

# A new deep-sea species of *Elliptiolumina* Cosel & Bouchet, 2008 (Bivalvia, Lucinida, Lucinidae) from cold seep of the South China Sea

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## Abstract

The increasing discoveries of new species of the family Lucinidae in the last two decades indicated a surprising diversity of chemosynthetic lucinids in the deep sea, especially in the Indo-West Pacific. However, only a few records have been reported from the South China Sea. A new lucinid species *Elliptiolumina subovalis* sp. nov. is here reported from a deep-sea cold seep site of the South China Sea. The new species is distinct from its congeners by possessing a strong anterior lateral tooth on the right valve and anterior tapering, subrectangular-oval shells. Sequences of three genes (18S rRNA, 28S rRNA, and CytB) were used to analyze its relationships with other species in the subfamily Myrteinae and confirm its taxonomic placement. The result supports the monophyly of Myrteinae but also demonstrates the polyphyly of *Elliptiolumina*. The new species has a close relationship with *E. williamsae* and *Rostrilucina garuda*, but is not closely related to congener *E. ingens*. By comparing morphological characters, we suggest that *E. ingens* should not belong to the genus *Elliptiolumina*. The basal two of three deep-sea clades recognized in Myrteinae may indicate the deep-sea origin of this subfamily. Our results add to the known diversity of deep-sea lucinids and molecular information for poorly studied Myrteinae and highlight the necessity of further investigation on deep-sea lucinids of the South China Sea.

## Key Words

Cold seep, *Elliptiolumina*, Lucinidae, Myrteinae, new species, South China Sea

## Introduction

Lucinidae J. Fleming, 1828 is a widespread family in Bivalvia with a known latitudinal range from 70°N to 55°S and a depth range from intertidal to 2570 m (Taylor and Glover 2021). Even though they are often diverse and prolific in shallow waters, recent surveys have shown remarkable diversity in deep seas (Cosel and Bouchet 2008; Glover and Taylor 2016). As the most diverse group of Bivalvia in the chemosynthetic environment, lucinids cultivate chemoautotrophic bacteria in the ctenidia, which serve as their primary source of nutrition (Taylor et al. 2011). Nowadays, a total of 374 accepted species in Lucinidae are reported worldwide, classified into seven

subfamilies and 96 genera (WoRMS 2023). The coral reef ecosystems of the Indo-West Pacific (IWP) demonstrate the highest diversity of coastal lucinids (Taylor and Glover 2006). As for the deep-water lucinid diversity, its hotspot was also believed to be located at IWP, in the South-East Asian seas from Taiwan to the Arafura Sea (Cosel and Bouchet 2008). In the last two decades, up to 28 new genera and 93 new species were reported from IWP (Jiao and Zhang 2022). Among the new species, 47 are collected from the deep sea (Taylor and Glover 2002, 2005, 2013, 2021; Glover et al. 2003, 2008; Bouchet and Cosel 2004; Glover and Taylor 2007, 2008, 2016; Cosel and Bouchet 2008; Okutani 2011). Bafflingly, despite the great diversity of deep-sea lucinids in the Okinawa

Trough and the region south of the Philippines in IWP, there are few reports of lucinids in the deep sea of the South China Sea, which represents a substantial part of IWP. We have grounds to expect that the South China Sea, similar to other areas of IWP, will yield a significant number of as yet unrecognized species.

The subfamily Myrteinae Chavan, 1969 currently contains 11 extant genera and one fossil genus. Species of this group are often associated with deep, offshore habitats, with only a few inshore species (Taylor and Glover 2021). Due to difficulties in sampling and investigation caused by deep-sea habitats, Myrteinae also is a poorly studied group. Ongoing molecular investigations have dramatically changed the composition and relationships of this subfamily since its establishment (Chavan 1969; Taylor et al. 2011, 2014, 2016, 2022; Kuhara et al. 2014; Glover et al. 2016). However, many taxonomic issues have not been fully resolved in Myrteinae: 1) status of some genera (*Eulopia* Dall, 1901, *Graecina* Cosel, 2006, *Jorgenia* Taylor & Glover, 2009, and *Tellidorella* S. S. Berry, 1963) have not been validated by molecular evidence due to the lack of sequences of representative species; 2) some genera remain polyphyletic; 3) molecular relationships and morphological similarity sometimes contradict (Taylor et al. 2022). The genus *Elliptiolucina* Cosel & Bouchet, 2008 is a relatively new and poorly studied group of Myrteinae that is strongly associated with deep-sea chemosynthetic habitats. To date, all five living species were reported in the hydrocarbon seeps of the IWP (Cosel and Bouchet 2008; Okutani 2011; Kuhara et al. 2014; Glover and Taylor 2016). Kuhara et al. (2014) confirmed that *Elliptiolucina* belongs to the subfamily Myrteinae using two genes (18S rRNA and 28S rRNA), by revealing a close relationship between *E. ingens* Okutani, 2011 with *Notomyrtea botanica* (Hedley, 1918), *Gloverina rectangularis* Cosel & Bouchet, 2008 and an uncertain species of *Myrtea* W. Turton, 1822. Taylor et al. (2022) demonstrated that *Elliptiolucina* is a paraphyletic group as *E. williamsae* Glover & Taylor, 2016 did not cluster with *E. ingens* in the 18S rRNA gene constructed tree.

