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Gigantidas niobengalensis sp. nov. (Bivalvia: Mytiloidea) from a methane seep in the Krishna–Godavari Basin, Bay of Bengal

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Abstract. A new species of a deep-sea Bathymodiolinae mussel is described as *Gigantidas niobengalensis* sp. nov. based on both molecular and morphological data. It was collected at a cold methane seep environment in the Bay of Bengal at 1750 m water depth. It is compared with other species of *Gigantidas*, especially the related *G. childressi*, *G. mauritanicus*, *G. platifrons*, and the *G. haimaensis* group.

Key words. Bathymodiolinae, Mytilidae, India, molecular systematics, anatomy, methane seep

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INTRODUCTION

In January 2018, an active cold seep was discovered in the Krishna–Godavari Basin of the Bay of Bengal, and this was followed in March 2018 by a transit cruise to investigate the macrofauna (Mazumdar *et al.* 2019; Sangodkar *et al.* 2023). Samples from around 1750 m revealed a benthic fauna of Bivalvia, shrimps of the family Caridea, Gastropoda, Malacostraca, Polychaeta, and a few Echinoidea, Ophuroidea, and Echiura. A total of 2313 individuals belonging to eight classes, 18 families, and 20 species were identified (Sangodkar *et al.* 2023). Among the Bivalvia were six specimens of a large bathymodioline mussel, the largest measuring 161 mm in length. A single specimen of *Acharax* Dall, 1908 (Solemyidae) was the only other bivalve obtained (Fig. 5F).

Species belonging to the chemosymbiotic Bathymodiolinae are associated with hot vents, cold seeps, and wood and whale falls, and they have been found in all temperate and tropical oceans (Taylor & Glover 2010). Following Thubaut *et al.* (2013), eight genera are now included of which three are represented by large to very large shells (to 200 mm): *Bathymodiolus* Kenk & B.R. Wilson, 1985; *Gigantidas* Cosel & B.A. Marshall, 2003, and *Vulcanidas* Cosel & B.A. Marshall, 2010.

Large species of Bathymodiolinae from oceans adjacent

to India are few. The first species of *Bathymodiolus* to be recorded from the western Indian Ocean was *B. marisindicus* Hashimoto, 2001, but it is now regarded as *B. septemdierum* Hashimoto & Okutani, 1994. More recently *Gigantidas vrijenhoeki* S.-J. Jang *et al.*, 2020 was described from the Onnuri Vent Field on the Central Indian Ridge. No large bathymodiolines have been described from the Bay of Bengal although both Mazumdar *et al.* (2019) and Sandokar *et al.* (2023) illustrated shells from the Krishna–Godavari Basin along with the often-associated, chemosymbiotic solemyid, *Acharax* (Subba Rao 2017).

This paper is taxonomic in nature and aims to identify the Bay of Bengal mussels, describe them, and discuss their relationships within the Bathymodiolinae.

MATERIALS AND METHODS

Specimen collection and deposition. The samples of the new species were collected during a transit cruise on-board RV *Sindhu Sadhana* in March 2018 in the Krishna–Godavari Basin, western Bay of Bengal, India. Six specimens were deposited in the National Repository for Marine Flora and Fauna at CSIR—National Institute of Oceanography, Dona Paula, Goa, India with the accession number NIO1006/21.

Methods. The morphology was recorded photographically using a Leica Z6 with a Nikon D750 or the same camera and with a 60 mm 1:1 macro lens. All photographs were stacked using Helicon Remote and rendered using Helicon Focus. Dissections were performed under a Leica MZ12 stereomicroscope, with some tissues stained in Methylene Blue to enhance contrast.

