*Zootaxa* 5160 (1): 001–158
https://www.mapress.com/zt/

Monograph

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5160.1.1
http://zoobank.org/urn:lsid:zoobank.org:pub:A9179C79-EE43-44E4-8723-919505500049

ZOOTAXA

5160

# Late Neogene Lophophaenidae (Nassellaria, Radiolaria) from the eastern equatorial Pacific

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Magnolia Press
Auckland, New Zealand

*Accepted by T. Pánek: 13 May 2022; published: 4 Jul. 2022*

SARAH TRUBOVITZ, JOHAN RENAUDIE, DAVID LAZARUS & PAULA NOBLE
**LATE NEOGENE LOPHOPHAENIDAE (NASSELLARIA, RADIOLARIA) FROM THE EASTERN EQUATORIAL PACIFIC**

(*Zootaxa* 5160)

158 pp.; 30 cm.

4 Jul. 2022

ISBN 978-1-77688-552-7 (paperback)

ISBN 978-1-77688-553-4 (Online edition)

FIRST PUBLISHED IN 2022 BY

Magnolia Press

P.O. Box 41-383

Auckland 1041

New Zealand

e-mail: magnolia@mapress.com

https://www.mapress.com/zt

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

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## ABSTRACT

Lophophaenidae is a clade of polycystine radiolarians that was highly abundant and diverse in the Late Neogene–Recent eastern equatorial Pacific (EEP). Despite their importance in fossil plankton assemblages, lophophaenids have been neglected because of their generally small size, complex morphology, and weak taxonomic framework. These challenges have left many lophophaenid concepts poorly defined or lacking formal description. Here we address this with a review of 101 lophophaenid taxa observed in EEP Middle Miocene–Recent marine sediments. We discuss existing lophophaenid genera *Amphiplecta* Haeckel 1881, *Arachnocorallium* Haeckel 1887, *Arachnocorys* Haeckel 1860, *Botryopera* Haeckel 1887, *Ceratocyrtis* Bütschli 1882, *Lithomelissa* Ehrenberg 1847, *Lophophaena* Ehrenberg 1847, and *Peromelissa* Haeckel 1881, including full species lists. We describe *Pelagomanes* n. gen., 23 new species: *Amphiplecta kikimorae* n. sp., *Arachnocorys jorogumoae* n. sp., *Botryopera amabie* n. sp., *Botryopera babayagae* n. sp., *Botryopera bolotniki* n. sp., *Ceratocyrtis? chimii* n. sp., *Ceratocyrtis vila* n. sp., *Lithomelissa alkonost* n. sp., *Lithomelissa babai* n. sp., *Lithomelissa dybbuki* n. sp., *Lithomelissa sirin* n. sp., *Lophophaena arie* n. sp., *Lophophaena casperi* n. sp., *Lophophaena domovoi* n. sp., *Lophophaena gozui* n. sp., *Lophophaena ikiryo* n. sp., *Lophophaena ikota* n. sp., *Lophophaena kaonashii* n. sp., *Lophophaena leshii* n. sp., *Lophophaena rusalkae* n. sp., *Lophophaena shishigae* n. sp., *Lophophaena ushionii* n. sp., and *Pelagomanes ibburi* n. sp., and one new subspecies, *Arachnocorys pentacantha wanii* n. subsp. In addition, we document 35 taxa in open nomenclature, and revise generic assignments of 10 species. The names of 32 previously-described species are upheld, but with clarified synonymies, discussion, and illustrations. This work contributes a practical framework for identifying tropical Late Neogene–Recent lophophaenid taxa, and demonstrates their rich morphological diversity.

**Key words:** Micropaleontology; radiolarians; Lophophaenidae; Neogene; tropical Pacific; new species; new genus

## INTRODUCTION

Lophophaenids are a group of nassellarians in the superfamily Plagiacanthoidea, which have two skeletal segments: a cephalis and a thorax, as well as an internal structure of spines and arches (Figure 1). In the eastern equatorial Pacific (EEP), taxa belonging to the family Lophophaenidae have been among the most abundant and species-rich radiolarians in plankton fossil assemblages since the Late Miocene (Trubovitz *et al.*, 2020). However, due to their relatively small size compared to other nassellarians, high morphological diversity, and rare use in biostratigraphy, the lophophaenids have been notoriously overlooked in radiolarian literature, leaving many taxa in open nomenclature or entirely undocumented. In the Neptune Sandbox Berlin (NSB) Database (Renaudie *et al.,* 2020), which is the primary collection of microfossil data from IODP/DSDP/ODP expeditions, there are only three valid lophophaenid species reported from the equatorial Pacific (within 20 degrees of the equator) over the last 10 million years (*Lophophaena cylindrica*, *Lophophaena hispida*, and *Lithomelissa ultima*). By contrast, Trubovitz *et al.* (2020) found an average of 60 lophophaenid taxa and hundreds of lophophaenid specimens per sample, comprising approximately 10–15% of the total radiolarian assemblages they observed in the EEP (Figure 2). Lophophaenids make up the majority of Plagiacanthoidea specimens observed in every sample, and approximately half of the Plagiacanthoidea species in each sample are classified as lophophaenids (Figure 2). Renaudie and Lazarus (2016) also found that lophophaenids are abundant and comprise approximately half of the Plagiacanthoidea (informally called "plagonid") species richness in the Late Neogene Southern Ocean assemblages; many of these species had not previously been documented nor described. Thus, lophophaenids are very important in terms of both abundance and taxonomic diversity in both low and high latitude oceans, but regrettably have been historically underreported.

Here we aim to address this problem by comprehensively documenting the lophophaenids from the Middle

Miocene–Recent at IODP Site U1337 in the EEP. We also provide concise discussions of the common lophophaenid genera present during this interval: *Amphiplecta, Arachnocorallium, Arachnocorys, Botryopera, Ceratocyrtis, Lithomelissa, Lophophaena,* and *Peromelissa*. In total, we discuss and illustrate our observations of 101 lophophaenid taxa from the Middle Miocene—Recent in the EEP. Additionally, this manuscript lists all species belonging to the genera mentioned above, including our remarks and revisions to these concepts where relevant. We describe 1 new genus, *Pelagomanes* n. gen., which unites several taxa that were questionably assigned to other genera in previous literature. We also describe 23 new species: *Amphiplecta kikimorae* n. sp., *Arachnocorys jorogumoae* n. sp., *Botryopera amabie* n. sp., *Botryopera babayagae* n. sp., *Botryopera bolotniki* n. sp., *Ceratocyrtis? chimii* n. sp., *Ceratocyrtis vila* n. sp., *Lithomelissa alkonost* n. sp., *Lithomelissa babai* n. sp., *Lithomelissa dybbuki* n. sp., *Lithomelissa sirin* n. sp., *Lophophaena arie* n. sp., *Lophophaena casperi* n. sp., *Lophophaena domovoi* n. sp., *Lophophaena gozui* n. sp., *Lophophaena ikiryo* n. sp., *Lophophaena ikota* n. sp., *Lophophaena kaonashii* n. sp., *Lophophaena leshii* n. sp., *Lophophaena rusalkae* n. sp., *Lophophaena shishigae* n. sp., *Lophophaena ushionii* n. sp., and *Pelagomanes ibburi* n. sp. In addition, we describe one new subspecies, *Arachnocorys pentacantha wanii* n. subsp. Sandin *et al.* (2019)'s recent revision of nassellarian classification based on an integrated genetic-morphologic approach found that both internal and external skeletal morphology should be considered when developing nassellarian taxonomy, so our species and generic concepts follow this principle.

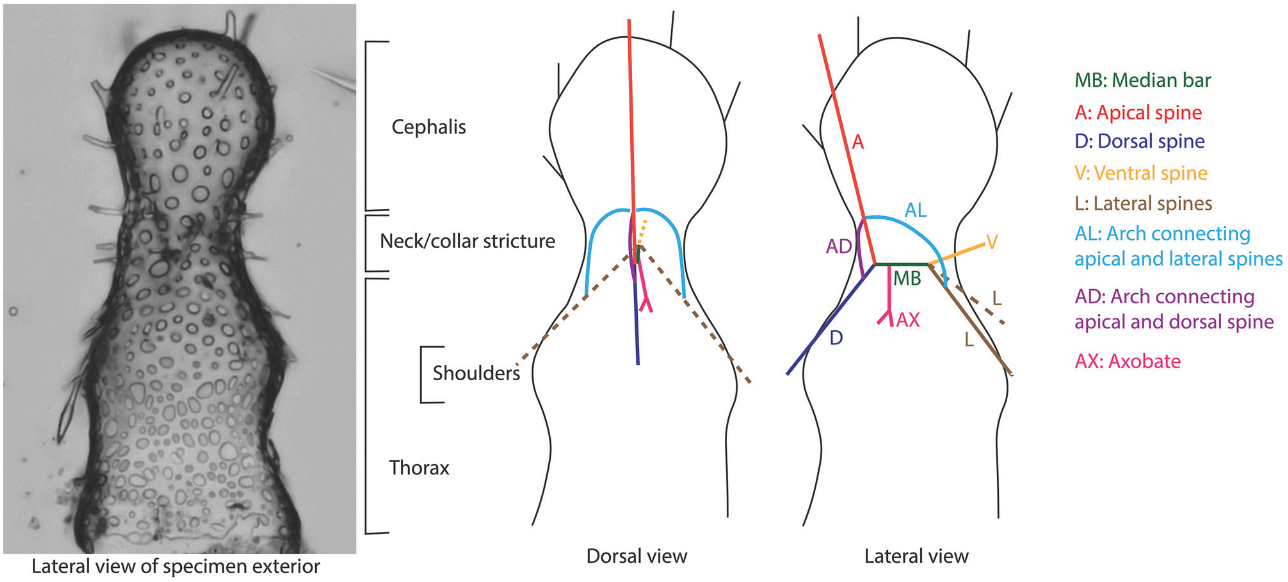

**FIGURE 1.** Diagram illustrating the general skeletal morphology of Lophophaenidae, and terminology used in this manuscript. Dashed lines indicate spines that are not visible from the angle shown, as they extend into the skeleton. An example specimen of *Lophophaena casperi* n. sp. is included for comparison to the diagrams.

## HISTORY OF STUDY

Although lophophaenids have not received the same amount of attention as some other radiolarian groups, several previous authors have contributed greatly to our understanding of their morphology and taxonomy. Ehrenberg (1795—1876) was an important early pioneer of the field of micropaleontology, and in the mid 1800s described the first species and genera that are now considered to be lophophaenids. Haeckel (1882) later established the concept of this group (as Lophophaenida). Haeckel (1834–1919) was a prolific radiolarian taxonomer who described a staggering number of taxa from his observations on the HMS Challenger Expedition (1887), including many of the lophophaenid species and genera discussed in this manuscript. While Haeckel made revisions to some of Ehrenberg's taxonomic concepts, he did not usually explain his rationale. Although both Ehrenberg and Haeckel made great strides in developing our modern framework of radiolarian systematics, and initially described most of the lophophaenid taxa in use today, many of their species names lacked detail and illustration. This has led to considerable confusion in subsequent radiolarian literature. Bütschli (1848–1920) was a student of Haeckel's, who published a manuscript (1882) tackling radiolarian systematics and revising some of Ehrenberg's early concepts.

Bütschli is the original author of the lophophaenid genus *Ceratocyrtis* (Bütschli, 1882). In the early 1900s, Popofsky made important contributions to lophophaenid taxonomy by describing and illustrating many new species, often with much greater detail than his predecessors. Popofsky occasionally included illustrations of both the external and internal skeletal morphology, with the primary spines labelled. Petrushevskaya built on previous knowledge of lophophaenids with her many publications from the 1960s–1980s. She produced high-quality illustrations and descriptions of many lophophaenid taxa encountered in this study, and she made extensive revisions to outdated species and genus concepts. Her work was among the first to include detailed discussion of species' internal skeletal morphology, and she established thorough and consistent terminology for nassellarian skeletal elements. In the 1990s and early 2000s, Funakawa (1994, 1995a, 1995b), Nishimura (1990), O'Connor (1997–2000), and Sugiyama (1992–1994) largely adopted Petrushevskaya's terminology, and vastly improved our understanding of lophophaenid morphology with their photographic illustrations (both scanning electron and transmitted light microscopy), and their detailed diagrams of the internal skeletal structure of lophophaenid taxa. More recently, Renaudie and Lazarus described 40 lophophaenid species from the Late Neogene Southern Ocean, and include high-quality transmitted light microscopy photos along with their detailed taxonomic descriptions (Renaudie and Lazarus, 2012, 2013a, 2015, 2016). The present study aims to summarize and review the concepts of these previous authors, and relies on the foundation they built for describing new lophophaenid taxa.

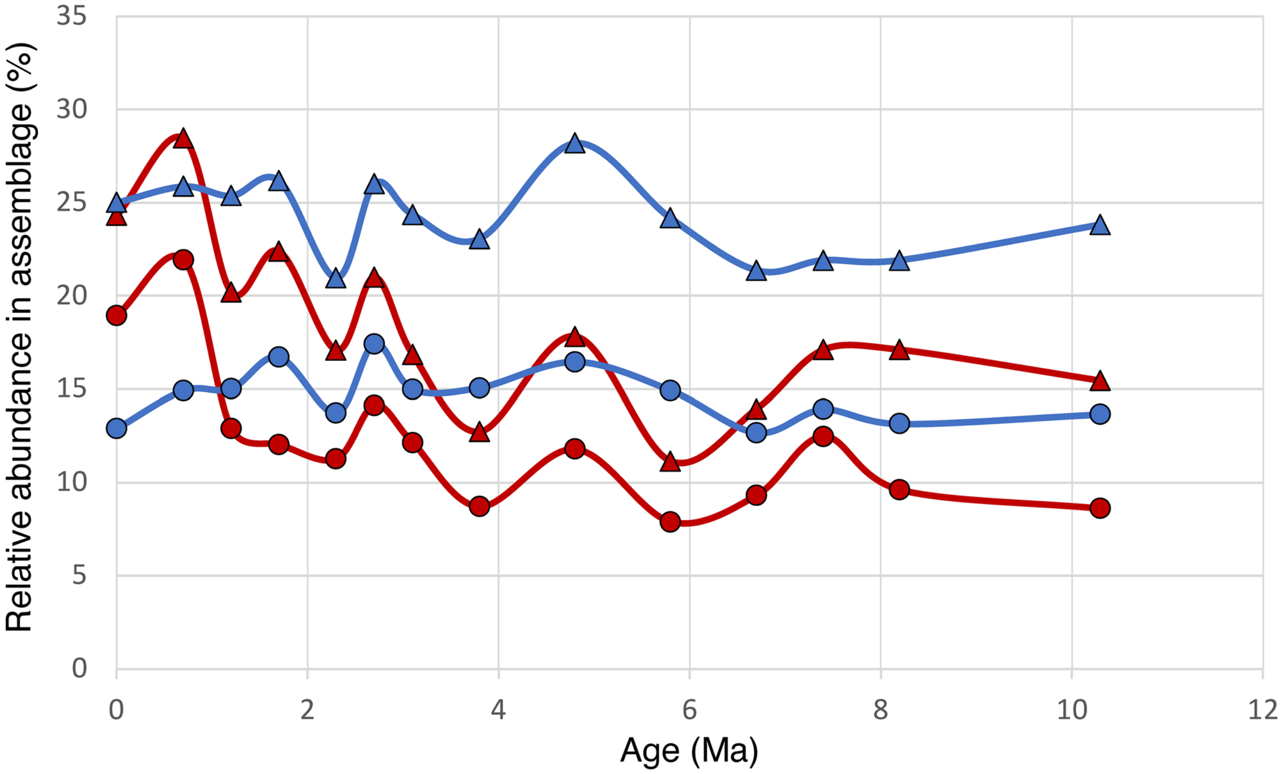

**FIGURE 2.** Relative abundance of specimens and taxa belonging to Plagiacanthoidea and Lophophaenidae per sample, from IODP Site U1337 in the EEP over the last ~10 Ma. The relative percentages of total taxa are represented by the blue lines and the red lines represent the percentages of total specimens (triangles = Plagiacanthoidea; circles = Lophophaenidae). The Plagiacanthoidea was among the most abundant and speciose of radiolarian groups encountered in Trubovitz *et al.* (2020), with at least 10% of the specimens and 20% of the taxonomic richness in every sample. Within the Plagiacanthoidea, lophophaenids consistently made up the majority of specimens (~67%) and taxa (~61%). Data are from Trubovitz *et al.* (2020).

Although we hope this manuscript will clarify some of the confusion and inconsistencies in previous lophophaenid literature, we acknowledge that there is still much work to be done. The original genus definitions in this family are very tenuous in most cases, which has occasionally led to artificial or conflicting groupings of taxa. Recent developments in combining genetic sequencing technology with classic morphologic observations (e.g., Biard *et al.,* 2015; Sandin *et al.,* 2019, 2021) will likely provide vital new insights into lophophaenid taxonomy in the near future. Another challenge with lophophaenid taxonomy —and radiolarian taxonomy in general— is that the type material of many original species erected in the 1800s and early 1900s is sometimes not available for examination, poorly illustrated, or not illustrated at all. Lophophaenids are also among the smaller-sized radiolarian families, making them more difficult to detect in micropaleontological studies. It is common practice in micropaleontology to use a sediment sieve size of 63 microns, to exclude broken specimens and focus on the larger biostratigraphic marker taxa. However, some of the lophophaenid skeletons observed in this study are only ~40–60 microns wide when fully developed, giving these taxa poor chances of being detected in most studies. Lophophaenids have a great deal of morphological complexity and species diversity, which has not been fully characterized in previous studies. Here, in addition to many newly named species we report on 37 lophophaenids that we have left in open nomenclature—a small indication of how much more primary taxonomic description is needed for this group. As a result of their fragile taxonomic framework, inconsistent name usage in the literature, small size, lack of developed biostratigraphy, morphological complexity, and species richness, lophophaenids have so far been underrepresented in the literature, but will be a fruitful topic of future study.

Suzuki *et al.* (2021) recently published a new family-level taxonomy for superfamily Plagiacanthoidea, as part of a comprehensive revision of Cenozoic radiolarian taxonomy. Molecular phylogenetic evidence supports the new divisions and groupings within some radiolarian superfamilies, but for Plagiacanthoidea the molecular data was insufficient for determining clear relationships among taxa, and so family-level groups defined by Suzuki *et al.* (2021) were based on morphological characteristics only (as they have been historically). Suzuki *et al.* (2021) cite a molecular phylogenetic analysis by Sandin *et al.* (2019), which found that Plagiacanthoidea is a paraphyletic group with specimens clustered together in two distinct groups (Clade G and Clade X). Clade G included all specimens visually identified as lophophaenids, and interestingly also included taxa that had previously been considered within the superfamily Cannobotryoidea (Sandin *et al.,* 2019). While this analysis provided valuable insight into the classification of nassellarians, it only included a small number of Plagiacanthoidea specimens, and so was not used by the authors to determine the family, genus, or species level taxonomy for this group. According to Sandin *et al.* (2019), all but one of the specimens visually identified as Lophophaenidae (*Ceratocyrtis* cf. *galea*) clustered together, suggesting that Lophophaenidae is a useful taxonomic grouping that largely reflects both overall morphology and natural phylogenetic relationships. However, additional molecular analyses that include more Plagiacanthoidea specimens are necessary to refine our understanding of lophophaenids and the other plagonid families. These future analyses may indeed show that Lophophaenidae should be revised to include or exclude different genera, but for now this group's lower-level taxonomy is based solely on morphological observations. Therefore, Sandin *et al.* (2019) cannot be invoked in support of the new family and genus level classification scheme for Plagiacanthoidea in Suzuki *et al.* (2021).

The Plagiacanthoidea are broken down into the following family-level groups by Suzuki *et al*. (2021): Ceratocyrtidae, Dictyocryphalidae Suzuki, n. fam., Dimelissidae, Phaenocalpididae, Plagiacanthidae, Pseudodictyophimidae Suzuki, n. fam., Tripodisciidae, and Ximolzidae Dumitrica, nom. nov. The genera discussed in this manuscript (which we consider to be Lophophaenidae) would fall under Ceratocyrtidae, Dictyocryphalidae, and Dimelissidae according to Suzuki *et al.* (2021)'s new classification scheme, but these names are problematic for us to adopt. Suzuki *et al.* (2021) erected the new family Dictyocryphalidae as a replacement for the name Lophophaenidae, because they consider the type species of *Lophophaena* to be a *nomen dubium* (*Lophophaena galeaorci* Ehrenberg). However, the International Code of Zoological Nomenclature (ICZN) does not state that a type species being a *nomen dubium* should invalidate the genus (or family) name. Thus, *Lophophaena* and Lophophaenidae should remain available names regardless of the status of *Lophophaena galeaorci* Ehrenberg. While we agree with Suzuki *et al.* (2021) that the initial documentation of *Lophophaena* (hence Lophophaenidae) was quite poor, the revisions of subsequent authors over the last century and a half have now adequately defined *Lophophaena* and most other genera widely considered to be lophophaenids today. Moreover, many of Ehrenberg's original *Lophophaena* specimens have since been reexamined and photographically illustrated (Ogane *et al.,* 2009), providing a clear basis for understanding Ehrenberg's original genus concept. Thus, we reject the idea that *Lophophaena* and Lophophaenidae are *nomina dubia* and require replacement with new names. The preamble to the ICZN states that the stability of names, and conservation of historical name usage should be prioritized over strict application of the ICZN. Because *Lophophaena*, and Lophophaenidae (including its derivatives) have been used extensively and continuously since the 1800s, have been accepted as valid in multiple prior taxonomic reviews by acknowledged authorities (e.g., Haeckel, 1887; Riedel, 1967; Petrushevskaya, 1971, 1984; Funakawa, 1995a, 1995b; Afanasieva *et al*., 2005), and because a comprehensive molecular-based classification system is likely coming very soon for Plagiacanthoidea, the acceptance of Suzuki *et al.* (2021)'s scheme would undermine the stability of widely-used taxonomic names and contribute to great confusion in radiolarian literature. We believe that a new classification scheme that integrates morphology with molecular data is imminent and will greatly improve our understanding of taxonomic relationships within Plagiacanthoidea; it will also probably require substantial revision of our current concept of Lophophaenidae. However, without the support of sufficiently comprehensive and verified molecular data, we do not think that an upheaval of established taxonomic names is justified at this time. Thus, in this manuscript we have chosen to conserve historical taxonomic names when possible in order to prevent more confusion in this already extremely convoluted group. But, in the near future, we look forward to the results of ongoing molecular phylogenetic research that will support an objective revision of family, genus, and species-level taxonomy within Plagiacanthoidea.

## MATERIALS AND METHODS

This study utilized samples from International Ocean Discovery Program (IODP) Site U1337, holes A and D, in the eastern equatorial Pacific (3°50.009′ N, 123°12.352′ W, 4463 meters below sea level; Figure 3). Samples were obtained from the IODP Gulf Coast Repository, and prepared into slides at the Museum für Naturkunde in Berlin.

To prepare slides, samples were soaked in a weak solution of sodium hexaphosphate and hydrogen peroxide to break down the sediment matrix, and 10% hydrochloric acid to dissolve out the carbonate content. The remaining siliceous material was sieved at 45µm in order to retain small species that would likely be overlooked using the 63µm sieve standard in most micropaleontological studies. A gelatin solution was applied to glass slide coverslips and allowed to dry, before being submerged in beakers of distilled water. A measured fraction of the rinsed >45µm cleaned sample was pipetted into beakers for random settling onto glass coverslips. After settling (~2 hours), the distilled water was siphoned to near the slide surface, and the rest was evaporated out of the beakers using heat lamps. Once fully dry, the coverslips with settled material were affixed to glass slides using warm Canada balsam. Finished slides were heated at 60°C until dry enough to handle (~48 hours). These procedures follow those of Renaudie and Lazarus (2013b), an adaptation of that originally developed by Moore (1973).

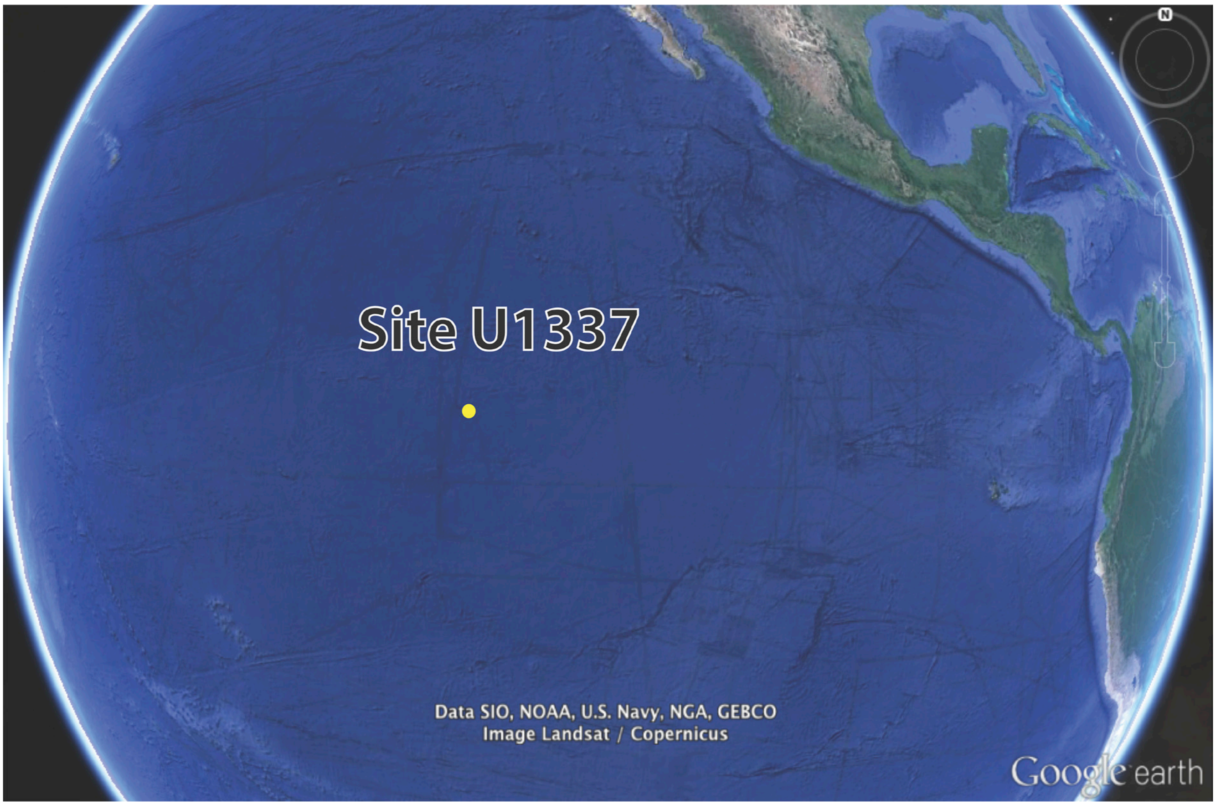

**FIGURE 3.** Locality map of IODP Site U1337, where all samples for this study were collected. Map from Google Earth™.

Slides were observed under transmitted light at 100–400x magnification using an Olympus BX51 microscope, and mounted cameras (OMax 10.0 megapixel model A35100U, and Meiji Techno model HD1500MET-AF). ToupLite imaging software and built-in Meiji Techno software were used for taking photographs. Photographs were organized and measured using Graphic Converter 10 software, and composite images were constructed using HeliconFocus version 7.6.6 Lite. The measurements used in our species descriptions are illustrated in Figure 4. Morphological terminology used throughout the paper generally follows Petrushevskaya (1971) and Funakawa (1995a, 1995b), and is illustrated in Figure 2. These skeletal elements include the median bar (MB), apical spine (A)—when referring specifically to the portion of the apical spine that extends outside the shell we use the term "apical horn," ventral spine (V), dorsal spine (D), lateral spines (L), arches connecting the apical spine to the dorsal and lateral spines (AD and AL, respectively), and axobate (AX). Although additional skeletal elements have been observed in lophophaenids, these are not easily distinguished using transmitted light microscopy, so for practical identification purposes they are not included in the present study. At a minimum, the genera included here exhibit a median bar, apical spine, dorsal spine, and lateral spines. Most genera have arches connecting the apical-dorsal and apical-ventral spines and a distinct ventral spine (*Arachnocorallium* is the exception). Only *Ceratocyrtis* and some species of *Botryopera* consistently show a well-developed axobate. The neck (or collar structure) is indicated as the narrow point of the skeleton, between the cephalis and thorax. The shoulders are defined as the first flare (and often widest point) of the upper thorax, which is often (but not always) where the dorsal and lateral spines meet the thoracic wall and sometimes protrude from it. The shoulders are not always the widest point of the thorax, alternatively the base of the thorax can be wider in some species, but the shoulders provide a consistent point of measurement on the thorax for lophophaenids, which often have an irregular termination at the base, or poor preservation of the lower part of the thorax.

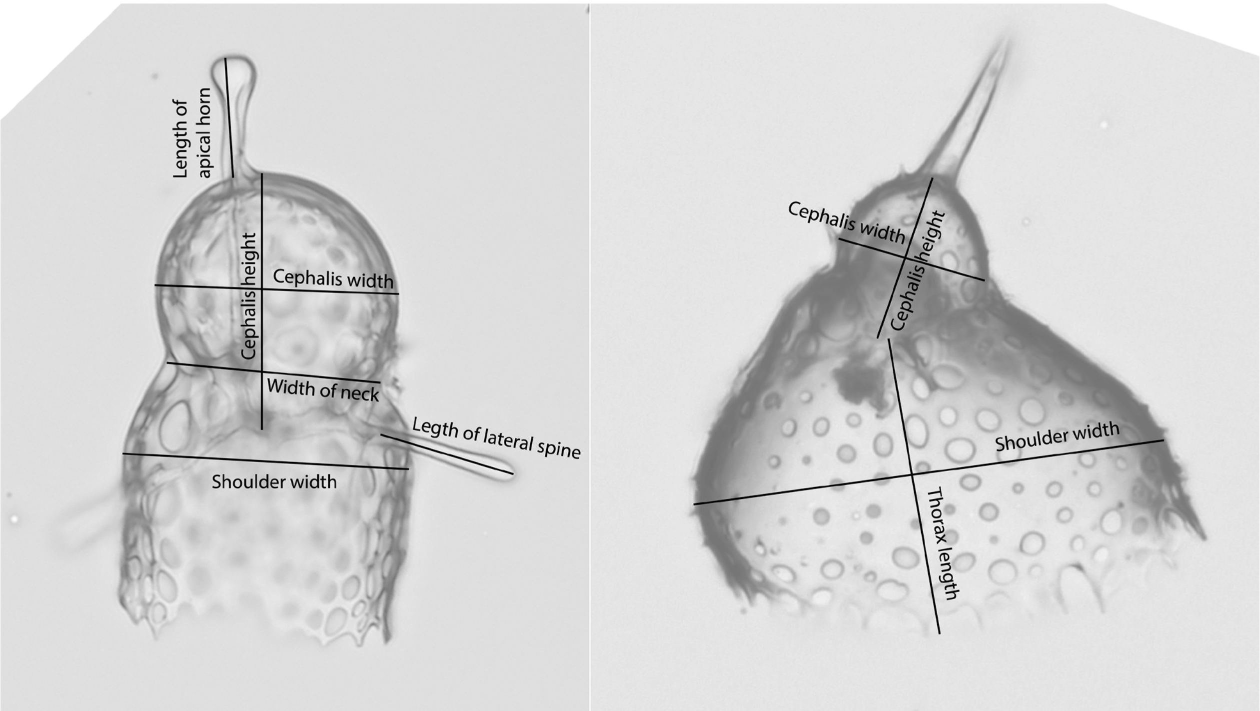

**FIGURE 4.** Examples of specimen measurements discussed in the Systematic Paleontology section of this study.

All type material is deposited in the micropaleontological collection of the Museum für Naturkunde in Berlin, accession numbers ECO-xxx, which refer to single slides. (A slide may have more than one type specimen on it). Holotypes and paratypes are indicated by England Finder coordinates, which are listed in the species descriptions of the Systematic Paleontology section below, and provided in Supplementary Table 1. New taxonomic names in this manuscript follow the general theme of being named after ghosts, and other supernatural creatures in folklore, due to the overall resemblance of the lophophaenid skeletal outline to popular depictions of ghosts. Species left in open nomenclature were done so due to insufficient number of specimens, incomplete preservation of specimens, and/or poor understanding of morphological variability. Taxa in open nomenclature are included here in an effort to fully document the range of lophophaenid morphologies among the genera presented in this study, even if we have only a limited understanding of them. The range of each taxon is given for the material we examined in the EEP, and extended to include other locations when that information is known and relevant.

Sample ages were determined using the best age models available for a given time interval. An astronomically-tuned age model is available for the last 12.2 million years (m.y.) at Site U1337 (Tian *et al.,* 2018). Older samples were dated using the age model in the NSB Database, an improvement of the original age model constructed for this site in the Proceedings of IODP Volume 320/321 (Pälike *et al.,* 2010). In some cases, the NSB model gives ages up to 900,000 years older than those of the astronomically-tuned age model by Tian *et al.* (2018). In addition, the tuned age model of Holbourn *et al.* (2015) spans 14.9—20 Ma for Site U1337, but begins at a depth of 337 meters below the seafloor, which is lower than any of the samples examined during this study. Thus, our sample dated to 16 Ma (at a depth of 329 meters below the seafloor) must be at least 1.1 m.y. younger than the NSB age model suggests, and our younger Middle Miocene samples may be several hundred thousand years younger than they are reported in this study. A revised age model extending to the base of the Miocene is needed for Site U1337, but as this would require new, orbitally tuned data for the middle Miocene interval, this is outside the scope of our study. Here our primary aim is to document and describe Late Neogene - Recent lophophaenid taxonomic diversity from the EEP; high-resolution stratigraphic ranges for these species will require future work with more closely-spaced sampling intervals. Epoch names are subdivided into Early, Middle, and Late, following Gradstein *et al.* (2012).

A taxonomic occurrence chart is given in Table 1. This chart lists the sample numbers and age names for each lophophaenid taxon occurrence, as well as the best numerical age estimate available for each sample. The 14 samples dated between 0–8.2 Ma and 10.3 Ma, were fully enumerated by Trubovitz *et al.* (2020), to include the whole radiolarian assemblage. Thus, for these samples we provide qualitative metrics of taxonomic abundances. These categories are: Extremely rare (<0.1% of the total radiolarian assemblage), Rare (0.1–0.5%), Common (0.5–1%), and Abundant (>1%). The exact number of specimens indicated by each metric varies due to slight differences in sample sizes, but generally, Extremely Rare refers to <4 specimens per sample, Rare indicates approximately 4–20 specimens, Common is about 20–40 specimens, and Abundant can be from 40 up to ~200 specimens. Assemblages throughout the study interval at Site U1337 were remarkably diverse with high species evenness, so most taxa fall into the Rare category; the average number of specimens of a given lophophaenid taxon per sample is only ~9. Samples dated to 9.4 Ma, and 11.2– 16.0 Ma were not systematically enumerated but were scanned for taxonomy, so we cannot report species' relative proportions of the full radiolarian assemblage. Instead, we use "X" to indicate that 1–2 specimens were observed in a given sample, and "XX" to indicate 3+ specimens.

The plates referenced in the Systematic Paleontology section are organized such that morphologically similar taxa appear on the same plate as much as possible. As this does not always concur with the alphabetical listing of taxonomic names, sometimes the plates and figures within them are not referenced in strict numerical order. We hope this strategy will help readers compare and understand the taxonomic concepts we present. Plates 1–2 include all *Amphiplecta* species. *Arachnocorallium* and *Arachnocorys* are illustrated on Plate 3. Additional *Arachnocorys* species appear on Plates 4–6. *Botryopera* spans Plates 6–9. *Ceratocyrtis* is included on Plates 10–14. Plates 15–20 are comprised of *Lithomelissa. Lophophaena*, and a related nassellarian morphotype are illustrated on Plates 21–38. All *Peromelissa* species are included on Plate 38. *Pelagomanes* n. gen. is shown on Plates 39–42.

## SYSTEMATIC PALEONTOLOGY

### Infrakingdom RHIZARIA Cavalier-Smith, 2002, sensu emend. Cavalier-Smith, 2003

### Phylum RETARIA Cavalier-Smith, 1999

### Class RADIOLARIA Müller, 1858

### Superorder POLYCYSTINEA Ehrenberg, 1839, emend. Riedel, 1967

### Order NASSELLARIA Ehrenberg, 1876, *sensu* Petrushevskaya, 1984

### Superfamily PLAGIACANTHOIDEA Hertwig, 1879, emend. Sandin *et al.* 2019

### Family LOPHOPHAENIDAE Haeckel, 1882, *sensu* Petrushevskaya 1971

### Genus *Amphiplecta* Haeckel 1881, emend. Petrushevskaya 1971 sensu Funakawa 1994

Type species: *Amphiplecta acrostoma* Haeckel, 1887

**Description.** A two-segmented lophophaenid with a conical cephalis that reaches maximum width at the top, can be left open, and often has a corona of spines. The thorax is widely flared and typically has an irregular termination. The internal skeletal structure of this genus includes an apical spine that runs along the side of the cephalis, a relatively short median bar, and dorsal, left lateral, and right lateral spines that extend from the base of the cephalis to run along the outside of the thorax as ribs (Figure 5), similar to *Lampromitra*. The arches at the base of the apical spine, AD and AL are well defined and prominent in skeletal outline.

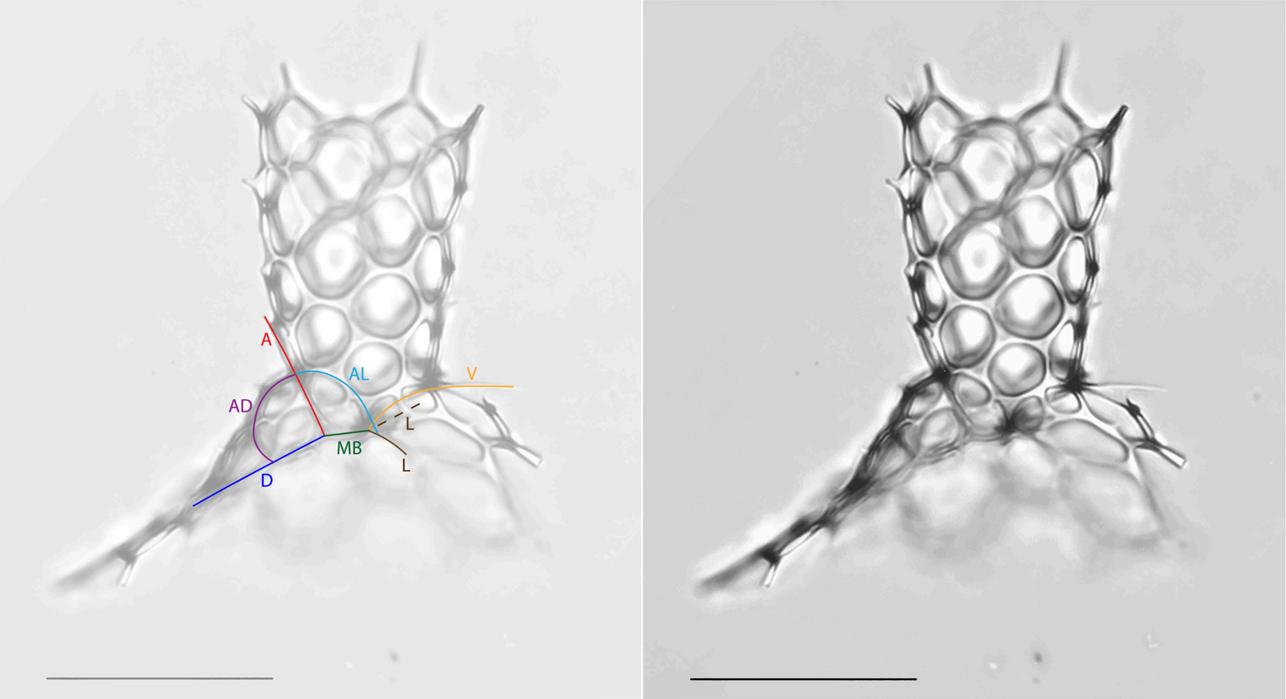

**FIGURE 5.** Internal skeletal structure of *Amphiplecta acrostoma* Haeckel, 1887.

**Remarks.** This genus was briefly mentioned in Haeckel's (1881) prodromus, but a more detailed description and illustrations were first published in Haeckel (1887). *Amphiplecta amphistoma* Haeckel, 1887 was designated as the type species by Campbell (1954). To clarify the genus concept, Petrushevskaya (1971) emended and clarified the genus description and redesignated the type species as *Amphiplecta acrostoma* Haeckel 1887 because *A. amphistoma* had not been illustrated. Petrushevskaya (1981) noted that Miocene species can have smaller, circular pores resembling those of the genus *Lophophaena.* Petrushevskaya (1971) also illustrated one specimen (*Amphiplecta* sp., Middle Miocene; pl. 54 fig. 1) with a closed cephalic apex. This characteristic would contradict the definition of the genus, as originally described by Haeckel (1881, 1887) and by Petrushevskaya (1971) herself. Funakawa (1994) uses a slightly looser definition of the genus, that does not require the cephalis to be open at the top. Two new *Amphiplecta* species without open tops have been described since Petrushevskaya's (1971) emendation, *Amphiplecta tripleura* Funakawa, 1995b and *Amphiplecta? satoshii* Renaudie and Lazarus, 2015. Funakawa's major contribution was the recognition of internal skeletal elements in SEM photography. We adopt Funakawa's (1994) revision as it is most congruent with common usage.