The discovery of chemosymbiosis in bivalves and the broad biological interest in chemosynthetic environments such as vents, hydrocarbon seeps, and organically enriched habitats have stimulated many recent offshore samplings. It has been revealed that there is a surprising diversity of Lucinidae in offshore shelf and bathyal depths (Taylor et al. 2014). In recent years, with the increased interest in deep-sea exploration, many cold seep sites have been found in the northern part of the South China Sea (Klaucke et al. 2015; Hsu et al. 2017; Liang et al. 2017; Fang et al. 2019). Various benthic macrofauna were collected and recognized from these cold seeps, and numerous species were reported new to science (Li 2017; Dong et al. 2020; Zhao et al. 2020). In this paper, we describe a new species of *Elliptiolucina* collected from a cold seep in the South China Sea at a depth of 1146 m. Morphological examination and molecular analyses of three genes (18S rRNA, 28S rRNA, and CytB) were used

to confirm the taxonomic status of this specimen. We also discuss the ascription and relationships of species assigned to *Elliptiolucina* and the relationships among shallow water and deep-sea species of Myrteinae. This study adds to the known diversity of deep-sea lucinids providing more molecular information for poorly studied Myrteinae. It also implies a potential uncovered diversity of Lucinidae in the South China Sea.

## Materials and methods

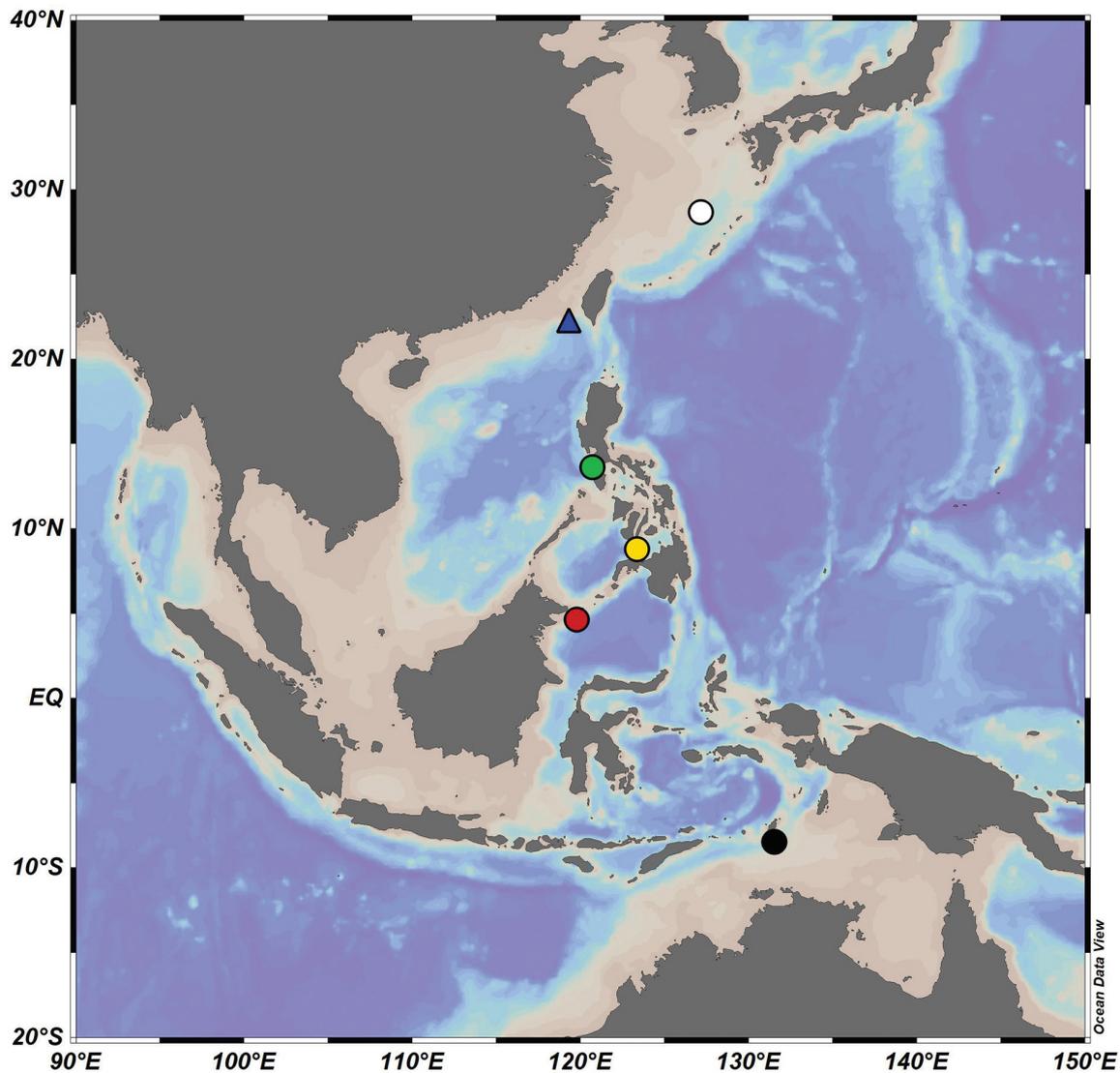
### Sample collection and morphological observation

The specimen of this study was collected during a survey of Site F (also called Jiaolong Seep No. 1, Formosa Ridge or Taixinan cold seep), a cold seep of the South China Sea, by a TV grab on Aug. 3, 2018 (Fig. 1). The morphological features were observed under a Zeiss STEREO Discovery V12 stereo microscope (Zeiss, Wetzlar, Germany) equipped with a Zeiss AxioCam 503 digital camera. Photos of the specimen were taken with a SONY ILCE-7RM4 camera. The shell length (SL), shell height (SH), shell width (SW), and length of lunule (LL) were measured by a vernier caliper with an accuracy of 0.01 mm.