Molecular methods. Whole genomic DNA was extracted from mantle tissue samples. The conventional hexadecyltrimethyl-ammonium bromide (CTAB) protocol, modified from Doyle and Dickson (1987), was used for the extraction of DNA (Folmer et al. 1994). The mitochondrial cytochrome oxidase subunit I gene (COI) fragment was amplified using 1 μ l of the extracted DNA as the template for a 50 μ 1 PCR reaction with four units of Taq polymerase (Promega) per reaction. Amplifications were conducted through 35 cycles at the following parameters: 1 min at 95 °C, 1 min at 40 °C, and 1.5 min at 72 °C, followed by a final extension step at 72 °C for 7 min. Amplifications were confirmed by gel electrophoresis, using 2% w/v agarose gel stained with ethidium bromide. Primers LCO1490 (5' -GGTCAACAAATCATAAAGATATTGG - 3') and HCO 2198 (5' – TGATTTTTGGTCACCCTGAAGTTTA – 3') were used for cycle-sequencing of the double-stranded PCR products (Folmer et al. 1994). Direct sequencing of the purified double-strand PCR product was performed using a sequencing ready reaction kit (Brand name) according to the manufacturer's directions. Sequence data were deposited in GenBank (GB) database under accession number ON964868. A specimen identification was attempted using a *blastn* analysis (Johnson *et al.* 2008) and the BOLD Systems platform (Ratnasingham & Hebert 2007). The preliminary DNA barcoding approach guided our further phylogenetic analyses. The entire COI dataset of Bathymodiolinae sequences published by Xu et al. (2019) was downloaded from GenBank. Sequence alignment was performed between our sequence ON964868 and the GenBank dataset using MAFFT v. 7.490 (Katoh & Standley 2013) under the default parameters. Clean sequences were trimmed to the start and length of baseline barcode sequences downloaded from GenBank and exported as FASTA files for molecular evolutionary analysis.

Maximum-likelihood (ML) analyses were performed to assess the phylogenetic relationship of our specimen with the rest of the species within the subfamily Bathymodiolinae. The ML tree was obtained using IQ-TREE v. 1.6.12 (Trifinopoulos & Nguyen 2016) based on the best substitution model determined for each gene fragment by the ModelFinder module (Kalyaanamoorthy et al. 2017) under the cAIC criterion. Node support was assessed with 1,000 ultrafast bootstrapping pseudoreplicates (uBS). IQ-TREE analyses were performed using the W-IQ-TREE web server (Trifinopoulos et al. 2016). The interspecific genetic divergences of the subfamily Bathymodiolinae were calculated using a neighbour-joining (NJ) analysis which was performed under the Kimura-2-parameter (K2P) evolutionary model (Kimura 1980) using MEGA11 (Tamura et al. 2021). The topology of ML and NJ trees were visualized and edited using FigTree v. 1.4.4 (Rambaut & Drummond 2009). Both ML and NJ trees were rooted according to the phylogenetic results showed in Xu et al. (2019). The COI interspecific genetic distance values based on K2p and p-distance models were calculated using MEGA11 (Tamura et al. 2021) with pairwise deletion option.

RESULTS

Molecular results

The COI fragment of the Bay of Bengal mussel (ON964868) is 602 bp long. The *blastn* analysis sequence revealed similarity of 97.23% with Gigantidas mauritanicus isolate 2859 (accession no. KU597623) (Assié et al. 2016). Specimen identification using BOLD Systems (Ratnasingham & Hebert 2007) revealed similarity of 98.35% with an unidentified sequence "Bathymodiolus sp. AA-2016 isolate 28, Makran coast, Pakistan" (accession no. KU597624) (Assié et al. 2016). The other matches were with Gigantidas species with less than 97% of similarity. The ML analyses confirmed that the Bay of Bengal bathymodioline belongs to the genus *Gigantidas* with a high statistical support (uBS = 93; Fig. 1). Both ML and NJ trees show a sister relationship between the Bay of Bengal bathymodioline and the Atlantic G. mauritanicus (Cosel, 2002), and a close relationship with G. childressi (Gustafson et al., 1998) as well as the Indo-Pacific G. platifrons (Hashimoto & Okutani, 1994) and G. haimaensis T. Xu et al., 2019 (Figs 1, 2). The Bay of Bengal bathymodioline species presents close interspecific divergences with the previous mentioned species ranging between 2.38 and 3.49% (K2p), and 2.23 and 3.39% (*p*-distance) (Fig. 2; Table 1).

Systematics

Bivalvia

Order Mytilida A. Férussac, 1822 Family Mytilidae Rafinesque, 1815 Subfamily Bathymodiolinae Kenk & B.R. Wilson, 1985



Figure 1. Maximum-likelihood phylogenetic tree of Bathymodiolinae based on COI sequences. Black circles indicate nodes with an ultrafast bootstrap support uBS > 90. The new species from the Bay of Bengal is shown in red.