Here we observed the following species belonging to *Amphiplecta: Amphiplecta acrostoma* Haeckel, 1887, *Amphiplecta cylindrocephala?* Dumitrica, 1973, *Amphiplecta kikimorae* n. sp., and *Amphiplecta tripleura?* Funakawa, 1995b. *Amphiplecta amphistoma* Haeckel, 1887 is considered a *nomen dubium* because it has never been illustrated and the verbal description alone is not sufficient to identify the species. *Amphiplecta callistoma* Haeckel, 1887 is not included because it has a flat rather than conical cephalis, and was transferred to *Lampromitra* by Petrushevskaya (1971).

**Range.** Middle Miocene—Recent.

### *Amphiplecta acrostoma* **Haeckel, 1887**

Plate 1, Figs. 1A–2.

*Amphiplecta acrostoma* n. sp., Haeckel, 1887, p. 1223–1224, pl. 97, fig. 10.
*Amphiplecta acrostoma* Haeckel; Benson, 1966, pl. 32, fig. 2.
*Amphiplecta acrostoma* Haeckel; Petrushevskaya, 1971, p. 104, fig. 54, II–VII.
*Amphiplecta acroctoma* Haeckel [sic]; Nishimura and Yamauchi, 1984, pl. 24, fig. 2.
*Amphiplecta acrostoma* Haeckel; Funakawa, 1994, p. 462–463, fig. 6, 1a–1b.
*Amphiplecta acrostoma* Haeckel; Okazaki *et al.,* 2005, pl. 12, fig. 21.
*Amphiplecta acrostoma* Haeckel; Hatakeda and Bjørklund, 2009, pl. 5, fig. 3.
? non *Amphiplecta acrostoma* Haeckel; Sandoval, 2018, fig. 7A.
*Amphiplecta acrostoma* Haeckel, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This is a well-documented species with consistent taxonomic usage. The material we observed compares favorably with most of the figured specimens in previous literature.

**Range.** Late Miocene—Recent in the EEP (Table 1).

### *Amphiplecta cylindrocephala*? **Dumitrica, 1973**

Plate 1, Figs. 3A–4C.

? *Amphiplecta cylindrocephala* n. sp., Dumitrica, 1973, p. 836, pl. 24, figs. 4–5.
non *Amphiplecta cylindrocephala* Dumitrica, Benson, 1983, pl. 8, fig. 5.

**Remarks.** This species is very close to *Amphiplecta acrostoma* Haeckel, 1887, but according to Dumitrica (1973), it differs in that it has a "very long cephalis, less spiny shell, and non-denticulate spines." This species is rare, and only two Quaternary specimens were illustrated by Dumitrica (1973), so it is difficult to know the true variability of this species. In our material we encountered two specimens with an unusually long cephalis, suggestive of *Amphiplecta cylindrocephala* Dumitrica, but one specimen differed in that it had a slight pinch in the cephalis outline toward the top. Thus, we questionably place these specimens in *Amphiplecta cylindrocephala* Dumitrica. Other than the two illustrations by Dumitrica (1973), we are only aware of one other illustration of *Amphiplecta cylindrocephala* by Benson (1983). This specimen appears to be within the range of *Amphiplecta acrostoma* Haeckel, so we do not consider it to be synonymous with our *Amphiplecta cylindrocephala*? specimens.

**Range.** Early Pliocene in the EEP (Table 1).

### *Amphiplecta kikimorae* **n. sp.**

Plate 2, Figs. 1A–5B.

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**Diagnosis.** Broad, elongated, inverted-conical cephalis that is widest and fully-enclosed at the top; thorax flares widely, has three ribs, and a distinct constriction or termination at the base.

**Description.** *Amphiplecta* with a broad, conical cephalis that is enclosed and flat on the top, is surrounded by a crown of short spines, and reaches its widest point at the top. The apical horn is strong and three-bladed. The AL arches and the AD arch are well defined, as in other *Amphiplecta* species. The thorax flares widely, and has a distinct termination or constriction where the dorsal and lateral ribs penetrate the thorax. Some specimens show additional skeletal development below the constriction (i.e., figs 1 and 3), while others appear to terminate the shell at this point (i.e., fig. 2).

**Remarks.** This species differs from *Lampromitra schultzei* (Haeckel) Takahashi, 1991 in that its cephalis is significantly larger and more angular. It differs from *Amphiplecta acrostoma* Haeckel (pl. 1, figs. 1A–2) in that its cephalis is wider and fully enclosed. It differs from *Amphiplecta cylindrocephala* Dumitrica, 1973 in that it has a broader and enclosed cephalis, but has a similar crown of short thorns around the top. The thorax is relatively short compared to other *Amphiplecta* species. The relatively broad, enclosed nature of the cephalis and constricted thorax produce some uncertainty as to the genus designation. However, the structure of the internal skeleton, the continuity of the cephalis and thorax without a clear neck region, as well as the external shape of the shell resemble other species assigned to *Amphiplecta* more than any other genera we are aware of.

**Material examined.** 7 specimens from sample 321-1337A-7H-6, 104–107cm (Early Pliocene).

**Holotype.** Pl. 2, figs. 1A–C; sample 321-1337A-7H-6, 104–107cm; ECO-134; L4-1.

**Paratypes.** (1) Pl. 2, figs. 2A–B; sample 321-1337A-7H-6, 104–107cm; ECO-134; S32-2. (2) Pl. 2, figs. 3A–B; sample 321-1337A-7H-6, 104–107cm; ECO-135; K5-1. (3) Pl. 2, fig. 4; sample 321-1337A-7H-6, 104–107cm; ECO-135; R6-2. (4) Pl. 2, figs. 5A–B; sample 321-1337A-7H-6, 104–107cm; ECO-134-Q17-1. (5) [not figured] sample 321-1337A-7H-6, 104–107cm; ECO-135; U31-4.

**Measurements.** Height of cephalis 37–43 (40)µm; maximum width of cephalis 39–48 (44)µm; maximum width of thorax 59–68 (64)µm; length of thorax 26–36 (32)µm. Based on 6 specimens.

**Etymology.** Named for the female house spirit in Slavic folklore, Kikimora.

**Range.** Early Pliocene in the EEP, as far as known (Table 1).

*Amphiplecta* **sp. cf.** *A. kikimorae*
Plate 2, Figs. 6A–7B.

*Amphiplecta acrostoma*?, Renz, 1974, pl. 18, fig. 12.
Unknown plagonid group C sp 73, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species resembles *Amphiplecta kikimorae* n. sp. (Pl. 2, Figs. 1A–5B) except that it has significantly larger pores, is overall larger in size, has a more widely flared thorax, and a less pronounced apical horn. However, it does have a cephalis of similar shape, and the same prominent AL and AD arches. It differs from *Amphiplecta acrostoma* Haeckel (Pl. 1, Figs. 1A–2) and *A. cylindrocephala* Dumitrica in that the cephalis is closed at the top. A specimen similar to ours was figured by Renz (1974) and identified as *Amphiplecta acrostoma?*, but the poor image quality makes it difficult to discern the pore size of Renz's specimen, and say with certainty it is conspecific with ours. However, we believe *Amphiplecta* sp. cf. *A. kikimorae* does not match any *Amphiplecta* species so far described, and could be justified as a new species after more specimens can be documented.

**Material Examined.** 2 specimens from samples 321-1337A-7H-6, 104–107cm (Early Pliocene) and 321-1337D-1H-1, 0–3cm (Recent).

**Range.** Early Pliocene—Recent in the EEP (Table 1). The specimen figured by Renz (1974) was listed as Quaternary in age.

*Amphiplecta tripleura?* **Funakawa, 1995b**
Plate 1, Figs. 5A–7C.

*Amphiplecta* sp. Petrushevskaya, 1971, pl. 54, fig. 1.
*Amphiplecta tripleura* n. sp., Funakawa, 1995b, p. 18–20, text fig. 5, pl. 1, figs. 1a–3b.

**Remarks.** The specimens observed in this study were observed in Middle and Late Miocene samples (~15.5—8.2 Ma), which is younger than the lower Miocene range given in Funakawa (1995b)'s description. Our specimens differ from those illustrated by Funakawa in that they have a gradational decrease in pore size from the bottom to top of the cephalis. The apical spine is also less pronounced in our specimens, and the cephalis appears to be slightly wider. However, not enough specimens have been observed or figured in previous literature to fully understand the intraspecific variation or the true stratigraphic range of this taxon. It is possible that the specimens we observed are within the range of variation for *Amphiplecta tripleura* Funakawa, but it is also possible that they are a related Middle–Late Miocene form that will later be determined to be a distinct species.

**Range.** Middle– Late Miocene in the EEP. Lower limit not determined. See Table 1.

### Other *Amphiplecta* species not observed in this study:

### *Amphiplecta? satoshii* Renaudie and Lazarus, 2015

*Amphiplecta? satoshii* n. sp., Renaudie and Lazarus, 2015, p. 191, pl. 5, fig. 10–12B, 14A–15; pl. 8, fig. 11.

## Genus *Arachnocorallium* Haeckel, 1887, emend. Petrushevskaya, 1971

Type species: *Arachnocorys* (*Arachnocorallium) hexaptera* Haeckel, 1887
(= *Psilomelissa calvata* Haeckel, 1887)

**Description.** Lophophaenid genus often comprised of only a cephalis, with inconsistent and usually minimal development of a thoracic segment. The base of the cephalis is narrow, and clearly exhibits the median bar, dorsal, and lateral spines extending out from the base of the cephalis, usually with minimal obstruction from any thorax development. Apical and ventral spines are not usually as well expressed as in other Lophophaenidae.

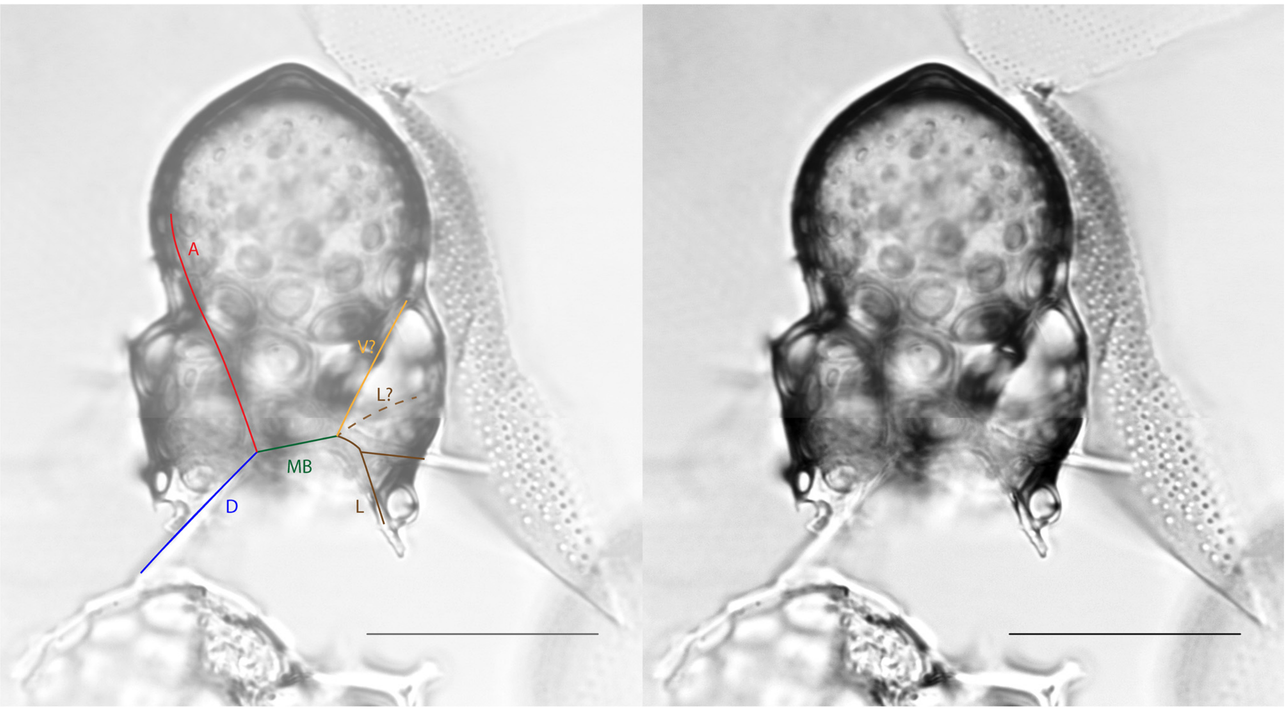

**FIGURE 6.** Internal skeletal structure of *Arachnocorallium calvata* (Haeckel, 1887) Petrushevskaya, 1971.

**Remarks.** *Arachnocorallium* was originally described as a subgenus of *Arachnocorys* by Haeckel (1887). He described it somewhat vaguely, as having a "thorax with six divergent ribs or radial beams." *Arachnocorys hexaptera* was the first species Haeckel (1887) listed under this subgenus, and it was designated as the type species of *Arachnocorys (Arachnocorallium)* by Campbell (1954, p. D126). However, this species was not illustrated by Haeckel (1887) nor Campbell (1954). In 1971, Petrushevskaya emended *Arachnocorallium,* elevating it to the genus level and synonymizing *Arachnocorys (Arachnocorallium) hexaptera* Haeckel, 1887 with *Psilomelissa calvata* Haeckel, 1887 to revise the concept of the type species (*Arachnocorallium calvata*; the only species of this genus described at that time). Petrushevskaya elevated *Arachnocorallium* to the genus level because she considered the type species of *Arachnocorys* (*Arachnocorys circumtexta*) to be sufficiently different from *Arachnocorallium calvata*. Since *Arachnocorallium calvata* (Haeckel) Petrushevskaya, 1971 has triradial symmetry, rather than the six divergent ribs mentioned in the subgenus description by Haeckel (1887), it seems that Petrushevskaya significantly changed the original meaning of *Arachnocorallium* when she elevated it to the genus level. For many decades, the species *Arachnocorallium calvata* Haeckel was the only taxon belonging to this genus, but recently three new species of *Arachnocorallium* have been described by Renaudie and Lazarus (2015) from the Southern Ocean. Furthermore, the high level of variation in *Arachnocorallium calvata* could potentially justify breaking this group into multiple species (see species discussion below).

The apical spine is not always easy to determine, particularly in *Arachnocorallium calvata,* which either has no clearly visible spines on the cephalis, or otherwise has three thin, conical spines of equal strength. Petrushevskaya (1971) noted that *Arachnocorallium calvata* does not have an apparent ventral spine. In the annotated specimen below, we mark the probable location of the ventral spine, although it is not overtly distinct from the wall of the cephalis.

Here we observed the following species of *Arachnocorallium*: *Arachnocorallium calvata* (Haeckel 1887) Petrushevskaya, 1971 and *Arachnocorallium stilla* Renaudie and Lazarus, 2015.

**Range.** ?Miocene—Recent in the tropical world oceans, and Miocene—Recent in the Southern Ocean, so far as known.

### *Arachnocorallium calvata* (Haeckel, 1887) Petrushevskaya, 1971

Plate 3, Figs. 1A–3B.

*Arachnocorys circumtexta* (juv.?), Hertwig, 1879, p. 79, pl. 8, fig. 2a.
*Arachnocorys hexaptera* n. sp., Haeckel, 1887, sp. 1271.
? *Lychnodictyum scaphopodium* n. sp., Haeckel, 1887, pl. 56, fig. 4.
*Psilomelissa calvata* n. sp., Haeckel, 1887, p. 1212, pl. 56, fig. 3.
*Peridium spinipes* Haeckel, Popofsky, 1913, text-figs. 33–34 (non text-figs. 31–32).
*Arachnocorallium calvata* Haeckel, emend., Petrushevskaya, 1971, pl. 70, figs. 1–8.
*Arachnocorallium calvata* Haeckel group, Boltovskoy and Riedel, 1987, pl. 3, fig. 24.
*Arachnocorallium calvata* Haeckel, Itaki *et al.,* 2008b, pl. 4, fig. 27 (? fig. 26).
*Arachnocorallium calvata* Petrushevskaya, Bjørklund *et al.*, 2012, pl. 4, figs. 8–9.
*Arachnocorallium calvata* Petrushevskaya group, Matsuzaki *et al.*, 2019, pl. 2, figs. 6–9.
*Arachnocorallium calvata* Haeckel, Matsuzaki *et al.*, 2020, pl. 6, fig. 7, 9–10 (?figs. 6, 8).
*Arachnocorallium calvata* Haeckel, Trubovitz *et al.*, 2020, supplementary data 7.
? *Arachnocorallium* cf. *calvata* Haeckel, Trubovitz *et al.*, 2020, supplementary data 7.

**Remarks.** This species appears to be often confused with species of *Archiperidium* (formerly *Peridium*), another lophophaenid that lacks a thoracic segment, in the literature. Here we follow Petrushevskaya's (1971) concepts of *Arachnocorallium* and *Archiperidium. Archiperidium* differs from the former in that the apical spine is more clearly expressed, usually with a set of relatively large, paired pores on the cephalis running along the apical spine. However, even ignoring the confusion regarding *Archiperidium* and *Arachnocorallium*, *Arachnocorallium calvata* (Haeckel) Petrushevskaya, 1971, seems to have highly variable development and/or preservation of cephalic horns and the thoracic segment. In the material we observed, some *Arachnocorallium* specimens had short spines on the cephalis, or none at all, which we identified as *Arachnocorallium calvata* sensu Petrushevskaya (1971), pl. 70, figs. 1–6, 8 (Pl. 3, Figs. 1A–B in this manuscript). Other specimens we observed resembled *Arachnocorallium calvata* in most characteristics, except that these specimens exhibited three long, thin cephalic horns, that extended upward by approximately the same length as the cephalis (Pl. 3, Figs. 2A–B). Petrushevskaya (1971) mentioned observing an alternate form of *Arachnocorallium calvata* with three horns on the cephalis. She illustrated one such specimen on pl. 70, fig. 7, but this individual differs from our specimens in that its spines are shorter and relatively weaker. In Trubovitz *et al.* (2020) these 3-horned specimens were considered *Arachnocorallium* cf. *calvata*; however, it is possible that spine development could constitute intraspecific variation or be a preservational artifact. Future work involving well-preserved specimens and genetic diversity within this genus is needed to determine whether specimens showing different types of cephalic spines, and different levels of thorax development should be considered multiple species.

**Range.** *Arachnocorallium calvata* was present from the early Late Miocene—Recent in the EEP. The form of this species exhibiting three equally-prominent spines on the cephalis was observed only from the Early Pleistocene–Recent in the EEP. See Table 1.

### *Arachnocorallium stilla* Renaudie and Lazarus, 2015
Plate 3, Figs. 3A–C.

? *Arachnocorallium* group Motoyama, 1996, pl. 3, fig. 17 (non fig. 18).
*Arachnocorallium stilla* n. sp., Renaudie and Lazarus, 2015, pl. 5, figs. 3–5, 7.
*Arachnocorallium stilla* Renaudie and Lazarus, Trubovitz *et al.*, 2020, supplementary data 7.

**Remarks.** This species was designated relatively recently by Renaudie and Lazarus, and thus has few mentions in the literature. The specimens we observed in the EEP were confirmed by the species' authors to be conspecific with the Southern Ocean form. Therefore, this species is likely more widespread than its short synonymy would suggest.

**Range.** Middle Miocene—Late Pliocene in the Southern Ocean. Latest Miocene– Middle Pleistocene in the EEP (Table 1).

### Other *Arachnocorallium* species not observed during this study:

### *Arachnocorallium cerebellum* Renaudie and Lazarus, 2015

? *Peridium longispinum* Jørgensen, Nishimura, 1990, pl. 13, fig. 11 (non figs 9–10c).
*Arachnocorallium cerebellum* n. sp., Renaudie and Lazarus, 2015, pl. 5, figs. 1–2, 13, 16.

### *Arachnocorallium? pyroensis* Renaudie and Lazarus, 2015

*Arachnocorallium? pyroensis* n. sp., Renaudie and Lazarus, 2015, pl. 5, figs. 6, 8–9.

## Genus *Arachnocorys* Haeckel, 1860, 1887, emend. Petrushevskaya, 1971

Type species: *Arachnocorys circumtexta* (Haeckel, 1862) Petrushevskaya, 1971

**Description.** Lophophaenidae with a gap in the shell wall between cephalis and thorax. This gap can be large (as in *Arachnocorys circumtexta* Haeckel) or small (as in *Arachnocorys umbellifera* Haeckel). The thorax of *Arachnocorys* typically exhibits ~6–12 strong ribs, and the cephalis has multiple anastomosing spines.

**Remarks.** This genus was originally described by Haeckel (1860) as having two segments separated by a deep stricture, with many spines on the cephalis and a thorax with strong ribs, resembling the structure and shape of an umbrella. In 1887, Haeckel added to this description of *Arachnocorys* that there are numerous "siliceous threads" that form an "arachnoidal framework" around the exterior of the shell. Haeckel (1887) listed three subgenera under *Arachnocorys*: *Arachnocorallium, Arachnocoronium*, and *Arachnocorythium*. Petrushevskaya (1971) emended the concept of *Arachnocorys* to include Haeckel's subgenus *Arachnocoronium* but not *Arachnocorallium,* which she elevated to a separate genus. Haeckel (1887) only included one species under the third subgenus *Arachnocorythium* (*Arachnocorys polyptera* Haeckel), and he did not illustrate it. Although Campbell (1954) recognized *Arachnocorythium* as a valid subgenus, with *Arachnocorys polyptera* Haeckel as the type species, neither the species nor subgenus names have been used in subsequent literature. To our knowledge only one illustration of *Arachnocorys* (*Arachnocorythium*) *polyptera* Haeckel has been published; it was hand-drawn by Popofsky (1913), and it is questionable whether this specimen fits Haeckel (1887)'s original concept of the species and/or subgenus. Therefore, here we follow Petrushevskaya (1971)'s concept of *Arachnocorys*, which includes the broad genus concept defined by Haeckel (1860, 1887) as well as the subgenus concept of *Arachnocoronium* (Haeckel, 1887), but not the subgenera *Arachnocorallium* (which has been elevated to the genus level) nor *Arachnocorythium* (which has not been sufficiently documented and may not be distinct from other *Arachnocorys*).

Here we observed the following species of *Arachnocorys*: *Arachnocorys circumtexta* (Haeckel, 1862) Petrushevskaya, 1971, *Arachnocorys jorogumoae* n. sp, *Arachnocorys pentacantha* (Popofsky, 1913) Petrushevskaya, 1971, *Arachnocorys pentacantha wanii* n. subsp., *Arachnocorys spinosissima* (Tan and Tchang, 1976) n. comb., and *Arachnocorys umbellifera* (Haeckel, 1862) Petrushevskaya, 1971.

We consider the following *Arachnocorys* species to be *nomina dubia*, due to a combination of inadequate text description, lack of illustration, and unavailable type materials: *Arachnocorys* (*Arachnocoronium*) *arachnodiscus* Haeckel, 1887, *Arachnocorys* (*Arachnocorallium*) *discoides* Haeckel, 1887, *Arachnocorys* (*Arachnocoronium*) *enneaptera* Haeckel, 1887, *Arachnocorys* (*Arachnocorythium) polyptera* Haeckel, 1887, *Arachnocorys (Arachnocoronium) trifida* Haeckel, 1887. *Arachnocorys simplex* Pantanelli and Stefani, 1879 was misspelled as *Arachnocoris simplex* n. sp. when the name was first created. No description or illustration was provided by the authors, or any subsequent authors we are aware of, making *Arachnocorys simplex* Pantanelli and Stefani, 1879 a *nomen oblitum*. *Arachnocorys dubius* Dogiel and Reshetnyak, 1952 is not included here because it was transferred by Matsuzaki *et al.,* 2015 to the genus *Cryptogyrus* given that it does not fit the definition of *Arachnocorys. Arachnocorys? fimbria* Kozlova, 1984 was transferred to *Ceratocyrtis* by the same author in 1999.

**Range.** ?Eocene—Recent.

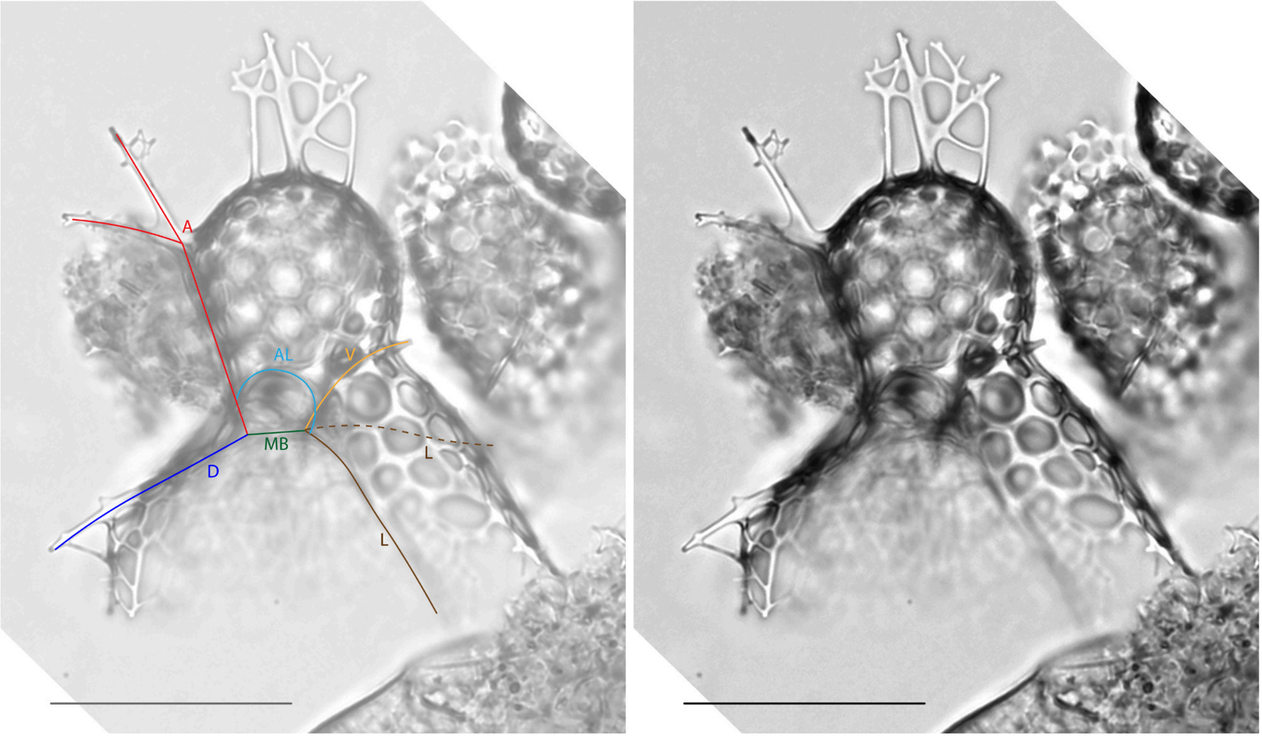

**FIGURE 7**. Internal skeletal structure of *Arachnocorys umbellifera* (Haeckel, 1862) Petrushevskaya, 1971.

## *Arachnocorys circumtexta* **(Haeckel, 1862) Petrushevskaya, 1971**

Plate 3, Figs. 4–5.

*Arachnocorys circumtexta* n. sp., Haeckel, 1862, pl. 6, figs. 9–11.
*Arachnocorys circumtexta* Haeckel, Hertwig, 1879, pl. 7, fig 2 (non fig. 2a).
*Arachnocorys araneosa* n. sp., Haeckel, 1887, pl. 56, fig. 11.
*Arachnocorys circumtexta* Haeckel, Popofsky, 1913, pl. 33, fig. 4; pl. 36, fig. 1; text-figs. 82–83.
*Arachnocorys circumtexta* Haeckel, emend. Petrushevskaya, 1971, pl. 65, figs. 3–5; pl. 67, figs. 1–2.
*Arachnocorys circumtexta* Haeckel, Nishimura and Yamauchi, 1984, pl. 24, figs. 10a–10b.
*Arachnocorys circumtexta* Haeckel, Boltovskoy and Riedel, 1987, pl. 3, fig. 25.
*Arachnocorys araneosa* Haeckel, Fujioka, 1990, pl. 43, fig. 4.
*Acanthocorys umbellifera* [sic] Haeckel, Ishitani and Takahashi, 2007, pl. 3, fig. c.
*Arachnocorys circumtexta* Haeckel, Kurihara and Matsuoka, 2010, fig. 3.2.
*Arachnocorys circumtexta* Haeckel, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** Use of this species name has been fairly consistent in the literature. In 1971, Petrushevskaya synonymized *Arachnocorys araneosa* Haeckel with *Arachnocorys circumtexta* Haeckel, broadening the concept to include multiple observed morphologies, which differ slightly in size, regularity of the skeleton, and shape of the thorax. The specimens we observed during this study were within the range of those illustrated by previous authors.

**Range.** Late Miocene—Recent in the EEP (Table 1).

### *Arachnocorys jorogumoae* **n. sp.**

Plate 4, Figs. 1A–11.

urn:lsid:zoobank.org:act:37C96B78-C0AF-40C6-8914-BE371896442F
unknown plagonid group C sp 1, partim., Trubovitz *et al.,* 2020, supplementary data 7.

**Diagnosis.** *Arachnocorys* with a relatively elongated cephalis that reaches maximum width ~3/4 of the way up and has several branching spines; the thorax is broad, ribbed, with irregular pores and no distinct gaps near the base of the cephalis.

**Description.** *Arachnocorys* with a well-developed, relatively long balloon-shaped cephalis that has several ridges and spines that can be branching. The cephalis has a narrow constriction at the neck area. The gaps/large pores between cephalis and thorax are diminished compared to other species in this genus. The thorax is broad, can grow up to twice the length of the cephalis, and has numerous strong ribs that form teeth at the base of the shell.

**Remarks.** This species is similar to *Arachnocorys umbellifera* (Haeckel) Petrushevskaya, 1971 (Pl. 3, Figs 6A–8B), except that the cephalis is proportionally longer and has a more distinct neck area. In the material we observed, this species also tends to be more heavily silicified and overall more robust than *A. umbellifera*. Although these two species have overlapping stratigraphic ranges, *A. umbellifera* was more common in the Pleistocene and Pliocene whereas *A. jorogumoae* was more common in the Late Miocene. A. *jorogumoae* differs from *A. circumtexta* (pl. 3, figs. 4–5) in that there are diminished gaps between cephalis and thorax, making it uncertain whether this species should be considered *Lophophaena* or *Arachnocorys*. However, many *A. umbellifera* specimens also have diminished gaps between cephalis and thorax. We place it into *Arachnocorys* due to its shared characteristics with *A. umbellifera* and *A. circumtexta*, which both also have dendritic spines on the cephalis and strong ribs on the thorax, diagnostic characteristics of *Arachnocorys*.

**Material examined.** 34 specimens; most were from Late Miocene samples 321-1337A-14H-7, 39–42cm and 321-1337A-16H-6, 121–124cm, and some were from samples 321-1337A-21H-1, 33–35cm (Late Miocene) and 321-1337D-30H-3, 103–104 (Middle Miocene).

**Holotype.** Pl. 4, figs. 2A–B; sample 321-1337A-14H-7, 39–42cm; ECO-138; X12-1.

**Paratypes.** (1) Pl. 4, figs. 1A–B; sample 321-1337A-16H-6, 121–124cm; ECO-141; L11-3. (2) Pl. 4, fig. 3; sample 321-1337A-14H-7, 39–42cm; ECO-138; Q20-3. (3) Pl. 4, figs. 4A–B; sample 321-1337A-21H-1, 33–35cm; ECO-144; E18-4. (4) Pl. 4, fig. 8; sample 321-1337A-16H-6, 121–124cm; ECO141; K29-1. (5) Pl. 4, fig. 9; sample 321-1337A-16H-6, 121–124cm; ECO-142; N34-3. (6) Pl. 4, fig. 7; sample 321-1337A-16H-6, 121–124cm; ECO-143; W5-1.

**Measurements.** Height of cephalis 53–68 (62), maximum width of cephalis 41–55 (48), width at neck constriction 28–40 (35). Based on 13 specimens.

**Etymology.** Named for the deadly spider-woman yokai of Japanese folklore, Jorôgumo.

**Range.** Middle—Late Miocene in the EEP, precise upper and lower limits not certain (Table 1).

### *Arachnocorys pentacantha* **(Popofsky, 1913) Petrushevskaya, 1971**

Plate 5, Figs. 8–9B.

*Arachnocorys pentacantha* n. sp., Popofsky, 1913, text-figs. 84–86; pl. 22, figs. 5–6.
*Arachnocorys pentacantha* Popofsky, Petrushevskaya, 1971, pl. 65, figs. 8–9; pl. 66, figs. 5–6.
? *Arachnocorys pentacantha* Popofsky, Nishimura and Yamauchi, 1984, pl. 55, figs. 8a–8b.
non *Arachnocorys* cf. *pentacantha* Popofsky, Nishimura and Yamauchi, 1984, pl. 24, figs. 11a–11b.
non *Arachnocorys pentacantha* Popofsky, Okazaki *et al.,* 2005, fig. 12.19.
*Arachnocorys pentacantha* Popofsky, Matsuoka, 2009, fig. 2-53, fig. 3-44, ?fig. 3-43.
non *Archiperidium pentacanthum* (Popofsky) nov. com., Matsuzaki *et al.,* 2014, pl. 3, fig 2.
*Arachnocorys* cf. *pentacantha* sp 1, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species was originally described by Popofsky (1913), but was amended by Petrushevskaya (1971).

It often has variable development/preservation of the thorax and arachnoidal filaments, so shows some variation in the fossil record. Petrushevskaya (1971) noted that some specimens of *Arachnocorys pentacantha* were significantly larger, and have relatively smaller gaps between the cephalis and thorax, than others. It is unclear whether or not she considered these specimens to belong to *Arachnocorys pentacantha*, as they were referred to as *Arachnocorys* cf. *pentacantha* in the caption of pl. 65, figs. 10–11, but were not explicitly referred to as cf. *pentacantha* in the species description. In our study, we also observed that there were two similar forms resembling *Arachnocorys pentacantha*; the larger form we have broken out as the separate subspecies *Arachnocorys pentacantha wanii* n. subsp. (Pl. 5, Figs. 1A–7B). Matsuzaki *et al.* (2014) listed *Arachnocorys pentacantha* as *Archiperidium pentacanthum* (Popofsky) nov. com., but did not provide a justification for the genus reassignment. In addition, the specimen figured by Matsuzaki *et al.* (2014) appears to have a relatively larger, more triangular cephalis, negligible gaps between thorax and cephalis, and weaker apical spine, compared to the specimens figured by Petrushevskaya (1971) and those observed in this study. These characteristics may indeed justify placing the species figured by Matsuzaki *et al.* (2014) into *Archiperidium*; however, we do not consider this species to be the same as the one described by Popofsky (1913) and amended by Petrushevskaya (1971).

**Range.** Late Pliocene—Recent in the EEP (Table 1).

*Arachnocorys pentacantha wanii* **n. subsp.**
Plate 5, Figs. 1A–7B.

urn:lsid:zoobank.org:act:7E6BF77B-06FF-4793-8326-6554CC6B0823
*Arachnocorys* cf. *pentacantha* Petrushevskaya, 1971, pl. 65, figs. 10–11.
*Arachnocorys* cf. *pentacantha* sp. 3 Trubovitz *et al.,* 2020, supplementary data 7.

**Diagnosis.** Subspecies of *Arachnocorys pentacantha* that has a relatively larger and wider cephalis than the typical form, and a thorax that attaches relatively lower toward the base of the cephalis.

**Description.** This subspecies of *Arachnocorys pentacantha* has consistently larger measurements and a larger cephalis:thorax ratio. It also has the thorax attachment relatively lower on the cephalis than typical in *A. pentacantha pentacantha*. While *A. p. pentacantha* often has arches of the thorax reaching the upper third of cephalis, this subspecies has arches reaching only the lower third of the cephalis. In the material used for this study, we observed an average cephalis height of 59 microns for *A. p. wanii,* whereas typical *A. p. pentacantha* specimens had a cephalis height of approximately 45 microns.

**Remarks.** This form was first recognized by Petrushevskaya (1971) as *Arachnocorys* cf. *pentacantha*. She illustrated it beside *Arachnocorys pentacantha* to show its relatively larger size. In her emendation of *Arachnocorys pentacantha,* she determined that the cephalis height of this species is between 35–45 microns. By contrast, the *Arachnocorys* cf. *pentacantha* form she identified has a cephalis height of approximately 60 microns. She did not mention observing any specimens with intermediate dimensions, suggesting that they could be different taxa. Petrushevskaya (1971) also noted that *Arachnocorys* cf. *pentacantha* differs in that it has smaller gaps between the cephalis and thorax, and the pores on the anterior side of the cephalis are proportionally smaller. In our material, many specimens similar to Petrushevskaya's *Arachnocorys* cf. *pentacantha* were observed. The cephalis height of these specimens averaged 59 microns, ranging between 54–67 microns, making it approximately the same size as Petrushevskaya's specimens. Some specimens had relatively smaller pores on the anterior side of the cephalis whereas others did not, suggesting that this may be a developmental feature and should not be used to strictly distinguish this subspecies from classic *A. p. pentacantha*. Another difference between *A. p. pentacantha* and this new subspecies, is that the apical horn protrudes near the cephalis maximum height in *A. p. pentacantha,* whereas in *A. p. wanii* n. subsp., the apical horn tends to depart from the wall of the cephalis before it reaches its maximum height. A few specimens were observed that did not neatly fit into the classic concept of *A. p. pentacantha* nor the new subspecies *wanii*; they exhibited a cephalis height between ~45 and 55 microns. Because of these somewhat intermediate forms, we are establishing a subspecies rather than a new species until the range of variability can be confidently determined.

**Material examined.** 64 specimens from samples 321-1337A-6H-3, 29–32cm (Late Pliocene), 321-1337A-5H-5, 11–14cm (Late Pliocene), 321-1337A-4H-6, 115–118cm (Early Pleistocene), 321-1337A-4H-2, 16–19cm

(Middle Pleistocene), 321-1337A-3H-2, 103–106cm (Middle Pleistocene), 321-1337A-2H-3, 76–79cm (Late Pleistocene), 321-1337D-1H-1, 0–3cm (Recent).