### Marker gene acquisition

Genomic DNA was extracted from the muscle tissue of the specimen using QIAamp DNA Mini Kit (Qiagen). The DNA was fragmented with Covaris E220 and selected using AMPure XP beads to obtain fragments around 200 bp. After that, the DNA was sequenced on the MGI-T7 platform with a layout of pair-end 150 bp. All of the generated short reads were filtered using SOAPnuke v.1.5.2 (Chen et al. 2018), and the draft genome (unpublished data) was assembled using SPAdes v.3.15.0 with the kmer of 31, 51, 71, 91 (Bankevich et al. 2012). Both 18S and 28S rRNA sequences were obtained by aligning the genomic assembly to corresponding gene sequences of *Fimbria fimbriata* (see Suppl. material 1) using BLAST v.36. The mitochondrial genome was assembled using NOVOPlasty v4.2 (Dierckxsens et al. 2017), and the mitochondrial genome of *Loripes lacteus* (GenBank, <https://www.ncbi.nlm.nih.gov/genbank/>, accession number: NC\_013271.1) (Dreyer and Steiner 2006) as the ‘Seed Input’ in the configuration file. The genome was annotated using the online tool MITOS (<http://mitos2.bioinf.unileipzig.de/index.py>) (Donath et al. 2019), and the CytB sequence was extracted from the annotation results.

Additional sequences of three genes (18S rRNA, 28S rRNA, and CytB) were retrieved from GenBank according to the accession numbers provided in previous studies on the phylogeny of Lucinidae (Williams et al. 2004; Taylor et al. 2007, 2011, 2014, 2016, 2022; Glover et al.



**Figure 1.** The locations of *Elliptiolucina* species. Blue triangle, *E. subovalis* sp. nov.; green circle: *E. magnifica*; red circle: *E. labeyriei*; yellow circle: *E. williamsae*; black circle, *E. virginiae*; white circle: *E. ingens*.

2008, 2016; Kuhara et al. 2014; see Suppl. material 1). These studies provided detailed information on mapping different markers to certain individuals and included almost all species of lucinids that possess molecular information. Our analyses included most of the species in these previous studies to increase the stability and reliability of our inferred phylogenetic relationship. Species names of these sequences used in this study followed the latest study rather than the original species name in GenBank. Seven species of Thyasiridae Dall, 1900 (1895) and Cyrenoididae H. Adams & A. Adams, 1857 (1853) were selected as outgroups.

### Phylogenetic analysis

Three datasets of different genes were aligned separately using MAFFT v.7.037b (Katoh and Standley 2013) with the iterative refinement method L-INS-i. Then the aligned sequences were uploaded to BioEdit v7.0.9.0 (Hall 1999)

for quality checking and editing. The untrimmed bases from both ends of the sequences were removed manually. Ambiguously aligned sites in the ribosomal gene were removed using GBLOCKS v. 0.91b (Castresana 2000) with the least stringent settings. The final dataset used in phylogenetic trees was constituted of 856 bp of 18S (70% of 1215 bp before Gblock), 1152 bp of 28S (64% of 1774 bp before Gblock), and 324 bp of CytB. The three gene datasets were concatenated into a single dataset by SequenceMatrix v.1.8 (Vaidya et al. 2011) for those individuals with some sequence for at least two genes.

The Maximum likelihood (ML) and Bayesian inference (BI) analysis based on concatenated and 18S datasets were used for phylogenetic analyses. The ML tree was conducted using IQ-TREE v.2.2.0-Linux (Nguyen et al. 2015). The most suitable evolution model was found by ModelFinder (Kalyaanamoorthy et al. 2017) and adopted automatically to infer the ML tree. Bootstrap supports (BS) were calculated with 1,000 replicates to assess branch supports. Gene partition models chosen

for IQ-TREE were 18S rRNA, TNe + FQ + I + R3; 28S rRNA, GTR + F + R4; and cytb, TPM3u + F + I + G4. The concatenated tree was inferred by the edge-proportional partition model with separate substitution models and separate rates across sites. jModeltest v.2.1.10 (Darriba et al. 2012) was used to find the best-fitting evolution models of each group of sequences for Bayesian phylogenetic trees. The best model for all separate genes was GTR + G + I by the Akaike information criterion (AIC). Genes were allowed to have their own model and rate in the concatenated gene analysis. The BI tree was carried out using MrBayes v.3.2.7 (Ronquist et al. 2012) with the best model of each dataset. The posterior probability (PP) was estimated using four chains running 10,000,000 generations and sampled every 1000 generations. The first 25% of sampled trees were discarded as burn-in. The results of ML and BI trees were visualized and rendered using Figtree v.1.4.4 (<http://tree.bio.ed.ac.uk/software/figtree/>).

