal view of left valve.

sent. Sculpture irregularly spaced weak growth margins; some specimens nearly smooth. Margins sharp and smooth. Internal surface and margin smooth; muscle scars and pallial line inconspicuous. Hinge only known from right valve; wide hinge plates at 150°; posterior plate longer; nine anterior teeth, 13 posterior teeth (in right valve with length 3.3 mm), chevron-shaped in cross-section, central teeth in either row most pronounced. Triangular, oblique resilifer behind umbo.

Remarks.—*Yoldiella retusa* (Hinds, 1843) is known from the Northern Indian Ocean (Huber 2010) and is similar to *Yoldiella umbostriata* Hoffman & Little sp. nov. Hinds (1843: 99) reported the outline of this species as being nearly equilateral with a pointed anterior margin, and a length of 4.6 mm. Our shells are inequilateral with a more convex anterior and a maximum length of 3.3 mm.

Stratigraphic and geographic range.—Type locality and horizon only.

Infraclass Pteriomorphia Beurlen, 1944

Order Mytilida Férussac, 1822

Family Modiolidae Termier & Termier, 1950

Genus *Gigantidas* Cosel & Marshall, 2003

Type species: *Gigantidas gladius* Cosel & Marshall, 2003, by original designation; Recent, SW Pacific, off North Island, New Zealand, cold seeps and active hydrothermal vent sites.

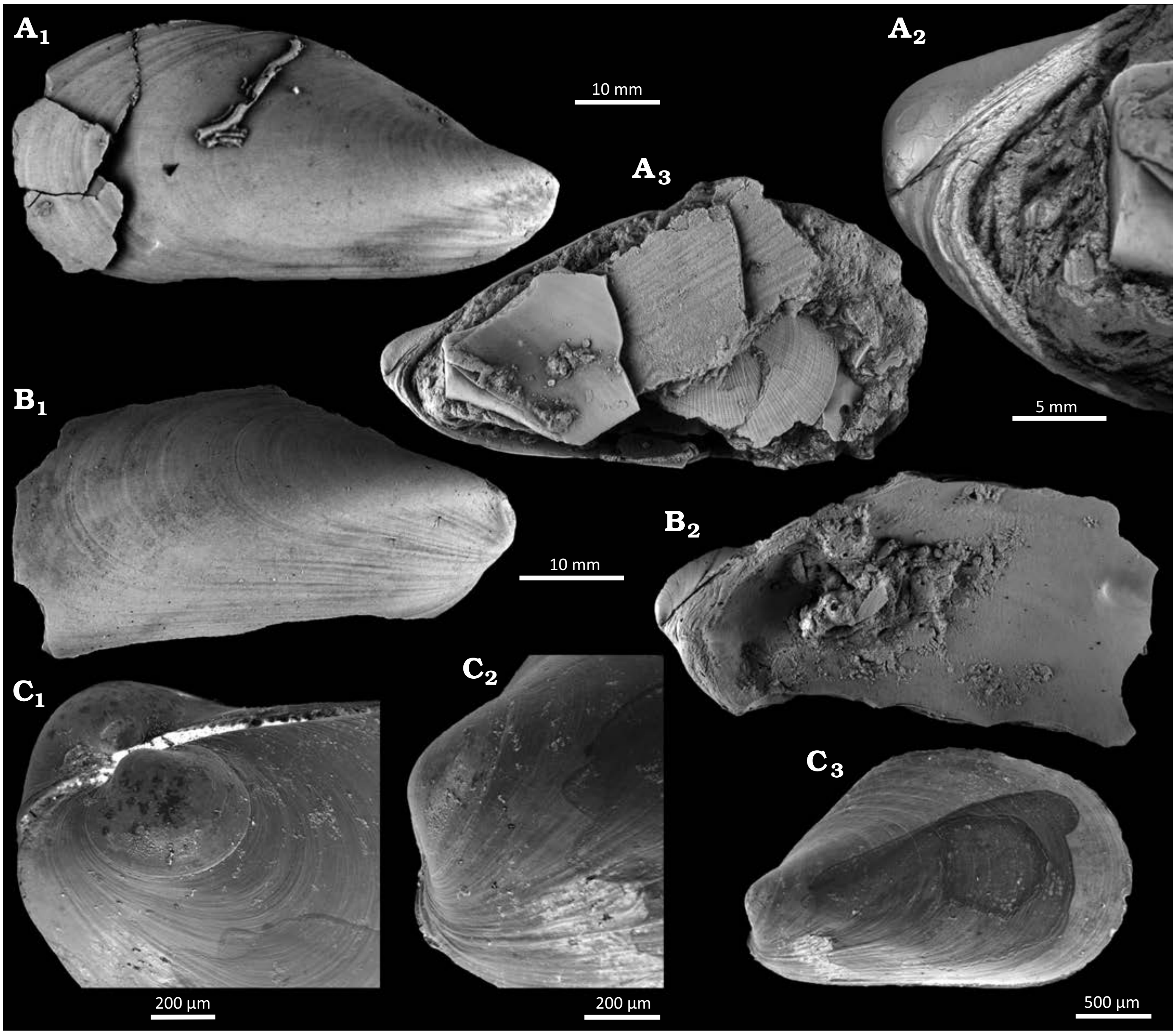

Fig. 15. The bathymodiolin bivalve *Gigantidas* cf. *platifrons* (Hashimoto & Okutani, 1994) from Upper Pleistocene seep deposits from core NGHP-01-12A, Krishna-Godavari Basin, offshore eastern India. **A**. SMF373094, right valve external view (A_1), internal umbonal detail (A_2), and internal view (A_3). **B**. SMF373100, right valve external (B_1) and external (B_2) views. **C**. SMF373099, articulated juvenile specimen, oblique dorsal view showing prodissoconchs (C_1), left valve detail of umbo (C_2), and left valve (C_3).

Gigantidas cf. *platifrons* (Hashimoto & Okutani, 1994)

Fig. 15.

Material.—One adult valve, SMF373100; one adult valve, SMF373094; one juvenile shell, SMF373099; one juvenile valve, SMF373096; two juvenile valves, SMF373098; one juvenile valve, SMF373101; one shell and three valves (all juveniles), SMF373097. Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335' N, 81°50.2274' E, 1046 m water depth, 16.18–16.78 mbsf level, core NGHP-01-12A; Upper Pleistocene. For additional material see Table 1. A single, small poorly preserved valve SMF373095 from 42.01 mbsf level, core NGHP-01-10D may belong to this species.

Description.—Large bathymodiolid shell, piriform. Prodissconch, ovate with straightened dorsal margin and inflated umbo, length 470 µm. Dissoconch piriform with slightly raised umbo near anterior end on dorsal margin. Posterodorsal margin concave near umbo, convex posteriorly, straight ventral margin, maximum convexity at anterior end. Sculpture fine irregular growth lines. Maximum length 52 mm.

Remarks.—Our species is close in shape to *Gigantidas platifrons* Hashimoto & Okutani, 1994, which was described from chemosynthetic environments off Japan. However, the umbones in the Japanese specimens are at the anterior end (Hashimoto and Okutani 1994), whereas our shells have umbones protruding above the anterior-dorsal end. *Gigantidas niobengalensis* Oliver et al., 2024, has been described from an active cold seep in the Krishna-Godavari Basin, depth 1750 m. This species has its umbo located anteriorly on the dorsal margin and has a convex anterior margin and a straightened posterior-dorsal margin (Oliver et al. 2024: holotype figs. 3A–C). Our species has a terminal umbo at the pointed anterior end and its posterior-dorsal margin is convex. For these reasons we think our fossil specimens do not belong to *Gigantidas niobengalensis*, although we note there is quite a lot of morphological variation in bathymodiolin species. The type species of *Gigantidas* has large narrowly elongated shells with protruding umbones on the dorsal margin (Cosel and Marshall 2003). Currently, the genus contains 11 species (MolluscaBase 2024) with a wide morphological variation; ranging from typical modioliform shape towards the elongated shape of the type species. The juvenile shell (Fig 13C_1) of the fossil *Gigantidas* cf. *platifrons* specimens has a typical modiolid outline and the large prodissoconch (length 470 µm) confiming a planktonic stage.

Order Pectinida Gray, 1854
Superfamily Pectinoidea Rafinesque, 1815
Family Propeamussiidae Abbott, 1954
Genus *Parvamussium* Sacco, 1897

Type species: *Pecten duodecimlamellatus* Bronn, 1831, by original designation; Cenozoic, Italy.

Parvamussium? aff. *scitulum* (Smith, 1885)

Fig. 16A, B.

Material.—One valve, SMF373093; one valve, SMF376540; one valve, SMF373094. Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335' N, 81°50.2274' E, 1046 m water depth, 16.18–16.28 mbsf level, core NGHP-01-12A; Upper Pleistocene. For additional material see Table 1.

Description.—Small fragile, thin, flat, pectiniform shell. Right valve flattened with regular commarginal growth lines and microscopic radial etchings; large anterior auricle with irregular growth lines and deep byssal notch; smaller posterior auricle. Left valve flattened smooth with irregular growth lines; large anterior auricle without byssal notch; smaller posterior auricle. Largest incomplete valve diameter 14 mm.