**Holotype.** Pl. 5, Figs. 1A–C; sample 321-1337A-4H-2, 16–19cm; ECO-127; P21-1.

**Paratypes.** (1) Pl. 5, figs. 3A–B; sample 321-1337A-3H-2, 103–106cm; ECO-126; G2-2. (2) Pl. 5, figs. 6A–B; sample 321-1337A-3H-2, 103–106cm; ECO-126; J42-3. (3) Pl. 5, figs. 7A-B; sample 321-1337A-3H-2, 103–106cm; ECO-126; Y4-3. (4) Pl. 5, fig. 5; sample 321-1337A-4H-2, 16–19cm; ECO-127; P19-3. (5) Pl. 5, figs. 2A-B; sample 321-1337A-3H-2, 103–106cm; ECO-126; D37-3.

**Measurements.** Height of cephalis 64–67 (59)µm; maximum width of cephalis 42–50 (47)µm; width of thorax at emergence of primary spines, approximately the maximum width 53–63 (59)µm. Based on 13 specimens.

**Etymology.** Named for the Japanese sea monster yokai, Wani.

**Range.** Late Pliocene—Recent in the EEP (Table 1).

### *Arachnocorys spinosissima* **(Tan and Tchang, 1976) n. comb.**

Plate 6, Figs. 1A–4B.

*Lithomelissa spinosissima* n. sp., Tan and Tchang, 1976, pl. 68, figs. 50a–e.
*Lithomelissa spinosissima* Tan and Tchang, Tan and Su, 2003, text-fig. 108.
*Lithomelissa spinosissima* Tan and Tchang, Aita *et al.,* 2009, pl. 5, figs. 6a–c.
?*Lithomelissa spinosissima* Tan and Tchang, Trubovitz *et al.,* 2020, supplementary data 7.
unknown plagonid group C sp 58, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** Tan and Tchang (1976) originally assigned this species to *Lithomelissa* but we are of the opinion that *L. spinosissima* does not fit the definition of *Lithomelissa* due to the apical spine running along the wall of the cephalis rather than passing freely through it. Tan and Tchang (1976) did not provide a discussion of the rationale for their genus assignment, and the only differential diagnosis was with the species *Lithomelissa thoracites*. *L. thoracites* has since been transferred to the genus *Peromelissa*, so it is problematic to keep *L. spinosissima* within *Lithomelissa* for multiple reasons. Here we propose that this species should be transferred to *Arachnocorys* due to similarities with *A. pentacantha,* namely the segment proportions, arches connecting the cephalis and thorax, and positioning of the apical spine.

**Range.** Late Miocene—Recent in the EEP (Table 1).

### *Arachnocorys umbellifera* **(Haeckel, 1862) Petrushevskaya, 1971**

Plate 3, Figs 6A–8B.

*Arachnocorys umbellifera* n. sp., Haeckel, 1862, pl. 6, fig. 12.
*Acanthocorys (Acanthocoronium) umbellifera* Haeckel, Haeckel, 1887, p. 1263 [not figured].
? *Acanthocorys umbellifera* Haeckel, Cleve, 1899, p. 25, not figured.
*Arachnocorys umbellifera* Haeckel, Jørgensen, 1905, pl. 18, fig. 107.
*Arachnocorys umbellifera* Haeckel, Petrushevskaya, 1962, pl. 5, figs. 2–4 (non fig. 1).
*Arachnocorys umbellifera* Haeckel, Benson, 1966, pl. 24, fig. 20 (non fig. 21).
*Arachnocorys umbellifera* Haeckel, emend. Petrushevskaya, 1971, pl.65, figs. 5–6; pl.66, figs. 1–4.
*Arachnocorys umbellifera* Haeckel, Tan and Tchang, 1976, text-fig. 58.
non *Arachnocorys umbellifera* Haeckel, Benson, 1983, pl. 8, fig. 6.
? *Acanthocorys umbellifera* Haeckel, Ishitani and Takahashi, 2007, pl. 3, figs. a–b (non fig. c).
*Arachnocorys umbellifera* Haeckel, Onodera *et al.*, 2011, pl. 8, figs. 8–9 (non fig. 7).
? *Acanthocorys umbellifera* Haeckel, sensu Cleve 1899, Bjørklund *et al.,* 2014, pl. 10, figs.11a–b.
unknown plagonid group C sp 12 cf, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species has been interpreted differently by authors in the literature. It is probable that several distinct species have been illustrated under the name *Arachnocorys umbellifera* Haeckel. In an attempt to clarify the species concept, our synonymy most closely follows the concepts and illustrations of Petrushevskaya (1971) and Tan and Tchang (1976). The specimen from Cleve's collection illustrated by Bjørklund *et al.* (2014) appears to have a relatively smaller cephalis that is sunken into the thorax, compared to illustrations by other authors. Its apical spine also appears to be stronger than the other illustrated specimens. It is difficult to say with certainty that this specimen belongs to a different species based on only two images, so both Cleve (1899) and Bjørklund *et al.* (2014) are questioned but not excluded in our synonymy.

**Range.** Late Miocene—Recent, with greatest abundances from the Late Miocene to Early Pliocene in the EEP (Table 1).

### *Arachnocorys*? **sp.**

Plate 3, Fig. 9.

Arachnocorys sp. 4, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species has a narrow thorax, with large pores at the top of thorax. These gaps suggest it could be *Arachnocorys*, but the overall shape of the skeleton is also consistent with *Lophophaena*. Few specimens were documented in Trubovitz *et al.* (2020), so further study is needed before this species can be confidently described.

**Material examined.** 9 specimens from samples 321-1337A-7H-6, 104–107cm (Early Pliocene), 321-1337A-4H-2, 16–19cm (Middle Pleistocene), 321-1337A-3H-2, 103–106cm (Middle Pleistocene), 321-1337A-2H-3, 76–79cm (Late Pleistocene), and 321-1337D-1H-1, 0–3cm (Recent).

**Range.** Early Pliocene—Recent in the EEP, so far as known (Table 1).

## Genus *Botryopera* Haeckel, 1887, emend. Petrushevskaya, 1975

Type species: *Botryopera cyrtoloba* Haeckel, 1887

**Description.** No clear consensus exists for the definition of this genus, and even the family assignment has been debated in the literature. Here we loosely follow the description given by Petrushevskaya (1986), which states that *Botryopera* species are small in size, with a sub-cylindrical, elongated skeletal shape, a thorax that is ~45–75 microns wide and never broader than 100 microns, and have arches connecting the thorax to the cephalis that reach ~⅓ of the way up the cephalic segment. Here we add that species in this genus often exhibit an axobate, which is a character common to the lophophaenid genera *Ceratocyrtis* and *Antarctissa,* but is otherwise not widely observed in this family. *Botryopera* species also tend to have a cephalis that is heavier and better developed than the thorax.

**Remarks.** Haeckel (1887) first described the genus *Botryopera* as one of two genera in the family Cannobotryida (Haeckel, 1881). He described *Cannobotrys* as the genus with porous tubes on the cephalis (a clear indication that these taxa should belong to the family *Cannobotryidae*), and *Botryopera* as the genus without these tubes. Two species previously described by Ehrenberg (1844), *Lithobotrys triloba* and *Lithobotrys quadriloba*, were placed into Haeckel's new genus *Botryopera*. However, Ehrenberg's first published illustrations of *Lithobotrys triloba* in 1854c (pl. 19, fig. 55; pl. 22, figs. 30A–B) suggests that it is a lophophaenid due to its cephalis shape, lack of lobes or tubes, and pore structure. Haeckel (1887) states that the cephalis is trilobate, but there appears to be some confusion, as it is the thorax, not the cephalis, that has three lobes in this species. Reexamination and photo documentation of Ehrenberg's collections by Suzuki *et al.* 2009 clearly indicates that the species *Lithobotrys triloba* Ehrenberg, 1854c should belong to the family Lophophaenidae (Suzuki *et al.,* 2009; pl. 20, figs. 3A–B, 9A–E). These photographs show that the overall shape, proportions, and internal skeletal structure are consistent with other lophophaenid taxa, and in particular there are common characteristics to the genus *Trisulcus* Popofsky, such as the three-lobed thorax and relatively small cephalis. Therefore, Ehrenberg's species concept cannot be easily confused with a cannobotryid; Haeckel (1887) must have either have mislabeled the cephalis and thorax in his description, or perhaps he misidentified a specimen as Ehrenberg's species. To our knowledge, *Lithobotrys quadriloba* Ehrenberg, 1844 was never illustrated, and is not often discussed in the literature. Accompanying his original genus description of *Botryopera*, Haeckel only illustrated two of the five species he placed in that genus: *Botryopera cyrtoloba* Haeckel, 1887 and *Botryopera quinqueloba* Haeckel, 1887. *Botryopera quinqueloba* is most likely a true cannobotryid, given its apparently tri-lobed cephalis. However, *Botryopera cyrtoloba* is depicted only in apical view, making it difficult to tell whether all three lobes actually belong to the cephalis (as Haeckel states), or if the species has a typical lophophaenid-type cephalis with a lobed or strongly-shouldered thorax (resembling a species like *Trisulcus triacanthus* or *Botryopera triloba*).

Popofsky (1913) synonymized *Botryopera* Haeckel under *Botryopyle* Haeckel, and placed it in the new family, Acrobotrusidae. However, he did not explain why all species in *Botryopera* should belong in *Botryopyle*, or the new family, Acrobotrusidae. While some *Botryopera* species described at the time could easily be considered cannobotryids, others, such as *Botryopera triloba* (Ehrenberg) Haeckel, 1887, could not. Subsequent authors did not follow Popofsky (1913)'s synonymy.

In 1954, Campbell listed *Botryopera* as a junior objective synonym of *Lithobotrys*, but did not provide any explanation for this. The type species of *Lithobotrys* was designated as *Lithobotrys quadriloba* Ehrenberg, 1844, which Haeckel (1887) had previously transferred to *Botryopera*, although neither author had illustrated it. Thus, the type species of the genus *Lithobotrys* is cryptic and may be either a cannobotryid or a lophophaenid. No type species of *Botryopera* was designated until Petrushevskaya's (1975) emendation of Haeckel's genus concept. She considered this genus to be in the family Lampromitridae Haeckel, along with *Antarctissa* and *Ceratocyrtis*, two genera now widely accepted to be lophophaenids. Petrushevskaya (1975) listed *Botryopera cyrtoloba* Haeckel, 1887 as the type species, and rejected Campbell (1954)'s synonymization with *Lithobotrys*. In addition, Petrushevskaya (1975) placed three species from *Trisulcus* into the revised concept of *Botryopera*. These species were discussed and illustrated in Petrushevskaya (1971) as *Trisulcus borealis*, *Trisulcus braevispicula,* and *Trisulcus boldyrae*. Petrushevskaya (1975) states that *Botrypera triloba* Ehrenberg is the most "typical" species group within this genus; therefore, it is unclear why she designated the poorly-illustrated *Botryopera cyrtoloba* Haeckel as the type species instead. Petrushevskaya (1981) considered *Botryopera* to be within Lithocampaninae, a new subfamily under Lampromitridae that also included the genus *Trisulcus*. Petrushevskaya (1986) showed that *Botryopera* is closely related to *Antarctissa* Petrushevskaya, 1967, but differs in having reduced skeletal dimensions, including a thorax never wider than 100 microns, which is often sub-cylindrical in shape. Sugiyama (1993) followed the genus concept established by Petrushevskaya (1975, 1981, 1986) but considered *Botryopera* to be in the family Lophophaenidae rather than Lampromitridae or the subfamily Lithocampaninae, which he determined to be junior synonyms of Lophophaenidae based on their internal skeletal structures. Sugiyama (1993) described several new species of *Botryopera*, all of which are well illustrated and in our opinion, clearly lophophaenids. However, each of these new species were given only a tentative generic assignment due to our poor understanding of the internal skeletal structure for all *Botryopera* species.

This genus is a problematic one and it is beyond the scope of this paper to resolve it. The majority of species in this genus are endemic to polar oceans, so it will require close examination of high latitude *Botryopera* species to gain a better understanding of the characteristics of this genus. However, several species observed during this study are tentatively assigned to the genus *Botryopera* due to their resemblance to species already placed in this genus. The modern concept of this genus is still very blurry, but most authors agree that it resembles the lophophaenid genera *Trisulcus* and *Antarctissa,* and should thus be considered a lophophaenid.

Here we observed the following species, which we provisionally consider to be *Botryopera*: *Botryopera amabie* n. sp., *Botryopera babayagae* n. sp., *Botryopera bolotniki* n. sp., *Botryopera? daleki* Renaudie and Lazarus, 2013a*,* and *Botryopera setosa* (Jorgensen, 1900) Kruglikova, 1989. We do not include *Botryopera equiceps* (Campbell and Clark, 1944) Petrushevskaya, 1986 as the original illustration by Campbell and Clark (1944) appears to indicate the apical spine passing through the center of the cephalis (likely placing this species in *Lithomelissa*). Campbell and Clark (1944) tentatively placed the species in *Dictyocephalus*. Petrushevskaya (1975) illustrated the species as *Antarctissa equiceps* (Campbell and Clark) group; these illustrations do not show the apical spine at all, so it does not seem to pass through the center of the cephalis. It is not clear to us whether these specimens are even conspecific. Because the original illustration would appear to fit *Lithomelissa* better than *Botryopera* or *Antarctissa*, we do not include it in our list of *Botryopera* species and hope that additional study can clarify this species concept in the future. *Botryopera piperata* Renaudie and Lazarus (2015) is tentatively transferred to *Pelagomanes* n. gen. later in this manuscript. *Botryopera conica* Gladenkov and Devyatkin, 1992 appears to fit better in *Antarctissa,* and so is not included here. *Botryopera deflandrei* (Petrushevskaya, 1975) was transferred to *Antarctissa* by Lazarus (1990). *Botryopera multiloba* Haeckel, 1887 was never illustrated and to our knowledge has never been used or better documented in subsequent literature, so it is likely a *nomen oblitum*. *Botryopera quinqueloba* Haeckel, 1887 appears to be a cannobotryid rather than a lophophaenid, so we do not include it here.

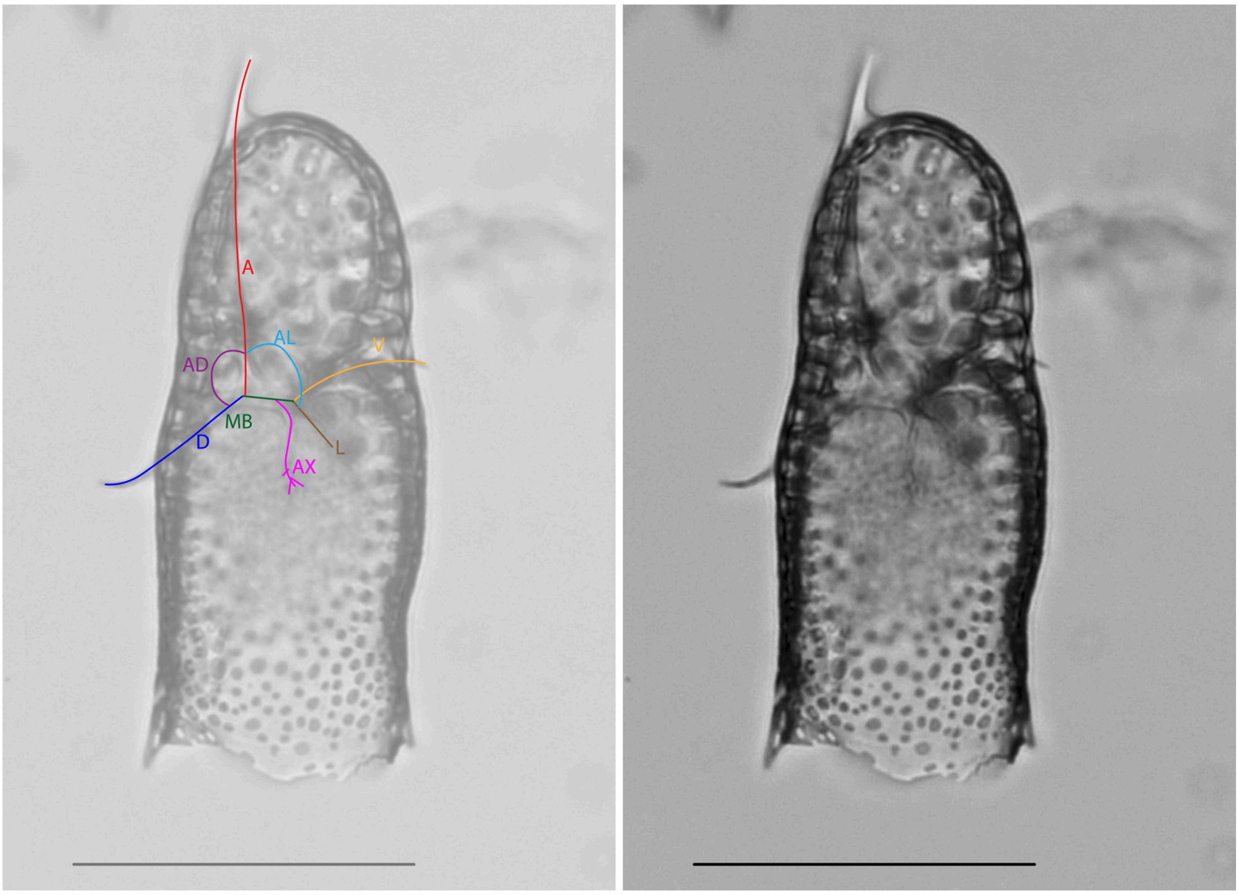

**FIGURE 8.** Internal skeletal structure of *Botryopera amabie* n. sp.

*Botryopera amabie* **n. sp.**
Plate 7, Figs. 1A–6.

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**Diagnosis.** Lophophaenid with characteristics shared by *Botryopera* species, as well as a narrow, elongated overall shape, thickly-silicified neck region, distinct apical spine fused to the cephalis wall, and dendritic axobate extending into the thorax.

**Description.** The cephalis of this species is somewhat thumb-shaped and elongated; it is similar in width to the thorax, giving the skeleton an overall subcylindrical shape. The apical spine runs alongside the wall of the cephalis and terminates in a relatively short and thin apical horn. Besides the apical horn, the cephalis has no other spines. The shell wall attains peak thickness where the thorax attaches to the cephalis, and thins both upward and downward. This species has an atypical pore structure on the shell wall, compared to most other lophophaenids observed in this study. The unframed straight-walled pores resemble those of other described *Botryopera* species. The neck area exhibits the largest pores on the skeleton, which decrease in size in both upwards and downwards. Dorsal and lateral spines pierce the thorax but do not form long wings or external spines.

**Remarks.** This species differs from described *Botryopera* taxa in that it has a short, thin apical spine that runs along the side of the cephalis (similar to *Lophophaena*). However, the dendritic axobate is an indicator that this species does not belong in *Lophophaena*. It differs from typical *Antarctissa* species in the elongated shape of the cephalis, and the single horn on the cephalis that is an extension of the apical spine.

**Material examined.** 10 specimens from samples 321-1337A-35X-1, 106–108cm (Middle Miocene), 321-1337A-31X-6W, 4–6cm (Middle Miocene), 321-1337D-30H-3, 103–104cm (Middle Miocene), and 321-1337D-26H-3W, 142–144cm (Late Miocene).

**Holotype.** Pl. 7, Fig. 4A–B; sample 321-1337D-30H-3, 103–104cm; ECO-150; O43-4.

**Paratypes.** (1) Pl. 7, Fig. 5; sample 321-1337D-30H-3, 103–104cm; ECO-149; D4-3. (2) [not figured] sample 321-1337D-30H-3, 103–104cm; ECO-149; O36-2.

**Measurements.** Cephalis height 40–47 (43)µm; minimum thorax length (of specimens not obviously broken) 40–70 (50)µm; width of thorax at shoulders 38–45 (41)µm. Based on 10 specimens.

**Etymology.** Named for the Japanese yokai, Amabie, who emerges from the sea to tell the future and whose image can protect people from disease.

**Range.** Middle–Late Miocene in the EEP; lower limit was not determined (Table 1).

### *Botryopera babayagae* **n. sp.**

Plate 9, Figs. 1A–8.

urn:lsid:zoobank.org:act:D591961F-2E7F-46FD-B2B5-CAECE92178A0
unknown plagonid group C sp 30 cf, partim., Trubovitz *et al.,* 2020, supplementary data 7.
unknown plagonid group C sp 36, Trubovitz *et al.,* 2020, supplementary data 7.

**Diagnosis.** Lophophaenid sharing characteristics with some *Botryopera* species, and has particularly heavy cephalis with relatively large pores, paired with a thorax of similar width that is lightly silicified and has significantly smaller pores.

**Description.** This cephalis of this species is very thick compared to the wall of the thorax. The apical spine is visible inside the shell and along the cephalis wall, but it rarely extends past the top of the cephalis. If it does, the apical spine is thin and weak. Pores on the cephalis are large and framed, while the thorax has much smaller pores and a very thin shell wall. The point of attachment between cephalis and thorax is the widest part of the skeleton, and is characterized by at least three muted upper thoracic lobes. The dorsal and lateral spines are clearly visible through the thin thorax wall, and have a branching appearance. These spines may pierce the thorax and extend as short, thin spines, but in many specimens these small appendages are absent.

**Remarks.** Like *Botryopera amabie* n. sp. (Pl. 7, Figs. 1A–6), the cephalis of this species is relatively thick, the overall shape is subcylindrical, and the thorax is relatively thin. *B. babayagae* n. sp. differs from *B. amabie* n. sp. in that it lacks a distinct apical horn, is less elongated in shape, and does not have an extended axobate. This species differs from *B. oceanica* (Ehrenberg) group Petrushevskaya, 1975 in that it is larger, has a more distinct separation between cephalis and thorax, and has more organized, numerous pores on both the cephalis and thorax.

**Material examined.** >100 specimens from samples 321-1337A-16H-6, 121– 124cm (Late Miocene), 321-1337A-12H-5, 23–26cm (Late Miocene), 321-1337A-10H-2, 91–94cm (Early Pliocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), 321-1337A-6H-3, 29–32cm (Late Pliocene), 321-1337A-5H-5, 11–14cm (Late Pliocene), 321-1337A-4H-6, 115–118cm (Early Pleistocene), 321-1337A-4H-2, 16–19cm (Middle Pleistocene), 321-1337A-3H-2, 103–106cm (Middle Pleistocene), 321-1337A-2H-3, 76–79cm (Late Pleistocene), and 321-1337D-1H-1, 0–3cm (Recent).

**Holotype.** Pl. 9, figs. 2A–B; sample 321-1337A-3H-2, 103–106cm; ECO-126; E35-2.

**Paratypes.** (1) Pl. 9, figs. 1A–B; sample 321-1337A-3H-2, 103–106cm; ECO-126; E35-2. (2) Pl. 9, figs. 6A-B; sample 321-1337A-4H-6, 115–118cm; ECO-130; S19-4. (3) Pl. 9, figs. 5A–B; sample 321-1337A-4H-2, 16-19cm; ECO-127; P21-1. (4) Pl. 9, fig. 7; sample 321-1337A-3H-2, 103–106cm; ECO-126; K30-1.

**Measurements.** Cephalis height 49–55 (51)µm; cephalis width 37–48 (42)µm; width at shoulders 42–50 (46)µm. Based on 8 specimens.

**Etymology.** Named for Baba Yaga, the fearsome forest witch of Slavic folklore who lives in a house on chicken legs.

**Range.** Late Miocene—Recent, EEP (Table 1).

### *Botryopera bolotniki* **n. sp.**

Plate 8, Figs. 1A–6B.

urn:lsid:zoobank.org:act:A713A6DA-F8AC-4111-BBFA-731495FC4DA7
unknown plagonid group C sp 51 cf, Trubovitz *et al.,* 2020, supplementary data 7.

**Diagnosis.** Small lophophaenid with similarities to *Botryopera*, including a narrow cephalis and subcylindrical shell outline, but in addition has strong conical dorsal, lateral and apical spines, often with distinctly thickened tips.

**Description.** This species is overall subcylindrical in shape, with a small and narrow thumb-shaped cephalis and a slightly wider thorax. The apical spine is fused to the wall of the cephalis and extends upward as a distinct conical spine with a thickened tip. The thorax attaches to the bottom third of the cephalis with several small lobes. The dorsal and lateral spines extend outward from the thorax as conical spines with thickened tips, closely resembling the characteristics of the apical spine. The cephalis is slightly more heavily silicified than the thorax, but both segments are relatively thin compared to other *Botryopera* species. This species has a short, thin, dendritic axobate, which is not always preserved in every specimen. The specimen in figure 5 is aberrant, with a deformity that apparently caused the growth of two apical spines.

**Remarks.** This species closely resembles *Botryopera amabie* n. sp. (Pl. 7, Figs. 1A-6), except that it has a thinner shell wall throughout the skeleton, more consistent pore sizes, and long, conical dorsal, lateral, and apical spines that are usually thickened at their tips, resembling cotton swabs. Transitional forms between the two species were not observed, and their ranges do not overlap, suggesting that they may be separate but related species. The genus designation was tentatively made due to the overall shell proportions and presence of an axobate, which would likely exclude it from *Lophophaena* and make *Botryopera* the best fit, despite this genus being poorly defined.

**Material examined.** 15 specimens observed from samples 321-1337D-23H-6, 134–137cm (Late Miocene), 321-1337A-16H-6, 121–124cm (Late Miocene), 321-1337A-14H-7, 39–42cm (Late Miocene), and 321-1337A-10H-2, 91–94cm (Early Pliocene).

**Holotype.** Pl. 8, Figs. 1A–B; sample 321-1337A-14H-7, 39–42cm; ECO-138; F36-4.

**Paratypes.** (1) Pl. 8, figs. 2A–B; sample 321-1337A-14H-7, 39–42cm; ECO-138; D30-1. (2) Pl. 8, figs. 3A–B; sample 321-1337A-14H-7, 39–42cm; ECO-140; M12-3. (3) Pl. 8, figs. 6A–B; sample 321-1337A-14H-7, 39–42cm; ECO-140; T27-2. (4) Pl. 9, figs. 4A–B; sample 321-1337A-14H-7, 39–42cm; ECO-139; Y34-3. (5) Pl. 8, figs. 5A–B [deformed specimen]; sample 321-1337A-14H-7, 39–42cm; ECO-138; S33-3. (6) [not figured] sample 321-1337A-14H-7, 39–42cm; ECO-138; N10-4. (7) [not figured] sample 321-1337A-14H-7, 39–42cm; ECO-140; Z14-4.

**Measurements.** Cephalis height 31–34 (32)µm; cephalis width 25–26 (26)µm; neck width 23–25 (24)µm; shoulder width 28–35 (32)µm. Based on 9 specimens.

**Etymology.** Named for the swamp spirit, bolotnik, in Slavic folklore.

**Range.** Late Miocene—earliest Pliocene in the EEP (Table 1).

### *Botryopera? daleki* **Renaudie and Lazarus, 2013a**

Plate 6, Figs. 5A–9B.

*Lophophaenoma* sp. M, Petrushevskaya, 1971, pl. 63, figs. 3–4.
*Botryopera? daleki* n. sp., Renaudie and Lazarus, 2013a, pl. 6, figs. 1A–C, 4A–6B; Pl. 8, figs. 1–2B, 5.
unknown plagonid group C sp 63, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** In the EEP, specimens vary widely in their degree of silicification. In general, specimens older than ~12Ma tend to be more heavily silicified; however, the degree of silicification can vary even within a single sample. Specimens 7 and 9 we consider to be questionably assigned to this species as they are substantially more silicified than the type material designated by Renaudie and Lazarus (2013a). Additional specimens will be needed to show that differing degrees of silicification should be accepted within the range of this species, or that there is a clear break between the two morphotypes justifying separate species.

**Range.** In the Southern Ocean, this species is rare in the Early Miocene and sporadic from the Middle to Late Miocene. In the EEP, it is present from the Middle to Late Miocene, but the lower limit was not determined (see Table 1). Petrushevskaya's specimen is from the Middle Miocene equatorial Pacific.

### *Botryopera setosa* **(Jørgensen, 1900) Kruglikova, 1989**

Plate 9, Figs. 9A–10B.

non *Botryopyle setosa* n. sp., Cleve, 1899, pl. 1, fig. 10a–b.
*Lithomelissa setosa* (Cleve) Jørgensen, 1900, pl. 4, fig. 21.
*Lithomelissa setosa* (Cleve) *var. belonophora* Jørgensen, 1900, pl. 4, fig. 21.
*Lithomelissa setosa* n. Sp., Jørgensen, 1905, pl. 16, figs. 81–83, pl. 18, fig. 108a–b.
*Lithomelissa setosa* Jørgensen, Popofsky, 1908, pl. 31, figs. 6, 7 (non figs. 2, 8, 10).
*Lithomelissa setosa* Jørgensen, Schröder, 1914, text-figs. 54–57.
*Lithomelissa setosa* Jørgensen, Wailes, 1937, text-fig. 25.
*Lithomelissa setosa* (?) Jørgensen, Petrushevskaya, 1967, pl. 46, fig. 4.
*Lithomelissa* sp. A, Petrushevskaya, 1967, pl. 46, figs. 1–2, ?fig. 3.
*Lophophaena setosa* Jørgensen, Petrushevskaya, 1971, pl. 60, fig. 6.
*Lithomelissa setosa* Jørgensen, Bjørklund, 1974, text-figs. 8a–h.
*Lithomelissa setosa* Jørgensen, Aarseth *et al.,* 1975, pl. 14, fig. g.
*Lithomelissa setosa* Jørgensen, Bjørklund, 1976, pl. 8, figs. 1–13.
*Lithomelissa setosa* Jørgensen, Boltovskoy and Riedel, 1980, pl. 5, fig. 1.
*Botryopera setosa* (Jørgensen), Kruglikova, 1989, pl. 2, figs. 17–23.
*Lithomelissa setosa* Jørgensen, Takahashi, 1991, pl. 25, figs. 21–22, ?figs. 19–20 (non 16–18).
non *Lithomelissa setosa* Jørgensen, Sashida and Kurihara, 1999, pl. 7, figs. 5–6, 17.
*Lithomelissa* sp., Sashida and Kurihara, 1999, pl. 7, fig. 3.
*Lithomelissa setosa* Jørgensen, Bjørklund *et al.,* 2014, pl. 7, figs. 10–13.
*Lithomelissa setosa* Jørgensen, Dolven *et al.,* 2014, pl. 6, figs. 10–17.
non *Lithomelissa setosa* Jørgensen, Chen *et al.,* 2017, pl. 66, figs. 6–8.
*Lithomelissa setosa* Jørgensen, Matul and Mohan, 2017, fig. 2.30.
*Lithomelissa setosa* Jørgensen, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** Jørgensen (1899) intended to questionably transfer Cleve's species *Botryopyle setosa* to *Lithomelissa.* However, the illustrations of Jørgensen show a species that is clearly not synonymous with Cleve's species, and is in fact a cannobotryid rather than a plagonid. Jørgensen (1905) corrected this mistaken synonymy, indicating that *Botryopyle setosa* Cleve, 1899 is not the same as *Lithomelissa setosa* Jørgensen, 1900. These two species are recognized as separate in subsequent literature, although *Botryopyle setosa* Cleve was later transferred to *Amphimelissa*, and designated as the type species of that genus by Petrushevskaya (1971). This species does not fit the definition of *Lithomelissa* because it does not have an apical spine that passes freely through the cephalis. Kruglikova (1989) transferred *L. setosa* to the genus *Botryopera*, and herein we accept this transfer although it has not yet been widely adopted in the literature.

**Range.** Middle Miocene—Late Pleistocene in the EEP, lower boundary not determined (Table 1).

### *Botryopera* sp. A

Plate 6, Figs. 7A–9B.

**Remarks.** This species is similar to *Botryopera amabie* n. sp. (Pl. 7, Figs. 1A–6) except that the cephalis is proportionally shorter and narrower, compared to the thorax dimensions. On average, the cephalis height is ~33 microns, rather than the 43 micron mean of *B. amabie.* The shoulders on the thorax are also more distinct, and the thorax tapers more dramatically, causing the shape to be less cylindrical in outline. The overall size is smaller than in *B. amabie* n. sp.

**Material examined.** 4 specimens observed from the following samples: 321-1337A-31X-6W, 4–6cm (Middle Miocene), 321-1337D-30H-3, 103–104cm (Middle Miocene), and 321-1337D-26H-3W, 142–144cm (Late Miocene).

**Range.** Middle–Late Miocene in the EEP (Table 1).

### *Botryopera* sp. B

Plate 8, Figs. 7A–8.

**Remarks.** The pore structure and segment dimensions are nearly identical to *Botryopera* sp. A (Pl. 6, Figs. 7A–9B), but this species differs in that it has a horn on the top of the cephalis that is not related to the apical spine. This characteristic also distinguishes *Botryopera* sp. B from *Botryopera amabie* n. sp. (Pl. 7, Figs. 1A–6). The horn on the cephalis is conical and relatively large, approximately the length of the cephalis itself.

**Material examined.** 2 specimens observed from samples 321-1337D-30H-3, 103–104cm (Middle Miocene), and 321-1337D-26H-3W, 142–144cm (Late Miocene).

**Range.** Middle–Late Miocene in the EEP (Table 1).

### Other Botryopera species not observed in this study:

### *Botryopera brevispicula* (Popofsky, 1908) Petrushevskaya, 1986

*Lithomelissa* (?) *brevispicula* n. sp., Popofsky, 1908, pl. 32, figs. 7–8.
*Lithomelissa brevispicula* Popofsky, Petrushevskaya, 1967, pl. 44, figs. 1–6.
*Botryopera brevispicula* (Popofsky), Petrushevskaya, 1986, pl. 1, fig. 8.

### *Botryopera boldyrae* (Petrushevskaya, 1971) Petrushevskaya, 1975

*Lithomelissa* sp., Petrushevskaya, 1966, pl. 6, fig. 1.
*Trisulcus boldyrae* n. sp., Petrushevskaya, 1971, pl. 73, figs. 4–6.
*Botryopera boldyrae* (Petrushevskaya), Petrushevskaya, 1975, p. 591 [not figured].
Aff. *Boryopera* sp. aff. *B. boldyrae* (Petrushevskaya), Petrushevskaya, 1975, pl. 11, fig. 35.

### *Botryopera* (?) *chlamida* Petrushevskaya, 1975

*Botryopera* (?) *chalmida* n. sp., Petrushevskaya, 1975, pl. 20, figs. 5–6.

### *Botryopera oceanica* (Ehrenberg, 1873a) group Petrushevskaya, 1975

*Lithopera oceanica* n. sp. Ehrenberg, 1873a, pl. 4, fig. 21.
*Sethopera oceanica* (Ehrenberg), Haeckel, 1887, p. 1232 [not figured].
*Lithomelissa hystrix* n. sp., Jørgensen, 1905, pl. 16, fig. 85.
*Botryopera oceanica* (Jørgensen), Petrushevskaya, 1975, pl. 18, figs. 7, 10; pl. 19, figs. 4–5.

### *Botryopera* (?) *pseudoantarctissa* Petrushevskaya and Kozlova, 1979

*Botryopera* (?) *pseudoantarctissa* n. sp., Petrushevskaya in Petrushevskaya and Kozlova, 1979, figs. 331–338.

### *Botryopera chippewa* Renaudie and Lazarus, 2013a

*Dimelissa* sp. P, Petrushevskaya, 1971, pl. 46, fig. 12.
? *Pseudodictyophimus* (?) sp., Petrushevskaya, 1975, pl. 11, fig. 18.
? *Lithomelissa* sp. B aff *L. mitra* Bütschli, Chen, 1975, pl. 8, figs. 4–5.
*Botryopera chippewa* n. sp., Renaudie and Lazarus, 2013a, pl. 5, figs. 12A–B; pl. 6, figs. 2A–3B, 7, 10.

### *Botryopera? gibbera* Renaudie and Lazarus, 2012

*Botryopera? gibbera* n. sp., Renaudie and Lazarus, 2012, pl. 7, figs. 3A–6B.

### *Botryopera* (?) *leptostraca* Sugiyama, 1993

*Botryopera* (?) *leptostraca* n. sp., Sugiyama, 1993, pl. 14, figs. 1A–4B.

### *Botryopera vavato* **Renaudie and Lazarus, 2015**

*Botryopera vavato* n. sp., Renaudie and Lazarus, 2015 pl. 4, figs. 6–8, 13.

### *Botryopera cyrtoloba* **Haeckel, 1887**

*Botryopera cyrtoloba* n. sp., Haeckel, 1887, pl. 96, fig. 1.

**Remarks.** This species is not well illustrated, making it unclear whether the species should be considered *Botryopera, Trisulcus, Antarctissa*, or another genus. However, as we are unable to examine the type material and it is currently designated the type species of *Botryopera*, we provisionally accept this species as *Botryopera*.

### *Botryopera triloba* **(Ehrenberg) Haeckel, 1887**

*Lithobotrys triloba* n. sp., Ehrenberg, 1844, p. 84 [not figured].
*Lithobotrys triloba* Ehrenberg, Ehrenberg, 1854c, pl. 19, fig. 55; pl. 22, figs. 30A–B.
*Botryopera triloba* (Ehrenberg), Haeckel, 1887, p. 1108 [not figured].
*Lithomelissa boreale* (Ehrenberg) Petrushevskaya, 1967, pl. 48, figs. 1–4.
*Lithomelissa* sp. B, Petrushevskaya, 1967, fig. 47.
*Trisulcus borealis* (Ehrenberg), Petrushevskaya, 1971, pl. 74, figs. 1–8.
*Botryopera triloba* (Ehrenberg) group, Petrushevskaya, 1975, pl. 11, figs. 27–29, 36–39; pl. 20, figs. 3–4.
*Lithobotrys triloba* Ehrenberg, Suzuki *et al.,* 2009, pl. 20, figs. 3A–B, 9A–B.

### Genus *Ceratocyrtis* Bütschli 1882, emend Sugiyama, 1993

Type species: *Cornutella? cucullaris* Ehrenberg, 1874

**Description.** Two-segmented lophophaenid with a small cephalis relative to the width of the thorax. The thorax is usually conical in shape. The dorsal and lateral spines protrude from the base of the cephalis rather than forming thoracic ribs, differentiating this genus from *Lampromitra.* The dorsal spine points downward relative to the near-horizontal lateral spines. The lateral spines are oriented at nearly a right angle from the dorsal spine, making them difficult to identify in the same plane as the dorsal, ventral, and apical spines. *Ceratocyrtis* also has a distinctively elongated axobate, which extends straight downward from near the junction of the median bar and lateral spines into the interior of the thorax. The axobate is often dendritic.

**Remarks.** *Ceratocyrtis* was first described by Bütschli (1882). He recognized two separate forms in the previously described genus *Cornutella* (Ehrenberg, 1839), and broke out several species as belonging to the new genus *Ceratocyrtis*. Bütschli (1882) described this genus as having a muted cephalis that is difficult to distinguish in exterior outline, primary spines likely corresponding to those of *Lithomelissa*, and a downward-pointing apophyse (referred to as the axial spine by Sugiyama (1993), and the axobate in this paper). This definition has remained fairly consistent in the literature, with subsequent authors adding clarification to the internal skeletal characteristics. However, there has been some disagreement as to the higher-level taxonomy and the species that should be included in this genus.

Petrushevskaya (1971) considered *Ceratocyrtis* to be a lophophaenid, and designated the type species of *Ceratocyrtis* as *Cornutella? cucullaris* Ehrenberg 1874. She determined that the type species of *Ceratocyrtis, Helotholus,* and *Bathrocalpis* were not sufficiently different to justify separate genera, so she synonymized these three genera under the senior name *Ceratocyrtis*. Although we agree that the type species of *Helotholus*, *H. histricosa* Jørgensen, 1905*,* should be in the genus *Ceratocyrtis,* we do not consider all species in *Helotholus* to fit this definition. *H. praevema* Weaver, 1983, for example, we do not consider to be *Ceratocyrtis*, but a revision of its taxonomy is outside the scope of this paper. Nishimura (1990) considered *Ceratocyrtis* to belong to Sethophormidae rather than Lophophaenidae. However, she accepted the genus concepts of Bütschli, 1882, Haeckel, 1887, Petrushevskaya, 1971, Petrushevskaya and Kozlova, 1979, and Bjørklund, 1976. Like Petrushevskaya (1971), Nishimura (1990) considered *Ceratocyrtis* to be synonymous with *Helotholus* (sensu Jørgensen, 1905, and Campbell, 1954) and *Bathrocalpis* (Clark and Campbell, 1942, and Campbell, 1954). Sugiyama (1993) closely followed the genus concept of Petrushevskaya (1971), but included detailed diagrams illustrating and clarifying the internal skeletal structure of *Ceratocyrtis* (figs. 21–22). Matsuzaki *et al.* (2015) remarked that *Ceratocyrtis* species often have a large or wide thorax with a small cephalis, whereas *Helotholus* species have a shorter thorax and more distinct cephalis. Therefore, they consider these to be two separate and valid genera. In the present study, we consider the type species of *Helotholus* (*H. histricosa)* to be within the range of variation among our other observed *Ceratocyrtis* species, and thus follow Petrushevskaya (1971)'s synonymy.