## Results

### Systematics

#### Family Lucinidae J. Fleming, 1828

#### Subfamily Myrteinae Chavan, 1969

#### Genus *Elliptiolumina* Cosel & Bouchet, 2008

#### *Elliptiolumina subovalis* sp. nov.

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Figs 2, 3, 4F

**Material examined.** *Holotype*: MBM229033, one complete specimen collected on Aug. 3, 2018, by a TV grab, deposited in the Marine Biological Museum, Chinese Academy of Sciences (MBMCAS), Qingdao.

**Description.** Shell medium-sized, 44.7 mm long, thick, elongate (SH/SL 0.78), sub-rectangular oval, inequilateral, nearly equivalve, slightly inflated (SW/SL 0.44). Umbones slightly prominent and prosogyrous, situated in front of the vertical midline, anterior umbonal slope slightly concave, postero-dorsal margin straight. Anterior margin narrowly rounded, posterior margin broad, rounded-truncate, and the vertical part slightly convex. Postero-dorsal corner obtuse. Ventral margin broadly rounded but slopes distinctly upswept in front.

Shell white, flaky periostracum pale-brownish, dense, and slightly wrinkled towards the margin of the shell. Exterior with dense, irregular commarginal growth ribs, fine commarginal striae, and few irregular vertical lines which diverge from the commarginal sculpture and running in a more upward direction on the postero-dorsal area (Fig. 3A), visible on 5× magnification. Both of anterior and posterior dorsal area with one very slight radial depression. Lunule rather long, generally symmetrical, deeply sunken, lanceolate. Escutcheon long, completely covered by ligament which almost occupies the whole postero-dorsal margin and situated on a strong nymph.

Inner shell surface dull white to slightly orange inside pallial line, and glossy at the margin. Dense radial stria from umbonal cavity to the shell margin. Hinge plate narrow, with only very faint and low indications of cardinal teeth in both valves, but a strong anterior lateral tooth in right valve, and a corresponding socket in left valve. Anterior adductor scar elongate, detached from pallial line for less than 1/2 of length. A distinct but shallow pedal retractor scar above the anterior adductor scar. Posterior adductor scar reniform, with a dorsal notch, open to the anterior. Pallial line entire. Shell margin smooth.

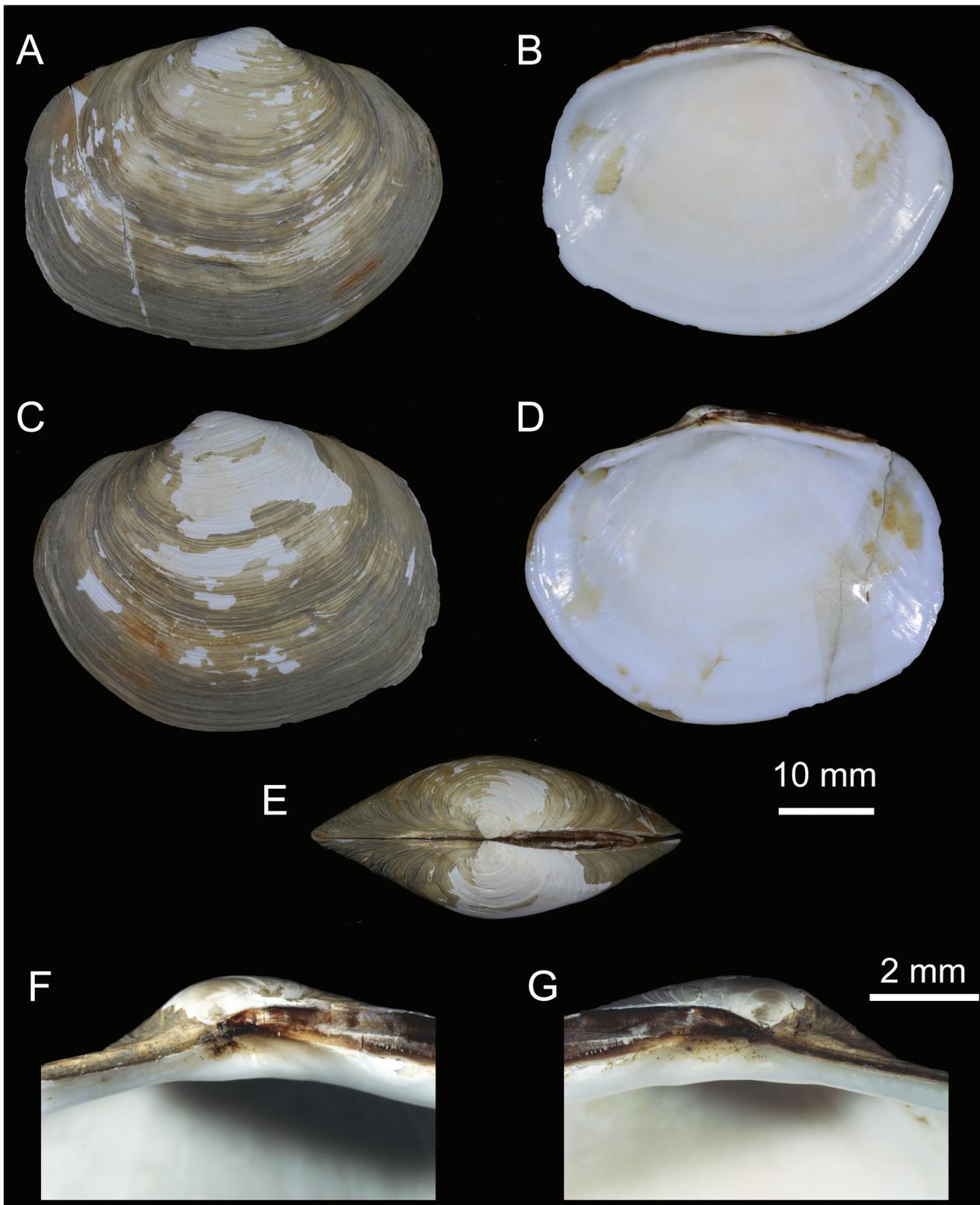
**Etymology.** The specific name *subovalis* was derived from the Latin *sub* + *oval* in reference to the shape of the shell, sub-rectangular oval but more ovate than most congeners.