Remarks.—*Parvamussium scitulum* was reported from the South-West Indian Ocean (Dijkstra and Maestrati 2015) and the Red Sea (Dijkstra and Janssen 2013). Our species has a similar sculpture and outline but it is larger and margins of the auricles are aligned with anterior and posterior margins; the auricles of *Parvamussium scitulum* end at an angle to the

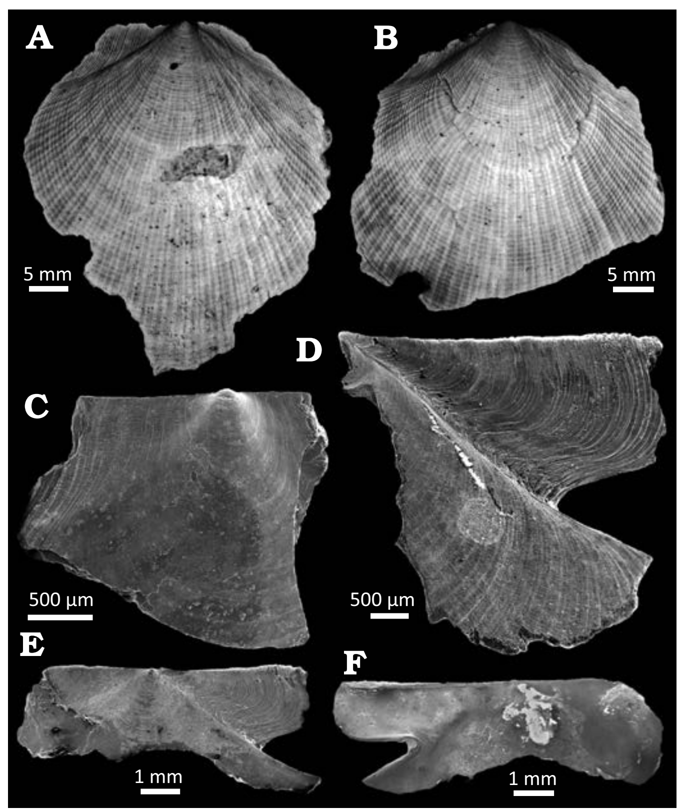

Fig. 16. Propeamussiid bivalves from core NGHP-01-12A, Krishna-Godavari Basin, offshore eastern India. **A**, **B**. *Parvamussium*? aff. *scitulum* (Smith, 1885). **A**. SMF373093, left valve external view. **B**. SMF376540, left valve external view. **C**–**F**. Propeamussiidae? gen. et sp. indet. **C**. SMF373091, left valve external view. **D**. SMF373092, partial right valve external view. **E**. SMF373089, partial right valve, external view. **F**. SMF373090, partial right valve, internal view.

dorsal margins. We refrain from describing a new species on the basis of our fragmentary material.

Propeamussiidae? gen. et sp. indet.

Fig. 16C–F.

Material.—One valve, SMF373091; one valve, SMF373092; one valve, SMF373089; one valve, SMF373090. Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335' N, 81°50.2274' E, 1046 m water depth, 16.18–16.48 mbsf level, core NGHP-01-12A; Upper Pleistocene. For additional material see Table 1.

Description.—Small fragile, thin, flat, pectiniform shell. Right valve flattened with regular commarginal growth lines and microscopic radial etchings; large anterior auricle with irregular growth lines and deep byssal notch; smaller posterior auricle. Left valve flattened smooth with irregular growth lines; large anterior auricle without byssal notch; smaller posterior auricle. Prodissoconch subcircular, convex, length 100 µm. Largest incomplete valve has a diameter of 3 mm.

Remarks.—Only fragments of smooth left and right valves were found. The placement in Propeamussiidae is speculative; an alternative placement in Pectinidae is feasible.

Infraclass Heteroconchia Gray, 1854

Order Lucinida Gray, 1854

Superfamily Thyasiroidea Dall, 1900 (1895)

Family Thyasiridae Dall, 1900 (1895)

Genus *Conchocele* Gabb, 1866

Type species: *Conchocele disjuncta* Gabb, 1866, junior synonym of *Conchocele bisecta* (Conrad, 1849), by monotypy; Miocene, Oregon, USA.

Conchocele sp.

Fig. 17A.

Material.—One valve, SMF373083. Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335' N, 81°50.2274' E, 1046 m water depth, 16.88 mbsf level, core NGHP-01-12A; Upper Pleistocene. For additional material see Table 1.

Description.—Medium-sized, solid, subcircular, thyasirid shell, inequivalve, equilateral. Large protruding umbo directed anteriorly, posteriorly two keeled radial ridges with sharp intermediate channel. Sculpture of coarse irregular growth lines and margins, a small semi-circular lunule and a long deep escutcheon demarcated by a sharp ridge. Hinge with elongated grooves both anteriorly and posteriorly. Length of largest incomplete valve 29 mm

Remarks.—We refrain from formally naming this species based on the small number of fragmentary specimens. Our species is similar to the Miocene *Conchocele majimai* Kiel et al., 2020, and *Conchocele visayaensis* Kiel et al., 2020, from the Philippines (Kiel et al. 2020); both these species have a large keeled area surrounding the lunule anteriorly; the lunule in our species is small without a surrounding demarcated area. Another similar thyasirid species is *Ascetoaxinus ravichandrani* Ravinesh et al., 2024, that was described off Tamil Nadu, southern India, depth 1007–1038 m. This species has narrow sulci placed more posteriorly and its lunule is demarcated by a coarsely sculptured margin (Ravinesh et al. 2024: figs. 3–5). Our species has broader sulci starting immediately behind the umbo and the demarcation of the lunule is smooth. Since we have only few fragmentary shells, we cannot rule out that the species belongs in the genus *Ascetoaxinus* Oliver & Frey, 2014.

Order Venerida Gray, 1854

Superfamily Glossoidea Gray, 1847 (1840)

Family Vesicomyidae Dall & Simpson, 1901

Subfamily Vesicomyinae Dall & Simpson, 1901

Remarks.—Currently, the subfamily only contains the genus *Vesicomya* Dall, 1886. Species in Vesicomyinae are not known to harbour chemosymbiotic bacteria (e.g., Krylova et al. 2018).

Genus *Vesicomya* Dall, 1886

Type species: *Callocardia atlantica* Smith, 1885, by original designation; Recent, Atlantic.

Vesicomya prashadi Hoffman & Little sp. nov.

Fig. 17B–D.

Zoobank LCID: urn:lsid:zoobank.org:act:8D92F14F-BB4A-41D9-92BF-F326FA809A7F.

Etymology: After Baini Prashad (1894–1969), Indian malacologist, particularly known for his study of the deep-water bivalves from the Siboga expedition (Prashad 1932).

Type material: Holotype, one shell, SMF373074. Paratypes, one valve, SMF373072; one valve, SMF373073, from the type locality and horizon.

Type locality: Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335' N, 81°50.2274' E, 1046 m water depth.

Type horizon: 16.38–16.88 mbsf level, core NGHP-01-12A; Upper Pleistocene.

Material.—Type material and several specimens from core NGHP-01-12A (for details see Table 1).

Diagnosis.—Small, solid, smooth, equivalve, inequilateral shell with oval outline, convex on all sides, beaks anteriorly, demarcated lunule and escutcheon, smooth prodissoconch.

Dimensions.—Holotype height 5.0 mm, length 6.0 mm, tumidity 4.2 mm. Maximum dimensions of shells in type set height as in holotype.

Description.—Prodissoconch single stage evident only, subcircular, truncated dorsally, flattened, smooth. Transition to dissoconch clear by change in sculpture. Length 300 µm. Dissoconch widely convex with prosogyrous umbos at 30% from anterior end; moderately inflated. Posterio-dorsal margin straightened, slightly convex, obliquely truncated pos-