Here we observed the following species belonging to *Ceratocyrtis: Ceratocyrtis? chimii* n. sp., *Ceratocyrtis cucullaris* (Ehrenberg) Petrushevskaya, 1971, *Ceratocyrtis histricosus* (Jørgensen 1905) Petrushevskaya, 1971, *Ceratocyrtis spinosiretis* (Takahashi, 1991) Matsuzaki *et al.,* 2015, and *Ceratocyrtis vila* n. sp. *Ceratocyrtis? pseudoadvena* Kozlova, 1999 is poorly documented, but does not appear to fit the description of *Ceratocyrtis* due to the nature of the cephalis. *Ceratocyrtis erosa* (Cleve) Petrushevskaya, 1971 was transferred from Cleve's designation as *Lampromitra*, but it is our opinion that it should remain in *Lampromitra*. Similarly, *Ceratocyrtis sinuosa* (Popofsky) Petrushevskaya, 1971 was also transferred from *Lampromitra* by Petrushevskaya, but we consider it to fit better in *Lampromitra* than *Ceratocyrtis* so do not accept this transfer.

**Range.** ?Eocene—Recent

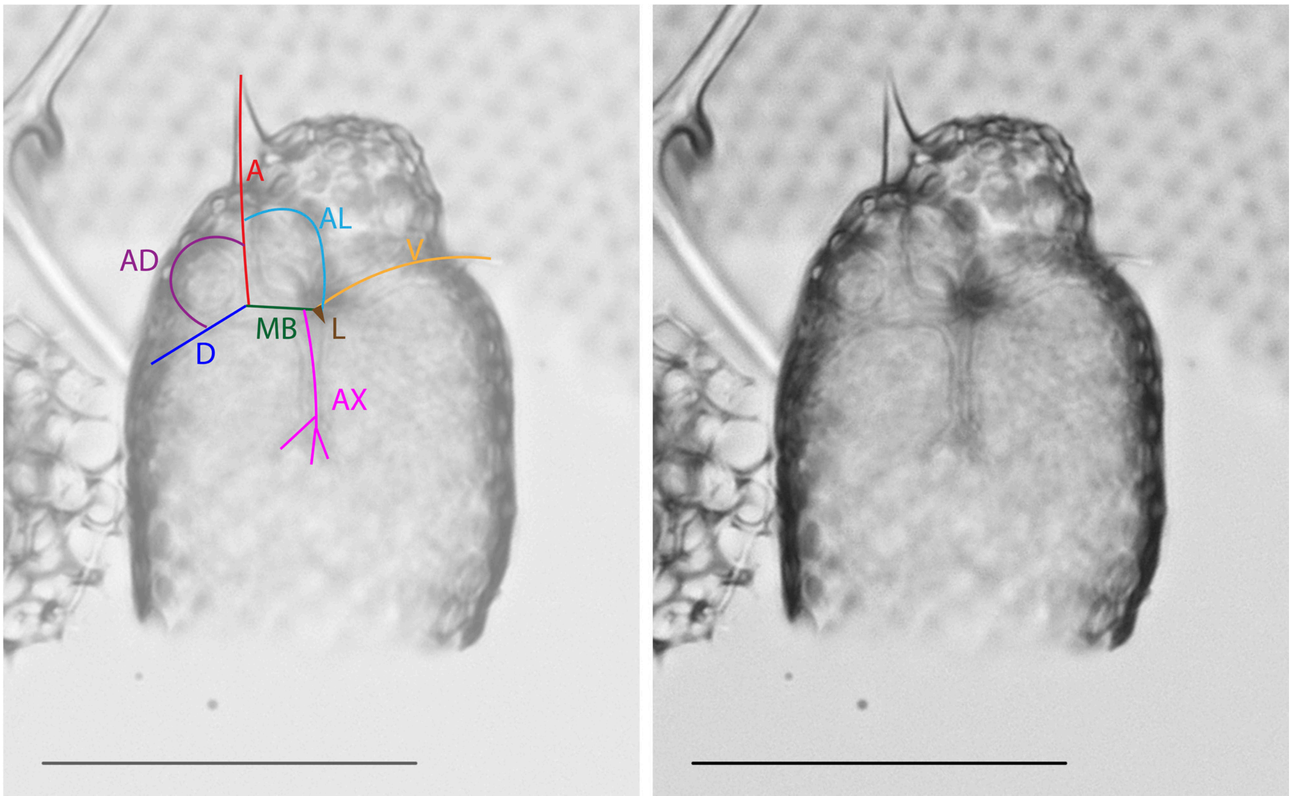

**FIGURE 9.** Internal skeletal structure of *Ceratocyrtis* sp. C.

*Ceratocyrtis? chimii* **n. sp.**
Plate 11, Figs. 1A–9.

urn:lsid:zoobank.org:act:3C24AD7B-0B4E-480E-8681-9B1EDAE03FCA
unknown plagonid group E sp 15, Trubovitz *et al.,* 2020, supplementary data 7.

**Diagnosis.** *Ceratocyrtis* with a single large conical spine on the cephalis that is not an extension of the apical spine. Thorax is usually asymmetrical in outline, and has distinctive shoulders, which tend to be hyaline or have a reduced number of small pores.

**Description.** This species has a relatively large and well-developed cephalis compared to many other *Ceratocyrtis* species, but it is small compared to lophophaenids in general. The apical and ventral spines are similarly thin and short, sometimes barely protruding from the cephalis. The cephalis also exhibits a conical horn and the apex, the height and thickness of which varies considerably between specimens, but is always the most robust spine on the skeleton. There are sometimes delicate and thin, needle-like spines preserved throughout the surface of the cephalis and thorax as well. The thorax is asymmetrical in shape, with a more pronounced, sometimes nearly lobed shoulder on the dorsal side of the skeleton that varies in development between specimens. Pores are small throughout the shell, but tend to become smaller or have more hyaline spaces on the shoulders and on the cephalis. A set of large pores are present where the lateral spines intersect with the wall of the thorax, near the base of the cephalis. When adequately preserved, the thorax ends in a jagged termination that resembles short teeth. An axobate was observed in several specimens, however it often appears to be small or broken off.

**Remarks.** The overall skeletal proportions of this species best fit *Ceratocyrtis* out of all the other lophophaenid genera we observed, but the poorly-developed axobate and relatively large cephalis are uncharacteristic of this genus, so we only make a tentative genus assignment.

**Material examined.** 29 specimens from the Late Miocene samples 321-1337D-26H-3W, 142–144cm, 321-1337D-23H-6, 134–137cm, 321-1337A-21H-1, 33–35cm.

**Holotype.** Pl. 11, Figs. 5A–C; sample 321-1337A-21H-1, 33–35cm; ECO-144; X28-2.

**Paratypes.** (1) Pl. 11, fig. 8; sample 321-1337A-21H-1, 33–35cm; ECO-144; W7-1. (2) Pl. 11, fig. 4; sample 321-1337A-21H-1, 33–35cm; ECO-144; D34-1. (3) Pl. 11, figs. 6A–B; sample 321-1337D-23H-6, 134–137cm; ECO-145; G31-4. (4) Pl. 11, fig. 9; sample 321-1337D-23H-6, 134–137cm; ECO-145; K6-1. (5) Pl. 11, fig. 7; sample 321-1337D-23H-6, 134–137cm; ECO-145; O27-2. (6) Pl. 11, figs. 1A–C; sample 321-1337D-23H-6, 134–137cm; ECO-146; V40-3. (7) Pl. 11, figs. 2A–C; sample 321-1337D-23H-6, 134–137cm; ECO-146; O31-2. (8) Pl. 11, fig. 3; sample 321-1337D-23H-6, 134–137cm; ECO-146; K30-1.

**Measurements.** Height of cephalis 25–31 (28)µm; maximum width of thorax 67–83 (77)µm; length of thorax 48–66 (56)µm; height of horn on cephalis 13–43 (28)µm. Based on 15 specimens.

**Etymology.** Named for the mischievous mountain wilderness spirits in Japanese folklore, chimi.

**Range.** Late Miocene in the EEP (Table 1).

### *Ceratocyrtis cucullaris* **(Ehrenberg) Petrushevskaya, 1971**

Plate 10, Fig. 1.

*Cornutella? cucullaris* n. sp., Ehrenberg, 1874, p. 221 [not figured].
*Cornutella? cucullaris* Ehrenberg, Ehrenberg, 1876, pl.2, fig. 7.
*Ceratocyrtis cucullaris* (Ehrenberg), Bütschli, 1882, pl. 33, fig. 36a–b.
*Sethoconus cucullaris* Haeckel, Haeckel, 1887, p. 1290–1291 [not figured].
*Ceratocyrtis cucullaris* (Ehrenberg), Petrushevskaya, 1971, pl. 52, fig. 1
? *Ceratocyrtis cucullaris* (Ehrenberg) group, Dzinoridze *et al.*, 1978, pl. 26, fig. 12; pl. 37, figs. 4–6.
*Ceratocyrtis cucullaris* (Ehrenberg) group, Dzinoridze *et al.*, 1978, pl. 41, figs. 14–16.
*Ceratocyrtis* ex. gr. *cucullaris* (Ehrenberg), Dumitrica, 1978, pl. 7, figs. 7–8.
*Ceratocyrtis cucullaris* (Ehrenberg), Petrushevskaya and Kozlova, 1979, fig. 290.
*Ceratocyrtis cucullaris* (Ehrenberg), Petrushevskaya, 1986, pl. 1, fig. 1.
non *Ceratocyrtis* sp. aff. *C. cucullaris* (Ehrenberg), Tsoy and Shastina, 1999, pl. 35, fig. 6.
non *Sethoconus cucullaris* (Ehrenberg), Tan and Su, 2003, pl. 11, fig. 6.
*Cornutella cucullaris* Ehrenberg, Ogane *et al.,* 2009, pl. 80, figs. 2a–c, pl. 81, figs. 3a–g.
*Ceratocyrtis cucullaris* (Ehrenberg), Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** The specimens observed in the EEP are within the range of morphological variation illustrated by previous authors.

**Range.** Middle Pleistocene in the EEP (Table 1).

### *Ceratocyrtis histricosus* **(Jørgensen, 1905) Petrushevskaya, 1971**

Plate 10, Figs. 2–3.

*Helotholus histricosa* n. sp., Jørgensen, 1905, p. 137, pl. 16, figs. 86–88.
non *Helotholus histricosa* Jørgensen, Riedel, 1958, pl. 3, fig. 8.

non *Helotholus histricosa* Jørgensen, Benson, 1966, pl. 31, figs. 4–8.
*Helotholus histricosa* Jørgensen, Petrushevskaya, 1967, pl. 51, fig. 2.
*Ceratocyrtis histricosa* (Jørgensen), Petrushevskaya, 1971, pl. 52, figs. 2–4.
*Ceratocyrtis histricosa* (Jørgensen) forma A, Petrushevskaya, 1971, pl. 29, figs. 3–4; pl. 52, figs. 5–7.
*Helotholus histricosa* Jørgensen, Tan and Tchang, 1976, text-fig 53a–c.
*Ceratocyrtis histricosus* (Jørgensen) [sic], Bjørklund, 1976, pl. 8, figs. 19–24.
*Ceratocyrtis histricsus* (Jørgensen) [sic], Bjørklund, 1976, pl. 11, figs. 4–5.
non *Ceratocyrtis* sp. aff. *C. histricosus* (Jørgensen) [sic], Bjørklund, 1976, pl. 15, figs. 6–8.
non *Helotholus histricosa* Jørgensen, Casey, 1977, pl. 6, fig. 1.
non *Ceratocyrtis* cf. *hystricosa* (Jørgensen) [sic], Dumitrica, 1978, pl. 6, figs. 9 and 19.
*Ceratocyrtis* sp. aff. *C. histricosus* (Jørgensen), Dzinoridze *et al.,* 1978, pl. 41, fig. 13.
*Ceratocyrtis* sp., Dzinoridze *et al.,* 1978, pl. 41, fig. 20.
non *Ceratocyrtis histricosa* (Jørgensen), Takahashi and Honjo, 1981, pl. 7, figs. 6–7.
non *Helotholus histricosa* Jørgensen group, Benson, 1983, pl. 8, figs. 1–3.
? *Ceratocyrtis histricosa* (Jørgensen), Nigrini and Lombari, 1984, pl. 15, fig. 6.
*Ceratocyrtis histricosus* (Jørgensen), Funakawa, 1994, pl. 7, fig 1a–b.
non *Helotholus histricosa* Jørgensen, Chen *et al.,* 2017, pl. 68, figs 12–13.
? *Clathromitra* sp. 2, Chen *et al.,* 2017, pl. 68, fig. 4 (non figs. 7–11).
*Helotholus histricosa* Jørgensen, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** Petrushevskaya (1971) transferred this species from *Helotholus* to *Ceratocyrtis*, as discussed in the genus discussion above. Since then, not all authors have recognized this name change, some of them retaining *Helotholus.* Many illustrated specimens of *Ceratocyrtis* (or *Helotholus*) *histricosa* in previous literature are typical of those observed during this study. However, there have been a number of specimens of *Sethoconus tabulatus* (Ehrenberg, 1873b) Haeckel, 1887*,* forms similar to *Helotholus vema* (Hays, 1965) or possibly species of *Botryopera*, specimens of *Antarctissa* and *Pseudodictyophimus*, as well as different *Ceratocyrtis* taxa that have been misidentified as *Ceratocyrtis histricosus* (Jørgensen), indicating multiple contradictory concepts in the literature. Here we follow the species concept and genus transfer of Petrushevskaya (1971).

**Range.** Late Miocene—Late Pleistocene, EEP (Table 1).

### *Ceratocyrtis spinosiretis* **(Takahashi, 1991) Matsuzaki** *et al.,* **2015**
Plate 10, Fig. 4.

*Helotholus histricosa* Jørgensen, Benson, 1966, pl. 31, figs. 7–8 (non figs. 4–6).
*Ceratocyrtis galeus* (Cleve), Nishimura and Yamauchi, 1984, pl. 32, figs. 8, 10–11.
*Lampromitra spinosiretis* n. sp., Takahashi, 1991, p. 110, pl. 34, figs. 1–2, 7.
*Lampromitra spinosiretis* Takahashi, Okazaki *et al.,* 2004, pl. 2, figs. 27, 28.
*Lampromitra spinosiretis* Takahashi, Ikenoue *et al.,* 2012, pl. 3, fig. 15.
*Lamprocyrtis nigrinae* (Caulet), Tanaka and Takahashi, 2008, pl. 3, fig. 14.
*Ceratocyrtis galeus* (Cleve), Itaki, 2009, pl. 19, figs. 3–10.
*Ceratocyrtis spinosiretis* (Takahashi), Matsuzaki *et al.,* 2015, pl. 8, figs. 1–2.
*Lampromitra spinosiretis* Takahashi, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** In his original description of this species, Takahashi (1991) listed part of Benson (1996)'s illustration of *Helotholus histricosa* Jørgensen in the synonymy. Takahashi lists Benson's plate 31, figs. 6–7 (only) in his synonymy, but upon examination of both sets of plates, it appears there was a typo in Takahashi's list; Benson (1966)'s pl. 31, figs. 7–8 are conspecific with *Lampromitra spinosiretis* Takahashi (1991), pl. 34, figs. 1–2, 7. Benson (1966)'s pl. 31, fig. 6 is clearly a *Pseudodictyophimus* specimen, due to its long feet, short thorax, and lack of an axobate. Therefore, we have indicated the corrected synonymy citation in the list above. Matsuzaki *et al.* (2015) transferred this species from *Lampromitra* to *Ceratocyrtis* due to the skeletal structure of the cephalis in Takahashi (1991)'s paratype specimen. Here we follow Matsuzaki *et al.* (2015)'s genus transfer, and add that the absence of three thoracic ribs and presence of an axobate are additional evidence that this species belongs in *Ceratocyrtis* rather than *Lampromitra.*

**Range.** Late Miocene—Middle Pleistocene, EEP (Table 1).

### *Ceratocyrtis vila* **n. sp.**

Plate 12, Figs. 1A–8B.

urn:lsid:zoobank.org:act:FC86AA1D-642B-4331-A956-BB44601D2D56
*Ceratocyrtis* sp 6, partim., Trubovitz *et al.,* 2020, supplementary data 7.
*Ceratocyrtis* sp 8, Trubovitz *et al.,* 2020, supplementary data 7.

**Diagnosis.** *Ceratocyrtis* with a very small cephalis surrounded by four small but prominent thoracic lobes where the thorax attaches to the cephalis, and the overall shape is highly elongated and generally conical.

**Description.** This species has a small, spherical cephalis that appears somewhat sunken into the thorax. The cephalis sits between a set of four strong thoracic lobes, which are each approximately the same size as the cephalis, and are located where the thorax attaches to the cephalis. Although this character is not always preserved, there is a single strong conical horn slightly longer than the height of the cephalis, and sometimes 1–2 minor thorns on the cephalis as well. This species has a long, conical thorax, with pores gradually increasing in size from top to bottom. Thorax wall is mostly smooth, without any prominent spines or thorns. Most specimens have a slight inflection in the thorax outline just below the four shoulders, where the pore size begins to increase more dramatically and shell silicification begins to decrease towards the base of the thorax. A dendritic axobate is present in most specimens, but in others the axobate does not appear to be dendritic.

**Remarks.** The relatively small, symmetrical shoulders surrounding the cephalis and the elongated cone-shaped thorax differentiate this species from the other *Ceratocyrtis* taxa observed in this study.

**Material examined.** 72 specimens observed from samples 321-1337A-35X-1, 106–108cm (Middle Miocene), 321-1337D-23H-6, 134–137cm (Late Miocene), 321-1337A-21H-1, 33–35cm (Late Miocene), 321-1337A-18H-6, 77–80cm (Late Miocene), 321-1337A-16H-6, 121–124cm (Late Miocene), 321-1337A-14H-7, 39–42cm (Late Miocene), 321-1337A-12H-5, 23–26cm (Late Miocene), and 321-1337A-10H-2, 91–94cm (Early Pliocene).

**Holotype.** Pl. 12, figs. 1A–B; sample 321-1337D-23H-6, 134–137cm; ECO-146; R41-3.

**Paratypes.** (1) Pl. 12, fig. 7; sample 321-1337A-21H-1, 33–35cm; ECO-144; P12-1. (2) Pl. 12, fig. 4; sample 321-1337A-21H-1, 33–35cm; ECO-144; Y23-1. (3) Pl. 12, figs. 3A–B; sample 321-1337D-23H-6, 134–137cm; ECO-145; O6-4. (4) Pl. 12, figs. 2A–B; sample 321-1337D-23H-6, 134–137cm; ECO-145; H13-2. (5) Pl. 12, fig. 5; sample 321-1337D-23H-6, 134–137cm; ECO-146; V16-2. (6) Pl. 12, fig. 6; sample 321-1337D-23H-6, 134–137cm; SCO-146; P16-3. (7) [not figured] sample 321-1337A-16H-6, 121–124cm; ECO-141; G35-4.

**Measurements.** Cephalis height 20–23 (22)µm; cephalis width 15–20 (18)µm; thorax width 77–111 (89)µm; thorax length 68–108 (90)µm; width of thorax at shoulders 30–38 (42)µm. Based on 11 specimens with variable preservation of the thoracic segment. Thus, the length and width of the thorax measurements should be considered the minimum possible dimensions, as all specimens had irregular terminations of the thorax, suggesting that they were partially broken.

**Etymology.** Named for the nymphs often portrayed wearing long white dresses in Slavic folklore, vilas.

**Range.** Middle Miocene—Early Pliocene, in the EEP. Lower limit not determined. (Table 1).

### *Ceratocyrtis* **sp. A**

Plate 10, Figs 5A–6B.

*Ceratocyrtis* sp 2, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species has a smooth shell surface that has three small lobes surrounding the cephalis. Furrows between lobes are associated with the dorsal and lateral spines, which become incorporated into the thorax. The concept of this species is poorly defined and in need of additional study; it may be a group containing multiple species.

**Material examined.** 92 specimens observed from samples 321-1337A-16H-6, 121–124cm (Late Miocene), 321-1337A-14H-7, 39–42cm (Late Miocene), 321-1337A-12H-5, 23–26cm (Late Miocene), 321-1337A-10H-2, 91–94cm (Early Pliocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), 321-1337A-6H-3, 29–32cm (Late Pliocene), 321-1337A-5H-5, 11–14cm (Late Pliocene), 321-1337A-4H-6, 115–118cm (Early Pleistocene), 321-1337A-4H-2, 16–19cm (Middle Pleistocene), 321-1337A-3H-2, 103–106cm (Middle Pleistocene), 321-1337A-2H-3, 76–

79cm (Late Pleistocene), and 321-1337D-1H-1, 0–3cm (Recent).

**Range.** Late Miocene—Recent in the EEP (Table 1).

### *Ceratocyrtis* **sp. B**

Plate 10, Figs. 7A–9B.

unknown plagonid group E sp. 3 cf, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species has pores on the thorax that increase in size dramatically from top to base. Thorax flares outward more widely than most other *Ceratocyrtis* species. The shell wall was thickly silicified in the specimens observed during this study. The axobate is dendritic, clearly placing this species within *Ceratocyrtis*. This species differs from *Tetraphormis dodecaster* Haeckel, 1887 in that it is much larger, has thicker bars between pores, has a dendritic axobate, and does not have ribs running down the thorax.

**Material examined.** 12 specimens from samples 321-1337D-23H-6, 134–137cm (Late Miocene), 321-1337A-16H-6, 121–124cm (Late Miocene), 321-1337A-14H-7, 39–42cm (Late Miocene), 321-1337A-12H-5, 23–26cm (Late Miocene), 321-1337A-6H-3, 29–32cm (Late Pliocene), 321-1337A-5H-5, 11–14cm (Late Pliocene), 321-1337A-4H-6, 115–118cm (Early Pleistocene), 321-1337A-4H-2, 16–19cm (Middle Pleistocene), and 321-1337D-1H-1, 0–3cm (Recent).

**Range.** Late Miocene—Recent in the EEP (Table 1).

### *Ceratocyrtis* **sp. C**

Plate 13, Figs. 1A–2B.

*Ceratocyrtis* sp 5, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** The cephalis of this species is relatively large for the genus. It has a strong conical apical spine that protrudes out the side of the cephalis before nearing the apex, which can have a slightly triangular shape in some specimens (as in pl. 13, fig. 1). This species has a tapering thorax, which is unusual among the *Ceratocyrtis* species observed in this study. The shell reaches its widest point approximately 1/3 down the thorax. Pore size is mostly uniform throughout the cephalis and thorax. Only three specimens were observed, so additional study is needed.

**Material examined.** 3 specimens observed from samples 321-1337A-6H-3, 29–32cm (Late Pliocene), and 321-1337A-4H-6, 115–118cm (Early Pleistocene).

**Range.** Late Pliocene– Early Pleistocene in the EEP (Table 1).

### *Ceratocyrtis* **sp. D**

Plate 14, Figs. 7A–8B.

*Ceratocyrtis* sp 5 cf, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species has a thorax that tends to taper slightly towards the base, similar to *Ceratocyrtis* sp. C (pl. 13, figs. 1A–2B). However, it is much smaller in overall size and has relatively larger pores and a proportionally smaller cephalis.

**Material examined.** 9 specimens observed from samples 321-1337D-23H-6, 134–137cm (Late Miocene), 321-1337A-18H-6, 77–80cm (Late Miocene), 321-1337A-10H-2, 91–94cm (Early Pliocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), 321-1337A-6H-3, 29–32cm (Late Pliocene), and 321-1337A-5H-5, 11–14cm (Late Pliocene).

**Range.** Late Miocene—Late Pliocene in the EEP (Table 1).

### *Ceratocyrtis* **sp. E**

Plate 13, Figs. 7A–8.

*Ceratocyrtis* sp 9, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species has at least two long, thin conical spines on its cephalis, one of which is an extension of the apical spine. It has a broad, dome-shaped thorax, with semi-irregular pores that do not increase in size toward the base, but do have the tendency to become elongated. The small cephalis, overall skeletal proportions, and dendritic axobate clearly place this species in *Ceratocyrtis,* but it does not match any species descriptions we are aware of.

**Material examined.** 14 specimens observed from samples 321-1337D-23H-6, 134–137cm (Late Miocene), 321-1337A-18H-6, 77–80cm (Late Miocene), 321-1337A-14H-7, 39–42cm (Late Miocene), 321-1337A-10H-2, 91–94cm (Early Pliocene), and 321-1337A-5H-5, 11–14cm (Late Pliocene).

**Range.** Late Miocene—Late Pliocene in the EEP (Table 1).

### *Ceratocyrtis* **sp. F**

Plate 12, Figs. 9A–11.

*Ceratocyrtis* sp 10, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species typically has a slightly thorny cephalis and thorax, with small, regular pores, and one slight dimple on thorax. The cephalis exhibits one main forked spine. This species is very similar to *Ceratocyrtis* sp. E (pl. 13, figs. 7A–8), but differs in that the primary cephalic horn is forked.

**Material examined.** 54 specimens observed from samples 321-1337D-23H-6, 134–137cm (Late Miocene), 321-1337A-18H-6, 77–80cm (Late Miocene), 321-1337A-16H-6, 121–124cm (Late Miocene), 321-1337A-14H-7, 39–42cm (Late Miocene), 321-1337A-12H-5, 23–26cm (Late Miocene), and 321-1337A-5H-5, 11–14cm (Late Pliocene).

**Range.** Late Miocene—Latest Pliocene, EEP (Table 1).

### *Ceratocyrtis* **sp. G**

Plate 14, Figs. 1A–2B.

*Ceratocyrtis* sp 11, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species resembles *Ceratocyrtis* sp. F (pl. 12, figs. 9A–11), except that the thorax is longer and more narrow, often with teeth present at the base. The overall shell dimensions are larger as well.

**Material examined.** 2 specimens observed from sample 321-1337A-18H-6, 77–80cm (Late Miocene).

**Range.** Late Miocene in the EEP (Table 1).

### *Ceratocyrtis* **sp. H**

Plate 13, Figs. 3A–6B.

unknown plagonid group E sp 16 **,** Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species is unusual for its very strong ventral spine, which is as strong, and nearly as long, as the apical horn. The axobate and small cephalis indicate that this species belongs in *Ceratocyrtis*, but more specimens are needed before it can be adequately described.

**Material examined.** 4 specimens observed from samples 321-1337D-26H-3W, 142–144 (Late Miocene) and 321-1337D-23H-6, 134–137cm (Late Miocene).

**Range.** Middle—lower Late Miocene, EEP (Table 1). Lower limit not determined.

### *Ceratocyrtis* sp. I group

Plate. 14, Figs. 3A–6B.

*Ceratocyrtis* sp 7 cf, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species group is unique for its relatively heavily silicified cephalis, and long, thin thorax with semi-irregular pores that remain similar in size throughout the length of the thorax. It differs from *C. cucullaris* (Pl. 10, Fig. 1) in that the thorax does not flare as widely outward, and it has a relatively thin thorax wall. It differs from *C. histricosus* (Pl. 10, Figs. 2–3) in that it generally grows a much longer thorax, and the pores on the thorax do not substantially increase in size toward the bottom. We list this as a species group rather than a single species because the simple morphology and lack of constraint in morphological variability make it difficult to determine whether this is one species or multiple.

**Material examined.** 10 specimens observed from Late Miocene samples 321-1337D-23H-6, 134–137cm, 321-1337A-18H-6, 77–80cm, and 321-1337A-16H-6, 121–124cm.

**Range.** Late Miocene in the EEP (Table 1).

## Other species of *Ceratocyrtis* not observed in our study:

### *Ceratocyrtis? arthuri* Renaudie and Lazarus, 2015

*Ceratocyrtis? arthuri* n. sp., Renaudie and Lazarus, 2015, pl. 6, figs. 4A–B, 6A–B.

**Remarks.** It is not certain that this species belongs in *Ceratocyrtis* because the axobate was not observed, and the nature of the cephalis and thorax termination are unusual for this genus. However, it appears to be more closely related to other species of *Ceratocyrtis* than to any other genus.

### *Ceratocyrtis broeggeri* Goll and Bjørklund, 1989

*Ceratocyrtis cucullaris* (Ehrenberg) f. *goetheana*, Petrushevskaya and Kozlova, 1979, fig. 294.
*Ceratocyrtis broeggeri* n. sp., Goll and Bjørklund, 1989, pl. 5, figs. 14–18.

### *Ceratocyrtis campanula* (Clark and Campbell, 1942) Petrushevskaya, 1971

*Bathrocalpis campanula* n. sp., Clark and Campbell, 1942, pl. 9, fig. 27.
*Ceratocyrtis campanula* (Clark and Campbell), Petrushevskaya, 1971, pl. 51, figs. 1–4.
*Ceratocyrtis campanula* (Clark and Campbell) Petrushevskaya, Kozlova, 1999, pl. 30, fig. 6.
non *Ceratocyrtis campanula* (Clark and Campbell), Dzinoridze *et al.,* 1978, pl. 26, fig. 13.

### *Ceratocyrtis dolvenae* Renaudie and Lazarus, 2012

*Ceratocyrtis dolvenae* n. sp., Renaudie and Lazarus, 2012, pl. 5, figs. 2A–B, 5A–6B.

### *Ceratocyrtis galeus* (Cleve, 1899) Bjørklund, 1976

*Sethoconus galea* n. sp., Cleve, 1899, pl. 4, fig. 3.
*Sethoconus* (?) *galea* Cleve, Petrushevskaya, 1967, pl. 52, fig. 2.
*Ceratocyrtis galeus* (Cleve), Bjørklund, 1976, pl. 11, figs. 1–3.
*Ceratocyrtis galeus* (Cleve) Bjørklund, Renaudie, 2014, pl. 18, figs. 4A–B.

### *Ceratocyrtis manumi* **Goll and Bjørklund, 1989**

*Ceratocyrtis manumi* n. sp., Goll and Bjørklund, 1989, pl. 5, figs. 21–23.

### *Ceratocyrtis mashae* **Bjørklund, 1976**

*Ceratocyrtis* sp. aff. *C. cucullaris* (Ehrenberg), Petrushevskaya and Kozlova, 1972, pl. 37, fig. 12.
*Ceratocyrtis mashae* n. sp., Bjørklund, 1976, pl. 17, figs. 1–5.
*Ceratocyrtis cucullaris* (Ehrenberg) *mashae* Bjørklund, Petrushevskaya and Kozlova, 1979, figs. 287–288, 466–468.
*Ceratocyrtis mashae* Bjørklund, Abelmann, 1990, pl. 4m figs. 15A–C.
*Ceratocyrtis mashae* Bjørklund, Nishimura, 1990, pl. 20, figs. 5A–B, 8A–B.
? *Ceratocyrtis mashae*? Bjørklund, O'Connor, 1999, pl. 9, fig. 9.
*Ceratocyrtis mashae* Bjørklund, Renaudie, 2014, pl. 18, fig. 6.

### *Ceratocyrtis multicornus* **Funakawa, 1994**

*Arachnocorys* sp. B group, Funakawa, 1993, pl. 2, figs. 1A–3B.
*Ceratocyrtis multicornus* n. sp., Funakawa, 1994, pl. 7, figs. 2A–B.

### *Ceratocyrtis panicula* **Petrushevskaya and Kozlova, 1979**

*Lithomelissa stigi* Bjørklund partim., Bjørklund, 1976, pl. 15, figs. 12–14, 17.
*Ceratocyrtis panicula* n. sp., Petrushevskaya in Petrushevskaya and Kozlova, 1979, fig. 289.

### *Ceratocyrtis rhabdophora* **(Clark and Campbell, 1945) group Petrushevskaya, 1986**

*Bathrocalpis rhabdophora rhabdophora* n. sp., Clark and Campbell, 1945, pl. 7, figs. 37–41.
? *Ceratocyrtis* sp. R, Petrushevskaya, 1975, pl. 11, fig. 12; pl. 18, fig. 1–3 (non fig. 4); pl. 19, fig. 1.
*Bathrocalpis* (?) *rhabdophora* (Clark and Campbell) group, Dzinoridze *et al.,* 1978, pl. 26, fig. 15.
? *Ceratocyrtis rhabdophora* (Clark and Campbell), Petrushevskaya, 1986, pl. 1, fig. 7.
*Ceratocyrtis rhabdophora* (Clark and Campbell), Kozlova, 1999, pl. 47, fig. 14.

**Remarks.** Petrushevskaya (1971) indicated that the genus *Bathrocalpis* Clark and Campbell, 1942 is a junior synonym of *Ceratocyrtis*, but she did not specifically mention *rhabdophora* in that publication. She first explicitly listed this species as *Ceratocyrtis rhabdophora* in 1986, but the illustration in that publication is a questionable match to the specimens figured by Clark and Campbell (1945).

### *Ceratocyrtis? ringisstola* **Renaudie and Lazarus, 2015**

*Ceratocyrtis? ringisstola* n. sp., Renaudie and Lazarus, 2015, pl. 6, figs. 5A–B, 7A–B.

**Remarks.** The axobate with this species was not observed, and the thorax has an unusual termination, which led the authors to only tentatively place this species in *Ceratocyrtis*.

### *Ceratocyrtis robustus* **Bjørklund, 1976**

*Ceratocyrtis robustus* n. sp., Bjørklund, 1976, pl. 17, figs. 6–10.
non *Ceratocyrtis robustus* Bjørklund, Nishimura, 1990, pl. 20, fig. 6.
*Ceratocyrtis robustus* Bjørklund, Renaudie, 2014, pl. 18, figs. 3A–B.
non *Ceratocyrtis robustus* Bjørklund, Chen *et al.,* 2017, pl. 73, figs. 20–22.

**Remarks.** None of the type specimens illustrated by Bjørklund (1976) clearly show the outer wall of the thorax, making it difficult to visualize the nature of the pores on that part of the shell, which are described by the author as "rounded to irregularly rounded pores of variable size, 5–25 µm." Both Nishimura (1990) and Chen *et al.* (2017) depict specimens with pores of fairly consistent size; small pores are visible on the specimen in Nishimura (1990) and large pores on both specimens in Chen *et al.* (2017). Thus, these specimens are excluded from our synonymy, and further illustration of the type material would likely aid in clarifying this species concept.

### *Ceratocyrtis shimodaensis* **Sashida and Kurihara, 1999**

*Ceratocyrtis* sp., Sashida and Uematsu, 1994, figs. 3-5; 4-4, 11, 12, 15.
*Ceratocyrtis shimodaensis* n. sp., Sashida and Kurihara, 1999, text-figs. 4.1–4.2; pl. 7, fig. 11; pl. 12, fig. 9.

**Remarks.** This species appears to be unusual for *Ceratocyrtis* in that the cephalis is barely distinguishable from the thorax and the thorax is very short, which are characteristics more common in genera such as *Helotholus* and *Steganocubus* than *Ceratocyrtis.* However, the authors note that this species has an axobate that is prominent and dendritic, so we accept their placement in *Ceratocyrtis*.

### *Ceratocyrtis stoermeri* **Goll and Bjørklund, 1989**

*Ceratocyrtis stoermeri* n. sp., Goll and Bjørklund, 1989, pl. 5, figs. 5–9.
*Ceratocyrtis stoermeri* Goll and Bjørklund, Sugiyama, 1993, pl. 20, figs. 4–6.
*Ceratocyrtis stoermeri* Goll and Bjørklund, Renaudie, 2014, pl.; 18, figs. 7A–B.
*Ceratocyrtis stoermeri* Goll and Bjørklund, Chen *et al.,* 2017, pl. 74, figs. 1–6.

### *Ceratocyrtis tons* **Vituchin, 1993**

*Ceratocyrtis tons* n. sp., Vituchin, 1993, pl. 8, figs. 1–2B.

### **Genus *Lithomelissa* Ehrenberg, 1847, emend. O'Connor, 1997**

Type species: *Lithomelissa microptera* Ehrenberg, 1854c

**Description.** A two-segmented lophophaenid that has an apical spine passing freely through the cephalis. Dorsal, ventral, and lateral spines protrude through the wall of the thorax, not forming ribs. Cephalis is large relative to the thorax, similar in proportion to *Lophophaena* and *Peromelissa*, but proportionally larger than it is in *Ceratocyrtis*. Thorax typically does not have a clear termination.

**Remarks.** *Lithomelissa* was first described rather vaguely, as a test with a single stricture, neither end lobate, and lateral wing-like spines (Ehrenberg, 1847). This description could fit the majority of lophophaenid taxa. Initially, no species were described by Ehrenberg (1847a), and no type species was designated for this genus. Thus, over the years there has been much confusion and disagreement in the literature regarding the definition of *Lithomelissa*. Haeckel (1881, 1887) understood a very broad concept of *Lithomelissa*, and split the genus into three subgenera: *Acromelissa* (with one horn), *Micromelissa* (with two horns), and *Sethomelissa* (with three or more horns). It appears that the species Haeckel placed in *Acromelissa* would best fit the modern usage of *Lithomelissa* (i.e., sensu Petrushevskaya, 1975 and O'Connor, 1997), but as many of Haeckel's species were not illustrated, it is difficult to be certain of this. Several of the lithomelissids Haeckel assigned to subgenera *Micromelissa* and *Sethomelissa* have since been reassigned to *Lophophaena* (i.e., *L. decacantha* and *L. buetschlii*). Bütschli (1882) described and illustrated several species of *Lithomelissa* (figs. 21–26), with all except for *Lithomelissa haeckeli* exhibiting a single apical horn passing freely through the cephalis (similar to those in Haeckel's subgenus *Acromelissa*). Jørgensen (1900, 1905) was also among the first to describe and illustrate the internal skeletal characteristics of *Lithomelissa*. But, confusingly, he abbreviated the dorsal spine as "A" and apical spine as "D," and indicated that the apical spine runs along the side of the cephalis, rather than passing freely through it. This was certainly true of some species assigned to *Lithomelissa* at that time (i.e., *Lithomelissa setosa* Jørgensen, *Lithomelissa thoracites* Haeckel, *Lithomelissa buetschlii* Haeckel), but did not represent many others, which have a free apical spine (i.e., *Lithomelissa ehrenbergi* Bütschli, *Lithomelissa mitra* Bütschli, and the species that would later be designated the type species of the genus: *Lithomelissa microptera* Ehrenberg). Schröder (1914) reproduced Jørgensen's illustrations and accepted his concept of the genus. Thus, by the early 1900s, there were at least two conflicting concepts of *Lithomelissa* and no designated type species.

Campbell (1954) designated the type species as *Lithomelissa tartari* Ehrenberg, 1854b, although this species had never been illustrated and was thus not a practical choice. Foreman (1968) remarked that any species assignments to *Lithomelissa* are "doubtful" due to the "inadequacy of the description of the type species." For this reason, Petrushevskaya (1971) suggested the type species be considered *Lithomelissa microptera* Ehrenberg, 1854c by subsequent monotypy, as it had been adequately illustrated. However, unlike her predecessors, Petrushevskaya (1971) did not consider *Lithomelissa* to be Lophophaenidae, due to the apical horn passing through the cephalis rather than running along the side. Later, Petrushevskaya (1981) erected the subfamily Dimelissinae, and placed *Lithomelissa* into this group. To our knowledge, all other subsequent authors have considered *Lithomelissa* to be in Lophophaenidae, and we are of the same opinion because this genus is very similar to the lophophaenids *Lophophaena* and *Peromelissa* in every respect other than the position of the apical spine.