**Type locality.** An active seepage site (22.1159°N, 119.2854°E), site F, in southwest Taiwan, South China Sea, 1146 m depth (Fig. 1). Buried in the muddy bottom near the seep.

**Remarks.** The new species possesses thick, elongated shells with fine commarginal sculptures, a relatively short anterior adductor muscle scar, and a narrow hinge, especially a dorsal notch in the posterior adductor scar, which are in accord with the key characteristics of Myrteinae. It corresponds to the genus *Elliptiolumina* in the elongated shells and fine irregular commarginal sculptures. The new species was found from IWP. The West-Atlantic genus *Jorgenia* shares similar general morphology of the outer shell with *Elliptiolumina*. But the limited distribution combined with the different hinge features (small but distinct cardinal teeth in both valves of *Jorgenia*) can differentiate the two genera.

*Elliptiolumina subovalis* sp. nov. is distinct from other congeners by possessing a strong anterior lateral tooth on the right valve and anterior tapering, subrectangular-oval shells (Table 1, Fig. 4). The new species is morphologically similar to *E. magnifica* Cosel & Bouchet, 2008 in outline but can be distinguished by the more prominent and prosogyrous umbones and the lateral tooth. *Elliptiolumina subovalis* sp. nov. is the second species after *E. williamsae* known to possess a lateral tooth. The distinct cardinal teeth of *E. williamsae* can be used to separate it from the new species. In addition, the tapering anterior shell of *E. subovalis* differentiates the two species. *E. virginiae* Cosel & Bouchet, 2008 can be distinguished from the new species by its almost rectangular outline. It has a straight dorsal margin and vertical posterior margin, while the shell shape of *E. subovalis* sp. nov. is rather sub-ovate. The more compressed shells of *E. virginiae* (SW/SL ratio = 26–29%) and *E. labeyriei* Cosel & Bouchet, 2008 (SW/SL ratio = 24–33%) are distinct from that of *E. subovalis* sp. nov. (SW/SL ratio = 44%). *E. ingens* can be separated from the new species by its ridges in the inner surface running from the umbonal cavity to both posterior and anterior adductor scars and the absence of a posterior dorsal corner on the external surface.

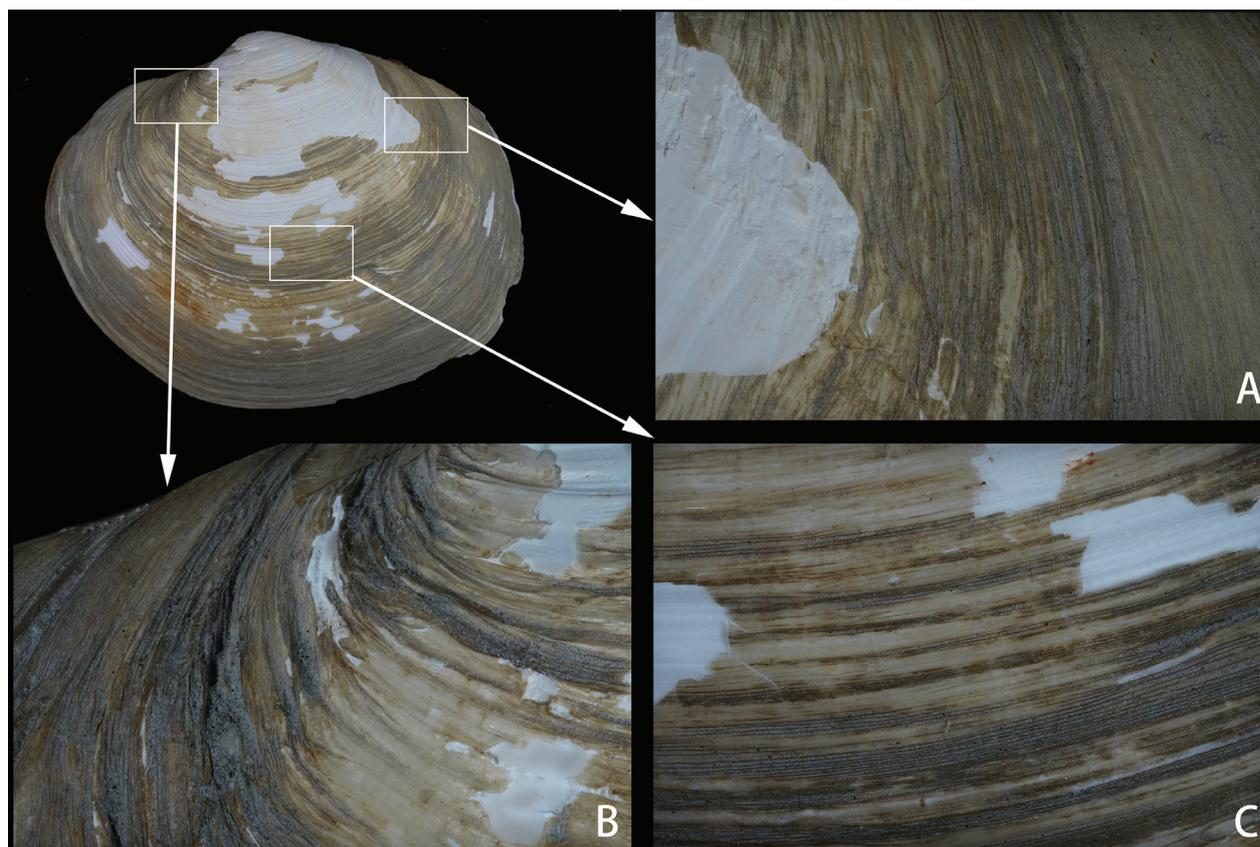
**Molecular analysis.** The obtained sequences were uploaded in GenBank (see Suppl. material 1). The entire dataset included sequences of 219 individuals from 146