Figure 2. Neighbour-joining tree of the subfamily Bathymodiolinae based on COI sequences using the K2p evolutionary model. The new species from the Bay of Bengal is shown in red. Genetic divergence values (K2p) are showed on branches.

	G. niobengalensis	G. mauritanicus	G. childressi	G. platifrons	G. haimaensis
G. niobengalensis ON964868	_	2.23%	3.21%	3.39%	3.03%
G. mauritanicus FJ890502	2.38%	—	3.11%	3.63%	3.90%
G. childressi KU597636	3.30%	3.20%	_	5.29%	4.97%
G. platifrons KU975036	3.49%	3.74%	5.53%	_	3.42%
G. haemaensis MK534977	3.11%	4.03%	5.18%	3.52%	

Table 1. COI interspecific genetic distances (K2p: lower; *p*-distance: upper) of the closest relatives of *Gigantidas niobengalensis* n. sp. according to our phylogenetic trees.

Genus Gigantidas Cosel & B.A. Marshal, 2003

Generic definition. Shells modioliform, large to very large; umbos subterminal to almost terminal; periostracum lacking hairs in adults. Chemosymbiotic; ctendium thick, fleshy; mantle edges smooth; valvular siphonal membrane present or absent. Posterior pedal and byssus retractor muscle attachments in a bundle, not widely separated from posterior adductor muscle.

Remarks. Morphological distinctions at the generic level between generic *Gigantidas* and *Bathymodiolus* are difficult to characterise. The type species of *Gigantidas* (*G. gladius* Cosel & B.A. Marshall, 2003) is very large (over 300 mm), with beaks well behind the anterior end of a narrow, sick-le-shaped (adulaform) shell. Additionally, Cosel & Marshall (2003) noted that it lacked the siphonal valvular membrane seen in other species of *Bathymodiolus* known at that time. Since then, with the application of DNA sequencing and the inclusion of other species of Bathymodiolinae into *Gigantidas*, the only character that has remained is the multiple bundling of the posterior pedal retractor muscle and byssus retractor muscles. Cosel (2008) alluded to this in his discussion, where he recognised two clades within *Bathymodiolus*,

Table 2. Type material of Gigantidas niobengalensis sp. nov.

the *B. childressi* clade with a multi-bundle posterior retractor complex and the *B. thermophilus* Kenk & B.R. Wilson, 1985 clade with two well-separated muscle bundles. The *B. childressi* clade is now included in *Gigantidas*.

Gigantidas niobengalensis sp. nov.

Figures 3, 4, 5A–E, 6A

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Type locality. Krishna–Godavari Basin, western Bay of Bengal, India; 15°42.9281′N, 082°03.8217′E, 1750 m deep; RV *Sindhu Sadhana*, March 2018.

Type material. Table 2.

Description of shell. Holotype (Fig. 3A–C) large, 161 mm long, moderately inflated, widest across posterior area of umbos, equivalve. Inequilateral beaks close to anterior end, 16 mm from anterior edge. Outline modioliform; beaks subterminal; ligament margin long, straight, angled with remainder of dorsal margin, straight to slightly concave; posterior broadly rounded; ventral margin long, slightly concave; anterior margin narrowly rounded. Ventral area weakly sulcate; byssal gape not apparent.

	Length (mm)	Height (mm)	Tumidity (mm) joined valves	Anterior edge to beak (mm)	Ligament length (mm)	Condition	Accession no.
Holotype (Fig. 3A–C)	161.0	87.5	58.2	16.0	69.9	Dry shell	NIO1006/21/1
Paratypes							
1 (Fig. 4)	93.0					Broken, body used for dissection	NIO1006/21/2
2 (Fig. 3E)	95.2	55.0	39.6	3.3	48.1	Tissues used for DNA extraction, only dry shell kept	NIO1006/21/3
3 (Fig. 5A–C)	100.2	57.5	49.1	2.0		Specimen in 70% ethanol	NIO1006/21/4
4 (Fig. 3F)	79.4	46.7				Broken, body in 70% ethnol	NIO1006/21/5
5 (Fig. 3D)	132.0	62.3	45.1	10.3		Specimen in 70% ethanol	NIO1006/21/6



Figure 3. Shells of *Gigantidas niobengalensis* n. sp. All to scale. A-C, holotype: (A) left valve exterior; (B) right valve interior (aa = anterior adductor scar; pa = posterior adductor scar; pprm = scar of posterior pedal retractor bundle); (C) dorsal view of joined valves. D, paratype 5, right valve exterior. E, paratype 2, left valve exterior. F, Paratype 4, left valve exterior.