Petrushevskaya (1975) synonymized *Lithomelissa* with *Acromelissa*, and proposed that *Lithomelissa microptera* Ehrenberg be considered the type species of *Acromelissa* Haeckel, and that the name *Lithomelissa* should be discontinued because it does not have a reliable type species. However, since *Acromelissa* Haeckel is a junior synonym and subgenus of *Lithomelissa* Ehrenberg, *Lithomelissa microptera* Ehrenberg should actually be considered the type species of *Lithomelissa* Ehrenberg, and *Acromelissa* Haeckel should not be used. *Lithomelissa microptera* Ehrenberg was finally formally designated as the new type species of *Lithomelissa* by Petrushevskaya and Kozlova (1979), and adopted in most subsequent literature (e.g., Petrushevskaya, 1981, O'Connor, 1997), but not all (i.e., Nishimura, 1990). In her emendation of *Lithomelissa,* Nishimura (1990) considered the type species to be *Lithomelissa tartari* Ehrenberg, 1854b, and did not mention Petrushevskaya (1971, 1981). O'Connor (1997) provided the most recent and comprehensive revision of *Lithomelissa,* which considers the emendations of both Petrushevskaya (1971) and Nishimura (1990). This is the definition we follow here. O'Connor (1997) suggested that species lacking secondary left and right lateral bars, and with an apical spine not free within the cephalis should not be considered *Lithomelissa*, and should likely be reassigned to *Lophophaena* (including several open nomenclature taxa in Nishimura, 1990).

Here we observed the following species of *Lithomelissa*: *Lithomelissa alkonost* n. sp., *Lithomelissa babai* n. sp., *Lithomelissa celsagula* Renaudie and Lazarus, 2015, *Lithomelissa cheni* Caulet, 1991, *Lithomelissa dybbuki* n. sp., *Lithomelissa ehrenbergi* Bütschli, 1882, *Lithomelissa mitra* Bütschli, 1882, and *Lithomelissa sirin* n. sp. Here we do not include *Lithomelissa capitata* Popofsky, 1908 because it was transferred to *Antarctissa* by Petrushevskaya (1975). *Lithomelissa jorgenseni* Popofsky, 1908 is excluded here because the apical spine runs along the side of the cephalis and thus does not meet the criteria for the modern usage of *Lithomelissa.* We suspect this species may fit best in *Botryopera* given its similarities to *Botryopera setosa* (Jørgensen, 1900) Kruglikova, 1989, but as it was not observed during this study we do not attempt to make a formal transfer here. Upon examination of the author's illustrations, *Lithomelissa curta* Kozlova, 1999 appears to be a trissocyclid rather than a lophophaenid, but it has not been officially transferred to our knowledge. We transfer *Lithomelissa*? *kozoi* Renaudie and Lazarus, 2013a to *Pelagomanes* n. gen. in this manuscript (see below). *Lithomelissa laticeps* Jørgensen, 1905 was transferred to *Lophophaena* by Kurihara and Matsuoka (2010), and we agree because the apical spine runs alongside the wall of the cephalis is this species, excluding it from *Lithomelissa*. *Lithomelissa setosa* Jørgensen 1900 and *Lithomelissa brevispicula* Popofsky 1908 were both transferred to *Botryopera* by Kruglikova 1989 and Petrushevskaya 1986, respectively (see above). We transfer *Lithomelissa spinosissima* Tan and Tchang 1976 to *Arachnocorys* due to the position of the apical spine and nature of the thorax attachment (see above). *Lithomelissa heros* Campbell and Clark 1944 was moved to *Botryometra* by Petrushevskaya 1975; this species is clearly a cannobotryid. *Lithomelissa hystrix* Jørgensen, 1905 was included in *Botryopera oceanica* (Ehrenberg) group by Petrushevskaya (1975), as it does not meet the criteria for *Lithomelissa*. *Lithomelissa robusta* Campbell and Clark, 1944 was transferred to the spumellarian genus *Lithelius* by Foreman (1968), and appears to be a fragment of a litheliid although details are not clear in the original illustration. *Lithomelissa amphora* Stöhr 1880 is clearly a carpocaniid, and so is not included here. *Lithomelissa haeckeli* Bütschli 1882 is not included because the apical spine does not pass freely through the cephalis, and the strong feet are very unusual for lophophaenids in general. O'Connor (1997) suggested that this species be considered *Lophophaena* instead of *Lithomelissa*, but we do not believe this species belongs in either genus due to the overall shell shape and strong feet. It likely would fit better in a genus such as *Cladoscenium, Clathromitra*, *Corythomelissa*, or *Pteroscenium*, but it is outside the scope of our study to formally transfer it. We also exclude as *nomina dubia*: *Lithomelissa tartari* Ehrenberg, 1854b, *Lithomelissa pycnoptera* Haeckel, 1887, and *Lithomelissa microstoma* Haeckel, 1887. The latter two names so far as we know have never been used in subsequent literature, and may actually be *nomina oblita*.

**Range.** ?Late Cretaceous –Recent.

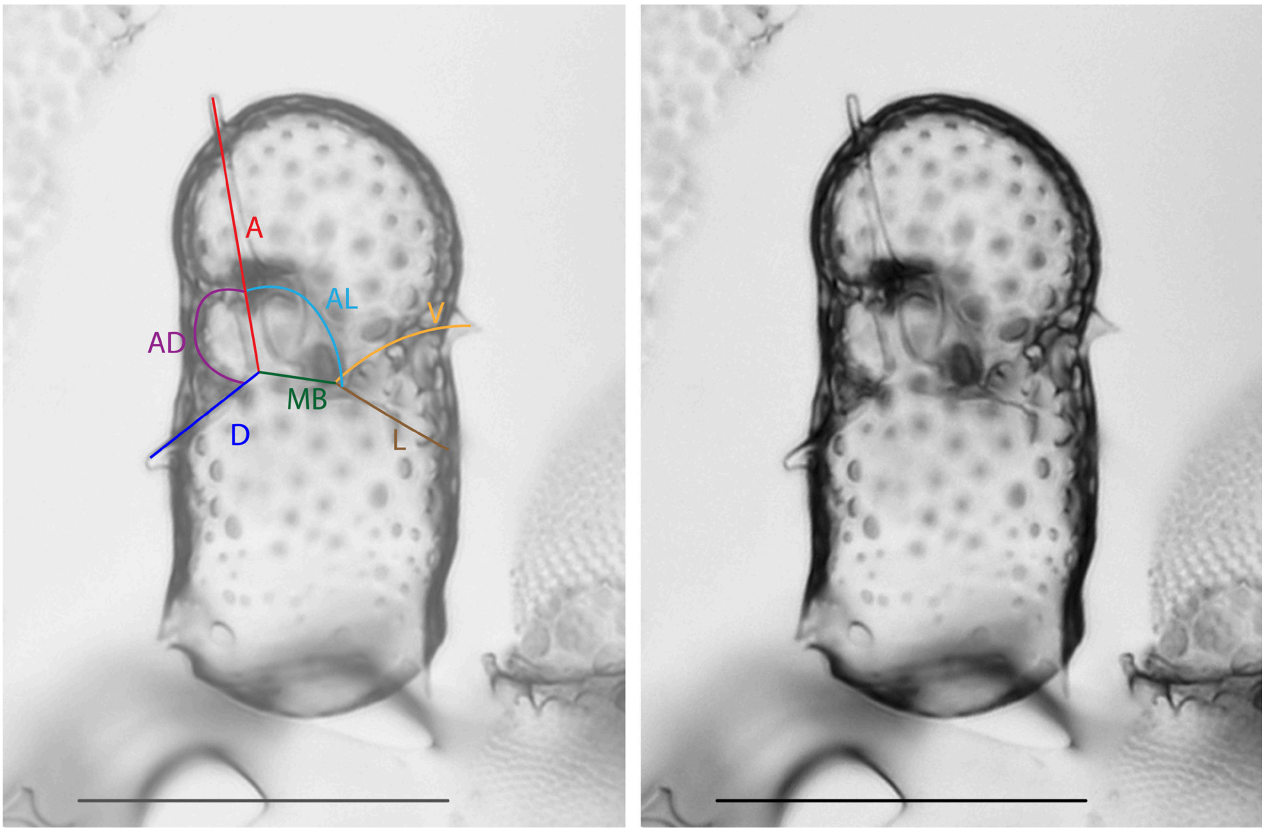

**FIGURE 10.** Internal skeletal structure of *Lithomelissa alkonost* n. sp.

*Lithomelissa alkonost* **n. sp.**
Plate 16, Figs. 1A–7B.

urn:lsid:zoobank.org:act:2904452E-3B02-47D6-9F23-0E37211ED8F2
? *Lithomelissa* sp. A, Kamikuri, 2019, pl. 6, fig. 5.
unknown plagonid group C sp 3, Trubovitz *et al.*, 2020, supplementary data 7.

**Diagnosis.** *Lithomelissa* with an elongated, irregular-shaped cephalis that has small pores and a distinctive bulge on the dorsal side of the neck area.

**Description.** This species is identifiable for its long, irregular-shaped cephalis, which typically has pores smaller in size than those on the thorax. The cephalis can be widest near the top third of the segment (i.e., figs. 3, 4, 6, and 7), or approximately the same width throughout (i.e., figs. 1, 2, and 5). The apical spine runs through the interior of the cephalis, clearly placing this species in *Lithomelissa*. The neck area is distinct for being approximately the same width as the rest of the shell, and having a large bulge on the bottom third of the cephalis on the dorsal side, where the AD and AL arches run along the wall of the cephalis. This forms an outward bulge on the dorsal side of the cephalis. The thorax is about the same width as the cephalis, but can be slightly narrower. Both the thorax and cephalis tend to have pores distributed irregularly, occasionally leaving hyaline areas on the shell. Appendages on the thorax derived from the dorsal and lateral spines are short and/or poorly-developed. At the junctions of the median bar with the lateral and dorsal spines, there are short, thornlike, downward hanging skeletal elements that do not connect to the thorax. The base of the thorax can fully enclose at the base with short feet, if the skeleton is fully developed and well preserved. However, such specimens were rare in our material.

**Remarks.** This species is similar in overall structure to *Lithomelissa sirin* n. sp. (Pl. 17, Figs. 1–11B), but differs in that the cephalis is larger, more irregular, and elongated, and is always at least as wide as thorax. This relatively wide cephalis and large bulge at the neck differentiates this species from both *Lithomelissa mitra* (Pl. 15, Figs. 4A–6) and *Lithomelissa sirin* n. sp. The thin, sometimes nearly hyaline nature of the cephalis wall and irregular pores throughout the shell differentiate this species from *Lithomelissa ehrenbergi* (Pl. 15, Figs. 7A–C), *L. cheni* (Pl. 15, Figs. 3A–B), and *L. celsagula* (Pl. 15, Figs. 1A–2B). This species shows significant variation in overall size, but the proportions remain consistent. The apical horn tends to be thin and short, compared to the other *Lithomelissa* species we observed. This species resembles a specimen figured by Kamikuri (2019) (pl. 6, fig. 5), but is on average is slightly smaller in size and has fewer, more irregular pores throughout the skeleton. However, once we have a better understanding of the variability within *L. alkonost*, it may be determined that they are conspecific.

**Material examined.** 76 specimens observed from samples 321-1337D-23H-6, 134–137cm (Late Miocene), 321-1337A-18H-6, 77–80cm (Late Miocene), 321-1337A-16H-6, 121–124cm (Late Miocene), 321-1337A-14H-7, 39–42cm (Late Miocene), 321-1337A-12H-5, 23–26cm (Late Miocene), 321-1337A-10H-2, 91–94cm (Early Pliocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), 321-1337A-6H-3, 29–32cm (Late Pliocene), 321-1337A-4H-6, 115–118cm (Early Pleistocene), and 321-1337A-3H-2, 103–106cm (Middle Pleistocene).

**Holotype.** Pl. 16, Figs. 1A–B; sample 321-1337A-14H-7, 39–42cm; ECO-138; U15-3.

**Paratypes.** (1) Pl. 16, figs. 3A–B; sample 321-1337A-16H-6, 121–124cm; ECO-141; Q26-3. (2) Pl. 16, figs. 4A-B; sample 321-1337A-16H-6, 121–124cm; ECO-143; P14-2. (3) Pl. 16, fig. 5; sample 321-1337A-16H-6, 121–124cm; ECO-143; M3-2. (4) Pl. 16, fig. 6; sample 321-1337A-16H-6, 121–124cm; ECO-143; C17-2. (5) Pl. 16, figs. 7A-B; sample 321-1337A-16H-6, 121–124cm; ECO-141; K17-2. (6) Pl. 16, figs. 2A-B; sample 321-1337A-16H-6, 121–124cm; ECO-143; Q5-2. (7) [not figured] sample 321-1337A-16H-6, 121–124cm; ECO-142; X34-3.

**Measurements.** Height of cephalis 39–56 (48)µm; width of cephalis 36–48 (42)µm; width of thorax at shoulder area 34–44 (39)µm; ratio of cephalis width:thorax width 0.9–1.2 (1.1). Measurements based on 24 specimens.

**Etymology.** Named for the woman-headed bird, Alkonost, the counterpart to Sirin in Slavic mythology.

**Range.** Late Miocene—Middle Pleistocene in the EEP (Table 1).

### *Lithomelissa babai* **n. sp.**

Plate 18, Figs. 1A–5B.

urn:lsid:zoobank.org:act:2B2D2DC5-3F5E-4BB8-B39A-795A513F78A2
unknown plagonid group C sp 27, Trubovitz *et al.*, 2020, supplementary data 7.

**Diagnosis.** *Lithomelissa* with a hemispherical cephalis exhibiting multiple long conical spines, and a cylindrical thorax that is slightly wider than the cephalis.

**Description.** The cephalis of this species is hemispherical in shape, and is very strongly silicified with large, framed pores. This species has several long, conical spines on the cephalis. These are easily broken off, but often at least two are preserved and our specimens showed up to six spines. One of the cephalic horns is connected to the apical spine, which is free within the cephalis like all *Lithomelissa* species. This apical horn is most often thin and conical like the others, but it can apparently develop into a stronger, tri-bladed horn in some individuals. The thorax is cylindrical in shape and is always wider than the cephalis. There are enlarged pores at the top of the thorax, near the connection to the cephalis. The dorsal and lateral spines protrude slightly through the wall of the thorax, but do not form long appendages.

**Remarks.** This species differs from *Lithomelissa dybbuki* n. sp. (Pl. 19, Figs. 1–7) in that it is larger overall, and has more spines on the cephalis. The collar structure is sunken into the thorax, so the species does not have a constriction at the base of the cephalis, differentiating it from *Lithomelissa mitra* (Pl. 15, Figs. 4A–6), *L. celsagula* (Pl. 15, Figs. 1A–2B), *L. alkonost* n. sp. (Pl. 16, Figs. 1A–7B) , and *L. sirin* n. sp. (Pl. 17, Figs. 1–11B).

**Material examined.** 42 specimens observed from samples 321-1337A-10H-2, 91–94cm (Early Pliocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), 321-1337A-6H-3, 29–32cm (Late Pliocene), 321-1337A-5H-5, 11–14cm (Late Pliocene), 321-1337A-4H-2, 16–19cm (Middle Pleistocene), 321-1337A-3H-2, 103–106cm (Middle Pleistocene), and 321-1337D-1H-1, 0–3cm (Recent).

**Holotype.** Pl. 18, Figs. 1A–C; sample 321-1337A-7H-6, 104–107cm; ECO-143; C26-3.

**Paratypes.** (1) Pl. 18, fig. 2; sample 321-1337A-7H-6, 104–107cm; ECO-143; U30-1. (2) Pl. 18, figs. 3A–B; sample 321-1337A-7H-6, 104–107cm; ECO-133; G15-3. (3) Pl. 18, figs. 4A–B; sample 321-1337A-7H-6, 104–107cm; ECO-133; X24-4. (4) Pl. 18, figs. 5A–B; sample 321-1337A-7H-6, 104–107cm; ECO-134; K38-2. (5) [not figured] sample 321-1337A-7H-6, 104–107cm; ECO-135; F37-4. (6) [not figured] sample 321-1337A-7H-6, 104–107cm; ECO-134; G27-1.

**Measurements.** Height of cephalis 36–43 (39)µm; width of cephalis 32–41 (36)µm; width of thorax at shoulder area 46–59 (51)µm.

**Etymology.** Named for the boogeyman in Russian folklore, Babai.

**Range.** Early Pliocene–Recent, EEP (Table 1).

### *Lithomelissa celsagula* Renaudie and Lazarus, 2015
Plate 15, Figs. 1A–2B.

? *Lophophenoma* sp G, Petrushevskaya, 1971, pl. 56, fig. 17 (non fig. 16).
*Lithomelissa celsagula* n. sp., Renaudie and Lazarus, 2015, pl. 7, figs. 10–11, 16; pl. 8, fig. 12.
*Lithomelissa celsagula* Renaudie and Lazarus, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** The specimens we observed in the EEP were confirmed to be conspecific with the Southern Ocean forms, by the authors of the species. There are no notable differences between the polar and tropical forms.

**Range.** Present from the Late Oligocene–Late Miocene in the SO. Observed in the Late Miocene in the EEP, lower limit not determined (Table 1).

### *Lithomelissa cheni* Caulet, 1991
Plate 15, Figs. 3A–B.

*Lithomelissa* sp. A aff. *L. ehrenbergi* (?) Bütschli, Chen, 1975, pl. 11, figs. 1–2.
*Lithomelissa ehrenbergi* Bütschli, Caulet, 1985, pl. 2, fig. 7.
*Lithomelissa cheni* n. sp., Caulet, 1991, pl. 2, figs. 1–2.
*Lithomelissa cheni* Caulet, Funakawa and Nishi, 2005, pl. 4, fig. 6.
*Lithomelissa cheni* Caulet, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** The specimens observed in the EEP were in good agreement with previously-published illustrations of this species.

**Range.** Late Miocene in the EEP, lower limit not determined (Table 1).

### *Lithomelissa dybbuki* n. sp.
Plate 19, Figs. 1–7.

urn:lsid:zoobank.org:act:9E726441-61BB-47AB-8B7B-B29E7A84ADBD
unknown plagonid group C sp 24, partim., Trubovitz *et al.*, 2020, supplementary data 7.
unknown plagonid group C sp 26 cf, partim., Trubovitz *et al.*, 2020, supplementary data 7.
unknown plagonid group C sp 43, Trubovitz *et al.*, 2020, supplementary data 7.

**Diagnosis.** A small *Lithomelissa* with a hemispherical cephalis that exhibits only one spine—the apical horn, and has a thorax ~1.5x the width of the cephalis.

**Description.** This species has a very small hemispherical cephalis and an apical spine passing freely through it, which extends as an apical horn that is at least as long as the cephalis itself. In some specimens, the apical horn has a bulb of extra silica at the tip (i.e., figs. 2, 5, and 6). The collar structure is sunken into the thorax, so that this species lacks the long neck constriction present in many other *Lithomelissa* species. The pores on the cephalis and thorax are approximately consistent in size and shape, except for the ring of enlarged pores present at the top of the thorax where it meets the cephalis. The thorax is roughly conical in shape, though may taper slightly toward the base. If present, appendages originating from the lateral and dorsal spines are very short and weak. The thorax has a jagged termination with short feet, when fully preserved (fig. 7).

**Remarks.** This species has somewhat similar segment proportions to *Lithomelissa babai* n. sp. (Pl. 18, Figs. 1A–5B.), but is smaller overall and is usually more weakly silicified. It also differs from *L. babai* in that it has only one spine (the apical horn) on the cephalis. These two species share the characteristic of having a collar structure sunken into the thorax, differentiating them from many other *Lithomelissa* taxa that exhibit a distinct neck constriction, and suggesting a possible close relationship between them. This species differs from *Lithomelissa sirin* n. sp. (Pl. 17, Figs. 1–11B) and *L. mitra* (Pl. 15, Figs. 4A–6) in that and the cephalis is smaller in both absolute size and proportion, with the thorax being significantly wider than the cephalis.

**Material examined.** 84 specimens observed from samples 321-1337A-14H-7, 39–42cm (Late Miocene), 321-1337A-12H-5, 23–26cm (Late Miocene), 321-1337A-10H-2, 91–94cm (Early Pliocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), 321-1337A-6H-3, 29–32cm (Late Pliocene), 321-1337A-5H-5, 11–14cm (Late Pliocene), 321-1337A-4H-6, 115–118cm (Early Pleistocene), 321-1337A-4H-2, 16–19cm (Middle Pleistocene), 321-1337A-3H-2, 103–106cm (Middle Pleistocene), and 321-1337A-2H-3, 76–79cm (Late Pleistocene).

**Holotype.** Pl. 19, Figs. 5A–B; sample 321-1337A-4H-6, 115–118cm; ECO-132; C25-1.

**Paratypes.** (1) Pl. 19, fig. 3; sample 321-1337A-4H-6, 115–118cm; ECO-131; C38-2. (2) Pl. 19, fig. 1; sample 321-1337A-4H-6, 115–118cm; ECO-131; O34-1. (3) Pl. 19, figs. 4A–B; sample 321-1337A-4H-2, 16–19cm; ECO-127; X18-3. (4) Pl. 19, figs. 6A–B; sample 321-1337A-4H-6, 115–118cm; ECO-132; Y35-2. (5) [not figured] sample 321-1337A-4H-2, 16–19cm; ECO-128; E20-4. (6) [not figured] sample 321-1337A-4H-2, 16–19cm; ECO-127; F21-1.

**Measurements.** Cephalis height 28–32 (30)µm; cephalis width 25–29 (27)µm; width of thorax at shoulder area 41–48 (44)µm.

**Etymology.** Named for the evil wandering spirit of Jewish folklore, the dybbuk.

**Range**: Upper Late Miocene—Late Pleistocene, EEP (Table 1).

### *Lithomelissa ehrenbergi* **Bütschli, 1882**

Plate 15, Figs. 7A–C.

*Lithomelissa macroptera* n. sp., Ehrenberg, 1874, p. 211, pl. 3, fig. 8 (non figs. 9–10).
*Lithomelissa ehrenbergi* n. sp., Bütschli, 1882, pl. 33, fig. 21a–b.
*Lithomelissa ehrenbergi* Bütschli, Dumitrica, 1973, pl. 25, figs. 6–7.
*Lithomelissa ehrenbergi* Bütschli, Caulet, 1991, pl. 2, fig. 3.
*Lithomelissa ehrenbergi* Bütschli, Hollis, 1997, pl. 3, figs. 17–20.
*Lithomelissa* sp., Kozlova, 1999, pl. 31, fig. 13.
*Lithomelissa ehrenbergi* Bütschli, O'Connor, 1999, pl. 9, fig. 20.
*Lithomelissa macroptera* Ehrenberg, Ogane *et al.,* 2009, pl. 4, figs. 3a–3c, ?4a–4d, 7a–7d (non pl. 19, fig. 6a–6d; pl. 79, fig. 6a–6c).
*Lithomelissa ehrenbergi* Bütschli, Pascher *et al.,* 2015, pl. 2, figs. 10–11.
*Lithomelissa ehrenbergi* Bütschli, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** Bütschli (1882) considered the species *Lithomelissa macroptera* described by Ehrenberg (1874) to actually contain two species. So, he split out one specimen figured by Ehrenberg (pl. 3, fig. 8) as representative of the new species *Lithomelissa ehrenbergi* Bütschli, 1882. This was adopted later by Haeckel (1887), and the subsequent authors we encountered in the literature.

**Range.** Late Miocene—Recent, EEP (Table 1).

### *Lithomelissa* **sp. cf.** *L. ehrenbergi* **Bütschli, 1882**

Plate 15, Fig. 8A–B; Plate 16 Fig. 9A–B.

*Lithomelissa* cf. *ehrenbergi*, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species resembles *Lithomelissa ehrenbergi* Bütschli, 1882 (Pl. 15, Figs. 7A–C) except that the wall of the cephalis is thinner and the cephalis is more elongated. It differs from *Lithomelissa mitra* Bütschli (Pl. 15, Figs. 4A–6) in that the cephalis is proportionally larger. This species is similar to *Lithomelissa alkonost* n. sp. (Pl. 16, Figs. 1A–7B), but differs in that the neck area is more clearly constricted. The pores on the cephalis and thorax are more regularly distributed and typically larger than in *L. alkonost* n. sp. and *L. sirin* n. sp. (Pl. 17, Figs. 1–11B). Appendages on the thorax are typically very strong and bladed, similar to *L. ehrenbergi* and *L. mitra,* but different from the thin, conical spines typical in *L. sirin* and the usually short thoracic spines on *L. alkonost.* Despite their differences, all of these species are apparently closely related and will require further study to determine true species-level distinctions versus intraspecific morphological variation.

**Material examined.** 65 specimens observed from samples 321-1337A-16H-6, 121–124cm (Late Miocene), 321-1337A-12H-5, 23–26cm (Late Miocene), 321-1337A-10H-2, 91–94cm (Early Pliocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), and 321-1337A-5H-5, 11–14cm (Late Pliocene).

**Range.** Late Miocene—Late Pliocene, EEP (Table 1).

### *Lithomelissa mitra* **Bütschli, 1882**

Plate 15, Figs. 4A–6.

*Lithomelissa mitra* n. sp., Bütschli, 1882, pl. 33, fig. 24.
*Lithomelissa mitra* Bütschli, Haeckel, 1887, p. 1204–1205 [not figured].
*Lithomelissa mitra* Bütschli, Petrushevskaya, 1971, pl. 44, figs. 1–2.

**Remarks.** Bütschli (1882) was the first to name and illustrate this species. In 1887, Haeckel provided a more detailed description but no additional illustrations. The specimens we observed compare favorably with the few specimens that have been previously illustrated.

**Range.** Late Miocene—Late Pliocene, EEP (Table 1).

### *Lithomelissa sirin* **n. sp.**

Plate 17, Figs. 1–11B.

urn:lsid:zoobank.org:act:E7AD61E4-915D-4C1A-B114-F5BEE876639A
cf. *Lithomelissa* sp. B aff. *L. mitra* Bütschli, Chen, 1975, pl. 8, figs. 4–5.
*Lithomelissa* sp. aff. *L. mitra* Bütschli, Weaver and Dinkelman, 1978, pl. 1, fig. 11.
cf. *Lithomelissa* cf. *mitra* Bütschli, O'Connor, 1999, pl. 9, fig. 25.
unknown plagonid group C sp 26, Trubovitz *et al.,* 2020, supplementary data 7.

**Diagnosis.** *Lithomelissa* with few or small and irregular pores on the cephalis, a strong and distinct apical spine, and a thorax of approximately the same width as the cephalis.

**Description.** The cephalis of this species ranges from broadly hemispherical in outline (i.e., figs, 2 and 4) to somewhat more elongated and kidney-shaped (i.e., figs. 1 and 3). However, having few and/or small pores irregularly distributed on the cephalis is a consistent characteristic of this species. Some species may even have a nearly-hyaline cephalis (i.e., figs. 4 and 6). The apical horn is the only spine present on the otherwise-smooth cephalis. This spine usually has a small rounded bulb of silica at its tip, and the base of the spine can be bladed where it exits the cephalis. This species has a strong ventral spine, and the dorsal and lateral spines protrude from the thorax about as far as the apical spine does from the cephalis. The thorax is cylindrical in shape, and exhibits larger and more numerous pores than the cephalis. When fully preserved, the thorax terminates with several small teeth (i.e., figs. 2, 7, 8, 9, and 10).

**Remarks.** Compared to *Lithomelissa mitra* (Pl. 15, Figs. 4A–6), this species has more irregular pores, particularly on the cephalis (which can be completely hyaline). It also has a less distinct constriction at the neck than *L. mitra*, with the cephalis appearing to sink slightly into the thorax rather than developing the clear neck area present in *L. mitra*. The shape of the cephalis is less spherical than *L. mitra*, and can be slightly elongated in some specimens. The apical spine of this species often presents a little rounded bulb of silica at the tip, which is not a character we observed in *L. mitra* or *L. alkonost* (Pl. 16, Figs. 1A–7B). This species also differs from *L. alkonost* in that it lacks the bulge at the base of the dorsal side of the cephalis. Both *L. sirin* and *L. dybbuki* (Pl. 19, Figs. 1–7) have a single spine on the cephalis that often has a distinct rounded tip; however, *L. sirin* differs from *L. dybbuki* in its overall larger size, proportionally larger cephalis compared to the thorax, and tendency to have very small or few pores on the cephalis.

This species was figured by Weaver and Dinkelman (1978) as *Lithomelissa* sp. aff. *L. mitra* Bütschli. A similar form was illustrated by Chen (1975) as *Lithomelissa* sp. B aff. *L. mitra* Bütschli, but those specimens differed in being much more heavily silicified than the individuals observed in the present study. Otherwise, however, they are extremely similar in segment proportions and irregularity of pores, particularly on the cephalis. Chen (1975)'s specimens are from the Oligocene, so it's possible that this species was the ancestor of *Lithomelissa sirin* n. sp. O'Connor (1999) also figured a specimen identified as *Lithomelissa* cf. *mitra* Bütschli, which was described as having a poreless cephalis. This specimen has a very similar cephalis to our new species, but differs in its thorax, which has strong downward-curving winglike appendages. *L. sirin* has much weaker spines that extend sub-horizontal from the thorax.

**Material examined.** More than 400 specimens observed from samples 321-1337D-23H-6, 134–137cm (Late Miocene), 321-1337A-18H-6, 77–80cm (Late Miocene), 321-1337A-16H-6, 121–124cm (Late Miocene), 321-1337A-14H-7, 39–42cm (Late Miocene), 321-1337A-12H-5, 23–26cm (Late Miocene), 321-1337A-10H-2, 91–94cm (Early Pliocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), 321-1337A-6H-3, 29–32cm (Late Pliocene), 321-1337A-5H-5, 11–14cm (Late Pliocene), 321-1337A-4H-6, 115–118cm (Early Pleistocene), 321-1337A-4H-2, 16–19cm (Middle Pleistocene), and 321-1337A-3H-2, 103–106cm (Middle Pleistocene).

**Holotype.** Pl. 17, Fig. 1; sample 321-1337A-16H-6, 121–124cm; ECO-141; X39-2.

**Paratypes.** (1) Pl. 17, fig. 2; sample 321-1337A-16H-6, 121–124cm; ECO-142; M3-3. (2) Pl. 17, figs. 4A–B; sample 321-1337A-16H-6, 121–124cm; ECO-143; Y10-4. (3) Pl. 17, fig. 7; sample 321-1337A-16H-6, 121–124cm; ECO-143; O8-3. (4) Pl. 17, figs. 3A–B; sample 321-1337A-14H-7, 39–42cm; ECO-138; P17-2. (5) Pl. 17, figs. 11A-B; sample 321-1337A-14H-7, 39–42cm; ECO-140; M17-2. (6) Pl. 17, figs. 8A–B; sample 321-1337A-14H-7, 39–42cm; ECO-140; R37-4.

**Measurements.** Height of cephalis 39–45 (42)µm; width of cephalis 35–42 (38)µm; width at neck 31–36 (34)µm; width of thorax at shoulders 41–53 (44)µm. Based on 15 specimens.

**Etymology.** Named for the mythological creature of Slavic folklore, the Sirin, which has the head of a woman and the body of a bird and sings captivating songs.

**Range.** Late Miocene—Middle Pleistocene, in the EEP (Table 1).

### *Lithomelissa* sp. A

Plate 20, Figs. 1A–5.

*Lithomelissa brevispicula* Popofsky, Trubovitz *et al.*, 2020, supplementary data 7.

**Remarks.** This species was misidentified as *Lithomelissa brevispicula* Popofsky in Trubovitz *et al.,* 2020. Unlike the Popofsky species, this species has a clear distinction between the cephalis and thorax segments. The cephalis is relatively large, sometimes approximately the same length as the cephalis, and the apical spine passes through the center of the cephalis.

**Material examined.** 12 specimens observed from samples 321-1337A-12H-5, 23–26cm (Late Miocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), 321-1337A-6H-3, 29–32cm (Late Pliocene), 321-1337A-5H-5, 11–14cm (Late Pliocene), 321-1337A-4H-6, 115–118cm (Early Pleistocene), and 321-1337A-3H-2, 103–106cm (Middle Pleistocene).

**Range.** Latest Miocene—Middle Pleistocene, EEP (Table 1).

### *Lithomelissa* sp. B

Plate 18, Figs. 6A–8B; Plate 20, Figs. 8–9.

unknown plagonid group C sp 32 cf sp 2, Trubovitz *et al.*, 2020, supplementary data 7.

**Remarks.** This species differs from *Lophophaena witjazii* Petrushevskaya (Pl. 25, Figs. 5A–B) in that the apical spine passes freely through the cephalis, and the neck area is not as constricted, instead blending into the thorax. In addition, placement of the spines on the cephalis is more irregular, not forming the "crown" of thorns typical of *L. witjazii*, but being scattered throughout the cephalis and the most prominent horn originating from the apical spine.

This species differs from *Lophophaena simplex* Funakawa (Pl. 33, Figs. 8A–9B) in that the apical spine passes freely through the cephalis, and it is overall much larger in size.

**Material examined.** 13 specimens observed from samples 321-1337A-18H-6, 77–80cm (Late Miocene), 321-1337A-12H-5, 23–26cm (Late Miocene), 321-1337A-10H-2, 91–94cm (Early Pliocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), 321-1337A-5H-5, 11–14cm (Late Pliocene), 321-1337A-3H-2, 103–106cm (Middle Pleistocene), 321-1337A-2H-3, 76–79cm (Late Pleistocene), and 321-1337D-1H-1, 0–3cm (Recent).

**Range.** Late Miocene—Recent, EEP (Table 1).

### *Lithomelissa* sp. C group?

Plate 20, Figs. 6A–7C.

unknown plagonid group C sp 38, partim., Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This morphotype was originally grouped with another morphotype as Unknown plagonid group C sp 38 in Trubovitz *et al.* (2020). However, the other morphotype has a lobed cephalis, suggesting that it belongs in a different genus, possibly *Euscenarium,* while the morphotype we figure here appears to fit the definition of *Lithomelissa*. The cephalis of this species is more typical of *Lithomelissa* in its overall shape and the characteristic of the apical spine passing freely through the cephalis. The spines on the thorax protrude well above the base of the shell, so cannot be considered "feet," in contrast to the other morphotype observed in Trubovitz *et al.* (2020). This group may possibly include two different species, but here we group them until more specimens can be observed to determine the morphological variability.

**Material examined.** 2 specimens observed from Late Miocene samples 321-1337D-23H-6, 134–137cm and 321-1337A-18H-6, 77–80cm.

**Range.** Late Miocene, EEP (Table 1).

### *Lithomelissa* sp. D

Plate 16, Figs. 8A–B.

*Lithomelissa* sp 1, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species has a compressed, asymmetrical cephalis, which is longer than it is wide. It differs from *L. ehrenbergi* (Pl. 15, Figs. 7A–C) in that it does not have an extended neck, and differs from *L. mitra* (Pl. 15, Figs. 4A–6) in that cephalis is not round. The large, framed pores differentiate this species from *L. alkonost* n. sp. (Pl. 16, Figs. 1A–7B) and *L. sirin* n. sp. (Pl. 17, Figs. 1–11B). Thus, this species does not seem to fit in any of the species categories for far described, but here we leave it in open nomenclature until a better understanding of its variability can be reached.

**Material examined.** 15 specimens observed from samples 321-1337A-16H-6, 121–124cm (Late Miocene), 321-1337A-10H-2, 91–94cm (Early Pliocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), 321-1337A-6H-3, 29–32cm (Late Pliocene), 321-1337A-4H-2, 16–19cm (Middle Pleistocene), 321-1337A-3H-2, 103–106cm (Middle Pleistocene), 321-1337A-2H-3, 76–79cm (Late Pleistocene).

**Range.** Late Miocene—Pleistocene, EEP (Table 1).

## Other species of *Lithomelissa* that were not observed during our study:

### *Lithomelissa (Acromelissa) acutispina* Clark and Campbell, 1942

*Lithomelissa (Acromelissa) acutispina* n. sp., Clark and Campbell, 1942, pl. 9, fig. 21.

**Remarks.** It is not possible to tell from the original description nor illustration whether this species has an apical spine passing freely through the cephalis, so its assignment to *Lithomelissa* will need to be confirmed by examination of the type material.

### *Lithomelissa? aitai* **Hollis, 1997**

aff. *Lophophaena? Polycyrtis* (Campbell and Clark), Foreman, 1968, pl. 3, figs. 3A–C.
*Ceratocyrtis? volubilis* n. sp., Petrushevskaya, 1977, pl. 1, fig. b (non figs. a, v).
*Lithomelissa? aitai* n. sp., Hollis, 1997, pl. 12, figs. 5–8.

### *Lithomelissa capito* **Ehrenberg, 1874**

*Lithomelissa capito* n. sp., Ehrenberg, 1874, p. 240–241 [not figured].
*Lithomelissa capito* Ehrenberg, Ehrenberg, 1876, pl. 3, fig. 14.
*Peromelissa capito* (Ehrenberg), Haeckel, 1887, p. 1237 [not figured].
*Lithomelissa capito* Ehrenberg, Ogane *et al.,* 2009, pl. 34, figs. 2A–F.

**Remarks.** Illustrated specimens of this species do not sufficiently portray the nature of the apical spine, so it is difficult to determine whether this species best fits *Lithomelissa* or instead *Peromelissa* (as Haeckel, 1887 suggested). It may also be within the range of *Lophophaena*, but Ehrenberg (1874) already described a separate species as *Lophophaena capito* (see above).

### *Lithomelissa challengerae* **Chen, 1975**

*Lithomelissa challengerae* n. sp., Chen, 1975, pl. 8, fig. 3.
*Lithomelissa challengerae* Chen, Takemura, 1992, pl. 4, figs. 11–12.

### *Lithomelissa dupliphysa* **Caulet, 1991**

*Lithomelissa dupliphysa* n. sp., Caulet, 1991, pl. 2, fig. 4.

**Remarks.** This species has an unusually large and wide cephalis for a lophophaenid, and very strong feet. We suspect that it may fit better in a different Plagiacanthidae genus such as *Euscenarium* or *Clathrocorys*.

### *Lithomelissa gelasinus* **O'Connor, 1997**

*Lithomelissa* aff. *sphaerocephalis* Chen, O'Connor, 1993, pl. 6, fig. 1.
*Lithomelissa gelasinus* n. sp., O'Connor, 1997, text-fig. 4; pl. 2, figs. 3–6; pl. 6, figs. 6–9.
*Lithomelissa gelasinus* O'Connor, Hollis, 1997, pl. 3, figs. 15–16.
*Lithomelissa gelasinus* O'Connor, O'Connor, 2000, pl. 1, figs. 7A–9B.

### *Lithomelissa macropter***a Ehrenberg, 1874**

*Lithomelissa macroptera* n. sp., Ehrenberg, 1874, p. 241 [not figured].
*Lithomelissa macroptera* Ehrenberg, Ehrenberg, 1876, pl. 3, figs. 9–10 (non fig. 8).
*Lithomelissa (Acromelissa) macroptera* Ehrenberg, Haeckel, 1887, p. 1204 [not figured].
? *Lithomelissa* cf. *macroptera* Ehrenberg, Petrushevskaya, 1971, pl. 44, figs. 4–6.
non Dictyophimus macropterus (Ehrenberg), Takahashi, 1991, pl. 39, figs. 8–11.
*Lithomelissa macroptera* Ehrenberg, Ogane *et al.,* 2009, pl. 19, fig. 6A–6D; pl. 79, fig. 6A–6C (non pl. 4, figs. 3A–3C, ?4A–4D, 7A–7D).

**Remarks.** Bütschli (1882) split Ehrenberg's original concept of this species into two groups: *Lithomelissa macropter*a Ehrenberg and *Lithomelissa ehrenbergi* Bütschli.

### *Lithomelissa matschigarica* **Vituchin, 1993**

*Lithomelissa matschigarica* n. sp., Vituchin, 1993, pl. 29, figs. 14, 18.
*Lithomelissa matschigarica* Vituchin, Tsoy and Shastina, 1999, pl. 34, fig. 9.