**Figure 2.** *Elliptiolumina subovalis* sp. nov. **A, B.** Exterior and interior of the right valve; **C, D.** Exterior and interior of the left valve; **E.** Dorsal view; **F, G.** Detail of the hinge of the right and left valves.

species. Because markers are not always available for the same species, somewhat different taxon sets are employed in three-gene and 18S trees. In particular, for *E. williamsae*, only the 18S rRNA gene was available. Phylogenetic frameworks of ML and BI methods showed similar topologies on each dataset. Thus, four trees were

presented in two summary cartoon trees in our study (Figs 5, 6). Our results based on three-gene (Fig. 5) have divided the species of Lucinidae into seven clades, corresponding to seven subfamilies. Phylogenetic results of two datasets displayed similar topologies within Myrteinae. Our new species *Elliptiolumina subovalis* sp. nov. was found to be



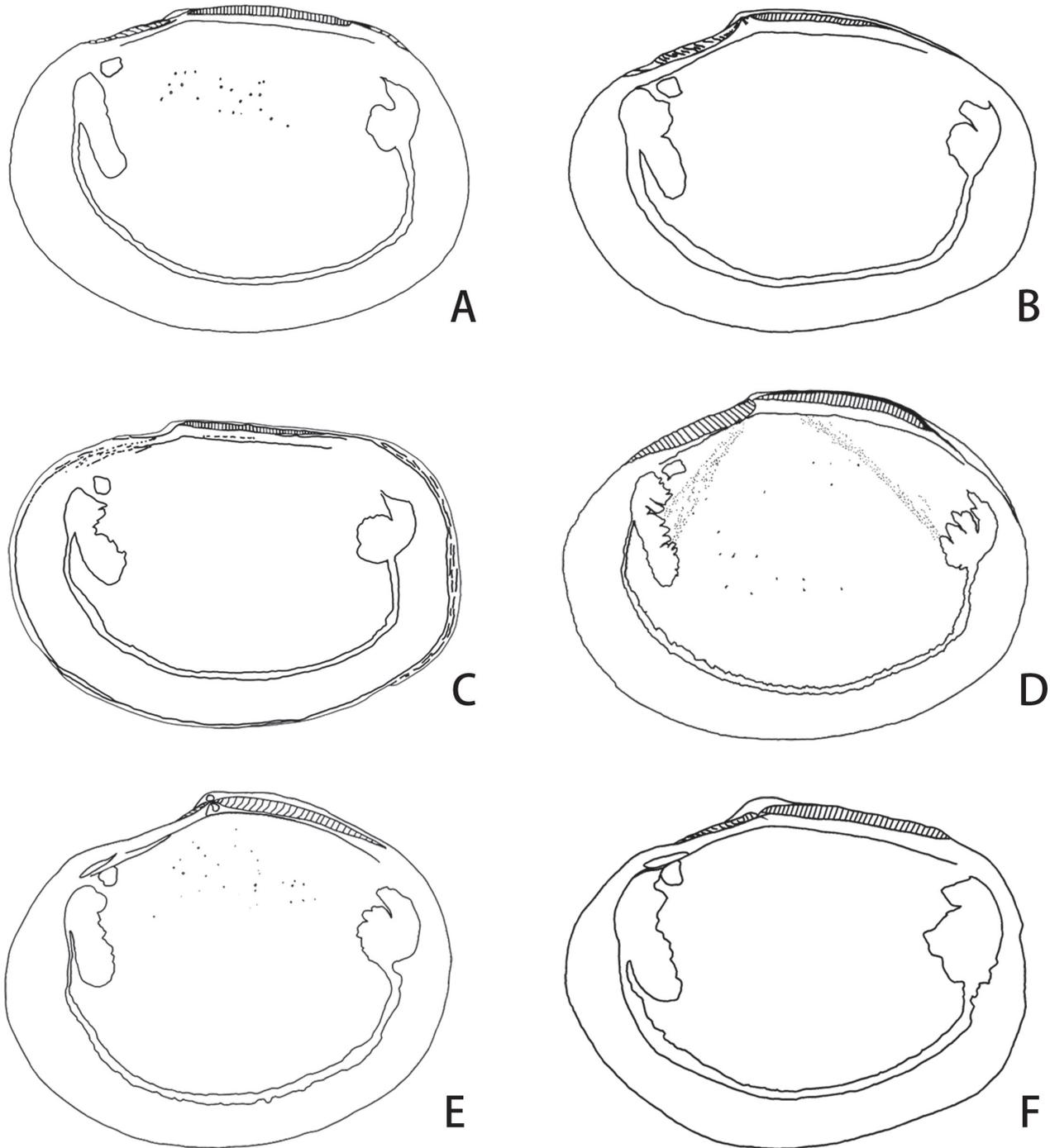
**Figure 3.** Shell sculptures of *Elliptiolumina subovalis* sp. nov. **A.** Posterior surface (~5×); **B.** Anterior surface (~5×); **C.** Middle surface (~5×).