Figure 4. Anatomy of *Gigantidas niobengalensis* n. sp. **A**, gross anatomy of holotype left valve and mantle removed. **B**, anterior of Paratype 1 (ct = ctenidium; f = foot; m = mouth; og = oral groove; pl = labial palps). C, posterior view of holotype (ea = exhalant siphon; imf = inner mantle fold; omf = outer mantle fold; vsm = valvular siphonal membrane). D, paratype 1, dissection of pedal musculature (aa = anterior adductor muscle; apr = anterior pedal retractor muscle; by = byssus; f = foot; pa = posterior adductor muscle; pbrA = anterior bundle of pedal byssus retractor muscles; ppr = posterior pedal retractor muscle).



Figure 5. A–E, *Gigantidas niobengalensis* n. sp., paratype 3, and attached stalked barnacle: (A, C) exterior of right and left valves; (B) posterior margin of right valve showing numerous attached byssi; (D) stalked barnacle, as seen in C; (E) anatomy after removal of left valve and mantle (aa = anterior adductor muscle; apr = anterior pedal retractor muscle; by = byssus; f = foot; imf = inner mantle fold; m = mouth pa = posterior adductor muscle; pl = labial palps; pprm = pedal and byssus retractor bundle). F, *Acharax* sp., the only other bivalve found at the type locality of the new species.

Interior lacking hinge teeth. Posterior adductor scar subcircular, coalescing with posterior pedal retractor scars; anterior adductor scar small, elliptical.

Exterior with periostracum persistent, weakly wrinkled

over posterior area, deep chestnut-brown. Interior slightly pearlescent, white to pale grey.

Variation in shells. The shells of the paratypes are 79–132 mm long. Unlike the holotype, the slightly concave hori-



Figure 6. Shell and muscle-scar outlines in species of *Gigantidas* belonging to the *G. childressi* clade. Partly after Xu *et al.* (2019). Scale bars = 10 mm.

zontal dorsal margin becomes less apparent; in the largest paratype (Fig. 3D) the posterior dorsal margin is straight but slopes into the posterior margin, whereas in the smaller shells (Fig. 3E, F) there is no distinct posterior dorsal margin and the broadly rounded posterior begins at the end of the ligament margin. Furthermore, the anterior area is prominent only in the two larger shells, while the umbos are almost terminal in the others.

In paratype 3 (Fig. 5A–C) the shell appears to have numerous periostracal hairs around the posterior margin (Fig. 5B), along with a few stalked barnacles (Fig. 5C, D). On closer examination, these hairs are not periostracal in origin but are the remnants of byssus threads from other mussels previously attached to this shell. Similar remnants can be found on the other shells, but they are very sparse.

Anatomy. The gross anatomy has been examined in the holotype and Paratype 3 while Paratype 1 was used for dissection.

Adductor and pedal musculature (Figs 4A–D, 7A): heteromyarian, posterior adductor muscle [pa] subcircular approximately four times larger than elliptical anterior adductor muscle [aa]. Pedal retractors with short joint stem, anterior pedal retractor [apr] divides into a number of strands and attachment points adhering just behind beaks in umbonal cavity; posterior pedal retractor small adhering to the dorsal area close to the centre of the ligament margin. Posterior pedal retractor attachment close to a bundle of anterior byssus retractor muscles [pbrA] formed of three strands.



Figure 7. Stylised diagrams of the musculature of three *Gigantidas* species. **A**, *G. niobengalensis*. **B**, *G. haimaensis* (after Xu *et al.* 2019). **C**, *G. vrjenhoeki* (after Jang *et al.* 2020).