### *Lithomelissa* **(?)** *hoplites* **Foreman, 1968**

*Lithomelissa* (?) *hoplites* n. sp., Foreman, 1968, pl. 3, figs. 2A–C.
? *Tripodiscium* sp. aff. *Lithomelissa hoplites*, Petrushevskaya and Kozlova, 1972, pl. 7, fig. 2.

**Remarks.** It is not clear whether or not this species belongs in *Lithomelissa*. Although it has an apical spine passing freely through the cephalis, the elongated and tapering/undulating nature of the thorax, relatively small and poreless cephalis, nature of the pores and ridges on the thorax, and very strong appendages high up on the thorax, are together very unusual characteristics for this genus, and unlike any of the other lophophaenids we observed in this study. If it really does belong in *Lithomelissa,* to our knowledge this species would be the only member of this genus that dating back to the Cretaceous. Furthermore, if correctly assigned, this species would make *Lithomelissa* the oldest lophophaenid genus of those included in this manuscript.

### *Lithomelissa lautouri* **O'Connor, 1999**

? *Lamptonium sanfilippoae* Foreman, Ling, 1975, pl. 9, fig. 23 (partim).
? *Lithomelissa* sp., Caulet, 1991, pl. 2, fig. 6.
*Lithomelissa lautouri* n. sp., O'Connor, 1999, text-fig. 7; pl. 2, figs. 23–27; pl. 6, figs. 11A–15.

### *Lithomelissa maureenae* **O’Connor, 1997**

*Lithomelissa* sp. A, O’Connor, 1993, pl. 6, figs. 2–3.
*Lithomelissa* sp. B, O’Connor, 1993, pl. 6, figs. 4–5.
*Lithomelissa maureenae* n. sp., O’Connor, 1997, text-fig. 5; pl. 2, figs. 7–10; pl. 6, figs. 10–11; pl. 7, figs. 1–6.
*Lithomelissa maureenae* O’Connor, O’Connor, 2000, p. 206 [not figured].

**Remarks.** This species has arches in the center of the cephalis connecting the apical spine to the lateral spines, and a bar that splits off from the apical spine to produce a secondary horn on the dorsal side. These characteristics are not typical of *Lithomelissa,* so future work may reveal that this species belongs better in a different genus.

### *Lithomelissa microptera* **Ehrenberg, 1854c**

*Lithomelissa microptera* n. sp., Ehrenberg, 1854c, pl. 36, fig. 2.
*Lithomelissa microptera* Ehrenberg, Haeckel, 1862, p. 303 [not figured].
*Lithomelissa microptera* Ehrenberg, Ehrenberg, 1874, p. 241 [not figured].
*Lithomelissa microptera* Ehrenberg, Ehrenberg, 1876, p. 78–79; pl. 3, fig. 13.
*Lithomelissa microptera* Ehrenberg, Bütschli, 1882, pl. 33, fig. 26.
*Micromelissa microptera* (Ehrenberg), Haeckel, 1887, p. 1230 [not figured].
? *Lithomelissa microptera* Ehrenberg, Petrushevskaya, 1971, pl. 44, fig. 3.
*Lithomelissa microptera* Ehrenberg, Ogane *et al.,* 2009, pl. 21, figs. 3A–C.

**Remarks.** Ehrenberg (1854c) first illustrated this species without a written description. Haeckel (1862) provided a description based on Ehrenberg’s illustration, but apparently without having physically observed any specimens himself. Ehrenberg (1874) then gave another description of the species, without referencing Haeckel but also not contradicting him. Petrushevskaya (1971)’s specimen is questioned, because the cephalis is shorter and broader with less of a constriction at the neck compared to Ehrenberg’s type material.

### *Lithomelissa parva* **(Gorbunov, 1977) Kozlova, 1999**

*Sethoconus* (?) *parvus* n. sp., Gorbunov, 1977, pl. 1, fig. 3
*Sethoconus* (?) *parvus* Gorbunov, Gorbunov, 1979, pl. 15, fig. 35.
*Lithomelissa parva* (Gorbunov), Kozlova, 1999, pl. 35, figs. 18–19.

### *Lithomelissa robusta* **Chen, 1975**

*Lithomelissa robusta* n. sp., Chen, 1975, pl. 9, figs. 1–2.
*Lithomelissa robusta* Chen, Abelmann, 1990, pl. 5, figs. 2A–B.

**Remarks.** This species was given the same name as a species described by Campbell and Clark (1944), but the two species are completely different. *Lithomelissa robusta* Campbell and Clark was transferred to *Lithelius* by Foreman (1968), long before *Lithomelissa robusta* Chen was described in 1975. Thus, Chen's species name is valid because it is a secondary homonym; the two species were never congeneric at the same time.

### *Lithomelissa* **?** *sakaii* **O'Connor, 2000**

*Lithomelissa* ? *sakaii* n. sp., O'Connor, 2000, pl. 2, figs. 9A–15.

**Remarks.** Like *Lithomelissa maureenae* O'Connor, 1997, this species has an atypical skeletal structure within the cephalis. In addition, it has very strong feet/wings that extend below the thorax, which are not present in most *Lithomelissa* species. Future work may find that this species fits better in a different genus, but since we did not observe it we do not make a formal transfer here.

### *Lithomelissa sphaerocephalis* **Chen, 1975**

*Lithomelissa sphaerocephalis* n. sp., Chen, 1975, pl. 8, figs. 1–2.
*Lithomelissa sphaerocephalis* Chen, Takemura, 1992, pl. 4, figs. 8–9.
*Lithomelissa sphaerocephalis* Chen, Funakawa, 2000, pl. 6, figs. 1A–4D; text-fig. 10.
*Lithomelissa sphaerocephalis* Chen, Funakawa and Nishi, 2005, pl. 4, figs. 9A–10.

### *Lithomelissa tricornis* **Chen, 1975**

*Lithomelissa tricornis* n. sp., Chen, 1975, pl. 8, figs. 6–7.
*Lithomelissa tricornis* Chen, Abelmann, 1990, pl. 5, fig. 3.
*Lithomelissa tricornis* Chen, Takemura, 1992, pl. 2, figs. 6–7.

### *Lithomelissa trifoliolata* **Funakawa, 1995a**

*Clathrolychnus* sp., Sugiyama, 1994, pl. 2, figs. 3A–B.
*Lithomelissa trifoliolata* n. sp., Funakawa, 1995a, pl. 10, figs. 3A–4C; text-fig. 9.

### *Lithomelissa ultima* **Caulet, 1979**

*Lithomelissa ultima* n. sp., Caulet, 1979, pl. 1, figs. 2–3.
*Lithomelissa ultima* Caulet, Sugiyama *et al.,* 1992, pl. 17, figs. 1A–B.

### *Lithomelissa vespa* **Renaudie and Lazarus, 2012**

*Lithomelissa vespa* n. sp., Renaudie and Lazarus, 2012, pl. 7, figs. 7A–B, 9A–B, 10.

### Genus *Lophophaena* Ehrenberg, 1847 emend. Petrushevskaya, 1971

Type species: *Lophophaena galeaorci* Ehrenberg, 1854b (=*Lophophaena apiculata* Ehrenberg, 1874)

**Description.** This genus has a relatively high cephalis, which is variable in shape but often reaches maximum width near the top. The cephalis may exhibit a distinct and elongated "neck" region, in which skeletal bars separate the main cephalic segment from the thorax, or the cephalis may be attached to the thorax near the median bar and expand upward without a clear neck. The cephalis also typically has numerous spines, which may be simple or branching. In all *Lophophaena*, the apical spine becomes embedded in the shell wall near the base of the cephalis, rather than being free through the length of the cephalis as it is in *Lithomelissa.* The embedded apical spine may protrude as a horn once it reaches the top of the cephalis, as it does in *Lithomelissa*. The thorax is wider than the cephalis, but it does not flare outward as widely as some other plagonid genera, such as *Lampromitra, Ceratocyrtis,* and *Amphiplecta.* Ribs and wings on the thorax are sometimes present, but rarely form strong feet as in *Pseudodictyophimus.*

**Remarks.** The original description of this genus by Ehrenberg (1847) was somewhat vague and not illustrated, leading to some of the confusion in subsequent taxonomic literature. The type species, *Lophophaena galea orci* Ehrenberg, 1854b (by monotypy) was first illustrated from different material by Stöhr (1880). Ehrenberg's original flow-chart describing this genus only specified that this taxon has two segments, a wide opening on the last segment, no ribs, often is crested, and has no posterior corona of spines. Ehrenberg (1874) described several additional species in this genus, and as some of these were also illustrated a clear basis for understanding the original meaning of *Lophophaena* is available. Furthermore, many of Ehrenberg's illustrated type series specimens have since been digitally re-imaged using modern light microscopy (Ogane *et al.*, 2009—see citations within individual species synonymy lists below). From these descriptions and images it is clear that the original concept was quite broad, and subsequent workers have further refined the scope of the genus concept Haeckel (1862) added further specifications to this genus, noting that it has a "ring-shaped cross-constriction" [translation from the German by David Lazarus], has a flared thorax (cylindrical or bell-shaped) that is not flattened, and has one or more spines on the cephalis that can be connected to one another. In 1887, Haeckel apparently revised this description, stating that the cephalis of *Lophophaena* should have a group of large spines (rather than a single spine being acceptable). This revision was adopted by Campbell and Clark (1945), who described the genus as having a "cephalis armed with several large horns." Haeckel (1887) considered *Lophophaena apiculata* Ehrenberg 1874 to be synonymous with *Lophophaena galea* Ehrenberg, 1854b, but omitted the second half of the name (*orci*). Petrushevskaya (1971) also included *Lophophaena apiculata* Ehrenberg, 1874 under *Lophophaena galea orci* Ehrenberg, 1854b.

Haeckel (1887) designated two subgenera within *Lophophaena*: *Lophophaenula* and *Lophophaenoma*. Campbell (1954) listed *Lophophaenula* as a junior synonym of *Lophophaena*. Petrushevskaya (1971) initially elevated the subgenus *Lophophaenoma* to the genus rank, and *Lophophaena circumtexta* Haeckel, 1887 was the type species of *Lophophaenoma* by monotypy, as well as a junior synonym of *L. radians* (Ehrenberg, 1874). While Haeckel (1887) defined the subgenus *Lophophaenoma* as: "Horns of the cephalis connected by anastomosing branches," Petrushevskaya (1971)'s genus description includes species without connected cephalic horns. She states that anastomosing branches on the cephalis are sometimes present, but particularly in more recent *Lophophaenoma* species, are not common. Later, Petrushevskaya (1981) considered *Lophophaenoma* to be a subjective synonym of *Arachnocorys*, presumably because the type species fit within *Arachnocorys*. Petrushevskaya (1981) decided that the differences between *Lophophaena* and *Lophophaenoma*, such as the variation in skeletal proportions and spine strength, were insufficient to justify separate genera, but instead of completely subsuming *Lophophaenoma* within *Lophophaena*, she suggested that some of the species would fit within *Peromelissa* and others in *Lophophaena*, but did not make any formal transfers. Subsequent usage of *Lophophaena* is inconsistent in the sense that some still use the narrower definition of *Lophophaena* and break out *Lophophaenoma*, sensu Petrushevskaya 1971 (i.e., Poluzzi, 1982, Matsuzaki *et al.*, 2016), whereas others use a broader genus definition of *Lophophaena* (i.e., Van de Paverd, 1995). Petrushevskaya (1971) was the first to describe the internal skeletal structure of *Lophophaena,* which was followed and clarified by Nishimura (1990), Funakawa (1994), and O'Connor (1997). All of these authors agree that the internal skeleton of *Lophophaena* includes the median bar, apical spine, dorsal spine, ventral spine, right and left lateral spines, and arches connecting the apical and ventral spines to the lateral spines. The arches connecting the apical and lateral spines are incorporated into the wall of the cephalis, as is the apical horn after it passes upward from the collar structure.

Here we observed the following species of *Lophophaena*: *Lophophaena amictoria* Renaudie and Lazarus, 2015, *Lophophaena arie* n. sp., *Lophophaena buetschlii* (Haeckel) Petrushevskaya, 1971, *Lophophaena casperi* n. sp., *Lophophaena cylindrica* (Cleve) Petrushevskaya, 1971, *Lophophaena domovoi* n. sp., *Lophophaena gozui* n. sp., *Lophophaena hispida* (Ehrenberg) Petrushevskaya, 1971, *Lophophaena ikiryo* n. sp., *Lophophaena ikota* n. sp., *Lophophaena kaonashii* n. sp., *Lophophaena laticeps* (Jørgensen) Kurihara and Matsuoka, 2010, *Lophophaena? leberu* Renaudie and Lazarus, 2016, *Lophophaena leshii* n. sp., *Lophophaena macrencephala* Clark and Campbell, 1945, *Lophophaena nadezdae* Petrushevskaya, 1971, *Lophophaena rhopalica* Renaudie and Lazarus, 2016, *Lophophaena rusalkae* n. sp., *Lophophaena shishigae* n. sp., *Lophophaena simplex* Funakawa, 1994, *Lophophaena undulatum* (Popofsky, 1913) n. comb., *Lophophaena ushionii* n. sp., *Lophophaena variabilis* (Popofsky) Petrushevskaya, 1971, and *Lophophaena witjazii* (Petrushevskaya) n. comb.

*Lophophaena circumtexta* Haeckel, 1887 is not included here because it is considered to be in *Arachnocorys,* following Petrushevskaya (1981)'s determination that *Lophophaenoma* (type species: *L. circumtexta*) is a subjective synonym of *Arachnocorys*. *Lophophaena galeata* Ehrenberg, 1874 does not fit the genus description, because the apical spine of this species is free within the cephalis, making it instead a *Lithomelissa*. Haeckel (1887) questionably synonymized *Lophophaena galeata* with *Lithomelissa ehrenbergi*, and we agree with this genus reassignment based on the position of the apical spine, but cannot confirm the species synonymy due to the poor quality of illustrated specimens. *Lophophaena? globeacuculla* Renaudie and Lazarus, 2015 has a nearly-spherical cephalis and very strong feet, which are not typical of this genus. However, it is not clear which genus would be a better fit for this species, so we do not make any formal transfer here. *Lophophaena tekopua* O'Connor, 1997 and *Lophophaena*? *thaumasia* Caulet, 1991 are not included because these species both have a cephalis relatively too small and horns too strong to be typical of *Lophophaena*. Here we transfer these species to a new genus, *Pelagomanes* n. gen., which is described later in this manuscript.

**Range.** ?Eocene–Recent.

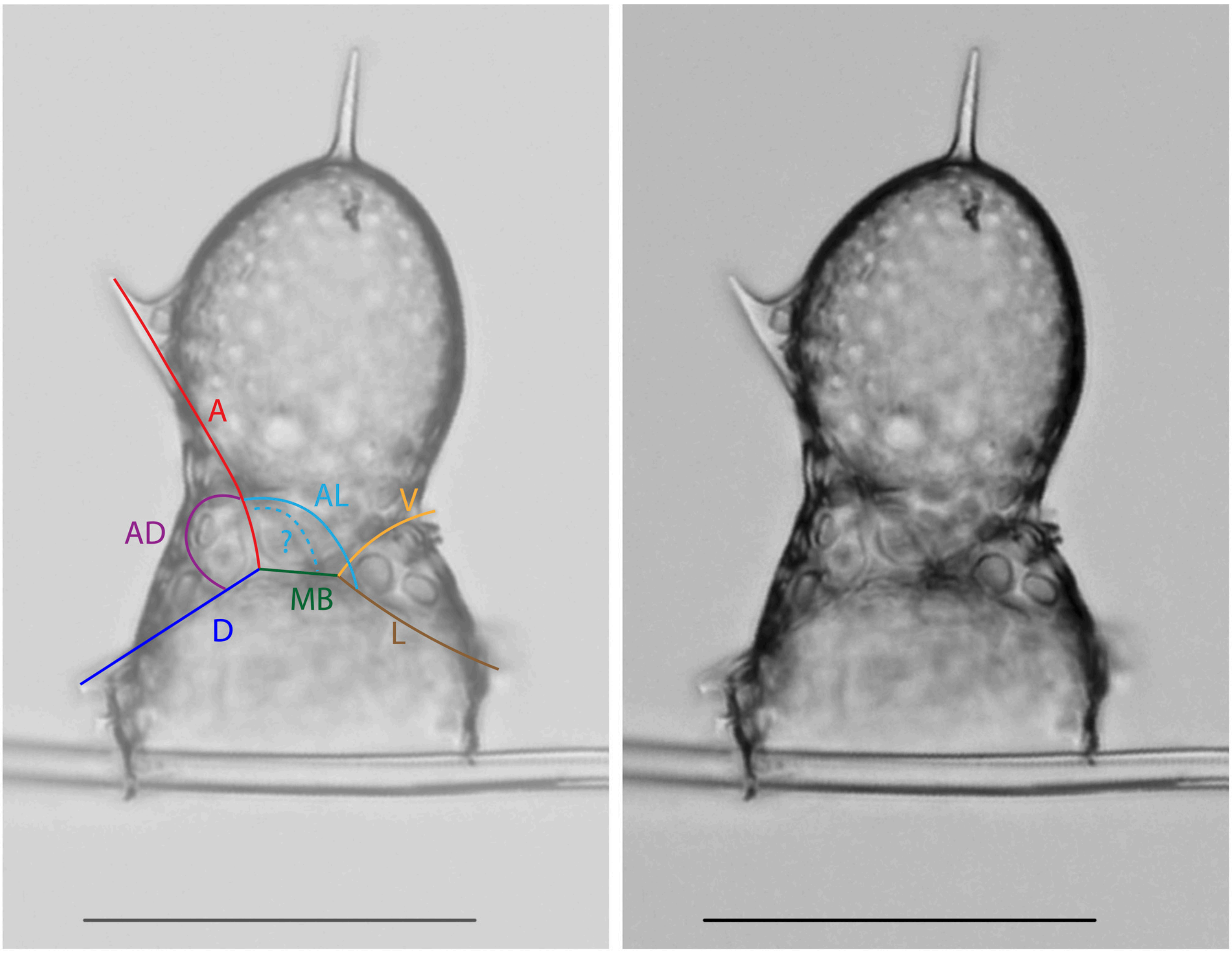

**FIGURE 11.** Internal skeletal structure of *Lophophaena domovoi* n. sp.

### *Lophophaena amictoria* **Renaudie and Lazarus, 2015**

Plate 21, Figs. 1A–3B.

*Peridium* spp., Lazarus and Pallant, 1989 (partim.), pl. 2, fig. 15.
*Lophophaena amictoria* n. sp., Renaudie and Lazarus, 2015, pl. 8 figs. 1–3.
*Lophophaena clevei,* Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species has a similar structure to *Lophophaena clevei* Petrushevskaya, 1971, and we misidentified it as such in our previous study. However, *L. amictoria* differs from *L. clevei* in that it is larger overall, has a more globular cephalis shape, and a relatively inflated neck area.

**Range.** Middle Miocene—Late Pleistocene in the EEP (Table 1). Early Miocene—Pleistocene in the Southern Ocean. Specimens from Lazarus and Pallant (1989) would indicate the range of this species extends back to the Early Oligocene.

### *Lophophaena arie* **n. sp.**

Plate 26, Figs. 1A–6 (?7A–C).

urn:lsid:zoobank.org:act:D0F6C5BB-51B6-4520-BFC8-09B0B331B0CB
unknown plagonid group C sp 23, Trubovitz *et al.,* 2020, supplementary data 7.

**Diagnosis.** Large *Lophophaena* with a cephalis that reaches its widest point near the top, and is flattened on the dorsal side where the apical spine is fused to the wall.

**Description.** This species is relatively large, with a high cephalis that becomes progressively wider toward the top until a point ~¾ of the way up, where it rounds smoothly toward the apex. The apical spine runs along the wall of the cephalis, and extends as a very short, thornlike spine where the cephalis reaches its maximum width. Pores on the cephalis are small, closely spaced, and regular in size and shape. They are close in size to those on the thorax, but may be slightly smaller. The neck area is long, and exhibits a bulge on the dorsal side where the AD and AL arches run along the shell wall. The ventral spine protrudes approximately perpendicular to the apical spine, and can be bladed and triangular in shape. The dorsal and lateral spines extend as thick appendages near the top of the thorax.

**Remarks.** This species resembles *Peromelissa thoracites* (Haeckel) Matsuzaki *et al.,* 2015 (Pl. 38, Figs. 7A–10) in general structure and proportions, but is significantly larger and no specimens of intermediate size were observed that would suggest an intraspecific morphological gradient. It also differs in having a short, thorn-like apical horn, rather than the straight and usually relatively longer horn present in *P. thoracites*. This species often stands out in assemblages for having an unusually large cephalis for a lophophaenid. A questionable specimen is included on Plate 26, Figs. 7A–C. This individual has an unusual flare on the ventral side of the cephalis, and a more pronounced gradient in pore size than the other specimens observed, but it shares the other characteristics and so is considered an atypical specimen of *L. aerie* rather than a different taxon. So far no specimen has been found with the thorax fully preserved, so the complete size and shape of the thorax of this species are not known.

**Material examined.** 17 specimens observed from samples 321-1337A-16H-6, 121–124cm (Late Miocene), 321-1337A-12H-5, 23–26cm (Late Miocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), 321-1337A-6H-3, 29–32cm (Late Pliocene), 321-1337A-5H-5, 11–14cm (Late Pliocene), 321-1337A-4H-6, 115–118cm (Early Pleistocene), 321-1337A-4H-2, 16–19cm (Middle Pleistocene), 321-1337A-3H-2, 103–106cm (Middle Pleistocene), and 321-1337A-2H-3, 76–79cm (Late Pleistocene).

**Holotype.** Pl. 26, Fig. 1A–B; sample 321-1337A-3H-2, 103–106cm; ECO-126; H11-1.

**Paratypes.** (1) Pl. 26, figs. 2A–B; sample 321-1337A-4H-2, 16–19cm; ECO-128; D11-4. (2) Pl. 26, figs. 4A–B; sample 321-1337A-4H-2, 16–19cm; ECO-129; L12-2. (3) Pl. 26, figs. 3A–B; sample 321-1337A-7H-6, 104–107cm; ECO-134; T26-1. (4) Pl. 26, figs. 5A–B; sample 321-1337A-4H-2, 16–19cm; ECO-128; U13-3. (5) [not figured] sample 321-1337A-7H-6, 104–107cm; ECO-134; R36-4.

**Measurements.** Cephalis height 65–81 (74)µm; cephalis width 55–68 (63)µm; width of neck 49–56 (52)µm. Based on 9 specimens.

**Etymology.** Named for Arie, the large, benevolent yokai that comes from the sea to tell prophecies and ward off evil.

**Range.** Late Miocene—Late Pleistocene, EEP (Table 1).

### *Lophophaena buetschlii* **(Haeckel 1887) Petrushevskaya, 1971**

Plate 24, Figs. 1A–2B.

*Lithomelissa buetschlii* n. sp., Haeckel, 1887, p. 1207, pl. 56, fig. 1.
*Acanthocorys variabilis* n. sp., Popofsky, 1913, p. 360–364, text-fig. 80 (non text-figs. 71–79, 81).
*Lophophaena buetschlii* Haeckel, Petrushevskaya, 1971, p. 109, 111, pl. 58, figs. 1–10.
*Lithomelissa buetschlii* Haeckel, Renz, 1976, pl. 6, fig. 19.
*Lithomelissa buetschlii* Haeckel, Tan and Tchang, 1976, text-fig. 51a–51b.
*Lophophaena buetschlii*, Boltovskoy and Riedel, 1987, pl. 4, fig. 9.
*Lophophaena buetschlii* (Haeckel) Petrushevskaya, Van de Paverd, 1995, pl. 65, fig. 10 (non-figs. 3–4).
*Lophophaena buetschlii* (Haeckel) Petrushevskaya, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** Haeckel (1887) originally described this species under the generic name *Lithomelissa,* subgenus *Micromelissa*. Petrushevskaya (1971) reassigned this species to *Lophophaena* and provided many detailed illustrations. Name usage has been mixed between these two genus assignments ever since, but here we follow Petrushevskaya (1971)'s assignment to *Lophophaena*, because the apical spine is not free within the cephalis as it is in *Lithomelissa*.

**Range.** Late Miocene—Recent, EEP (Table 1).

### *Lophophaena casperi* **n. sp.**

Plate 28, Figs. 1A–9B.

urn:lsid:zoobank.org:act:F96F8032-1408-4E90-B84F-CC30D80A16D0
? *Tripodocorys* sp. A., Sugiyama, 1994, pl. 5, figs. 3a–d.
unknown plagonid group C sp 28, Trubovitz *et al.,* 2020, supplementary data 7.

**Diagnosis.** *Lophophaena* with an hourglass shape in outline, exhibiting many thin spines around the cephalis and the shoulders of the thorax.

**Description.** This species has a high, balloon- shaped cephalis that reaches its widest point about ⅔ of the way up. From the circumference of this wide point, many thin spines extend upward from the cephalis. Pores on the cephalis are small and round. The neck area is proportionally narrow, and includes several short, thin spines in addition to the horizontally-orientated ventral spine. The thorax flares widely at the shoulders, contributing to the skeleton's overall hourglass shape. When well-preserved, many thin spines extend down and outward from the widest point of the shoulders. Below the shoulders, the thorax wall tends to become thinner and have smaller, more irregular pores. The base of the thorax is smooth, lacking teeth at the termination.

**Remarks.** This species shows a relatively high amount of size variation, but the shell shape and proportions are consistent. It differs from *Lophophaena rusalkae* n. sp. (Pl. 29, Figs. 1A–6) in its larger overall size, and more pronounced hourglass shape, with a long and narrow neck, and high, inflated cephalis. Figure 12 illustrates how the cephalis dimensions are different between these two species, which can appear similar at first glance.

**Material examined.** 85 specimens observed from Late Miocene samples 321-1337A-21H-1, 33–35cm, 321-1337A-18H-6, 77–80cm, 321-1337A-16H-6, 121–124cm, and 321-1337A-14H-7, 39–42cm.

**Holotype.** Pl. 28, figs. 1A–B; sample 321-1337A-21H-1, 33–35cm; ECO-144; G3-1.

**Paratypes.** (1) Pl. 28, figs. 4A–B; sample 321-1337A-21H-1, 33–35cm; ECO-144; S16-2. (2) Pl. 28, fig. 2; sample 321-1337A-14H-7, 39–42cm; ECO-139; W39-4. (3) Pl. 28, figs. 8A–B; sample 321-1337A-14H-7, 39–42cm; ECO-138; Q30-1. (4) Pl. 28, figs. 7A–B; sample 321-1337A-16H-6, 121–124cm; ECO-141; W22-1. (5) Pl. 28, figs. 5A–B; sample 321-1337A-16H-6, 121–124cm; ECO-142; M17-1. (6) Pl. 28, fig. 3; sample 321-1337A-16H-6, 121–124cm; ECO-141; J15-4. (7) Pl. 28, figs. 6A–B; sample 321-1337A-16H-6, 121–124cm; ECO-141; H39-4. (8) [not figured] sample 321-1337A-16H-6, 121–124cm; ECO-141; C2-2.

**Measurements.** Height of cephalis 44–58 (52)µm; width of cephalis 30–41 (38)µm; width at neck 23–33 (29)µm; width at shoulders 42–52 (48)µm. Based on 16 specimens.

**Etymology.** Named for Casper the friendly ghost, a mid-century American cartoon character.

**Range.** Late Miocene, EEP (Table 1).

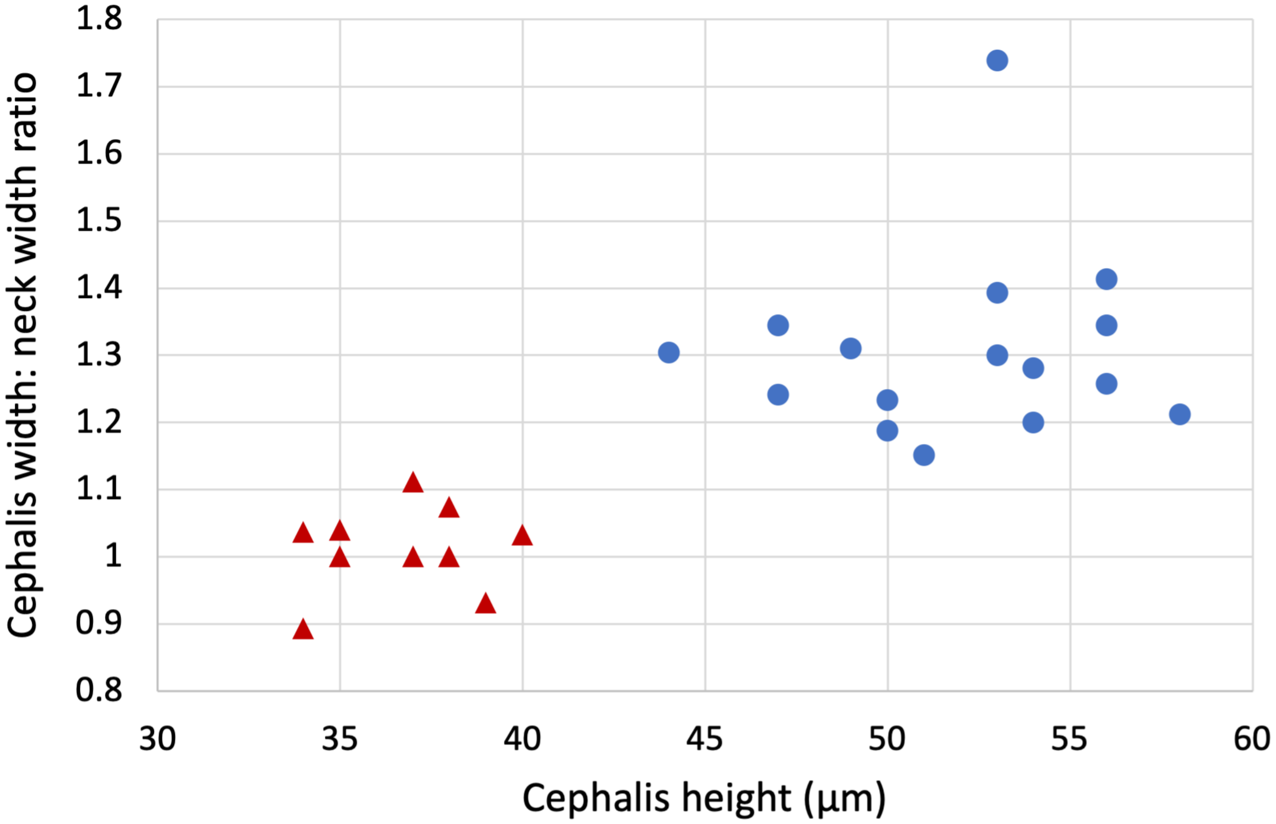

**FIGURE 12.** Chart illustrating the different cephalis dimensions of *Lophophaena casperi* n. sp. (blue squares) and *L. rusalkae* n. sp. (red triangles). *L. rusalkae* has a cephalis height ranging from 34-40 microns, and an average cephalis width:neck ratio of 1. By contrast, L. casperi has a higher cephalis, ranging from 44- 58 microns, and a cephalis width:neck ratio averaging 1.3. The specimen with a cephalis width:neck ratio of 1.7, which is visually the outlier on this chart, has a particularly narrow neck (23 microns), but a cephalis of typical width for this species (40 microns).

### *Lophophaena cylindrica* (Cleve, 1900) Petrushevskaya, 1971

Plate 22, Figs. 1A–4.

*Dictyocephalus cylindricus* n. sp., Cleve, 1900, p. 7, pl. 4, fig. 10.
*Lophophaena cylindrica* (Cleve), Petrushevskaya, 1971, p. 117, pl. 57, fig. 5; pl. 61, figs. 4–6.
non *Lophophaena cylindrica* Cleve, Renz, 1976, pl. 6, fig. 21.
*Lophophaena cylindrica* Cleve, Takahashi, 1991, pl. 25, fig. 3 (non figs. 4–5).
*Lophophaena cylindrica* Cleve, Hull, 1993, pl. 4, fig. 2.
*Lophophaena cylindrica* Cleve, Sashida and Kurihara, 1999, fig. 7.4.
unknown plagonid group C sp 30, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species is close to *Lophophaena hispida* (Ehrenberg) Petrushevskaya (Pl. 22, Figs. 5–8B), but differs in that pore size is consistent throughout the skeleton, whereas *L. hispida* has significantly larger pores on the cephalis. Well-preserved specimens of this species also tend to show an extra built-up layer of silica around the neck area, whereas *L. hispida* does not. The *Lophophaena cylindrica* specimen illustrated in Renz (1976), and some of the specimens illustrated in Takahashi (1991) appear to have large pores on the cephalis (although image quality is low), likely making these *L. hispida* specimens. There is significant variation in size within this species, including in our EEP material.

**Range.** Late Miocene—Recent, EEP (Table 1).

### *Lophophaena* cf. *decacantha* (Haeckel, 1887) Petrushevskaya, 1971

Plate 27, Figs. 3A–4C.

? *Lophophaenoma* cf. *decacantha* (Haeckel, 1887) Petrushevskaya, 1971, pl. 61, fig. 2.

**Remarks.** This species is similar to *Lophophaena decacantha* (Haeckel) Petrushevskaya, except that the top of the cephalis is not hyaline, and there are three horns on the cephalis rather than four. The two specimens we observed resemble a specimen illustrated by Petrushevskaya (1971) as *Lophophaenoma* cf. *decacantha*. Our specimens do not exhibit the strong ventral horn at the base of the cephalis, however, so it's not certain that these individuals are conspecific.

**Material examined.** 2 specimens observed from sample 3H2,103–106cm (Middle Pleistocene).

**Range.** Middle Pleistocene in the EEP (Table 1).

### *Lophophaena decacantha* (Haeckel, 1887) group sensu Takahashi, 1991

Plate 27, Figs. 1A–2B.

*Lophophaena decacantha* Haeckel group, Takahashi, 1991, pl. 25, figs. 2, 8.
*Lophophaena decacantha* Haeckel group, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species group differs from many others in *Lophophaena* in that the apical spine flares out from the cephalis, and is usually reinforced by skeletal buttressing where it separates from the cephalis, similar to the cephalic spine structure of *Lophophaena decacantha* (Haeckel) Petrushevskaya *sensu stricto*. However, it differs from *Lophophaena decacantha ss.,* in that the top of the cephalis is not hyaline, the neck area is not as constricted, and there is only one major spine on the cephalis, which is more poorly developed than the four strong cephalic horns of *L. decacantha*. Takahashi's group concept likely includes multiple distinct species.

**Material examined.** 22 specimens observed from samples 321-1337A-12H-5, 23–26cm (Late Miocene), 321-1337A-10H-2, 91–94cm (Early Pliocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), 321-1337A-6H-3, 29–32cm (Late Pliocene), 321-1337A-5H-5, 11–14cm (Late Pliocene), 321-1337A-4H-6, 115–118cm (Early Pleistocene), 321-1337A-4H-2, 16–19cm (Middle Pleistocene), 321-1337A-3H-2, 103–106cm (Middle Pleistocene), and 321-1337A-2H-3, 76–79cm (Late Pleistocene).

**Range.** Latest Miocene—Late Pleistocene, EEP (Table 1).

### *Lophophaena domovoi* n. sp.

Plate 30, Figs. 1A–7B.

urn:lsid:zoobank.org:act:2C507BDD-D308-40B4-A308-4A8A9E987A94
unknown plagonid group C sp 20, Trubovitz *et al.,* 2020, supplementary data 7.

**Diagnosis.** *Lophophaena* with a curved, hook-like apical spine and a thin, conical horn on the top of the cephalis.

**Description.** The cephalis of this species has two spines. One originates from the apical spine and is curved upward, resembling a hook or thorn, and extends outward from the dorsal side of the cephalis, well below the apex. The second spine is conical with a pointed tip, extends from the apex of the cephalis, and is not related to any of the primary skeletal spines. Pores on the cephalis are small and round, and decrease in size from the base to the top of the cephalis. The thorax is wider than the cephalis to varying degrees, but not dramatically so. There are strong indentations on the thorax where the lateral and dorsal spines run along the shell wall before extending outside the thorax as short appendages.

**Remarks.** Some specimens of this species can have few, or very small pores, such as the specimen in Figure 5 (seen from dorsal side). The size of this species is significantly smaller than *Lophophaena ikota* n. sp. (Pl. 33, Figs. 1A–7B), and it also differs in that the apical spine is more pronounced.

**Material examined.** 18 specimens observed from samples 321-1337A-31X-6W, 4–6cm (Middle Miocene) and 321-1337D-23H-6, 134–137cm (Late Miocene).

**Holotype.** Pl. 30, figs. 1A–C; sample 321-1337D-23H-6, 134–137cm; ECO-147; K30-4.

**Paratypes.** (1) Pl. 30, fig. 2; sample 321-1337D-23H-6, 134–137cm; ECO-147; F8-1. (2) Pl. 30, figs. 3A–B; sample 321-1337D-23H-6, 134–137cm; ECO-146; T35-1. (3) Pl. 30, figs. 7A–B; sample 321-1337D-23H-6, 134–137cm; ECO-145; K25-2. (4) Pl. 30, fig. 5; sample 321-1337D-23H-6, 134–137cm; ECO-146; M9-1. (5) [not figured] sample 321-1337D-23H-6, 134–137cm; ECO-146; N37-3.

**Measurements.** Cephalis height 40–49 (45)µm; cephalis width 29–38 (35)µm; neck width 25–31 (28)µm; width at shoulders 40–57 (46)µm. Based on 15 specimens.

**Etymology.** Named for the house spirit in Slavic folklore, the Domovoi.

**Range.** Middle—Late Miocene, EEP (Table 1). Lower limit not determined.

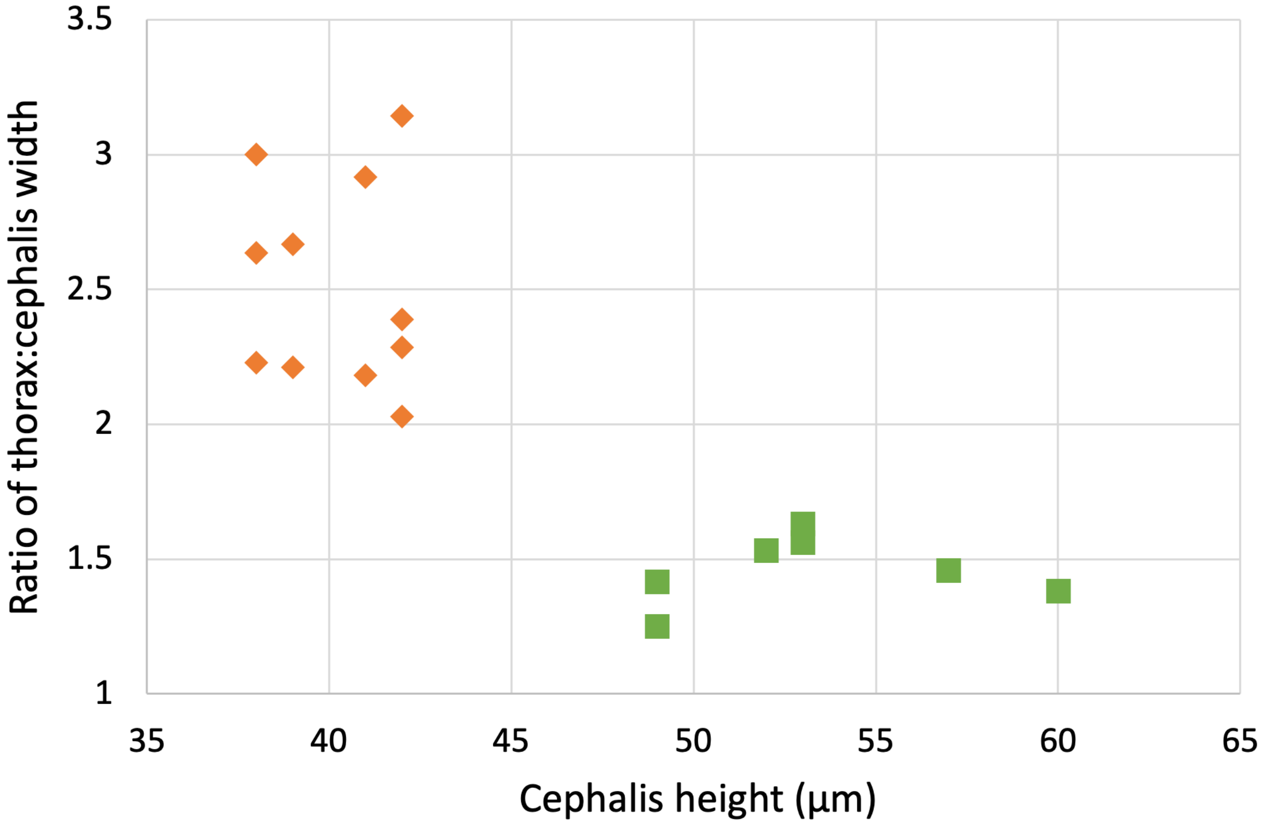

**FIGURE 13.** Chart illustrating the differences between *Lophophaena gozui* n. sp. (orange diamonds) and *L. ushionii* n. sp. (green squares), in terms of cephalis height and the ratio between thorax and cephalis width. *L. gozui* has a shorter average cephalis height (40 microns) compared to *L. ushionii* (average cephalis height = 54 microns). In addition, the thorax is proportionally wider compared to the cephalis in *L. gozui* (average ratio of thorax:cephalis width = 2.5). *L. ushionii* has a proportionally narrower thorax (average ratio of thorax: cephalis width = 1.5).