**Table 1.** Comparison of conchological features in all species of the genus *Elliptiolumina*. Modified by Kuhara (2014). Additional information was adapted from Cosel and Bouchet (2008); Okutani (2011); Glover and Taylor (2016).

	<i>E. ingens</i>	<i>E. magnifica</i>	<i>E. labeyriei</i>	<i>E. virginiae</i>	<i>E. williamsae</i>	<i>E. subovalis</i> sp. nov.
Outline	oval, somewhat discoid	subrectangular-oval	subrectangular-oval	sub-rectangular	subovate	subrectangular-oval
Shell length (mm)	53.2–98.4	80.4	18.5–43.6	23.0–78.5	20.5–44.1	44.7
SH/SL ratio	72–84%	72%	68–80%	63–69%	78–86%	78%
SW/SL ratio	29–45%	38%	27–33%	26–29%	36–44%	44%
Umbones	tumid and low	small and flattened	flattened	small	low	slightly prominent
Hinge teeth	edentulous	edentulous	occasionally cardinal tooth indications	edentulous	small cardinal teeth and lateral teeth	cardinal tooth indications and lateral teeth
Width of lunule	narrow	narrow	very narrow	very narrow	narrow	narrow
Length of lunule	rather long to long	rather long	long	short	–	long
LL/SL ratio	22–30%	ca. 22%	ca. 25%	ca. 14%	–	ca. 25%
Outline of posterodorsal corner	round	angular	rather angular	angular	angular	angular
Position of posterodorsal corner	low	high	slightly low	high	slightly low	slightly low

a member of Myrteinae. *E. williamsae* and *E. subovalis* sp. nov. formed a stable sister group in 18S trees. A close relationship between the group *E. subovalis* sp. nov. (+ *E. williamsae*) and *Rostrilucina garuda* Cosel & Bouchet, 2008 was shown in all trees. The new species formed a sister clade of all other Myrteinae species in conjunction with *Rostrilucina garuda* and *Myrtea flabelliformis* (Prasad, 1932) in concatenated trees. In 18S trees, the three species mentioned above, together with the *E. williamsae*, were also basal to other Myrteinae species. The monophyletic *Elliptiolumina* and *Myrtea* were not supported. *E. ingens* involved in a clade composed of *Gloverina* Cosel &

Bouchet, 2008, *Myrtea catonii* (Glover & J. D. Taylor, 2016), *Myrtea vincentia* (Glover & J. D. Taylor, 2007), and another undescribed *Myrtea* species in all trees. Deep-sea species of Myrteinae formed three monophyletic clades in the concatenated dataset (Fig. 5). Two stable monophyletic deep-sea clades (clade A and C) represented by species of *Elliptiolumina*, *Gloverina*, *Myrtea* and *Rostrilucina* Cosel & Bouchet, 2008. The polyphyletic genus *Elliptiolumina* and *Myrtea* were shared in the two clades. One species of *Taylorina* Cosel & Bouchet, 2008, *T. solomonensis* Cosel & Bouchet, 2008, formed a separate clade, as the sister group of clade A plus all of shallow-sea Myrteinae.