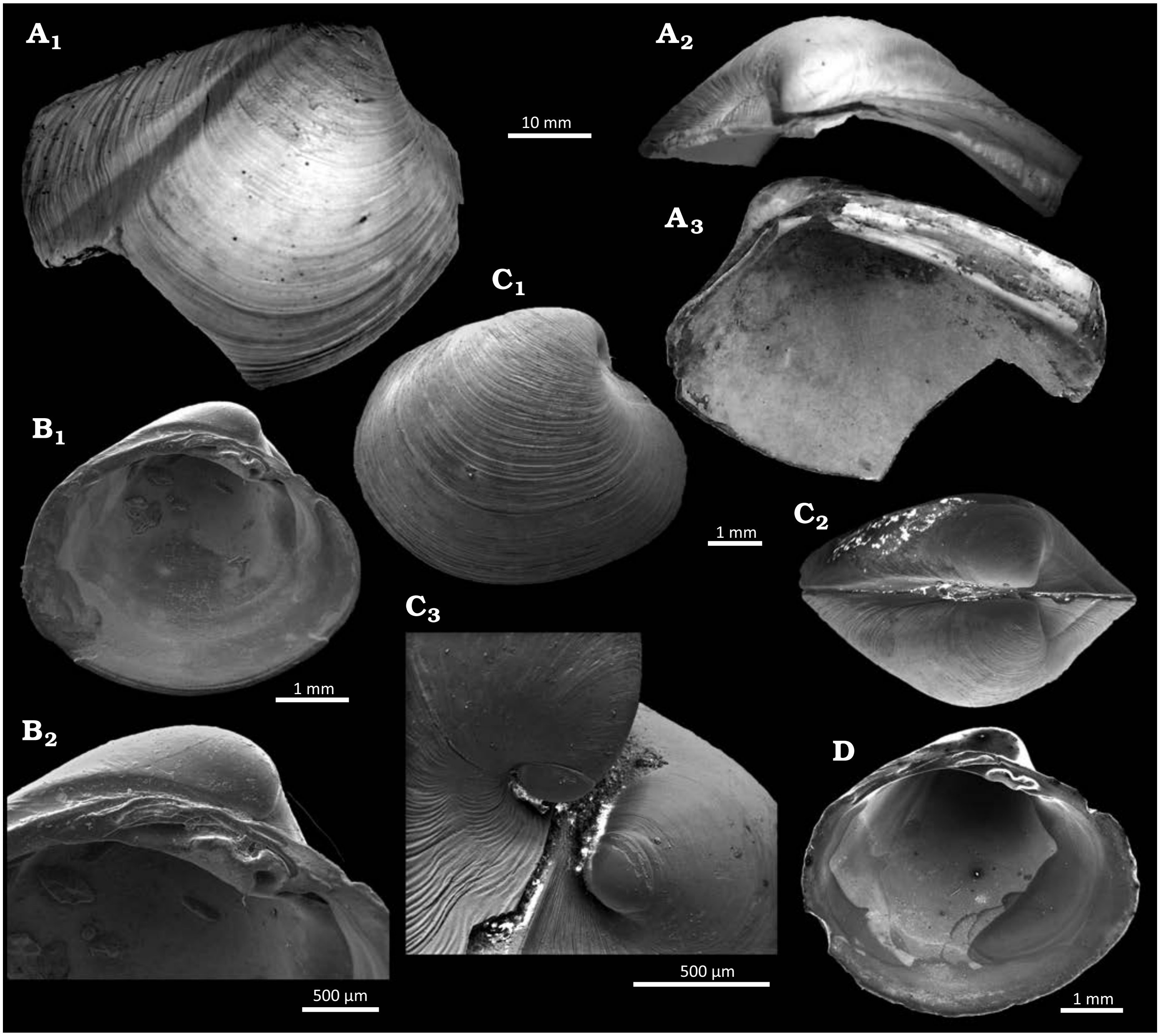

Fig. 17. Bivalves from Upper Pleistocene seep deposits from cores NGHP-01-12A and NGHP-01-10D, Krishna-Godavari Basin, offshore eastern India. **A**. Thyasirid *Conchocele* sp., SMF373083, right valve external (A_1), dorsal (A_2), and internal (A_3) views. **B**–**D**. Vesicomyid *Vesicomya prashadi* Hoffman & Little sp. nov. **B**. SMF373072, paratype, left valve internal view (B_1), internal view hinge detail (B_2). **C**. SMF373073, holotype, articulated specimen right valve (C_1), dorsal view (C_2), detail of umbonal area from anterior (C_3), prodissoconch. **D**. SMF373074, paratype, left valve internal view.

teriorly; ventral margin widely convex; anterior most convex; anterio-dorsal margin with indent at lunule; external sculpture with numerous fine growth margins of variable strength. Long lanceolate escutcheon, with fine growth lines, large lanceolate area for external ligament. Large triangular lunule with indented margins, with somewhat regular coarse growth lines. Ventral margin sharp, dorsal margin blunt. Internally surface and internal margin smooth; muscle scars and pallial line inconspicuous. Adductor scars of equal size; pallial line with minor sinus. Hinge only known from left valve; one curved elongated tooth posterior of umbo, elongated cavity for tooth right valve below; a second inverted w-shaped tooth below umbo, a short cavity for tooth right valve below posterior end w-tooth; one weak lateral tooth below posterio-dorsal margin; no anterior lateral tooth.

Remarks.—The genus *Vesicomya* has been based on the morphology of dentition in the left valve. The proximal curved tooth and the, long, more distal flexuous tooth *Vesicomya prashadi* Hoffman & Little sp. nov. is most similar to the dentition in the type species *Vesicomya atlantica* (Krylova et al. 2018: fig. 2C: teeth 2a, b, 4b) or that of the congener *Vesicomya alleni* (Krylova et al. 2018: fig. 3D). The type species of *Vesicomya* has a thin shell and narrow hinge plates whereas *Vesicomya prashadi* Hoffman & Little sp. nov. has a thick shell and heavy hinge plates. *Vesicomya alleni* has nearly identical teeth and hinge plate in the left valve but its shell is more elongated and the umbo is located further to the anterior (Krylova et al. 2018). *Vesicomya prashadi* Hoffman & Little sp. nov. has a more elevated outline and its umbos are in a nearly central position. *Vesicomya indica* (Knudsen, 1970) is known from abyssal depths in the Bay of Bengal (Huber 2010). That species has similar teeth compared to *Vesicomya prashadi* sp. nov but its hinge plate is narrower, its triangular outline is more elevated (height/length ±1) and the lunule is rounded. The escutcheon is also less pronounced; the co-marginal sculpture is fine and regular. *Vesicomya prashadi* Hoffman & Little sp. nov. is more flattened with a more triangular lunule, a pronounced escutcheon, an elongate-oval outline and a more irregular growth sculpture.

We considered placement of *Vesicomya prashadi* Hoffman & Little sp. nov. in other genera of small vesicomyids, for example *Waisiuconcha* Beets, 1942, and *Isorropodon* Sturany, 1896. *Waisiuconcha* was rejected as the dentition of the type species *Waisiuconcha alberdinae* Beets, 1942, are clearly different (Beets 1942: figs. 147–148: thick strong teeth). The same character is observed in, for example, the Atlantic *Waisiuconcha haeckeli* Cosel & Salas, 2001 (Zettler and Hoffman 2021: figs. 4, 12). We also rejected placement in *Isorropodon* because species in this genus have elongated, dorsally aligned teeth, as in evident in the original illustrations of the type species *Isorropodon perplexum* Sturany, 1896 (Sturany 1896: pl. 1: 24–27).

Stratigrapic and geographic range.—Type locality and horizon only.

Subfamily Pliocardiinae Woodring, 1925

Remarks.—The subfamily currently contains 19 genera. Species from all genera in Pliocardiinae are known to harbour chemosymbiotic bacteria (e.g., Krylova et al. 2018). In the Krishna-Godavari Basin fossil material species in the genera *Pliocardia* Woodring, 1925, *Callogonia* Dall, 1889a, and *Archivesica* Dall, 1908a, are present.

Genus *Pliocardia* Woodring, 1925

Type species: *Anomalocardia bowdeniana* Dall, 1903, by original designation; Pliocene, Jamaica.

Pliocardia cf. *solidissima* (Prashad, 1932)

Fig. 18A.

Material.—One valve (SMF373088) from Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335' N, 81°50.2274' E, 1046 m water depth, 16.68 mbsf level, core NGHP-01-12A; Upper Pleistocene.

Description.—Medium-sized, solid vesicomyid shell, equivalve, inequilateral. Outline oblong-ovate, strongly protruding umbo directed anteriorly, antero-dorsal margin concave, postero-dorsal and ventral margins weakly convex, anterior margin most convex, posterior widely convex. Sculpture with numerous irregular coarse growth lines. Elongated yet widely oval lunule, narrow elongated escutcheon. Internally, large teeth and hinge plate, pallial sinus absent. Length 36 mm.

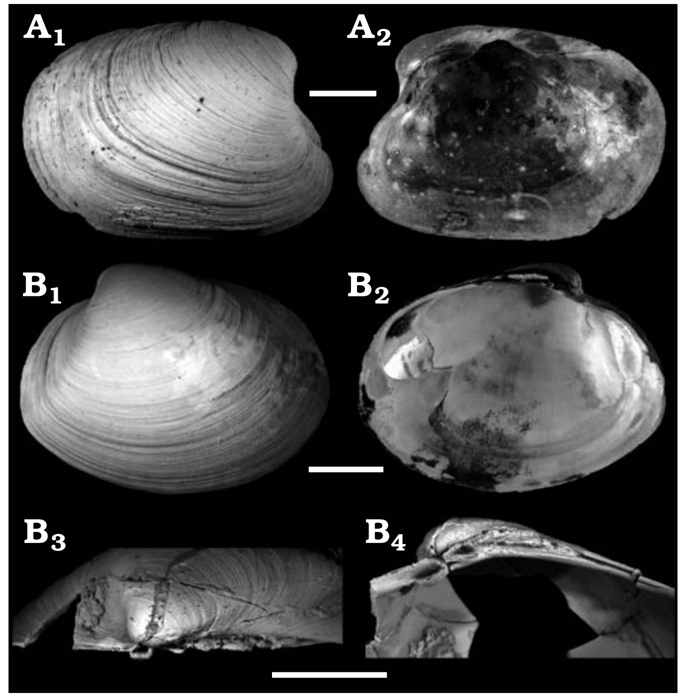

Fig. 18. Vesicomyid bivalves from core NGHP-01-12A and NGHP-01-10D, Krishna-Godavari Basin, offshore eastern India. **A**. SMF373088, *Pliocardia* cf. *solidissima* (Prashad, 1932), right valve external (A_1) and internal (A_2) views. **B**. SMF373082, *Callogonia* cf. *leeana* (Dall, 1889a), left valve external (B_1) and internal (B_2) views, partial right valve dorsal (B_3), and internal (B_4) views. Scale bars 10 mm.