### *Lophophaena gozui* n. sp.

Plate 31, Figs. 1A–6.

urn:lsid:zoobank.org:act:95177882-DC83-4974-8370-E9B904F3E4BA
unknown plagonid group C sp 32 cf, partim., Trubovitz *et al.,* 2020, supplementary data 7.

**Diagnosis.** *Lophophaena* with a thumb-shaped cephalis that is relatively small compared to the thorax and has two prominent bladed horns on the dorsal and ventral sides.

**Description.** This species has heavily silicified cephalis with framed pores. The apical spine extends broadly upward as a strong bladed horn on the dorsal side, and a second bladed horn extends at a slightly lower angle from the ventral side of the cephalis. The top of the cephalis can exhibit several small thorns, but additional spines do not develop on top of the cephalis. The ventral spine is relatively long and needlelike when preserved. The cephalis is small compared to the thorax, which reaches approximately twice its width and is at least double the length of the cephalis (though a fully preserved thorax has not yet been observed, so it is likely even larger). Pores on the thorax can be approximately the same size as those on the cephalis, or slightly larger. The dorsal and lateral spines join the wall of the thorax and do not form prominent appendages, although a short tip may protrude outside the thorax (i.e., fig. 1).

**Remarks.** This species has a similar overall appearance to *Lophophaena ushionii* n. sp. (Pl. 31, Figs. 7A–11B), but differs in that the cephalis is much smaller, the thorax is relatively wider (Figure 13), and it does not develop a third spine between the two prominent horns on the cephalis as does *L. ushionii.*

**Material examined.** 18 specimens from samples 321-1337A-31X-6W, 4–6cm (Middle Miocene), 321-1337D-26H-3W, 142–144cm (Late Miocene), and 321-1337D-23H-6, 134–137cm (Late Miocene).

**Holotype.** Pl. 31, Figs. 1A–B; sample 321-1337D-23H-6, 134–137cm; ECO-147; O22-1.

**Paratypes.** (1) Pl. 31, fig. 2; sample 321-1337D-23H-6, 134–137cm; ECO-145; Z26-1. (2) Pl. 31, fig. 5; sample 321-1337D-23H-6, 134–137cm; ECO-145; U8-3. (3) Pl. 31, figs. 4A–B; sample 321-1337D-26H-3, 142–144cm; ECO-148; Y41-1. (4) Pl. 31, fig. 6; sample 321-1337D-26H-3, 142–144cm; ECO-148; U32-1. (5) [not figured] sample 321-1337D-23H-6, 134–137cm; ECO-145; H13-3.

**Measurements.** Cephalis height 38–42 (40)µm; cephalis width 30–36 (34)µm; thorax width 71–110(87) µm; ratio of thorax:cephalis width 2.0–3.1 (2.5). Based on 12 specimens. Note: thorax width should be considered the minimum width, as the thorax is typically not fully preserved. In the two specimens that appeared to have a nearly-complete thorax, its width was 105 and 110 microns.

**Etymology.** Named for the ox-headed demon, Gozu, that guards the gates of hell in Japanese Buddhism, for its resemblance to an ox.

**Range.** Middle– Late Miocene, EEP (Table 1).

### *Lophophaena hispida* (Ehrenberg, 1862) Petrushevskaya, 1971

Plate 22, Figs. 5–8B.

*Dictyocephalus hispidus* n. sp., Ehrenberg, 1862, p. 298 [not figured].
*Dictyocephalus hispidus* Ehrenberg, Ehrenberg, 1873b, pl. 5, fig. 18.
*Dictyocephalus (Dictyocryphalus) hispidus* Ehrenberg, Haeckel, 1887, p. 1309 [not figured].
? *Theocapsa democriti* n. sp., Haeckel, 1887, p. 1427, pl. 66, fig. 8.
*Sethoconus crinitus* n. sp., Cleve, 1900, p. 11, pl. 3, fig. 13.
*Acanthocorys variabilis* n. sp. Popofsky, 1913, p. 360–364, text-figs. 74–77, ?73; non text-figs. 71–72, 78–81.
*Lophophaena hispida* (Ehrenberg), Petrushevskaya, 1971, p. 115, 117, pl. 61, figs. 1–3.
? *Lophophaena hispida* Ehrenberg, atyp., Petrushevskaya, 1971, pl. 57, fig. 4.
*Theocapsa democriti* Haeckel, Tan and Tchang, 1976, fig. 69a–c.
*Lophophaena cylindrica* Cleve, Renz, 1976, pl. 6, fig. 21.
*Lophophaena hispida* Ehrenberg, Kruglikova, 1978, pl. 22, fig. 7.
*Lophophaena hispida* Ehrenberg, Nishimura and Yamauchi, 1984, pl. 32, figs. 6–7.
*Lophophaena hispida* Ehrenberg, Boltovskoy and Jankilevich, 1985, pl. 4, fig. 6.
*Lophophaena hispida* Ehrenberg, Nishimura, 1990, p. 93–95, figs. 17.1a–17.3b.
*Lophophaena cylindrica* Cleve, Takahashi, 1991, pl. 25, figs. 4–5 (non fig. 3).
*Lophophaena hispida* Ehrenberg forma *hispida*, Van de Paverd, 1995, pl. 65, figs. 1–2.
*Lophophaena hispida* Ehrenberg, Itaki *et al.,* 2010, pl. 6, figs. 11–12.
*Lophophaena hispida* Ehrenberg, Matsuzaki *et al.,* 2016, figs. 9.17–9.18.
*Lophophaena hispida* Ehrenberg, Matsuoka 2017, fig. 22.1–22.8.
*Lophophaena hispida* Ehrenberg, Trubovitz *et al.*, 2020, supplementary data 7.

**Remarks.** The basionym of this species is *Dictyocephalus hispidus* Ehrenberg, 1862. The species was emended and transferred to the genus *Lophophaena* by Petrushevskaya (1971). Since then, the species has occasionally been confused with *Lophophaena cylindrica* (Cleve) Petrushevskaya, 1971 in the literature. Beyond the difference in pore sizes on the cephalis and thorax, *L. hispida* differs from *L. cylindrica* (Pl. 22, Figs. 1A–4) in that cephalic spines are directly related to the nodes of the pores. Van de Paverd (1995) split *Lophophaena hispida* into two forms, *L. hispida hispida* and *L. hispida cylindrica*, which are largely consistent with the species designations *Lophophaena hispida* and *Lophophaena cylindrica*. Here we maintain that these are two separate species, following the usage most common in the literature, and it is our opinion that the differences between the two justify separate species. Popofsky (1913) illustrated a wide variety of forms within *Acanthocorys variabilis*, which we herein divide into four species, including *L. hispida,* as well as *L. buetschlii, L. leshii* n. sp.*,* and *L. variabilis,* partially following the designations of previous authors as well as one new species. The specimens of *L. hispida* in our material varied considerably in their degree of silicification. Some specimens exhibited a closed base of the thorax. Haeckel designated specimens with the enclosed base and more elongated cephalis as a separate species, *Theocapsa democriti* Haeckel 1887. We observed a few *L. hispida* specimens with semi-enclosed and fully-enclosed thorax bases, suggesting this may be an ontogenetic character. However, the specimen Haeckel (1887) figured as *Theocapsa democriti* also appears to have a more elongated, thumb-shaped cephalis than is typical for *L. hispida*, so these may indeed be separate species.

**Range.** Late Pliocene—Recent, EEP (Table 1).

### *Lophophaena ikiryo* **n. sp.**

Plate 32, Figs. 1A–8.

urn:lsid:zoobank.org:act:80B504BF-6D68-448F-869B-E6BE8D8E82FB
*Lithomelissa thoracites* Haeckel, Boltovskoy and Riedel, 1987, pl. 4, fig. 7
unknown plagonid group C sp 8, partim., Trubovitz *et al.,* 2020, supplementary data 7.
unknown plagonid group C sp 54, Trubovitz *et al.,* 2020, supplementary data 7.

**Diagnosis.** *Lophophaena* with a large, sub-rectangular cephalis that tends to be increasingly hyaline towards the top and has a thorax with long, conical appendages extending from the dorsal and lateral spines.

**Description.** This species has a relatively large cephalis that is somewhat rectangular in shape, with slightly flattened sides. Pore size decreases from the neck to the apex of the cephalis, and in many cases the top ⅓ of the cephalis can be hyaline. The apical spine is subdued, barely extending from the top of the dorsal side of the cephalis. However, it forms a strong indentation where it runs along the wall of the cephalis, and appears to be pinched inwards. The largest pores on the skeleton occur around the neck area. The thorax is slightly more broad than the cephalis, and exhibits strong appendages extending from the dorsal and lateral spines. These spines are conical, and tend to be significantly thicker than the apical spine.

**Remarks.** This species differs from *Peromelissa thoracites* (Pl. 38, Figs. 7A–10) in that it is much larger, and the top of the cephalis tends to be hyaline or nearly so. It also has a consistently poorly developed apical horn, whereas *Peromelissa thoracites* usually has an apical horn of approximately the same strength as the dorsal and lateral spines on the thorax. The ranges of these two species overlap slightly, but *L. ikiryo* was restricted to the Late Miocene—Early Pliocene, whereas *P. thoracites* was present from the Latest Miocene—Recent, reaching greatest abundances in the Pleistocene.

**Material examined.** 50 specimens observed from samples 321-1337A-16H-6, 121–124cm (Late Miocene), 321-1337A-14H-7, 39–42cm (Late Miocene), 321-1337A-12H-5, 23–26cm (Late Miocene), and 321-1337A-10H-2, 91–94cm (Early Pliocene).

**Holotype.** Pl. 32, figs. 4A–B; sample 321-1337A-14H-7, 39–42cm; ECO-138; E37-1.

**Paratypes.** (1) Pl. 32, fig. 9; sample 321-1337A-12H-5, 23–26cm; ECO-137; C3-3. (2) Pl. 32, figs. 1A–B; sample 321-1337A-14H-7, 39–42cm; ECO-140; L33-4. (3) Pl. 32, figs. 3A–B; sample 321-1337A-16H-6, 121–124cm; ECO-142; K4-2. (4) Pl. 32, figs. 6A–B; sample 321-1337A-16H-6, 121–124cm; ECO-143; SS7-1. (5) Pl. 32, fig. 8; sample 321-1337A-16H-6, 121–124cm; ECO-143; R47-2. (6) Pl. 32, figs. 5A–B; sample 321-1337A-16H-6, 121–124cm; ECO-143; F33-1. (7) Pl. 32, figs. 7A–B; sample 321-1337A-14H-7, 39–42cm; ECO-138; J41-1.

**Measurements.** Cephalis height 51–59 (55)µm; cephalis width 41–49 (44)µm; neck width 32–40 (37)µm; width at shoulders 48–62 (52)µm. Based on 13 specimens.

**Etymology.** Named for the ghostly spirits of living people that temporarily leave their bodies in Japanese folklore, Ikiryô.

**Range.** Late Miocene—Pliocene in the EEP (Table 1).

### *Lophophaena ikota* **n. sp.**

Plate 33, Figs. 1A–7B.

urn:lsid:zoobank.org:act:ACF9629F-4970-42EE-ABE1-8F4E6A32EF32
unknown plagonid group C sp 16, Trubovitz *et al.,* 2020, supplementary data 7.

**Diagnosis.** *Lophophaena* with a cephalis that is widest at its center and has a single conical spine on the apex, unrelated to any of the primary spines; thorax is broadly conical and has weak ribs but no appendages.

**Description.** This species has a thickly-silicified, kidney-shaped cephalis with a strong conical spine extending from the apex. This horn is not connected to the apical spine, which runs along the side of the cephalis and does not extend significantly through the shell wall. The cephalis of this species is widest near its center and tapers toward the top, rather than reaching its widest point in the top 1/3 (as it does in many other *Lophophaena* species). The thorax is long and generally cone-shaped, with several weak ribs but no spines extending outward from the primary spines. The thorax typically becomes more thinly silicified toward the base. Pore size tends to decrease both upward and downward from the neck area.

**Remarks.** This species differs from *Lophophaena shishigae* n. sp. (Pl. 35, Figs. 1–6B) in that it is approximately twice its size, and has a more kidney-shaped cephalis that is widest at its middle. It differs from *Arachnocorys jorogumoae* n. sp. (Pl. 4, Figs. 1A–11) in that it does not develop several forked cephalic spines around the top third of the cephalis, and the cephalis wall tends to be thicker and more textured with strongly-framed pores. Another difference is that the thorax of *Lophophaena ikota* n. sp. usually has weaker ribs than *Arachnocorys jorogumoae* n. sp., and does not flare as widely outward. Despite its overall similar structure to *A. jorogumoae,* we place *L. ikota* in *Lophophaena* because it does not have any dendritic spines on the cephalis and lacks large pores at the base of the cephalis, excluding it from the definition of *Arachnocorys*. The cephalis shape of this species, which is slightly longer on the ventral side than the dorsal side, is common among *Lithomelissa*. However, since the apical spine is not free inside the cephalis, this species does not fit the definition of *Lithomelissa* and was placed in *Lophophaena* instead.

**Material examined.** 27 specimens observed from samples 321-1337D-26H-3W, 142–144cm (Late Miocene), 321-1337D-23H-6, 134–137cm (Late Miocene), 321-1337A-12H-5, 23–26cm (Late Miocene), 321-1337A-10H-2, 91–94cm (Early Pliocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), and 321-1337A-6H-3, 29–32cm (Late Pliocene).

**Holotype.** Pl. 33, Figs. 2A–B; sample 321-1337D-23H-6, 134–137cm; ECO-145; W7-3.

**Paratypes.** (1) Pl. 33, figs. 3A–B; sample 321-1337D-23H-6, 134–137cm; ECO-145; P30-1. (2) Pl. 33, fig. 4; sample 321-1337D-23H-6, 134–137cm; ECO-147; U11-1. (3) Pl. 33, fig. 5; sample 321-1337D-23H-6, 134–137cm; ECO-146; Z20-4. (4) Pl. 33, figs. 7A–B; sample 321-1337D-23H-6, 134–137cm; ECO-146; N33-3. (5) [not figured] sample 321-1337D-23H-6, 134–137cm; ECO-145; M28-1. (6) [not figured] 321-1337D-23H-6, 134–137cm; ECO-146; Q39-2.

**Measurements.** Cephalis height 52–61 (57)µm; cephalis width 38–48 (43)µm; width of neck constriction 36–43 (39)µm. Based on 14 specimens.

**Etymology.** Named for the ikota, a possession spirit in Russian folklore.

**Range.** Lower Late Miocene—Pliocene, EEP (Table 1).

### *Lophophaena kaonashii* **n. sp.**

Plate 34, Figs. 1A–8B.

urn:lsid:zoobank.org:act:8C9A5395-F8AD-43EE-BE0B-64C2173A99D2

*Arachnocorys?* sp 2/3 partim., Trubovitz *et al.,* 2020, supplementary data 7.

**Diagnosis.** *Lophophaena* with a heavily-silicified, spherical cephalis that has 1 or 2 conical horns unrelated to the apical spine, and a shouldered thorax with large pores around the top and no appendages.

**Description.** The cephalis of this species is spherical in shape and is more heavily silicified than the thorax. Well-preserved specimens show strongly-framed pores on the cephalis and many small bumps on the nodes of pores, which appear to have served as the bases of tiny, needle-like spines. 1, or rarely 2, prominent horns are present near the apex of the cephalis, but these are not related to the apical spine, which merges with the shell wall immediately above the collar structure and is so muted that it is difficult to detect. The thorax has a ring of large pores around the top where it connects to the cephalis. It reaches its widest point at the shoulders, and then tapers downward slightly. The lateral and dorsal spines merge with the thorax wall and do not form appendages. Pores on the thorax are small and tend to be more closely spaced than those on the cephalis.

**Remarks.** This species is structured similarly to *Lithomelissa dybbuki* (Pl. 19, Figs. 1–7)*,* but differs in heaving a more heavily silicified cephalis, with large pores around the base. In addition, the apical spine of *L. kaonashii* does not pass through the center of the cephalis, disqualifying it from being in *Lithomelissa*.

**Material examined.** 16 specimens from samples 321-1337A-31X-6W, 4–6cm (Middle Miocene), 321-1337D-30H-3, 103–104cm (Middle Miocene), 321-1337D-26H-3W, 142–144cm (Late Miocene), 321-1337D-23H-6, 134–137cm (Late Miocene).

**Holotype.** Pl. 34, Figs. 5A–B; sample 321-1337D-23H-6, 134–137cm; ECO-147; W22-4.

**Paratypes.** (1) Pl. 34, figs. 9A–B; sample 321-1337D-26H-3, 142–144cm; ECO-148; G8-4. (2) Pl. 34, figs. 4A–B; sample 321-1337A-31X-6, 4–6cm; ECO-151; O11-4. (3) Pl. 34, figs. 8A–B; sample 321-1337A-31X-6, 4–6cm; ECO-151; T25-1. (4) Pl. 34, fig. 7; sample 321-1337A-31X-6, 4–6cm; ECO-151; U32-2. (5) [not figured] sample 321-1337D-26H-3, 142–144cm; ECO-148; Z8-1.

**Measurements.** Cephalis height 34–41 (38)µm; cephalis width 30–40 (36)µm; neck width 25–34 (30)µm; width at shoulders 40–55 (48)µm. Based on 14 specimens.

**Etymology.** Named for the spirit Kaonashi (“No-Face”) in Hayao Miyazaki's animated film, *Spirited Away*.

**Range.** Middle—Late Miocene in the EEP, lower boundary not determined (Table 1).

### *Lophophaena laticeps* **(Jørgensen, 1905) Kurihara and Matsuoka, 2010**

Plate 23, Figs. 6A–7B.

*Lithomelissa laticeps* n. sp., Jørgensen, 1905, pl. 16, fig. 84.
*Lithomelissa laticeps* Jørgensen, Schröder, 1914, text-figs. 58–59.
*Lithomelissa laticeps* Jørgensen, Benson, 1966, pl. 24, figs. 14–15.
non *Botryopera laticeps* Jørgensen, Petrushevskaya, 1975, pl. 20, fig. 3.
*Lithomelissa laticeps* Jørgensen, Benson, 1983, pl. 9, fig. 3.
*Lophophaena laticeps* Jørgensen, Kurihara and Matsuoka, 2010, fig. 3.7.
*Lithomelissa laticeps* Jørgensen, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species was originally described under the genus *Lithomelissa*, but it does not have an apical spine passing freely through the cephalis and thus does not satisfy modern usage of this genus definition. Kurihara and Matsuoka (2010) listed this species in *Lophophaena* but did not discuss the genus transfer. We agree that this species best fits the definition of *Lophophaena* because the cephalis is relatively high with maximum width near the top, and the apical spine runs along the shell wall.

This species could be closely related to some morphotypes of *Stichopilium bicorne*, the notoriously cryptic group that is characterized by two strong spines running along opposite sides of the cephalis and has a wide variety of thorax shapes and sizes. In this paper, Plate 23, Figs. 8A–8B illustrate one such morphotype that is often identified (sometimes tentatively) as *Stichopilium bicorne* in the literature (e.g., Lazarus 1992, pl. 9, fig. 14). Comparison of this morphotype with *Lophophaena laticeps* (Pl. 23, Figs. 6A–7B) yields some striking similarities, such as the structure of the cephalis and pronounced lobe on the dorsal side of the neck area, suggesting a possible link between *Stichopilium bicorne* and the lophophaenids. However, even the most lophophaenid-like morphotype of *Stichopilium bicorne* figured in pl. 23, figs. 8A–B, differs in that it has a more reduced cephalis with relatively longer cephalic horns, lacks buttressing of the cephalic horns, and has a proportionally larger lobe in the neck region. Thus, we are not suggesting these specimens are conspecific, but rather that they could have an evolutionary relationship that justifies further study to potentially resolve this enigmatic group.

**Range.** Early Pliocene, EEP (Table 1).

### *Lophophaena? leberu* **Renaudie and Lazarus, 2012**

Plate 27, Figs. 5A–B.

*Lophophaena? leberu* n. sp., Renaudie and Lazarus, 2012, pl. 22, figs. 12A–14B.

**Remarks.** Our specimen differs slightly from the specimens figured by Renaudie and Lazarus (2012) in that the horns on the cephalis are less prominent. However, the positioning of these horns and the overall shell proportions are very similar, suggesting it is likely the same species.

**Range.** One specimen from the Early Pliocene in the EEP (Table 1). Present in the Southern Ocean from the Early–Late Miocene.

### *Lophophaena leshii* **n. sp.**

Plate 24, Figs. 3A–9.

urn:lsid:zoobank.org:pub:A9179C79-EE43-44E4-8723-919505500049
*Acanthocorys variabilis* Popofsky, 1913, text-fig. 81, non figs. 71–80.
? *Acanthocorys cf. variabilis* Popofsky, Takahashi, 1991, pl. 25, fig. 1.
*Lophophaena* cf. *buetschlii* sp. 2, Trubovitz *et al.,* 2020, supplementary data 7.

**Diagnosis.** *Lophophaena* with a very elongated cephalis that thins or is left open at the top, and a thorax only slightly wider than the cephalis with three long, conical appendages extending from the dorsal and lateral spines.

**Description.** This species has a very long and narrow cephalis, that becomes more thinly-silicified and increasingly hyaline, with fewer and smaller pores, towards the top. The apical spine runs along the wall of the cephalis, and extends upward from the inflection point where the cephalis begins to round toward the apex. The apical horn is conical and relatively thin. A short, needle-like ventral spine is present in the neck area, which is relatively compressed for a cephalis of this height. The thorax is slightly wider than the cephalis and has pores similar in size to those at the base of the cephalis. Near the top of the thorax, the lateral spines protrude as long, prominent appendages that are subhorizontal. The dorsal spine extends at a more acute downward angle, but matches the lateral spines in thickness and length.

**Remarks.** This species appears to be related to *L. buetschlii* (Haeckel) Petrushevskaya, 1971 (Pl. 24, Figs. 1A–2B) because both species have similar segment proportions, and an elongated cephalis that may be left open at the top. However, *Lophophaena leshii* n. sp. differs in that it has strong, conical thoracic appendages, usually with pointed tips, that are at least as long as the apical spine, and usually better-developed. These spines usually extend cleanly from the thorax, or with a small amount of buttressing, without the tendency to form “wings” of skeletal lattice as they often do in *L. buetschlii.* The cephalis of this species also has less variation in length than *L. buetschlii*. This species appears to have been first illustrated by Popofsky (1913) as *Acanthocorys variabilis* (text-fig. 81, non text-figs. 71–80). However, Petrushevskaya (1971) did not consider this to be part of her emended species concept of *Lophophaena variabilis*, and did not reassign Popofsky’s specimen in text-fig. 81 to a different name. It also appears that Takahashi (1991) may have illustrated this species under the name *Acanthocorys* cf. *variabilis* (Popofsky), but the image quality in that publication is too poor for us to be certain.

**Material examined.** 24 specimens observed from sample 321-1337D-23H-6, 134–137cm (Late Miocene).

**Holotype.** Pl. 24, Fig. 4; sample 321-1337D-23H-6, 134–137cm; ECO-147; D9-2.

**Paratypes.** (1) Pl. 24, figs. 3A–C; sample 321-1337D-23H-6, 134–137cm; ECO-145; H34-2. (2) Pl. 24, figs. 5A–B; sample 321-1337D-23H-6, 134–137cm; ECO-147; K27-2. (3) Pl. 24, figs. 7A-B; sample 321-1337D-23H-6, 134–137cm; ECO-145; H5-4. (4) Pl. 24, fig. 8; sample 321-1337D-23H-6, 134–137cm; ECO-145; L7-3. (5) Pl. 24, fig. 9; sample 321-1337D-23H-6, 134–137cm; ECO-145; P15-2. (6) Pl. 24, figs. 6A–B; sample 321-1337D-23H-6, 134–137cm; ECO-145; O14-4. (7) [not figured] sample 321-1337D-23H-6, 134–137cm; ECO-146; Q37-1. (8) [not figured] sample 321-1337D-23H-6, 134–137cm; ECO-146; J9-3.

**Measurements.** Cephalis height 47–56 (51)µm; cephalis width at its center 22–27 (25)µm; width at shoulder area at top of thorax 30–40 (33)µm; length that lateral/dorsal spines protrude from the thorax 23–41 (32)µm. Based on 13 specimens.

**Etymology.** Named for the forest spirit of Slavic folklore, the Leshi.

**Range.** Late Miocene in the EEP (Table 1).

### *Lophophaena macrencephala* **Clark and Campbell, 1945 partim.**

Plate 21, Figs. 7A–8B.

*Lophophaena macrencephala* n. sp., Clark and Campbell, 1945, pl. 7, figs. 6 and 9 (non figs. 7 and 8).
non *Lophophaena* sp. B, Petrushevskaya, 1971, pl. 56, figs. 1–3.
non *Lophophaena macrencephala* Clark and Campbell, Dzinoridze *et al.,* 1978, pl. 29, fig. 20; pl. 32, fig. 36.
non *Lophophaena macrencephala* Clark and Campbell, Petrushevskaya and Kozlova, 1979, figs. 348–349.
*Lophophaena macrencephala?*, Renaudie, 2014, pl. 23, fig. 5.
*Lophophaena macrencephala*? Clark and Campbell, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** There is a good deal of confusion regarding this species, and poor documentation in the literature. Clark and Campbell (1945) listed this species under the generic name *Lophophaena*, and the subgeneric name *Lophophaenula*. Because Campbell (1954) later synonymized the subgenus *Lophophaenula* under the genus *Lophophaena*, we drop the subgenus designation from the name. Clark and Campbell (1945) illustrated four specimens to accompany their species description. It is our opinion that at least two different species are included in these illustrations (pl. 7, figs. 6–9 in Clark and Campbell, 1945). Specimens 6 and 9 have a globular cephalis, slightly wider than the shoulder area of the thorax. However, specimens 7 and 8 have a relatively small, thumb-shaped cephalis, that is slightly narrower than the shoulders of the thorax. Specimen 7 also exhibits some cephalic pores more than twice the diameter of any pores on the other specimens. All specimens display a variable number of cephalic horns, and are broken in a way that does not show the full thorax. In their species description, Clark and Campbell (1945) note: "The 4 shells which we illustrate and assign to the present species may not all belong together. They have in common the swollen cephalis subequal in size, and very nearly in shape, but the horns are different. One of them (fig. 9) has no horns at all, while the others have one (fig. 8) or more (figs. 6–7). The last are considered to be typical of the species." Although we disagree with Clark and Campbell (1945) that all the shells exhibit a "swollen" cephalis and are similar in shape or size, we do agree that these four specimens do not belong to the same species. Specifically, the specimens considered "typical" by Clark and Campbell (figs. 6 and 7) are in our opinion almost certainly different species. Furthermore, the presence of multiple spines on the cephalis alone is not a sufficient reason to group the specimens in fig. 6 and fig. 7. Petrushevskaya and Kozlova (1979)'s concept of *L. macrencephala* includes Clark and Campbell (1945)'s figs. 7–8, but excludes figs. 6 and 9. Petrushevskaya and Kozlova (1979) consider this species to be similar to *L. apiculata* (= *L. galeaorci*), but is overall smaller in size. The specimens questionably assigned to *Lophophaena macrencephala* in Trubovitz *et al.* (2020) are most similar to Clark and Campbell (1945)'s illustrated specimens in figs. 6 and 9, in terms of segment proportions and pore size. Clark and Campbell's fig. 6 and fig. 9 appear to most closely match their own description of the species, as these could be described as having a "globular" or "swollen" cephalis. The specimens in figs 7–8 appear to belong to two different species due to the different pores sizes on the cephalis and the size of the cephalis itself, and so we do not follow Petrushevskaya and Kozlova (1979)'s revision of the species concept. As they also listed Petrushevskaya (1971)'s *Lophophaena* sp. B in their synonymy, we examined this specimen and concluded that it does not fit our concept of *L. macrencephala*. Instead, we adopt Clark and Campbell's fig. 6 and fig. 9 as the concept for *Lophophaena macrencephala.* In addition to some of the type specimens, our illustrations here and in Trubovitz *et al.* (2020), Renaudie (2014) also illustrated a similar specimen as *Lophophaena macrencephala?* (pl. 23, fig. 5 in Renaudie, 2014) that could be conspecific with ours, and our accepted part of Campbell and Clark (1945)'s concept. To fully resolve this concept however, the original type material will need to be examined, which is beyond the scope of this project.

**Range.** Late Miocene, EEP (Table 1).

### *Lophophaena nadezdae* **Petrushevskaya, 1971**

Plate 23, Figs 1A–2C.

*Lithomelissa* cf. *galeata* Ehrenberg, Benson, 1966, pl. 24, figs. 16–17 (non fig. 18).
*Lophophaena nadezdae* n. sp., Petrushevskaya, 1971, pl. 60, figs. 1–4.
*Lophophaena variabilis* Popofsky, Van de Paverd, 1995, pl. 65, figs. 5–6, 11.
*Lophophaena buetschlii* Haeckel, Van de Paverd, 1995, pl. 65, figs. 3–4 (non fig. 10).
*Lophophaena nadezdae* Petrushevskaya, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** Despite its abundance in our samples, this species is not commonly cited in the literature. Following Petrushevskaya (1971), we consider this species to have an elongated spiny cephalis with indistinct neck area, and a broad thorax (~2x the cephalis width) with numerous ribs and extended spines. Illustrations published under the names *Lithomelissa* cf. *galeata* Ehrenberg (Benson, 1966), *Lophophaena variabilis* Popofsky (Van de Paverd, 1995), and *Lophophaena buetschlii* Haeckel (Van de Paverd, 1995) best fit the description of *Lophophaena nadezdae* in our opinion, so these specimens are included in our synonymy.

**Range.** Late Miocene—Recent, EEP (Table 1).

### *Lophophaena rhopalica* **Renaudie and Lazarus, 2016**

Plate 25, Figs. 1A–4.

*Lophophaena rhopalica* n. sp., Renaudie and Lazarus, 2016, pl. 7, figs. 2, 5–6, ?fig. 8, non fig. 9.
unknown plagonid group C sp 68, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** Specimens observed in the EEP are within the range of those figured by Renaudie and Lazarus (2016) from the Southern Ocean. The authors of the species included two questionable identifications; one of which (fig. 9) we do not believe is within the range of this species, but it may be an aberrant specimen.

**Range.** Middle—Late Miocene in the EEP, but lower limit not determined with certainty (Table 1). In the SO, this species was reported by Renaudie and Lazarus (2016) as rare in the Early Miocene, with one possible occurrence in the Middle Miocene.

### *Lophophaena rusalkae* **n. sp.**

Plate 29, Figs. 1A–6.

urn:lsid:zoobank.org:act:ABD2BBA6-AD2F-4F87-BFE1-2489F79257E8
unknown plagonid group C sp 51, Trubovitz *et al.,* 2020, supplementary data 7.
unknown plagonid group C sp 53 cf, Trubovitz *et al.,* 2020, supplementary data 7.

**Diagnosis.** A small *Lophophaena* with many thin spines on the thumb-shaped cephalis, and a thorax with distinct shoulders that tapers toward the base.

**Description.** This species has a small, thumb-shaped cephalis that has many thin spines extending from the sides and top. The apical spine is embedded in the cephalis wall and is diminished to the point of being difficult to detect. The thorax is slightly wider than the cephalis, and reaches its widest point at the shoulders, where more thin spines extend downward. Pores on the cephalis and thorax are the same size, shape, and density. Both the cephalis and thorax show approximately the same degree of silicification. When the full skeleton is preserved, the thorax has a smooth termination at its base.

**Remarks.** This species differs from *Botryopera babayagae* n. sp. (Pl. 9, Figs. 1A–8) in that it has thin conical spines on top of the cephalis, and a longer, more narrow neck area. It differs from *Lophophaena cylindrica* (Pl. 22, Figs. 1A–4) and *Lophophaena hispida* (Pl. 22, Figs. 5–8B) in that it has a smaller, more thumb-shaped cephalis, with less of a constriction at the neck. It differs from *Lophophaena nadezdae* (Pl. 23, Figs. 1A–2C) in that it has fewer spines, and the cephalis is smaller, and more rounded at the top. The top of the cephalis is never open, differentiating this species from *Lophophaena variabilis* (Pl. 22, Figs. 9A–11C) and *Lophophaena buetschlii* (Pl. 24, Figs. 1A–2B). This species has similar overall structure to *Lophophaena casperi* n. sp. (Pl. 28, Figs. 1A–9B.)*,* but differs in its smaller size and cephalis shape (Figure 12).

**Material examined.** 33 specimens observed from samples 321-1337D-23H-6, 134–137cm (Late Miocene), 321-1337A-18H-6, 77–80cm (Late Miocene), 321-1337A-14H-7, 39–42cm (Late Miocene), 321-1337A-12H-5, 23–26cm (Late Miocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), and 321-1337A-6H-3, 29–32cm (Late Pliocene).

**Holotype.** Pl. 29, Fig. 4; sample 321-1337A-14H-7, 39–42cm; ECO-138; N20-4.

**Paratypes.** (1) Pl. 29, figs. 5A–B; sample 321-1337A-12H-5, 23–26cm; ECO-136; X10-2. (2) Pl. 29, figs. 2A–B; sample 321-1337A-14H-7, 39–42cm; ECO-140; Z14-2. (3) Pl. 29, figs. 1A–B; sample 321-1337A-14H-7, 39–42cm; ECO-139; Y39-3. (4) Pl. 29, figs. 2A–B; sample 321-1337A-14H-7, 39–42cm; ECO-139; X7-2. (5)

Pl. 29, fig. 3; sample 321-1337A-12H-5, 23–26cm; ECO-136; Z5-4. (6) Pl. 29, fig. 6; sample 321-1337A-14H-7, 39–42cm; ECO-139; O25-3. (7) [not figured] sample 321-1337A-14H-7, 39–42cm; ECO-138; C25-4.

**Measurements.** Cephalis height 34–40 (37)µm; cephalis width 25–32 (28)µm; width at neck 25–31 (28)µm; width at shoulders 36–44 (41)µm. Based on 10 specimens.

**Etymology.** Named for the malicious female water spirit in Russian folklore, the rusalka.

**Range.** Late Miocene—Pliocene, in the EEP (Table 1).

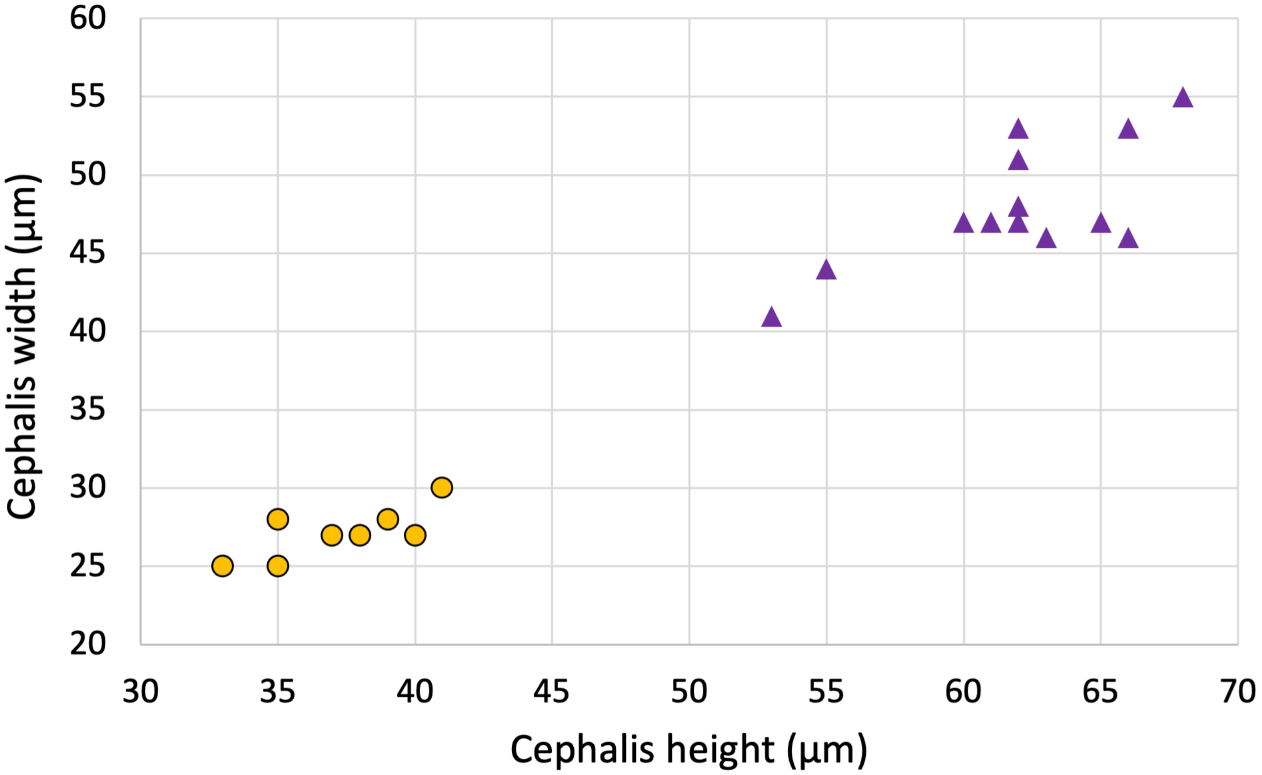

**FIGURE 14.** Chart illustrating the different cephalis sizes in *Lophophaena shishigae* n. sp. and *Arachnocorys jorogumoae* n. sp. The yellow circles indicate *L. shishigae*, with a small cephalis, and the purple triangles represent *A. jorogumoae*, with a significantly larger and proportionally higher cephalis.

### *Lophophaena shishigae* **n. sp.**

Plate 35, Figs. 1–6B.

urn:lsid:zoobank.org:act:A289D1AC-8B84-406E-B5E7-C6CF4358263F
unknown plagonid group C sp 17 (partim.), Trubovitz *et al.,* 2020, supplementary data 7.

**Diagnosis.** *Lophophaena* with a small, balloon-shaped cephalis that has numerous conical spines, and a flared conical thorax that has multiple strong ribs.

**Description.** The cephalis of this species is narrow at its base and reaches its widest point about ⅔ of the way up, giving it a balloon-like shape. There are many conical spines protruding from the cephalis, one of which is the apical spine, though it is not differentiated from the others. The small pores on the cephalis are about the same size, shape, and density as those on the thorax. The thorax extends down from the neck constriction in a roughly conical shape, flaring outward to varying degrees among specimens. The thorax has multiple strong ribs, and may become hyaline toward the base in some individuals (i.e., fig. 2).