Another bundle of byssus retractor muscles [pbrB], formed of four strands in two, adheres to the dorsal area close to the posterior adductor.

Foot (Figs 4A–C) [f]: small, finger-like, with a small heel [h] and byssal groove. Byssus [by] consists of up to 15 fine strands with flattened attachment areas.

Ctenidium (Fig. 4A, B) [ct]: large, formed of two demibranchs; details of fine structure not discernable due to state of preservation but filaments appear thickened. Labial palps [lp] triangular, with a long oral groove [og] to mouth [m] (Fig. 4B).

Mantle (Fig. 4A, C): rather thick; outer mantle fold narrow [omf], continuously separate from inner mantle fold [imf]. Inner mantle thin, smooth, wider close to the exhalent aperture; valvular siphonal membrane [vsm] thin, triangular. Exhalent aperture large [ea], with margins smooth.

Variation in anatomy. Paratype 3 has a flimsy anatomy (Fig. SE), and the ctenidia in particular appear almost transparent and, therefore, are probably devoid of symbiotic bacteria (Fig. SE). However, the arrangement of the pedal and byssal musculature (Fig. SE) agrees with that described above.

Habitat. The Krishna–Godavari Basin is a rift basin located in the Bay of Bengal, an area of more than 50,000 km². The study site is on the continental slope and is a seep environment at 1750 m water depth. The sediment was dark grey, clay-like, and had a hydrogen sulphide odour. The sediment temperature was 10 ± 0 °C, pH 7.66 \pm 0.02, and labile organic carbon 0.33 \pm 0.11% (Sangodkar *et al.* 2023).

Range. Known only from the type locality, in the Krishna–Godavari Basin, Bay of Bengal.

Etymology. The species epithet is a combination of the prefix *nio*, the abbreviation for the National Institute of Oceanography (India) that collected the species, and *bengalensis*, for the Bay of Bengal where the type locality is located.

DISCUSSION

The preliminary DNA-barcoding analyses on our specimen did not allow for a species identification. The closest match (<2% of genetic divergence) was with an unidentified specimen from the Pakistan Accretionary Wedge in the Gulf of Oman (Assié *et al.* 2016). This similarity was retrieved only by BOLD Systems, but not by the *blastn* algorithm. This led He *et al.* (2023) to conclude that the Indian and Pakistan mussels were likely to be the same species but with substantial interpopulation differentiation. At this time there are no morphological data on the Pakistan mussels.

The ML and NJ analyses based on the COI marker showed that *G. niobengalensis* n. sp. is part of a clade recognised by Xu *et al.* (2019) which includes both Atlantic and Indo-Pacific species and here termed the *childressi* clade (Fig. 2). The geographic distribution of species in this clade along with all other *Gigantidas* species is shown in Figure 8. The closest relationship is with the Atlantic *G. mauritianicus* (Cosel, 2002), with only 2.38% of divergence (K2p) based on COI. Other species in the clade also have very small divergence values from *G. niobengalensis* and each other ranging from 3.11% to 5.53% (K2p; Table 1). Genetic divergences between other *Gigantidas* species are also low. Genetic divergence between *G. haimaensis* and *G. platifrons* is 3.52% (K2p), that between *G. mauritianicus* and *G. chil*-



Figure 8. Distribution of *Gigantidas* species, as listed in MolluscaBase (2024). Species belonging to the *G. childressi* clade are shown in black, all others in red.

dressi is 3.20% (K2p). Other small genetic distances occur elsewhere as exemplified between G. tangaroa (Cosel & Marshall, 2003) and G. securiformis (Okutani, Fujikura & Sasaki, 2004) that is only 2.94% (K2p). Such small values in genetic divergences could suggest that species within Gigantidas had a recent speciation and distance values may not be a reliable indicator for distinguishing species. He et al. (2023), in discussing the relationships among the South China Sea and Indian Ocean seep faunas, suggested that they could have had an origin in the Philippines region, but gave no explanation for the similarities between the Indo-Pacific and Atlantic species. At no time did He et al. (2023) suggest that the Indian/Pakistan clade was conspecific with G. childressi or G. mauritanicus, nor did they find any conflict in the small genetic distances between all the species in the childressi clade.