Remarks.—Prashad's (1932) species is determined by its medium size, thick globose shell, elongated trapezoidal outline, demarcated lunule, hinge and pallial line without sinus. The type locality is from off Bali, Indonesia (SIBOGA sta. 18, 7°28.2' S, 115°24.6' E, 1018 m). A similar species is *Pliocardia kuroshimana* (Okutani et al., 2000), which is known in the Western Pacific off Japan (Okutani et al. 2000) and in the Miocene on Leyte, Philippines (Kiel et al. 2020). Another similar species is *Pliocardia atalantae* (Cosel & Olu, 2009) from off western Africa. *Pliocardia indica* (Smith, 1904) also lives in the Bay of Bengal (Smith 1904: 9; Huber 2010) in 767–1985 m. *Pliocardia indica* has a convex ventral margin, whereas our specimen has a flattened ventral margin and a trapezoidal outline.

Genus *Callogonia* Dall, 1889a

Type species: *Callocardia* (*Callogonia*) *leeana* Dall, 1889a; Recent, North-West Atlantic.

Callogonia cf. *leeana* (Dall, 1889a)

Fig. 18B.

Material.—One shell, SMF373082. Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern

India, 15°51.8647’ N, 81°50.0709’ E, 1050 m water depth, 15.73 mbsf level, core NGHP-01-10D; Upper Pleistocene.

Description.—Medium-sized, fragile vesicomyid shell, equivalve, subequilateral. Outline ovate, strongly protruding umbo directed anteriorly, all margins convex, anterior and posterior weakly truncated obliquely. Sculpture with numerous irregular coarse growth lines. Lunule not conspicuous, narrow elongated escutcheon. Internally, small elongated teeth, thin hinge plate, pallial sinus. Length 38 mm

Remarks.—Outline, sculpture, hinge and pallial sinus are similar to *Callogonia leeana* (Dall, 1889a) from the NW Atlantic; even though there is a morphological similarity, it may be a different species in view of the large oceanic distance to the type locality. The left valve of the present species shows a clear sinus in the pallial line, which is characteristic for the genus.

Genus *Archivesica* Dall, 1908b

Type species: *Callocardia gigas* Dall, 1896, by original designation; Recent, E Pacific.

Archivesica cf. *kawamurai* (Kuroda, 1943)

Fig. 19.

Material.—One juvenile shell, SMF373080; one adult valve, SMF373081; one adult valve, SMF373078; one adult valve, SMF373079; one juvenile valve, SMF373077. Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335’ N, 81°50.2274’ E, 1046 m water depth, 16.18–16.88 mbsf level, core NGHP-01-12A; Upper Pleistocene. For additional material see Table 1.

Description.—Large, solid vesicomyid shell, equivalve, inequilateral. Outline oblong-ovate, weakly protruding umbo at 25% from anterior margin, all margins convex, anterior and posterior most convex. Sculpture with numerous irregular coarse growth lines. Lunule not conspicuous, long lanceolate escutcheon. Length largest valve 43 mm

Remarks.—The large size, outline, sculpture and hinge of our specimens suggest that they are probably conspecific with *Archivesica kawamurai*, a species described off Japan, Sagami Bay (Kuroda 1943); the species also known from the Pliocene and Recent from various locations around Japan (Kuroda 1943; Amano and Kiel 2010: 158) and around Taiwan (Kiel et al. 2024: 10, figs. 8P–R). *Archivesica kawamurai* can be identified by the hinge and the widely convex ventral margin, a feature found in the holotype (Amano and Kiel 2010: 156–158, fig. 18). Many species in *Archivesica* have a straightened or slightly concave ventral margin. A morphologically similar species to our specimens is *Archivesica arctica* Hansen et al., 2017, from off NW Svalbard; this species has a similar outline and hinge, and its anterior margin seems less convex (Hansen et al. 2017). *Calyptogena marissinica* Chen et al., 2018, has a similar outline to our specimens, but this species has a different hinge with symmetrical cardinal teeth 2a, b of equal strength; our species has a strong 2b tooth and a weak 2a tooth, which are placed obliquely (Chen et al. 2018: figs. 2, 3).

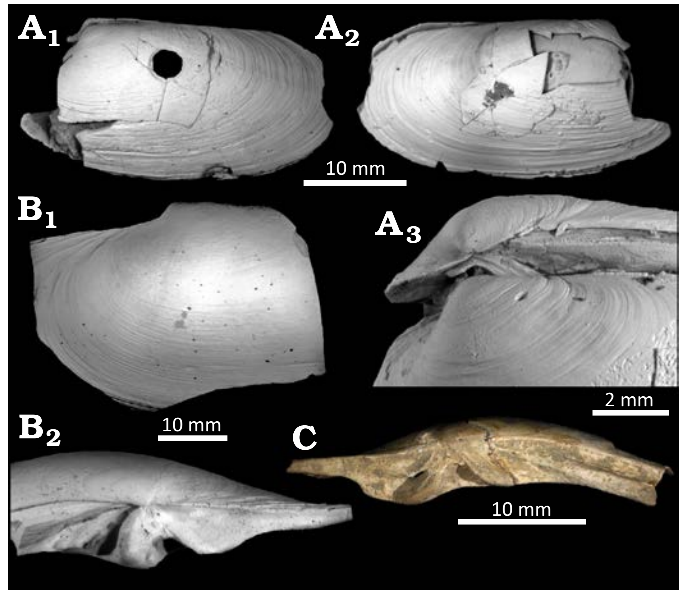

Fig. 19. The vesicomyid bivalve *Archivesica* cf. *kawamurai* (Kuroda, 1943) from Upper Pleistocene seep deposits from core NGHP-01-12A, Krishna-Godavari Basin, offshore eastern India. **A**. SMF373080, articulated specimen, left valve with *Oichnus paraboloides* Bromley, 1981 boring (A_1), right valve (A_2), and oblique dorsal view showing right valve hinge (A_3). **B**. SMF373081, left valve external (B_1) and hinge (B_2) views. **C**. SMF373078, right valve hinge view. A, B whitened and C not whitened.

Superorder Analodesmata Dall, 1889b

Family Cuspidariidae Dall, 1886

Cuspidariidae? gen. et sp. indet.

Fig. 20.

Material.—One fragmentary valve (SMF373084) from Northern Indian Ocean, Krishna-Godavari Basin, Bay of

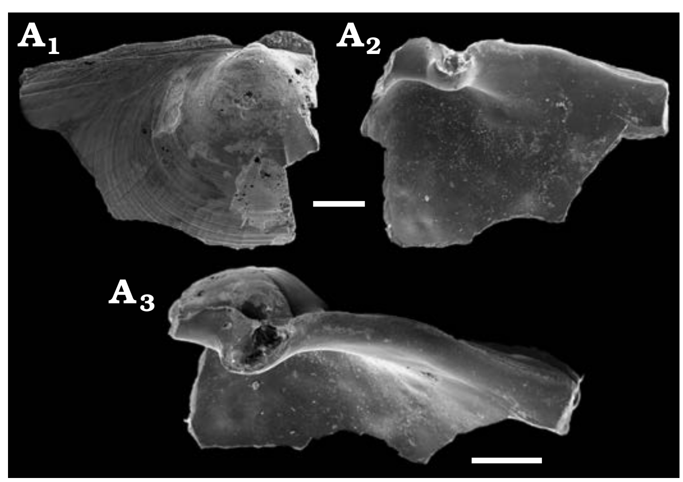

Fig. 20. The bivalve Cuspidariidae? gen. et sp. indet. from Upper Pleistocene seep deposits from core NGHP-01-12A, Krishna-Godavari Basin, offshore eastern India. **A**. SMF373084, partial right valve external (A_1), internal (A_2), and oblique dorsal (A_3) views. Scale bars 500 μm.

Bengal, offshore eastern India, 15°51.6335’ N, 81°50.2274’ E, 1046 m water depth, 16.88 mbsf level, core NGHP-01-12A; Upper Pleistocene.

Description.—Small fragile, flattened shell, inequilateral. Outline uncertain. Sculpture with fine radial and commarginal lines. Internal hinge with deep notch in external margin below the umbo, no teeth seen. Length about 3 mm.

Remarks.—Placement in Cuspidariidae is feasible from the external morphology and hinge. The radial sculpture suggests a species in the genus *Cardiomya* Adams, 1864, albeit that our species has relatively flat valves and known species in the Indo-Pacific are rather globose. Alternatively, it could be placed in another genus in Cuspidariidae or Protocuspidariidae. The material was deemed inadequate for a determination, or description as a new species.