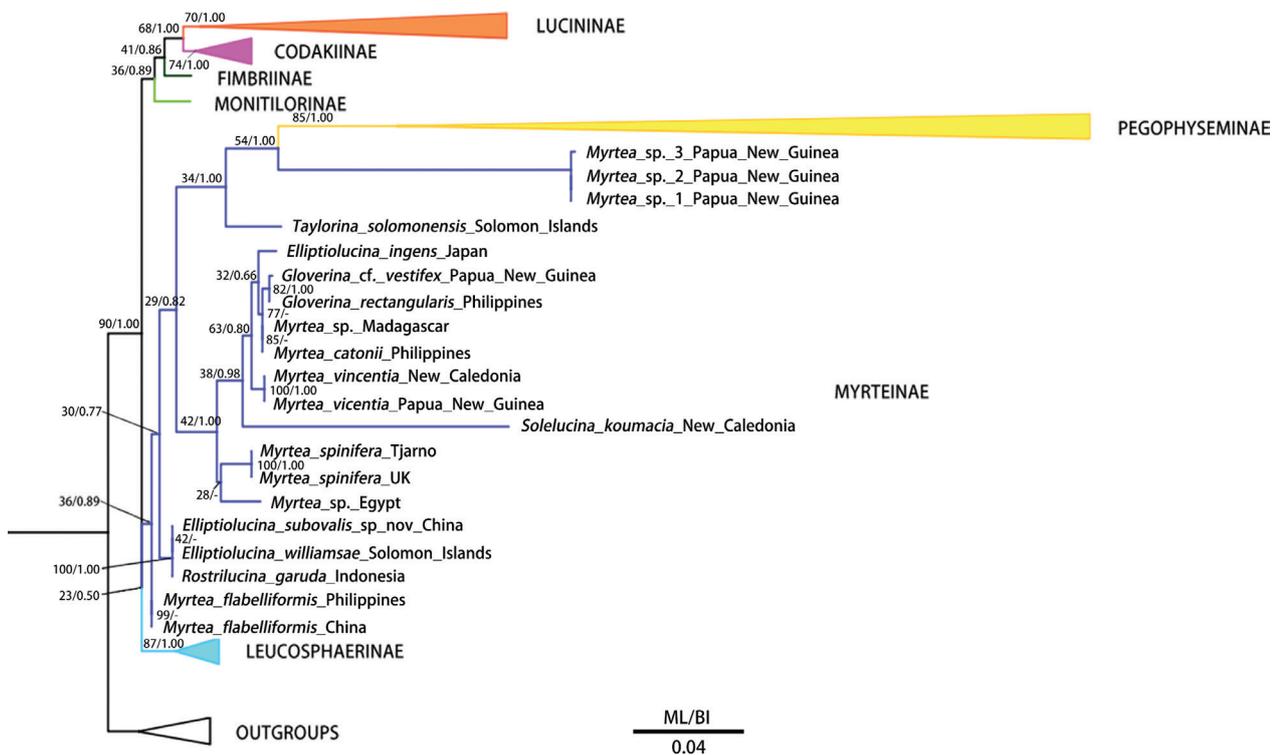
**Figure 4.** Outline drawing of shells interiors of *Elliptiolumina*. **A.** *E. magnifica*; **B.** *E. labeyriei*; **C.** *E. virginiae*; **D.** *E. ingens*; **E.** *E. williamsae*; **F.** *E. subovalis* sp. nov. Sketches of A–E. were adapted from Kuhara (2014, fig. 4) and Glover and Taylor (2016, figs 19, 20).

## Discussion

According to morphological and molecular results, we assign the new species to the genus *Elliptiolumina*. This genus was originally proposed to accommodate three species of Myrteinae, characterized by a large and oval-rectangular outline, compressed shells with irregular fine commarginal sculpture, living in deep-sea hydrocarbon seeps of IWP. Before our species, five living species of *Elliptiolumina* were limited to this region and patchily distributed

in the similar habitat, i.e., *E. magnifica*, *E. labeyriei* and *E. williamsae* from the Philippines, *E. virginiae* from Indonesia, and *E. ingens* from south Japan (Fig. 1). And for a long time, each species has only been found in its type locality. The IWP shows high diversity and endemism of Lucinidae. A total of 50 of 69 genera recorded from there are endemic to the region (Taylor et al. 2022). Many semi-enclosed basins with poor bottom water circulation and wide distribution of organic enrichment habitats (organic falls, hydrothermal vents, cold seeps, etc.) may





**Figure 6.** Phylogenetic tree inferred by Bayesian inference (BI) and Maximum likelihood (ML) based on 18S rRNA gene.

irregular vertical lines that diverge from other commarginal sculptures and run in a more upward direction in the dorsal area (Fig. 3A). *E. ingens* is distinct from other *Elliptiolumicina* species by the discoid rather than elongated shell (Okutani 2011). But the study involving more live-caught specimens indicated that the original description of *E. ingens* based on several dead shells was ambiguous (Kuhara et al. 2014). This species is highly variable in the outline, symmetry, and adductor scar characteristics. Although many parameters of *E. ingens* overlap with other species of this genus (Table 1), we found several characteristics of *E. ingens* that are obviously different from other species of *Elliptiolumicina*: 1) the postero-dorsal corner is absent in *E. ingens*, resulting in a round rather than a truncated posterior end; 2) the shells of *E. ingens* are more solid than other species; 3) the shell surface of *E. ingens* seems smoother than others with more regular sculptures; 4) the inner surfaces of *E. ingens* are distinct from others by having two ridges running from the umbonal cavity to both adductor scars and more slender slits in posterior adductor scar. According to these characteristics, we considered that *E. ingens* might not belong to the genus *Elliptiolumicina*. However, the assumption still needs more evidence, especially molecular data of the type species *E. magnifica*, which may help to confirm the assumption of relationships within *Elliptiolumicina* and recover the monophyly of this genus.

As the most diverse family of bivalves in the chemosynthetic habitat, Lucinidae is a significant taxon in the study of chemosymbiosis. In addition, it is an ideal subject for research on the evolutionary pattern between onshore and offshore species. We still need to learn more

about the diversity and phylogeny of lucinids, particularly the deep-sea taxa. To fully understand the diversity of deep-sea lucinids, more deep-sea surveys are needed, especially in IWP, the biodiversity hotspot of Lucinidae. And more molecular information on Myrteinae is needed to clarify its phylogeny and confirm its relationships with other subfamilies.

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## Supplementary material 1

### GenBank accession numbers of used sequences

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Data type: sequences

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