Based on morphology, affinity with the genus *Gigantidas* is supported by the arrangement of the pedal and byssus retractor mussels.

Xu *et al.* (2019), in describing *G. haimaensis*, made morphological comparisons with *G. platifrons*, *G. childressi*, and *G. mauritanicus*, as these species were sister taxa in their molecular phylogeny. On shell morphology alone Xu *et al.* distinguished *G. haimaensis* and *G. platifrons* from *G. childressi* and *G. mauritanicus*; the shells of the first pair have straight dorsal and ventral margins, whereas in the latter pair the dorsal margin is convex and the ventral margin concave. In *G. niobengalensis*, the ventral margin is concave, and the dorsal margin angulate in larger shells. Following Xu *et al.* 2019, the outlines of the species in the *G. childressi* clade, including that of *G. niobengalensis*, are reproduced here (Fig. 6).

Most *Gigantidas* species have been described from the West Pacific and Atlantic Oceans (Fig. 8). The only West Indian Ocean species, *G. vrijenhoeki*, differs both in shell and anatomy, but most significantly in the latter, where the base of the posterior pedal retractor is widely separated from the byssus retractor and the first strand of the posterior byssus retractor bundle is widely separated from the remainder (Fig. 7C). Figure 7A and B show the comparable arrangement of musculature in *G. niobengalensis* and *G. haimaensis*, respectively.

West Pacific species include *G. platifrons, G. haimaensis, G. horikoshii* (Hashimoto & Yamane, 2005), and *G. taiwanensis* (Cosel, 2008); the genetic distances place only the former two species in the same clade as *G. niobengalensis*.

A discussion on the differences in shell shape between smaller and larger shells is necessary, as it might be concluded on shell shape alone that within the six specimens from the Bay of Bengal, two distinct species may be present. The larger shells (Fig. 3A, D) have subterminal umbos, whereas the smaller shells (Fig. 3E, F) have almost terminal umbos.

Unfortunately, the sample size is too small to prepare a growth series, but relying only on the pedal musculature, it is concluded that all the specimens are conspecific. Cosel (2008) noted that the shell of *Bathymodiolus taiwanensis* Cosel, 2008, now *Gigantidas taiwanensis* (Cosel, 2008), varies in outline, with larger shells having a concave ventral margin contrasting with the straight ventral margin of smaller shells. Furthermore, the position of the umbos is more to the anterior in smaller shells; compare Cosel's (2008) figures 3E–J and 2C–H.

The distribution and dispersal of bathymodioline species have been studied in the Indo-West Pacific (Kyuno et al. 2009), where it is suggested that, despite wide separation of vent sites, there may be little genetic separation at the species level. Remarkably similar gene sequences were recognised, suggesting high levels of gene flow even between populations thousands of kilometres apart. Kyuno et al. (2009) hypothesised that populations could disperse along ocean spreading ridges or via isolated seeps, wood, and whale falls that would provide the necessary chemosynthetic settings. Populations living at methane seeps are not linked along rift margins and may be genetically isolated. He (2023) suggested that G. haimaensis is endemic to the Haima seep but that G. platifrons is more widely distributed. Figure 8 shows the distribution of Gigantidas species belonging to the G. childressi clade and other similar Gigantidas species as listed in MolluscaBase (2024).

Within the G. childressi clade a combination of shell morphology and a genetic distance between 2.38 and 3.49 is adopted as significant at the species level. Similar, low levels of genetic diversity are accepted for other sister taxa such as G. securiformis/G. tangaroa (2.94%) and Bathymodiolus boomerang Cosel & Olu, 1998/B. heckerae R.D. Turner et al., 1998 (1.4%; from Fig. 2). Only in the *B. septemdeirum/brev*ior/marindicus complex has the genetic distance of <1% led to the synonymisation of these three nominal taxa (Tunnicliffe & Breusing 2022). Despite the small genetic distances between species in the G. childressi clade, the morphology and wide geographical separation suggest that G. niobengalensis is not specific with G. mauritanicus. The slightly larger genetic distances and morphological difference further suggest that G. niobengalensis is not conspecific with G. childressi and neither with G. platifrons nor G. haimaensis. Further, more detailed molecular analyses of the closely related species within the Bathymodiolinae may clarify their evolutionary history.

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