Class Scaphopoda Bronn, 1862

Order Dentalida Starobogatov, 1974

Family Dentaliidae Children, 1834

Dentaliidae? gen. et sp. indet.

Fig. 21A–C.

Material.—Three shells (SMF373085–87) from Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335’ N, 81°50.2274’ E, 1046 m water depth, 16.78 mbsf level, core NGHP-01-12A; Upper Pleistocene. For additional material see Table 1.

Description.—small, weakly curved, solid scaphopod tooth-shaped shell with strong axial rib sculpture. small, globose, solid inflated gadilid-shaped shell. Apex small, pointed with circular hole, rectangular outline. Intial strong increase in diameter, less thickening in adult stage. Sculpture with large rounded axial ribs, apically 4 ribs increasing to 9 ribs abapically with incremental ribs progressively formed in between. Maximum length 7 mm.

Remarks.—Placement in Dentaliidae is plausible from the external morphology and outline in the few fragmentary shells. They likely belong to a single species in the genus *Antalis* Adams & Adams, 1854. Alternatively, they could be placed in another genus in Dentaliidae or in the genus *Entalina* Monterosato, 1872, in family Entalinidae Chistikov, 1979. The material was deemed inadequate for a determination, or description as a new species.

Order Gadilida Starobogatov, 1974

Family Gadilidae Stoliczka, 1868

Genus Cadulus Philippi, 1844

Type species: *Cadulus ovulum* (Philippi, 1844)†; Miocene, Sicily, Italy.

Cadulus chuni Jaeckel, 1932

Fig. 21D, E.

1932 *Cadulus chuni* Jaeckel, 1932: 309, text-fig. 6.
1995 *Cadulus chuni* Scarabino, 1995: 348–349, figs. 153, 160e.

Material.—One shell, SMF373076; one shell, SMF373075. Northern Indian Ocean, Krishna-Godavari Basin, Bay of Bengal, offshore eastern India, 15°51.6335’ N, 81°50.2274’ E, 1046 m water depth, 16.78–16.88 mbsf level, core NGHP-01-12A; Upper Pleistocene. For additional material see Table 1.

Description.—Small, smooth, swollen, solid gadilid-shaped shell. Apical aperture circular with thick rim. externally 0.6 mm, internally 0.4 mm; abapical aperture circular with thin rim, external diameter 0.9 mm. Lateral outline convexly swollen centre, slightly concave on apical and abapical shell faces. Maximum length 3 mm.

Remarks.—The species was described from off Somalia, eastern Africa, “Valdivia”, station 256, 01°49’ N, 45°30’ E, 1134 m. It is known as a recent species from the type locality and two locations in the Western central Pacific from Indonesia and the Philippines (Scarabino 1995: 349, fig. 153); the bathymetric range is 205–1134 m.

Stratigraphic and geographic range.—Recent, off Somalia, Philippines and Indonesia. Upper Pleistocene, Krishna-Godavari Basin, off eastern India.

Discussion

Palaeocology of the Upper Pleistocene Krishna-Godavari Basin seep assemblage.—The majority of the studied specimens come from the shell-rich horizon in core NGHP-01-12A situated between 16.18 mbsf and 17 mbsf (Table 1). Based on ^{14}C dating the age range of this material spans at least 10 000 years, and thus should be considered an assemblage of fossils representing a series of living seep communities. Nonetheless, the species composition seems to have been similar, so there is no obvious signature of changing community structure over time. Although the material from core NGHP-01-10D is undated, Mazumdar et al. (2019) report from a nearby sediment core U-Th based dates of carbonate tubules of ~46.2 ± 3.7 to 53 ± 1.6 ka at 16 mbsf. Based on these various dates Teichert et al. (2014; fig. 10) correlated the MDAC and shell-rich horizons between NGHP-01-12A and NGHP-01-10D. Consequently, we here consider the material present between 16.18 mbsf and 17 mbsf in the former and 15.3 mbsf and 15.73 mbsf in the latter to be roughly contemporary, and, therefore, below consider them as a single fossil seep assemblage.

The seep gastropod, bivalve and scaphopod assemblage comprises 29 species: 15 gastropods, 12 bivalves, and two scaphopods. Of these species nine are identified as new: six gastropods and three bivalves (Table 1). A comparison with living conspecifics and congenerics (e.g., Dubilier et al. 2008) suggests that six of these species are likely to have had chemosymbionts (*Acharax* sp., *Gigantidas* cf. *platifrons*, *Conchocele* sp., *Pliocardia* cf. *solidissima*, *Callogonia* cf. *leeana*, and *Archivesica* cf. *kawamurai*). These represent 21% of the diversity, but only 14% of the specimens complete enough for identification (Tables 1, 2).

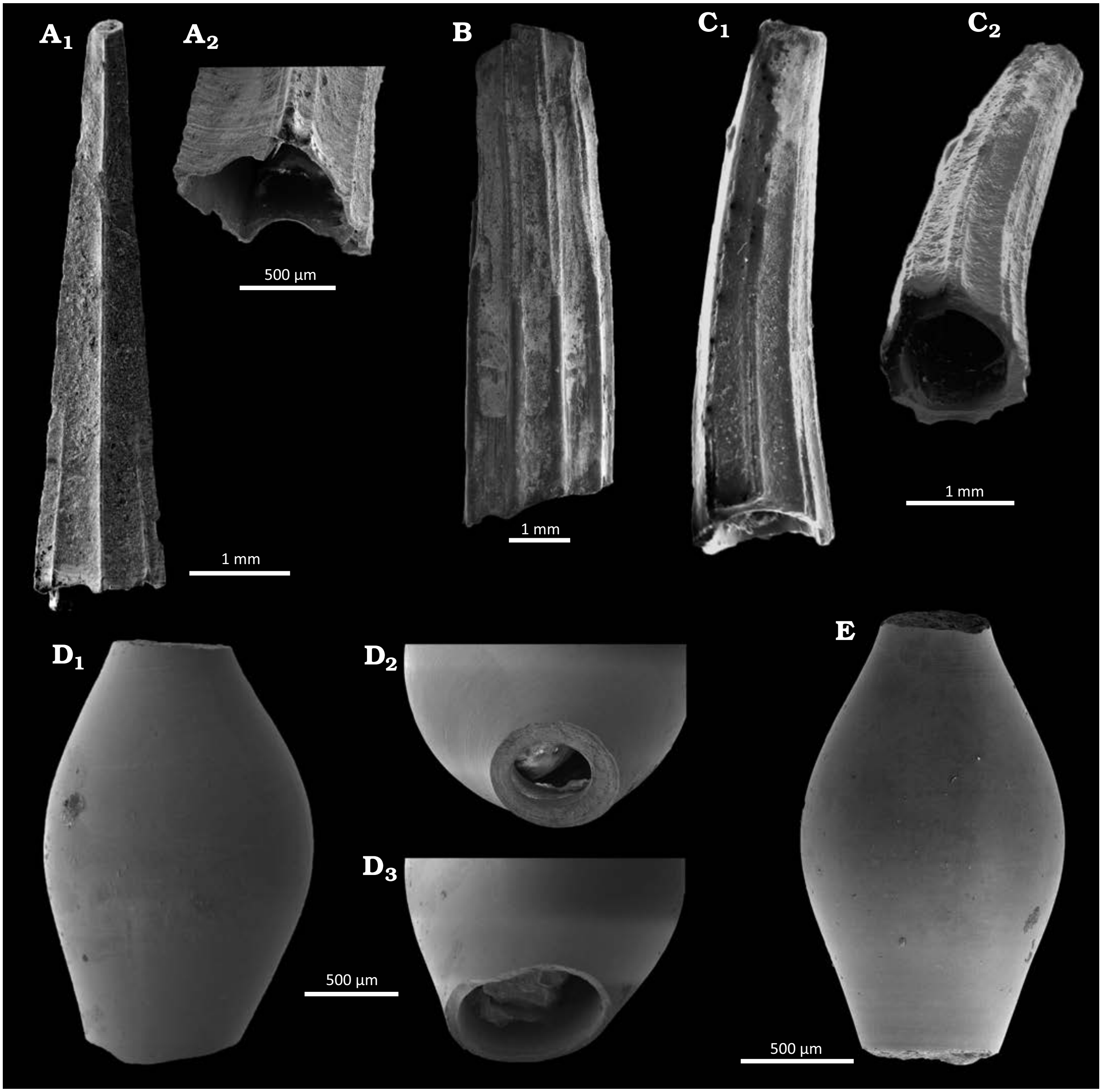

Fig. 21. Scaphopods from Upper Pleistocene seep deposits from core NGHP-01-12A, Krishna-Godavari Basin, offshore eastern India. **A**–**C**. Dentalidae? gen. et sp. indet. **A**. SMF373085, side view (A_1) and oblique view of aperture (A_2). **B**. SMF373086, side view. **C**. SMF373087, side view (C_1), oblique view of aperture (C_2). **D**, **E**. Gadilid *Cadulus chuni* Jaeckel, 1932. **D**. SMF373076, side view (D_1), abapical (D_2), and apical (D_3) openings. **E**. SMF373075, dorsal view.

However, shell fragments of bathymodiolins and vesicomyids are very common in most of sediment sub-samples, suggesting that originally these taxa represented a larger proportion of the molluscan faunal abundance in the seep communities. With the exception of *Acharax* sp., all these putative chemosymbiotic taxa were likely to have been obligate to seeps, based on the occurrence of living conspecifics and congenerics (e.g., Imhoff et al. 2003; Sasaki et al. 2005; Krylova and Sahling 2010; Lorion et al. 2013; Zanzerl et al. 2019). Most occurrences of *Acharax* species are from seeps (e.g., Neulinger et al. 2006; Mazumdar et al. 2019; Yang et al. 2024), but they are also known from organic-rich sediments associated with oxygen minimum zones, for example off Baja California (Suárez-Mozo et al. 2019), so this taxon is not always obligate to the seep environment. Obligacy is likely to have been the case for *Paralepetopsis bathyalus* Hoffman & Little sp. nov., as most living *Paralepetopsis* species are restricted to either

Table 2. Suggested palaeoecological determinations for bivalve, gastropod, and scaphopod taxa from cores NGHP-01-12A and NGHP-01-10D. CSV version of this table is available in SOM 3.

Taxon	Occurrence	Palaeoecology
Paralepetopsis bathyalus Hoffman & Little sp. nov.	obligate	epifaunal grazer
Mesopelex godavariensis Hoffman & Little sp. nov.	facultative	epifaunal grazer
Fissurellidae gen. et sp. indet.	facultative	spongivore
Anatoma bengalensis Hoffman & Little sp. nov.	?obligate	epifaunal grazer
Seguenzioidea gen. et sp. indet.	facultative	epifaunal grazer
Cirsonella aperta Hoffman & Little sp. nov.	facultative	epifaunal grazer
Dikoleps? *magnarota* Hoffman & Little sp. nov.	facultative	epifaunal grazer
Alvania axistriatus Hoffman & Little sp. nov.	facultative	epifaunal grazer
Benthonellania sp.	facultative	epifaunal grazer
Columbellidae gen. et sp. indet.	facultative	epifaunal predator/scavenger
Conoidea gen. et sp. indet.	facultative	epifaunal predator/scavenger
Eulimella sp. 1	facultative	epifaunal parasite
Eulimella sp. 2	facultative	epifaunal parasite
Odostomia sp.	facultative	epifaunal parasite
Cylichnidae? gen. et sp. indet.	facultative	infaunal predator/scavenger
Acharax sp.	facultative	infaunal chemosymbiotic
Ledella favus Hoffman & Little sp. nov.	facultative	infaunal deposit feeder
Yoldiella umbostriatus Hoffman & Little sp. nov.	facultative	infaunal deposit feeder
Gigantidas cf. *platifrons*	obligate	semi-infaunal chemosymbiotic
Parvamussium? aff. *scitulum*	facultative	epifaunal microcarnivore
Propeamussiidae? gen. et sp. indet.	facultative	epifaunal microcarnivore
Conchocele sp.	obligate	infaunal chemosymbiotic detritivore
Vesicomya prashadi Hoffman & Little sp. nov.	facultative	infaunal detritivore
Pliocardia cf. *solidissima*	obligate	infaunal chemosymbiotic
Callogonia cf. *leeana*	obligate	infaunal chemosymbiotic
Archivesica cf. *kawamurai*	obligate	semi-infaunal chemosymbiotic
Cuspidariidae? gen. et sp. indet.	facultative	epifaunal microcarnivore
Dentaliidae? gen. et sp. indet.	facultative	semi-infaunal microcarnivore
Cadulus chuni	facultative	semi-infaunal microcarnivore

seep or hydrothermal vent habitats (e.g., McLean 1990; Warén and Bouchet 2001, 2009). This could possibly also have been the case for *Anatoma sahlingi* Hoffman & Little sp. nov., as a small number of living *Anatoma* species have been reported from hydrothermal vent sites in the central Indian Ocean and not elsewhere (Hoffman et al. 2022). However, anatomids are found in a large variety of habitats from intertidal to deep bathyal depths in all oceans of the world (Geiger 2012). Including this taxon gives a value for obligacy in the Krishna-Godavari Basin seep assemblage diversity of 24% (Table 2). The remaining bivalve, gastropod and scaphopod species described here also have living relatives common in bathyal habitats and can probably be considered as facultative or "background" fauna in the assemblages (e.g., Scarabino 1995; Dijkstra and Janssen 2013; Dijkstra and Maestrati 2015; Krylova et al. 2018). They represent a wide variety of infaunal and epifaunal palaeoecologies, ranging from less specialized grazers to specialized microcarnivores (Table 2). Additional palaeoecological information comes from the small number of penetrative borings present in vesicomyid shells (Fig. 19A_1) and neolepadid plates (Fig. 22D). These are consistent with the ichnotaxon *Oichnus paraboloides* Bromley, 1981, which is commonly ascribed to the predatory drilling activities of naticid and muricid gastropods (e.g., Breton et al. 2017). Intriguingly, neither taxon is present as shells in the Krishna-Godavari Basin seep assemblage (Table 1).

Undoubtedly, both the species and palaeoecological diversity in the fossil seep assemblage was enhanced by the presence of abundant hard substrate, as shells and MDAC, in what was otherwise a fine-grained sedimentary environment. These hard substrates served as attachment sites for a diversity of epifauna, including the byssate bivalves (i.e., *Gigantidas* cf. *platifrons*, and probably the pectinids), corals (*Caryophyllia* sp.), serpulids and neolepadids (Fig. 2), sponges (suggested by the presence of spongivorous fissurellids), as well as, presumably, for the larvae of these and many other taxa. The bivalve and gastropod shells also acted as substrates for fungal microborings (Fig. 22A, B) and were grazed extensively, as inferred from the presence of *Radulichnus inopinatus* Voigt, 1977, trace fossils on many of the larger bivalve shell fragments (Fig. 22C), which probably resulted from gastropod and/or chiton grazing (e.g., Voigt 1977; De Gibert et al. 2007).

Material from deeper in core NGHP-01-10D (between 41.54 mbsf and 42.27 mbsf, and at 61.03 mbsf) represents

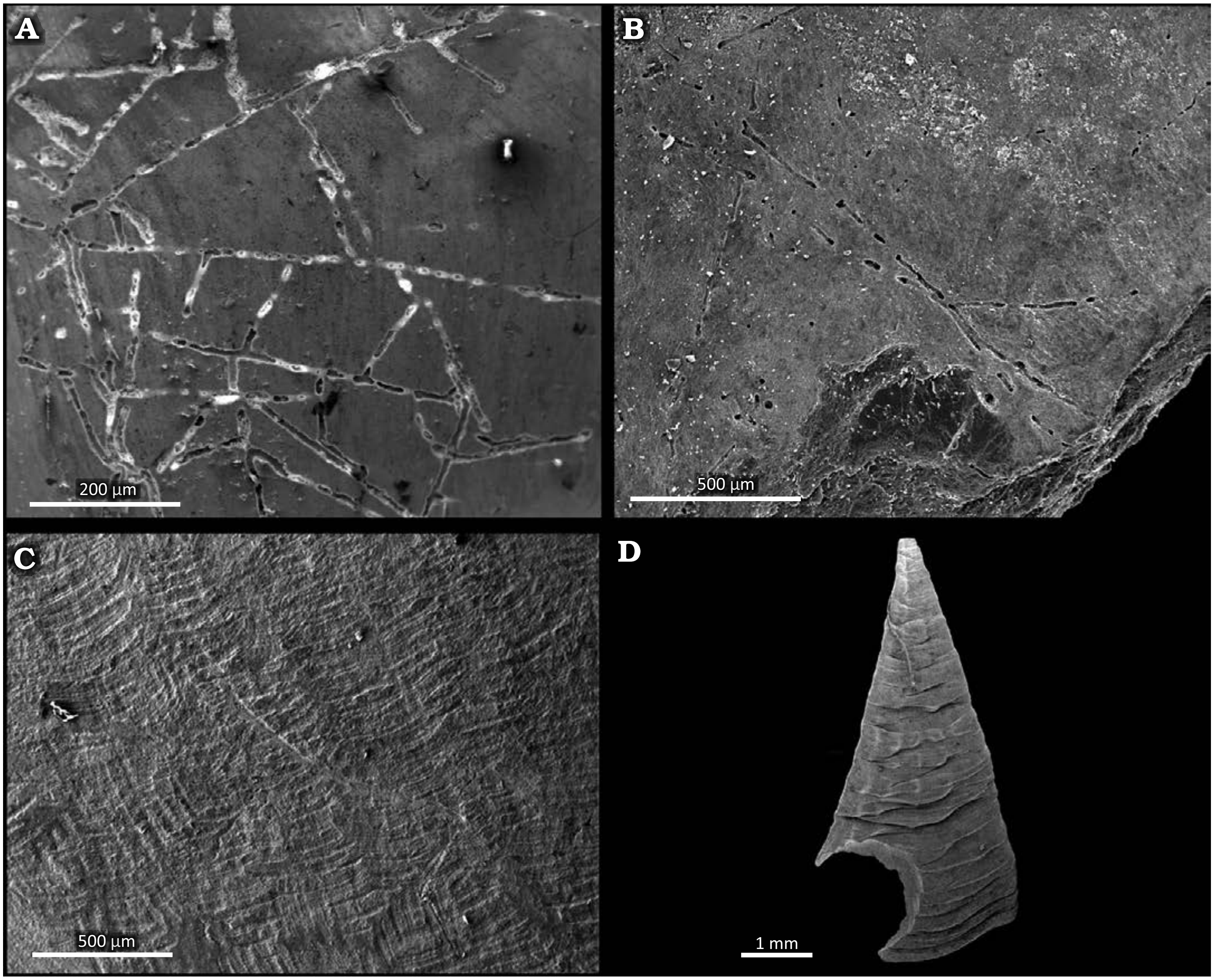

Fig. 22. Trace fossils from Upper Pleistocene seep deposit from core NGHP-01-12A, Krishna-Godavari Basin, offshore eastern India. **A**, **B**. Fungal microborings. **A**. SMF373120, external surface of *Cirsonella aperta* Hoffman & Little sp. nov. (see Fig. 8C). **B**. SMF373062, bivalve shell fragment. **C**. Grazing trace *Radulichnus inopinatus* Voigt, 1977, on vesicomyid bivalve shell fragment. **D**. NHMUK IC 1416, drillhole *Oichnus paraboloides* Bromley, 1981, boring in upper latus plate of *Ashinkailepas indica* Gale in Gale et al., 2020.

older fossil assemblages. The presence of MDAC at these levels (Teichert et al. 2014), fragments of large vesicomyid shells and a single, probable *Gigantidas* cf. *platifrons* shell at 42.01 mbsf (Table 1) strongly suggests that hydrocarbon seepage and associated faunas were present at this site before ~52 ka. A using the ^{14}C ages from Teichert et al. (2014) for core NGHP-01-12A to calculate a sedimentation rate (1 m per 3.25 ka) would give an age estimate of ~136 ka for the shell at 42.01 mbsf in core NGHP-01-10D.

Comparison with other putative fossil seep assemblages from offshore eastern India.—In addition to the material reported here there are several other likely occurrences of fossil seep assemblages from the Krishna-Godavari Basin. Mazumdar et al. (2009: fig. 4c) figure articulated and fragmented bivalves shells identified as *Calyptogena* sp. from 16 mbsf to 18 mbsf in a sediment core (MD161-8) recovered during cruise MD-161 of the R/V Marian Dufresne (May 2007). This site is close to NGHP-01-10D at 15°51.8624’ N, 81°50.0692’ E in a water depth of 1033 m (Fig. 1). The figured shells do not show the internal features that are needed for generic determination of vesicomyid genera, but the overall elongation and rounded posterior margin of the specimens are similar to the *Archivesica* cf. *kawamurai* specimens described here, so may be conspecific. Additional bivalve shell fragments from the same cruise were figured by Joshi et al. (2014) at 27–31 mbsf in sediment core MD161-15, recovered from 983 m water depth. These comprise one anterior portion of a shell identified as *Calyptogena* sp. (Joshi et al. 2014: fig. 9a, b) and the ventral portion of a shell identified as *Lucinoma* sp. (Joshi et al. 2014: fig. 9c). None of this material is complete enough for generic determination, but the shape of the vesicomyid shell is similar to the *Archivesica* cf. *kawamurai* specimens herein, and the "*Lucinoma* sp." shell bears some resemblance to our *Conchocele* sp. specimens. Joshi et al. (2014) state that scaphopods are incorporated into MDAC from this core. One specimen (Joshi et al. 2014: fig. 8v, vi) shows closely spaced longitudinal ribbing, so is likely to be a dentaliid, but being considerably larger than any of the specimens herein, cannot be compared directly with them. According to Joshi et al. (2014) age of the shells from MD 161-15 is undetermined.

Badesab et al. (2020) figure fragmentary bivalve shells from a short sediment core (SSD-045/Stn-9/GC-01) recovered from the Krishna-Godavari Basin during cruise SSD-045 of the R/V Sindhu Sadhana at 16°18.6027' N, 82°37.9809' E in 1 673 m water depth (Fig. 1). Associated with MDAC Badesab et al. (2020) identified *Calyptogena* sp. from 2.7 mbsf and 5.1 mbsf (Badesab et al. 2020: fig. 8j, k). Again, these shells are too incomplete for generic determination, although they are most similar in size and shape to our *Archivesica* cf. *kawamurai* specimens. The shells recorded in Badesab et al. (2020) are likely to be considerably younger than our Krishna-Godavari Basin seep specimens, as the former come from much shallower core depth horizons.

Comparison of the Krishna-Godavari Basin Upper Pleistocene seep assemblage with modern seep communities in the Indian Ocean.—Until all the taxa present in the modern seep communities from Krishna-Godavari Basin and Mannar Basin have been formally described it will be difficult to make definitive species comparisons between these and those present in the Upper Pleistocene Krishna-Godavari Basin seep assemblage. However, using the figures in Mazumdar et al. (2019), Dewangan et al. (2021) and Sangodkar et al. (2022), and the identifications of He et al. (2023) (which were based on the images in the above publications) for the Krishna-Godavari Basin and Mazumdar et al. (2021) for the Mannar Basin seeps allows us to make some initial comparisons.

Based on the seafloor photographs in Mazumdar et al. (2019: fig. 3a) and Dewangan et al. (2021: fig. 5a) the Krishna-Godavari Basin seep communities appear to be dominated by bathymodiolins and vesicomyids. The bathymodiolin specimen figured in Sangodkar et al. (2022: fig. 3a) looks similar to our *Gigantidas* cf. *platifrons*, so could be conspecific, but is also very similar to *Gigantidas niobengalensis* Oliver et al., 2024. The bathymodiolin images in Mazumdar et al. (2019: fig. 3a,q) and Dewangan et al. (2021: fig. 5a) are probably also the same species, but the images are not detailed enough to be sure. It is worth noting here that several superficially similar bathymodiolin species can be present in modern seeps, for example, the Haima Seep in the South China Sea has four co-occurring species (Lin et al. 2022). The large vesicomyid species figured in Mazumdar et al. (2019: fig. 3b, c) differs from the *Archivesica* cf. *kawamurai* specimens herein in being shorter and having a slightly concave ventral margin, so probably represents a different species. This is also the case for the vesicomyids figured in Sangodkar et al. (2022: fig. 3b) and Dewangan et al. (2021: fig. 5d). He et al. (2023) identify this taxon as *Calyptogena makranensis*.

Solemyids, thyasirids and pectinoids are present in the modern Krishna-Godavari Basin seep communities. The *Archarax* sp. figured in Mazumdar et al. (2019: fig. 3e) and Sangodkar et al. (2022: fig. 3c) look to be the same specimen. The *Archarax* sp. figured in Dewangan et al. (2021: fig. 5c) is probably the same species. It is likely that our *Acharax* sp. is conspecific with these modern specimens, but the fossil material is too fragmentary to be sure. The *Conchocele* sp. specimens figured in Mazumdar et al. (2019: fig. 3d) and Dewangan et al. (2021: fig. 5b) are probably the species as the Thyasiridae gen. et sp. indet. in Sangodkar et al. (2022: fig. 3d). These specimens have a slightly different shape to our *Conchocele* sp. in having a less projecting anterior margin and a deeper posterior sulcus. However, these differences may be ontogenetic, as the fossil specimens are considerably smaller than the modern figured ones. Mazumdar et al. (2019: fig. 3f) identify a ribbed pectinoid bivalve from the modern Krishna-Godavari Basin seeps as belonging to the Pectinidae. He et al. (2023) identify this as *Catillopecten*. This species could be conspecific with our *Parvamussium* aff. *scitulum*, although the image of the modern taxon is not good enough to make a definitive comparison. Gastropods are also present in the modern Krishna-Godavari Basin seep fauna. The limpets shown in Mazumdar et al. (2019: fig. 3g, h) could be conspecific with our *Paralepetopsis bathyalus* Hoffman & Little sp. nov. The "Phenocolepadidae" in Sangodkar et al. (2022: fig. 3m), which He et al. (2023) identify as *Bathyacmaea*, is a more questionable comparison to either of our fossil limpet species.

Molluscan taxa in the fossil seep assemblage that cannot be easily compared to taxon descriptions or figures in Mazumdar et al. (2019), Dewangan et al. (2021) or Sangodkar et al. (2022) are the gastropods *Mesopelex godavariensis* Hoffman & Little sp. nov., Fissurellidae gen. et sp. indet., *Anatoma sahlingi* Hoffman & Little sp. nov., Seguenzioidea gen. et sp. indet., *Cirsonella aperta* Hoffman & Little sp. nov., *Dikoleps*? *magnarota* Hoffman & Little sp. nov., *Alvania axistriata* Hoffman & Little sp. nov., *Benthonellania* sp., Columbellidae gen. et sp. indet., Conoidea gen. et sp. indet., *Eulimella* sp. 1, *Eulimella* sp. 2, *Odostomia* sp., and Cylichnidae? gen. et sp. indet., the bivalves *Ledella favus* Hoffman & Little sp. nov., *Yoldiella umbostriata* Hoffman & Little sp. nov., Propeamussiidae? gen. et sp. indet., *Vesicomya prashadi* Hoffman & Little sp. nov., *Pliocardia* cf. *solidissima* (Prashad, 1932), *Callogonia* cf. *leeana* (Dall, 1889a), and Cuspidariidae? gen. et sp. indet., and the scaphopod *Cadulus chuni* Jaeckel, 1932. Most of these are small taxa, so may have been overlooked in the samples of Mazumdar et al. (2019), Dewangan et al. (2021), and Sangodkar et al. (2022), or were present, and simply not reported in these publications. Alternatively, these fossil taxa are not present in the modern Krishna-Godavari Basin seep communities. Conversely, some of the gastropod taxa figured in Mazumdar et al. (2019), Dewangan et al. (2021), and Sangodkar et al. (2022) are not present in the fossil seep assemblage: neritids (Mazumdar et al. 2019: fig. 3j), "Provannidae" (Mazumdar et al. 2019: fig. 3i; identified as *Phymorhynchus* in He et al. 2023), and neither of the gastropods figured in Sangodkar et al. (2022: fig. 3o) as "gastropod unidentified spp.", which appear to be a buccinid (image on right in fig. 3o) and provannids (three left images in fig. 3o). The latter are also identified as *Provanna* by He et al. (2023). The absence of Provannidae from the fossil seep assemblage is interesting, as this is one of the most characteristic and species-rich taxon in modern and many fossil seep communities (e.g., Warén and Bouchet 2001; Sasaki et al. 2010; Betters and Cordes 2023).

In the non-molluscan elements of the modern and fossil Krishna-Godavari Basin seep faunas there are also differences and similarities. Shared taxa include echinoids, which are present in the fossil Krishna-Godavari Basin assemblage as very occasional isolated test ossicles, and serpulids, the tubes of which are very commonly found attached onto bivalve shells and neolepadid barnacle plates in the fossil material (Figs. 2, $15A_1$), and are figured attached onto bivalve shells in the modern communities (Dewangan et al. 2021: fig. 5d). This is also the case for neolepadids in the modern seep communities (Mazumdar et al. 2019: fig. 3q; Dewangan et al. 2021: fig. 5a). These modern neolepadids have been identified as *Neolepas* sp. in Mazumdar et al. (2019), Dewangan et al. (2021), and Peketi et al. (2022), and *Leucolepas* in He et al. (2023). It is possible that these are conspecific with *Ashinkailepas indica* Gale in Gale et al., 2020, the isolated plates of which are very common elements in most of NGHP-01-12A core samples and from the 15.54 mbsf level in core NGHP-01-10D (Table 1).

The modern Krishna-Godavari Basin seep communities include soft bodied taxa that would not be expected to be present in a fossil assemblage for purely taphonomic reasons, such as non-tubicolous polychaete worms (Mazumdar et al. 2019: fig. 3l, m; Sangodkar et al. 2022: fig. 3f, g). This may also pertain to taxa with lightly mineralized exoskeletons, such as decapod crustaceans (Mazumdar et al. 2019: fig. 3n, o; Sangodkar et al. 2022: fig. 3e, n), which are not present in the fossil assemblage. Siboglinid tubeworms are absent from the fossil Krishna-Godavari Basin seep assemblage. Whilst this is expected for the soft tissues of these worms, the chitin-rich tubes are known to get replaced in modern seep sites by carbonates (Haas et al. 2009), and have a rich fossil record (Georgieva et al. 2019). It is possible that some of the tubular carbonates present in Krishna-Godavari Basin sediment cores reported in Kocherla et al. (2015) and Mazumdar et al. (2019) represent replaced siboglinid tubes. One more taxon not present in the fossil seep assemblage is the Ophiuroidea (Mazumdar et al. 2019: fig. 3p; Sangodkar et al. 2022: fig. 3k).

The Mannar Basin seep community includes siboglinids (as *Lamellibrachia* sp., Mazumdar et al. 2021: fig. 2), munidopsids (Mazumdar et al. 2021: fig. 4a–d), and gastropods and bivalves. Some of the illustrated siboglinid tubes have neolepadid specimens attached to them, identified as *Neolepas* sp. (Mazumdar et al. 2021: fig. 2c, d). The gastropods are large buccinoid species (Mazumdar et al. 2021: fig. 4e); the bivalves are bathymodiolins and vesicomyids, identified as *Calyptogena* sp. (Mazumdar et al. 2021: fig. 4f). Based on the external morphology of the illustrated specimen, this latter taxon looks similar to the large vesicomyids from the modern Krishna-Godavari Basin seep communities, but not elongated enough to be conspecific with our *Archivesica* cf. *kawamurai* specimens.

Some of the taxa characteristic of deep-water seep communities are shared between the Krishna-Godavari Basin fossil seep assemblage and the modern seeps elsewhere in the Indian Ocean, at least at higher taxonomic levels. In the seeps off Indonesia shared taxa include serpulids and mytilids in the Semeulue seep community off northern Sumatra, vesicomyids, thyasirids and *Acharax* at the Snail Hill seep in the Sunda Arc, and *Archivesica garuda* (Okutani & Soh, 2005) at the seep off eastern Java. The latter species is not the same as our *Archivesica* cf. *kawamurai*, which is interesting, as *Archivesica kawamurai* is a species common in modern and fossil (Pliocene) seeps from Japan (Amano and Kiel 2010), geographically considerably further away from India than the Indonesian seeps. There are also shared higher taxa between the Krishna-Godavari Basin fossil seep assemblage and the modern seeps on the Makran accretionary margin below 1000 m water depth. These are neolepadids, bathymodiolins, *Archarax*, and *Calyptogena makranensis* Krylova & Sahling, 2006.

The non-obligate molluscan taxa in the Krishna-Godavari Basin fossil seep assemblage comprises typical representatives of taxa found in upper bathyal zone sediments globally, some already known from around the Indian continental margin (e.g., Conidae, *Acharax*, *Ledella*, *Yoldiella*, Propeamussidae, *Vesicomya*), and some that where previously not recorded from this area (e.g., *Mesopelex*, *Cirsonella*, *Cadulus*, and possibly *Dikoleps*). However, the latter observation may reflect the general poor state of knowledge of Indian deep water molluscs. For example, the compilation in Rajendra et al. (2021; Table 1) lists only 25 deep sea bivalve, gastropod and scaphopod species.

In summary, the Upper Pleistocene seep assemblage was structured ecologically and taxonomically very like modern deep water seep communities, from offshore India and elsewhere in the Indian Ocean in containing a small number obligate taxa, most of which likely had chemosymbionts (e.g., *Acharax*, *Gigantidas*, Pliocardiinae, *Conchocele*, *Ashinkailepas*), as well as a greater diversity of morphologically smaller species that represent common deep-sea taxa, with a wide variety of palaeoecologies (Table 2). However, pending taxonomic work on the modern seep fauna, the significance of the fossil seep faunas in the Krishna-Godavari Basin for understanding community evolution and palaeobiogeography in hydrocarbon seep environments in the Indian Ocean will be limited. What is certain is that many more seep communities are to be identified in the Indian Ocean, both modern and fossil. In the Recent this is evidenced, for example, by the occurrence of probable seep obligate pliocardiins in deep water off Bali (*Pliocardia solidissima* [Prashad, 1932] at SIBOGA sta. 18; Prashad 1932). Additional fossil evidence comes from the presence of the shells of large bathymodiolins and pliocardiins, together with MDAC, in horizons of sediment cores both younger and older than the Upper Pleistocene, in the Krishna-Godavari Basin and Mannar Basin (e.g., Teichert et al. 2014; Mazumdar et al. 2019, 2021; Kocherla et al. 2015).

Conclusions

The here described mollusc fauna of a bathyal Upper Pleistocene fossil methane seep deposit from between 15.3 mbsf and 17 mbsf in cores NGHP-01-12A and NGHP-01-10D in the Krishna-Godavari Basin comprises 29 taxa: 15 gastropods, 12 bivalves, and two scaphopods. Of these nine are new species: six gastropods and three bivalves. Six are likely to have had chemosymbionts, representing 21% of the diversity. The majority of these taxa were likely to have been obligate to seeps, as was probably the case for two of the new gastropod species. The rest of the mollusc taxa have living relatives common in bathyal habitats and were thus most likely facultative or "background" fauna in the fossil seep assemblage. The presence of a bathymodiolin mussel shell fragment from 42 mbsf level in Core NGHP-01-12A indicates that methane seep communities were also present sometime earlier in the Krishna-Godavari Basin. The molluscan assemblage from the Upper Pleistocene Seep deposit shares some taxa with recent seep communities from the east coast of India and elsewhere in the Indian Ocean, as well as with fossils from other sediment cores from the Krishna-Godavari Basin. The extent of taxonomic similarities between these Indian Ocean seep faunas awaits further systematic work.

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