**Remarks.** This species is similar to *Lophophaena variabilis* (Pl. 22, Figs. 9A–11C), except that the cephalis is always heavily-silicified, rounded, and closed at the top. It reaches its widest point about 2/3 up from the base of the cephalis. On the thorax, the numerous spines have a tendency to form long ribs, rather than protruding through the thorax wall as they commonly do in *L. variabilis*. It differs from *L. casperi* (Pl. 28, Figs. 1A–9B) in that the cephalis is relatively narrower, particularly at its widest point, and the thorax flares outward in a roughly conical shape, rather than expressing sharp shoulders before tapering inward toward the base. The more widely flared thorax, strong ribs, and more balloon-shaped cephalis also distinguish this species from *L. rusalkae* n. sp. (Pl. 29, Figs. 1A–6). This species differs from *Arachnocorys jorogumoae* n. sp. (Pl. 4, Figs. 1A–11) in that it is consistently much smaller in size, has relatively smaller pores, and does not have dendritic spines on the cephalis.

**Material examined.** 14 specimens observed from Late Miocene samples 321-1337D-23H-6, 134–137cm and 321-1337A-21H-1, 33–35cm.

**Holotype.** Pl. 35, Fig. 1; sample 321-1337D-23H-6, 134–137cm; ECO-146; W4-2.

**Paratypes.** (1) Pl. 35, figs. 2A–B; sample 321-1337D-23H-6, 134–137cm; ECO-146; W37-1. (2) Pl. 35, fig. 3; sample 321-1337A-21H-1, 33–35cm; ECO-144; V2-2. (3) Pl. 35, fig. 4; sample 321-1337D-23H-6, 134–137cm; ECO-147; W30-4. (4) Pl. 35, fig. 5; sample 321-1337D-23H-6, 134–137cm; ECO-146; Y6-1. (5) Pl. 35, figs. 6A–B; sample 321-1337D-23H-6, 134–137cm; ECO-146; A34-4.

**Measurements.** Cephalis height 33–41 (37)µm; cephalis width 25–30 (27)µm; width at neck 19–25 (23)µm; width at shoulders 39–68 (51)µm. Based on 8 specimens.

**Etymology.** Named for Shishiga, the troublesome female swamp creature in Russian mythology.

**Range.** Late Miocene in the EEP, range not well constrained (Table 1).

### *Lophophaena simplex* **Funakawa, 1994**

Plate 33, Figs. 8A–9B.

*Lophophaena simplex* n. sp., Funakawa, 1994, pl. 8, figs. 1a–2c.

**Remarks.** *Lophophaena simplex* is described by Funakawa (1994) as having short spines on the cephalis unrelated to the apical and ventral spines, which are relatively weak. It has irregularly spaced pores and thoracic ribs that terminate as teeth. These characteristics were certainly true of the specimens we observed in the EEP. However, Funakawa (1994) also notes that some specimens showed an axobate (termed "axial projection"). This character was not clearly visible in the author's published illustrations, and did not appear to be present on the two specimens we observed in the EEP (although it could have been broken off). Additional documentation will help clarify this species concept.

**Range.** Two specimens observed from the Middle Miocene, EEP (Table 1). Funakawa (1994) described this species from Upper Miocene sediments on the east coast of Hokkaido, Japan.

### *Lophophaena undulatum* **(Popofsky, 1913) n. comb.**

Plate 21, Figs. 4–5.

*Artopilium undulatum* n. sp., Popofsky, 1913, pl. 36, figs. 4–5.
*Artopilium undulatum* Popofsky, Benson, 1966, pl. 36, figs. 1–2.
*Artopilium undulatum* Popofsky, Renz, 1974, pl. 16, fig. 14.
*Lophocorys undulata* (Popofsky), Takahashi, 1991, pl. 40, figs. 9–10.
*Peromelissa undulata* (Popofsky), Van de Paverd, 1995, pl. 71, figs. 12–13.
*Lophophaena undulatum* (Popofsky), Renaudie, 2014, pl. 27, fig. 13.
*Artopilium undulatum* Popofsky, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** It is not entirely clear which genus this species should belong to, but it is included here in *Lophophaena* because it fits the basic genus definition, has been considered a lophophaenid by some authors, and because it has morphological similarities to many of the other *Lophophaena* species we encountered during this study. In the original illustration by Popofsky (1913), the spine that runs vertically alongside and extends upward from the cephalis is labelled the ventral spine, while the horizontally-oriented spine at the base of the cephalis is labelled the apical spine. It is our suspicion that the names of these two spines may be reversed, but since Popofsky's type material is not available for inspection, it is not possible to draw this conclusion with absolute certainty. If the upward-trending spine is indeed the apical spine, this species would fit the definition of *Lophophaena*. However, if the apical spine is truly a horizontal spine in the neck area, this would be a characteristic unique among the lophophaenids and indeed suggest that this species belongs in a different family. This species was originally described as a theoperid (genus: *Artopilium*) by Popofsky (1913), and many subsequent authors have upheld this designation. Takahashi (1991) states that *Artopilium* is a junior objective synonym of *Triacarthus*, and that this species, *undulata,* does not appear to be similar to the type species of that genus, *Artopilium elegans*. Takahashi therefore tentatively placed this species in the genus *Lophocorys*. The species was later moved to the genus *Peromelissa* by Van de Paverd (1995), but no discussion was provided to justify this. Here we follow the most recent genus designation of Renaudie 2014, and formally place the species in *Lophophaena*. In our opinion, this is the best genus for the species, provided that our interpretation of Popofsky's illustration is correct.

**Range.** Late Miocene—Recent in the EEP. Lower limit not determined. See Table 1.

### *Lophophaena ushionii* **n. sp.**

Plate 31, Figs. 7A–11B.

urn:lsid:zoobank.org:act:563EAE81-E06C-40F6-B180-33517AB17AB3
unknown plagonid group C sp 32 cf, partim., Trubovitz *et al.,* 2020, supplementary data 7.

**Diagnosis.** *Lophophaena* with a large cephalis that has two prominent bladed horns on the dorsal and ventral sides, and a third, often smaller horn that forms between them on the apex of the cephalis.

**Description.** This species has a large cephalis that is distinct for its two strong bladed horns that protrude from the widest part of the cephalis at approximately 45-degree angles. The horn on the dorsal side is an extension of the apical spine, and the other is not related to any of the primary spines, but sits just above the short and thin ventral spine. In one specimen we observed, the horn extending from the apical spine was strongly forked (fig. 11), but since few specimens were documented it is not clear how common this is. The thorax is approximately 1.5x as wide as the cephalis, and has extensions of the dorsal and lateral spines that form short appendages. Pores on the thorax are slightly larger than those on the cephalis.

**Remarks.** This species resembles *Lophophaena gozui* n. sp. (Pl. 31, Figs. 1A–6) except that the cephalis is much larger, has three horns rather than two, and the thorax is relatively more narrow compared to the width of the cephalis (Figure 13). In *L. gozui,* the average ratio of thorax:cephalis width is 2.52; for *L. ushionii*, this ratio averages 1.46. A chart showing the differences in cephalis dimensions is included above in the description of *L. gozui*. Another difference between these two species is that *L. ushionii* has short appendages on the thorax front he dorsal and lateral spines, whereas in *L. gozui* these primary spines join the wall of the thorax.

**Material examined.** 10 specimens observed from samples 321-1337A-31X-6W, 4–6cm (Middle Miocene) and 321-1337D-26H-3W, 142–144cm (Late Miocene).

**Holotype.** Pl. 31, Figs. 7A–B; sample 321-1337A-31X-6, 4–6cm; ECO-151; T6-1.

**Paratypes.** (1) Pl. 31, fig. 10; sample 321-1337A-31X-6, 4–6cm; ECO-151; O40-3. (2) [not figured] sample 321-1337A-31X-6, 4–6cm; ECO-151; U26-4.

**Measurements.** Cephalis height 49–60 (54)μm; cephalis width 40–52 (46)μm; thorax width 50–75 (65)μm; ratio of thorax:cephalis width 1.3–1.6 (1.5). Based on 9 specimens. Note: thorax width should be considered the minimum width, as the thorax is typically not fully preserved.

**Etymology.** Named for the Japanese yokai, ushi oni, which comes from the sea and has the head of an ox.

**Range.** Middle—Late Miocene, lower boundary not determined (Table 1).

### *Lophophaena variabilis* **(Popofsky, 1913) Petrushevskaya, 1971**

Plate 22, Figs. 9A–11C.

*Acanthocorys variabilis* n. sp., Popofsky, 1913, p. 360–364, text-figs. 71–72, 79 (non text-figs. 74–78, 80, 81).
? *Lithomelissa* cf. *galeata* Ehrenberg, Benson, 1966, pl. 24, fig. 18 (non figs. 16–17).
*Lophophaena* variabilis Popofsky, Petrushevskaya, 1971, pl. 57, figs. 2–3; pl. 59, figs. 5–6.
non *Acanthocorys* cf. *variabilis* Popofsky, Takahashi, 1991, pl. 25, fig. 1.
non *Lophophaena variabilis* Popofsky, Van de Paverd, 1995, pl. 65, figs. 5–6, 11.
*Lophophaena* cf. *buetschlii* (Haeckel) Petrushevskaya, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** The basionym of this species is *Acanthocorys variabilis* (Popofsky, 1913), but it was later emended to a narrower concept and placed in *Lophophaena* by Petrushevskaya (1971). Herein we follow Petrushevskaya's

(1971) concept of *Lophophaena variabilis*, although not all other authors have done this, some retaining Popofsky's broader species concept.

**Range.** Late Pleistocene—Recent, EEP (Table 1).

### *Lophophaena witjazii* **(Petrushevskaya, 1971) n. comb.**

Plate 25, Figs. 5A–B.

*Lophophaena* cf. *capito* Ehrenberg, Benson, 1966, pl. 24, figs. 22–23, pl. 25, fig. 1.
*Lophophaenoma witjazii* n. sp., Petrushevskaya, 1971, pl. 62, figs. 3–7.
*Lithomelissa horrida* (Popofsky), Petrushevskaya, 1971, pl. 57, fig. 8.
*Lophophaenoma witjazii* Petrushevskaya, Poluzzi, 1982, pl. 22, figs. 1–3.
*Lithomelissa* sp. A, Nishimura, 1990, figs. 14.6–8, 15.1–4c.
*Lophophaena witjazii* Petrushevskaya, Van de Paverd, 1995, pl. 66, figs. 1–3, 5a–b.
*Lophophaenoma witjazii* Petrushevskaya, Chen and Tan, 1996, pl. 30, figs. 7–10, pl. 51, figs. 8–9.
*Lophophaenoma witjazii* Petrushevskaya, Tan and Su, 2003, pl. 5, fig. 14; pl. 17, figs. 5–6; pl. 21, fig. 12.
*Lophophaena witjazii* Petrushevskaya, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** Generic names for this species have been used inconsistently in the literature. The basionym of this species is *Lophophaenoma witjazii* (Petrushevskaya, 1971), but Petrushevskaya (1981) later determined this genus to be a junior subjective synonym of *Arachnocorys*. She also noted that some of the species formerly placed in *Lophophaenoma* should actually belong to *Lophophaena* and *Peromelissa* rather than *Arachnocorys*. However, Petrushevskaya did not officially transfer *L. witjazii* to *Arachnocorys*, *Lophophaena,* or *Peromelissa*. Van de Paverd (1995) listed this species as *Lophophaena witjazii*, as did Renaudie and Lazarus (2016). We follow these authors' precedent here, because this species fits the criteria for *Lophophaena* better than any other lophophaenid genera we are aware of. The specimen illustrated by Petrushevskaya (1971) as *Lithomelissa horrida* (Popofsky) is included in our synonymy because we consider it a better match for *L. witjazii* due to its lack of pronounced feet. Van de Paverd (1995) also included this specimen in his synonymy for *L. witjazii*.

**Range.** Late Miocene—Recent, EEP (Table 1).

### *Lophophaena* **sp. cf.** *L. witjazii*

Plate 25, Figs. 6–8D.

*Lophophaena witjazii* cf sp 2, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species is similar to *Lophophaena witjazii* (Pl. 25, Figs. 5A–B), except that cephalis is more elongated, with a more distinct neck, less robust spines, and better-defined thorax shape. Pores tend to be smaller throughout cephalis and thorax. It differs from *Lophophaena arie* n. sp. (Pl. 26, Figs. 1A–6, ?7A–C) in that it has a crown of spines around the top third of the cephalis. The cephalic spines are smaller than on *L. witjazii*, but future work may show that this is a subspecies of *L. witjazii* if intermediate forms are discovered.

**Material examined:** 8 specimens observed from samples 321-1337A-16H-6, 121–124cm (Late Miocene), 321-1337A-14H-7, 39–42cm (Late Miocene), 321-1337A-4H-6, 115–118cm (Early Pleistocene), 321-1337A-3H-2, 103–106cm (Middle Pleistocene), 321-1337A-2H-3, 76–79cm (Late Pleistocene), and 321-1337D-1H-1, 0–3cm (Recent).

**Range.** Late Miocene—Recent EEP (Table 1).

### *Lophophaena* **sp. cf.** *Trisulcus testudus* **Petrushevskaya, 1971 group**

Plate 36, Figs. 5A–7B.

? *Trisulcus testudus* n. sp., Petrushevskaya, 1971, pl. 72, figs. 1–3.
unknown plagonid group C sp 65, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** The specimens we illustrate here resemble a species described by Petrushevskaya (1971), *Trisulcus testudus*. We believe our specimens may belong to two separate species, but it is unclear which of these, if either, fit Petrushevskaya's concept, due to her somewhat ambiguous illustrations (pl. 72, figs. 1–3) and no designation of a type specimen. Regardless, we suspect that *Trisulcus testudus* Petrushevskaya may fit the definition of *Lophophaena* better than *Trisulcus*, due to the proportions and characteristics of the cephalis and thorax. Here we call our specimens *Trisulcus testudus?* (group) to convey their similarity to Petrushevskaya's species, but also to indicate that there are multiple forms which may justify separate species after more specimens can be studied.

**Range.** Three specimens from Latest Pliocene—Recent, EEP (Table 1).

*Lophophaena* **sp. A**
Plate 36, Figs. 1A–2B.

*Lophophaenoma* sp., Petrushevskaya, 1971, pl. 57, fig. 7.
non *Lophophaena triangula* n. sp., Funakawa, 1994, p. 466, 468; pl. 8, figs. 31–4b.
unknown plagonid group C sp 75, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** The specimens we observed in the EEP closely resemble the specimen illustrated as *Lophophaenoma* sp. by Petrushevskaya (1971). Funakawa (1994) questionably synonymized Petrushevskaya's specimen with a new species, *Lophophaena triangula*. However, it is our opinion that the specimens figured by Funakawa differ in cephalis shape and overall size from Petrushevskaya's *Lophophaenoma* sp. specimen. Therefore, we suggest that our two specimens are conspecific with Petrushevskaya's *Lophophaenoma* sp., but none of these are the same as *Lophophaena triangula* Funakawa. This species was extremely rare in our material, so unfortunately we are not able to provide a formal description here (only two specimens were observed). As we do not accept *Lophophaenoma* as a valid genus, *Lophophaena* is used instead. However, the strong bladed feet on this species is not typical of *Lophophaena*, so future study of more complete specimens may yield a more appropriate genus assignment.

**Material examined.** 2 specimens observed from sample 321-1337A-2H-3, 76–79cm (Late Pleistocene).

**Range.** Late Pleistocene in the EEP, see Table 1.

*Lophophaena* **sp. B**
Plate 36, Figs. 3A–4B.

unknown plagonid group C sp 21, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species is distinct for its flat-topped cephalis, with irregular pore shapes and sizes. However, with only two specimens observed, we cannot formally describe it here.

**Material examined.** 2 specimens from Late Miocene samples 321-1337D-23H-6, 134–137cm and 321-1337A-12H-5, 23–26cm.

**Range.** Late Miocene, in the EEP (Table 1).

*Lophophaena***? sp. C**
Plate 23, Figs. 3A–5B.

unknown plagonid group C sp 5, Trubovitz *et al.*, 2020, supplementary data 7.

**Remarks.** This species has a pointed cephalis with at least one spine protruding from the top. Other, smaller spines are occasionally preserved on sides of cephalis. This species resembles *L. nadezdae* Petrushevskaya (Pl. 23, Figs. 1A–2C) except that the cephalis comes to a point at the top rather than flattening into a rectangular shape. It also differs from *L. nadezdae* and the other species in this genus in that it has a discernable axobate. Only one specimen had this character well-preserved, but some of the others hint at a broken-off axobate that was not preserved. This species has some morphological similarities to the genus *Antarctissa*, so the genus assignment to *Lophophaena* is tentative.

**Material examined.** 7 specimens from samples 321-1337A-12H-5, 23–26cm (Late Miocene), 321-1337A-10H-2, 91–94cm (Early Pliocene), 321-1337A-6H-3, 29–32cm (Late Pliocene), 321-1337A-5H-5, 11–14cm (Late Pliocene), 321-1337A-4H-2, 16–19cm (Middle Pleistocene), 321-1337A-3H-2, 103–106cm (Middle Pleistocene), and 321-1337A-2H-3, 76–79cm (Late Pleistocene).

**Range.** Late Miocene—Pleistocene, EEP (Table 1).

*Lophophaena* **sp. E group**
Plate 37, Figs. 1A–3C.

**Remarks.** These three specimens almost certainly belong to different species, but as we only observed three specimens with this very distinct morphology we are placing them together in one group until more specimens are found. All three have an unusually short and widely-flared thorax with teeth, and a proportionally large cephalis. This overall morphology is similar to a specimen figured by Popofsky (1913) as *Lampromitra circumtexta*, Popofsky, 1913, pl. 32, fig. 1, text-fig. 53. However, none of our specimens appear to be conspecific with Popofsky's. One specimen observed from sample 6H3, 31–32cm (Pliocene) differs from Popofsky's illustrated specimen in that pores on the thorax decrease significantly in size before the segment terminates in several prominent teeth. Our specimen also may have more pronounced shoulder humps, though it is difficult to tell whether this character was present on Popofsky's specimen due to the nature of the illustration. The overall morphology, shape of the cephalis, and size dimensions are very similar to Popofsky's specimen, however. A much smaller specimen was found in our Pleistocene EEP sample (3H2, 103–106cm). It shares several characteristics with our Pliocene specimen, including a large, thorny cephalis with a short, wide thorax that terminates in multiple long teeth, which is a highly unusual morphology for lophophaenids. A third specimen with similar characteristics to our other two was observed in sample 10H2, 91–93cm, although we do not consider any of them to be conspecific. Until additional material is studied, we include them here as a loose species group.

**Material examined.** 3 specimens form samples 321-1337A-10H-2, 91–94cm (Early Pliocene), 321-1337A-6H-3, 29–32cm (Late Pliocene), and 321-1337A-3H-2, 103–106cm (Middle Pleistocene).

**Range.** Pliocene– Pleistocene, EEP (Table 1). Range and morphological concept is not well constrained.

*Lophophaena* **sp. F**
Plate 38, Figs. 1A–2B.

unknown plagonid group C sp 29, Trubovitz *et al.* 2020, supplementary data 7.

**Remarks.** This species is notable for its smooth, thumb-shaped cephalis, with relatively large pores and no prominent spines. The thorax is wider than cephalis, and no thoracic spines are present. Due to a lack of characters, this species is difficult to distinguish from broken specimens of similar taxa that do have numerous spines, such as *Lophophaena nadezdae* (Pl. 23, Figs. 1A–2C).

**Material examined.** Over 300 specimens observed from samples 321-1337A-12H-5, 23–26cm (Late Miocene), 321-1337A-10H-2, 91–94cm (Early Pliocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), 321-1337A-6H-3, 29–32cm (Late Pliocene), 321-1337A-5H-5, 11–14cm (Late Pliocene), 321-1337A-4H-6, 115–118cm (Early Pleistocene), 321-1337A-4H-2, 16–19cm (Middle Pleistocene), 321-1337A-3H-2, 103–106cm (Middle Pleistocene), 321-1337A-2H-3, 76–79cm (Late Pleistocene), and 321-1337D-1H-1, 0–3cm (Recent).

**Range.** Latest Miocene—Recent, EEP (Table 1).

*Lophophaena* **sp. G**
Plate 30, Figs. 8A–9B.

unknown plagonid group C sp 44, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species has a thumb-shaped cephalis, with two strong spines. Pores around the base of cephalis are larger than any of its other pores.

**Material examined.** 11 specimens observed from samples 321-1337A-7H-6, 104–107cm (Early Pliocene), 321-1337A-6H-3, 29–32cm (Late Pliocene), 321-1337A-5H-5, 11–14cm (Late Pliocene), 321-1337A-4H-2, 16–19cm (Middle Pleistocene), 321-1337A-3H-2, 103–106cm (Middle Pleistocene), and 321-1337A-2H-3, 76–79cm (Late Pleistocene).

**Range.** Early Pliocene—Late Pleistocene, EEP (Table 1).

### *Lophophaena* **sp. H**

Plate 35, Figs. 7A–10B.

unknown plagonid group C sp 50, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species is large, and has many strong cephalic spines, differentiating it from *Lophophaena gozui* n. sp. (pl. 31, figs. 1A–6), which only has two spines. The thorax of this species is very thorny around the shoulder area and about three times as broad as the cephalis.

**Material examined.** 5 specimens observed from samples 321-1337A-14H-7, 39–42cm (Late Miocene), 321-1337A-12H-5, 23–26cm (Late Miocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), and 321-1337A-5H-5, 11–14cm (Late Pliocene),

**Range.** Upper Late Miocene—Latest Pliocene, EEP (Table 1).

### *Lophophaena* **sp. I**

Plate 19, Figs. 8A–10.

unknown plagonid group C sp 55, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species has a large, bulbous cephalis, that has very small pores and no spines beyond a muted apical spine. It has a distinctive, strongly-shouldered thorax with small appendages extending from the dorsal and lateral spines, with a bulging area between them. This species differs from *Amphiplecta jorogumoae* n. sp. (pl. 4, figs. 1A–11) in that the cephalis is rounded and smooth at the top rather than flat with a crown of short spines.

**Material examined.** 17 specimens observed from samples 321-1337A-16H-6, 121–124cm (Late Miocene), 321-1337A-14H-7, 39–42cm (Late Miocene), 321-1337A-12H-5, 23–26cm (Late Miocene), 321-1337A-10H-2, 91–94cm (Early Pliocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), 321-1337A-6H-3, 29–32cm (Late Pliocene), 321-1337A-5H-5, 11–14cm (Late Pliocene), and 321-1337A-4H-2, 16–19cm (Middle Pleistocene).

**Range.** Upper Late Miocene—Pleistocene, EEP (Table 1).

### *Lophophaena* **sp. J**

Plate 37, Figs. 4A–6B.

unknown plagonid group C sp 61, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species has a long cephalis, that is widest near the top and narrowest at the bottom. Pores decrease in size dramatically from the bottom to top of the cephalis. On the thorax, the dorsal and lateral spines form short and strong appendages that are approximately horizontal.

**Material examined.** 13 specimens observed from samples 321-1337A-18H-6, 77–80cm (Late Miocene), 321-1337A-16H-6, 121–124cm (Late Miocene), 321-1337A-14H-7, 39–42cm (Late Miocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), and 321-1337A-5H-5, 11–14cm (Late Pliocene).

**Range.** Late Miocene—Late Pliocene, EEP (Table 1).

*Lophophaena* **sp. L**
Plate 29, Figs. 7A–8D.

unknown plagonid group C sp 71, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species has a large hump on the upper part of the thorax, and relatively large AL arches. The cephalis is somewhat rectangular in shape, with flattened sides and a point at the apex. Pores on the thorax can be slightly irregular in size and shape. This species differs from *Lophophaena nadezdae* (Pl. 23, Figs. 1A–2C) in that it lacks spines on the thorax, other than the lateral and dorsal spines, and has a relatively broader cephalis.

**Material examined.** 4 specimens observed from samples 321-1337D-23H-6, 134–137cm (Late Miocene), 321-1337A-10H-2, 91–94cm (Early Pliocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), and 321-1337A-4H-6, 115–118cm (Late Pleistocene).

**Range.** Late Miocene—Late Pleistocene, EEP (Table 1).

*Lophophaena* **sp. M**
Plate 21, Figs. 6A–C.

**Remarks.** Only a single specimen of this unusual species was observed in our material, but it was so distinct that we chose to illustrate it here for completeness. The shape of the cephalis and bulge at the neck area closely resemble the structure of *Lophophaena amictoria* (Pl. 21, Figs. 1A–3B), but this species has an undulating thorax with much stronger feet and is more than twice its size. The curved, billowing nature of the thorax is similar to *Lophophaena undulatum* (Pl. 21, Figs. 4–5), but this species differs in its significantly larger size, larger and better developed cephalis, and more elongated neck area with prominent bulge on the dorsal side. *L. undulatum* also lacks the feet of *Lophophaena* sp. M and *L. amictoria*, although some specimens do develop long ribs from the dorsal and lateral spines that run partway down the thorax. This species appears to be distinct yet have some relationship to the previously-mentioned lophophaenid taxa; more material must be examined before it can be formally described.

**Material examined.** 1 specimen from sample 321-1337D-23H-6, 134–137cm (Late Miocene).

**Range.** Late Miocene in the EEP (Table 1).

*Lophophaena* **sp. N**
Plate 28, Figs. 9A–B.

**Remarks.** This species has a relatively narrow, thumb-shaped cephalis with at least four bladed, triangular horns near the apex of the cephalis. None of these horns appear to be related to the apical spine. The thorax is broad, and there is some indication of an axobate, though it is not fully preserved. This species differs from *Antarctissa evanida* Renaudie and Lazarus, 2013a in that the thorax does not flare outward as widely. Only one specimen was observed in our material, so more individuals will need to be examined to confirm the genus assignment and give this species a formal description.

**Material examined.** 1 specimen observed from sample 321-1337A-10H-2, 91–94cm (Early Pliocene).

**Range.** Early Pliocene, EEP (Table 1).

*Lophophaena* **sp. O**
Plate 27, Figs. 6A–7B.

*Lophophaena witjazii* cf sp 1, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species has a crown of bladed spines in the upper third of the cephalis, which is very elongated. It differs from *L. witjazii* (Pl. 25, Figs. 5A–B) in that its cephalis is more elongated and does not flare outward at the top, instead forming a cylinder shape. As only four specimens were observed, the range of morphology is not well understood.

**Material examined.** 4 specimens observed from samples 321-1337A-12H-5, 23–26cm (Late Miocene), 321-1337A-3H-2, 103–106cm (Middle Pleistocene), 321-1337A-2H-3, 76–79cm (Late Pleistocene), and 321-1337D-1H-1, 0–3cm (Recent).

**Range.** Latest Miocene—Recent, EEP (Table 1).

## Other *Lophophaena* species not observed during this study:

### *Lophophaena capito* Ehrenberg, 1874

*Lophophaena capito* n. sp., Ehrenberg, 1874, p. 242 [not figured].
*Lophophaena capito* Ehrenberg*,* Ehrenberg, 1876, pl. 8, fig. 6.
? *Lophophaenoma* sp. G, Petrushevskaya, 1971, pl. 56, fig. 15.
non *Lophophaena? capito* Ehrenberg group, Petrushevskaya and Kozlova, 1972, pl. 33, figs. 20–23.
non *Lophophaena? capito* Ehrenberg group, Petrushevskaya, 1975, pl. 9, fig. 21.
non *Lophophaena cf. capito* Ehrenberg, Takahashi, 1991, pl. 25, figs. 6–9.
*Lophophaena capito* Ehrenberg, Ogane *et al.,* 2009, pl. 19, fig. 8a–8c, pl. 34, fig. 3a–3c, pl. 79, fig. 2a–2c.

### *Lophophaena clevei* Petrushevskaya, 1971

*Dictyocephalus* sp. ?*,* Cleve, 1899, p. 20, pl. 2, fig. 1.
*Lithomelissa? laticeps* Jorgensen, Hülsemann, 1963, p. 27–28, fig. 18 (non *L . laticeps*
Jørgensen 1905, p. 136, pl. 16, fig. 84).
*Peromelissa? sp. L*, Petrushevskaya, 1971, pl. 45, fig. 10.
*Lophophaena* spp., Petrushevskaya, 1971, pl. 56, figs. 9–11.
*Lophophaena clevei* n. sp., Petrushevskaya, 1971, p. 107, 109, pl. 57, fig. 1.
*Lophophaena clevei* Petrushevskaya, Petrushevskaya and Kozlova, 1979, p. 126, 128, figs. 350–353, 492.
*Lophophaena clevei* Petrushevskaya, Renaudie and Lazarus, 2015, pl. 7, fig. 17.
non *Lophophaena clevei* Petrushevskaya, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** Since this species was formally described by Petrushevskaya (1971), usage in the literature has been consistent. However, the species appears in older literature under a variety of other names and genera, included in the synonymy above. In our previous study, we misidentified *L. amictoria* as *L. clevei*.

### *Lophophaena decacantha* (Haeckel, 1887) Petrushevskaya, 1971

*Lithomelissa (Sethomelissa) decacantha* n. sp., Haeckel, 1887, p. 1208, pl. 56, fig. 2.
*Lophophaenoma decacantha* Haeckel, emend., Petrushevskaya, 1971, pl. 62, fig. 1.
? *Lithomelissa* sp. cf. *L. decacantha* Haeckel, Nishimura, 1990, figs. 14.9a–c.
non *Lophophaena decacantha* Haeckel group, Takahashi, 1991, pl. 25, figs. 2, 8.
*Peromelissa decacantha* Haeckel, Van de Paverd, 1995, pl. 66, fig. 15.
non *Lophophaenoma decacantha* Haeckel, Itaki *et al.,* 2008b, pl. 4, figs. 12 and 18.

**Remarks.** To our knowledge, no authors have illustrated exactly the morphology described and figured by Haeckel; in particular, the combination of ribs, feet, and appendages on the thorax. However, some authors have come close, which are included in this synonymy. As no specimens were observed in our EEP material, it is beyond the scope of this project to evaluate this species concept, but some clarification is needed.

### *Lophophaena galeaorci* Ehrenberg, 1854b

*Lophophaena Galea Orci* [sic] n. sp., Ehrenberg, 1854b, p. 245.
*Lophophaena galea Orci* [sic] Ehrenberg, Haeckel, 1862, p. 298.
*Lophophaena apiculata* n. sp.*,* Ehrenberg, 1874, p. 242.
*Lophophaena apiculata* Ehrenberg, Ehrenberg, 1876, pl. 8, fig. 11.
*Lophophaena galea Orci* [sic] Ehrenberg, Stöhr, 1880, p. 99, pl. 3, fig. 17.

*Lophophaena galea* Ehrenberg, Haeckel, 1887, p. 1303 [not figured].
*Lophophaena galea orci* [sic] Ehrenberg, Petrushevskaya, 1971, p. 106–107 [not figured].
Plagoniids, gen. et sp. indet., Riedel and Sanfilippo, 1977, pl. 7, fig. 1.
? *Lophophaena apiculata* Ehrenberg, Petrushevskaya and Kozlova, 1979, fig. 491.
*Lophophaena galea orci* [sic] Ehrenberg, Petrushevskaya, 1981, fig. 83.
? *Lophophaena apiculata* Ehrenberg, Sarkisova, 2005, pl. 1, figs. 5–7.
*Lophophaena apiculata* Ehrenberg, Ogane *et al.,* 2009, pl. 19, figs. 3A–D.

**Remarks.** Ehrenberg (1854b) described only one species of *Lophophaena*: *Lophophaena Galea Orci* [sic]. Thus, it appears that "*orci*" is not a subspecies of *Lophophaena galea*; rather, it is part of a compound name. Ehrenberg named the species after the ship that led to its discovery, the "Brig Delphin," which roughly translates to "Galea Orci". Because it was intended as a single species name rather than a subspecies, the name must be corrected to *galeaorci* according to ICZN Article 32.5.2.2. In 1862, Haeckel followed Ehrenberg's original name, but put "*galea"* in lower case. Later, Haeckel (1887) dropped the "*orci*" from Ehrenberg's species, referring to it simply as *Lophophaena galea* Ehrenberg, subgenus *Lophophaenula*. Haeckel (1887) considered *Lophophaena galeaorci* Ehrenberg, 1854b and *Lophophaena apiculata* Ehrenberg 1874 to be junior synonyms of *Lophophaena galea* Ehrenberg. However, he did not provide a justification for the name change or the synonymy, and not all subsequent authors have not adopted it. Petrushevskaya (1971), also considered *L. apiculata* Ehrenberg, 1874 to be a junior synonym of *L. galea orci* [sic] Ehrenberg, 1854b. Here we follow the precedent of Haeckel (1887) and Petrushevskaya (1971) by adopting their synonymy, but we correct the species name to *galeaorci*.

### *Lophophaena gibba* **Dumitrica, 1978**

*Lophophaena gibba* n. sp., Dumitrica, 1978, pl. 7, fig. 6 and 11.

### *Lophophaena kamikurii* **Renaudie and Lazarus, 2016**

*Lophophaena kamikurii* n. sp., Renaudie and Lazarus, 2016, pl. 7, figs. 10A–12, ?pl. 6, figs. 5A–B.

### *Lophophaena larvata* **Ehrenberg, 1874**

*Lophophaena larvata* n. sp., Ehrenberg, 1874, p. 243 [not illustrated].
*Lophophaena larvata* Ehrenberg, Ehrenberg, 1876, pl. 8, fig. 10.
*Sethoconus (Conarachnium) larvatus* Haeckel, Haeckel, 1887, p. 1287 [not illustrated].
*Lophophaena larvata* Ehrenberg, Ogane *et al.,* 2009, pl. 4, figs. 6A–B; pl. 79, figs. 3A–C, 5A–B.

### *Lophophaena mugaica* **(Grigorjeva) Kozlova, 1983**

*Theocyrtis mugaicus* n. sp., Grigorjeva, 1975, pl. 1, fig. 2.
*Lophophaena* sp., Dumitrica, 1973, pl. 9, fig. 6; pl. 11, fig. 8 (non pl. 3, figs. 5–7).
*Lophophaena mugaica* (Grigorjeva), Kozlova, 1983, pl. 5, fig. 4.
*Lophophaena mugaica* (Grigorjeva), Kozlova, 1999, pl. 1, figs. 18–19; pl. 3, fig. 16; pl. 4, fig. 3.
*Lithomelissa* cf. *gelasinus* O'Connor, Hollis, 1997, pl. 12, figs. 13–14.
*Lophophaena mugaica* (Grigorjeva), Hollis, 2002, pl. 4, figs. 3–6.

### *Lophophaena? neuma* **Renaudie and Lazarus, 2015**

*Lophophaena? neuma* n. sp., Renaudie and Lazarus, 2015, pl. 7, figs. 1–3, pl. 8, fig. 9.

### *Lophophaena pileata* **Renaudie and Lazarus, 2015**

*Lophophaena pileata* n. sp., Renaudie and Lazarus, 2015, pl. 7, figs. 4–5.

### *Lophophaena radians* Ehrenberg, 1874

*Lophophaena radians* n. sp., Ehrenberg, 1874, p. 243 [not figured].
*Lophophaena radians* Ehrenberg, Ehrenberg, 1876, pl. 8, figs. 7–9.
*Lophophaenoma radians* (Ehrenberg), Petrushevskaya, 1981, p. 86, fig. 78.
? *Lophophaena lynx* n. sp., Ehrenberg, 1876, pl. 8, fig. 13.
*Lophophaena radians* Ehrenberg, Kamikuri, 2015, pl. 13, fig. 30.
*Lophophaena radians* Ehrenberg, Ogane *et al.,* 2009, pl. 3, figs. 3a–b, 5a–d; pl. 79, figs. 4a–c.

**Remarks.** This species has a very convoluted history in the literature. After it was described and figured by Ehrenberg (1874, 1876), Haeckel (1887) split the concept into two separate species, apparently on the basis of isolated versus interconnected horns on the cephalis. He asserted that Ehrenberg (1876)'s pl. 8, figs. 7–8 (with interconnected spines) should be considered a junior synonym of *Lophophaena circumtexta* Haeckel (not to be confused with *Arachnocorys circumtexta* Haeckel), which to our knowledge was never illustrated beyond Ehrenberg's illustrations of *Lophophaena radians*. Haeckel (1887) retained the name *Lophophaena radians* for Ehrenberg (1876)'s pl. 8, fig. 9 only (which is identical to figs. 7–8, except for the lack of interconnected horns), and questionably synonymized it with *Lophophaena lynx* Ehrenberg. *L. lynx* does indeed appear to be very similar in overall shape and proportions to *Lophophaena radians* Ehrenberg 1876, pl. 8, fig. 9, but may have fewer horns and is smaller in size. Therefore, it is questionably included in our synonymy. It is our opinion that all three specimens of *L. radians* illustrated by Ehrenberg (1876) are the same species, so we do not adopt Haeckel's revision or synonymy here. Interconnections between horns can sometimes be an ontogenetic character, as evidenced by other lophophaenid species, so should not be the sole basis of splitting species concepts. Petrushevskaya (1971) designated *L. circumtexta* (junior synonym: *L. radians* Ehrenberg) as the type species of *Lophophaenoma*, which she elevated to the genus rank after it was described as a subgenus of *Lophophaena* by Haeckel (1887). However, in the taxonomic remarks section, she states that *L. radians* Ehrenberg is the type species of *Lophophaenoma*, and that *L. circumtexta* Haeckel is its junior synonym. Petrushevskaya (1971) also considered all specimens figured by Ehrenberg (pl. 8, figs. 7–9) to be part of *L. radians*, including forms with and without interconnected cephalic spines (contrary to Haeckel). Later, Petrushevskaya (1981) found that *Lophophaenoma* should be demoted back to a subgenus as it is largely a junior synonym of *Arachnocorys,* although some species in *Lophophaenoma* should be placed in *Peromelissa* or *Lophophaena* instead. It is unclear to which genus Petrushevskaya (1981) thought *L. radians* should belong, since it was the type species of a genus determined to be a junior synonym of *Arachnocorys* (p. 86–87), but figured as an example of *Lophophaenoma* with the genus name *Lophophaena* (fig. 78). Here we do not believe this species should be in *Arachnocorys*, because it lacks gaps between the cephalis and thorax and has a more cylindrical, ribless thorax than other species in *Arachnocorys.* Petrushevskaya (1971) also considered *L. radians* to be different from *Arachnocorys* for its lack of gaps between cephalis and thorax. Kamikuri (2015) was the most recent author to illustrate this species; he did so under its original name, *Lophophaena radians* Ehrenberg. Here we follow Kamikuri (2015) and also use the original name, although no specimens were observed during our study. Other than Kamikuri (2015) and the re-illustrations of Ehrenberg's collection by Ogane *et al.* (2009), we do not know of other photographs of *L. radians*, so this species is in need of additional documentation to be fully understood.

### *Lophophaena rioplatensis* Boltovskoy *et al.,* 2003

*Lophophaena rioplatensis* n. sp., Boltovskoy *et al.,* 2003, figs. 4a–g, 5.

### *Lophophaena sibirica* Gorbovetz ex Petrushevskaya and Kozlova, 1979

*Lophophaena sibirica* (Gorbovetz), Dzinoridze *et al.,* 1978, pl. 29, figs. 19, 24–25; pl. 32 figs. 33–35.
*Lophophaena sibirica* Gorbovetz n. sp., Petrushevskaya and Kozlova, 1979, figs. 354, 355, and 490.
*Lophophaena sibirica* Gorbovetz, Kozlova, 1999, pl. 14, fig. 12; pl. 44, figs. 7 and 9.

**Remarks.** Petrushevskaya and Kozlova (1979) listed this species as "*Lophophaena sibirica* Gorbovetz, sp. n.," but attribute the species name to A. N. Gorbovetz. They also note that some of the specimens used in their description came from Gorbovetz's collections.

### *Lophophaena triangula* Funakawa, 1994

*Lophophaena triangula* n. sp., Funakawa, 1994, p. 466, 468; pl. 8, figs. 31–4b.

## Genus *Peromelissa* Haeckel, 1881, emend. Petrushevskaya, 1971, sensu Matsuzaki *et al.*, 2015

(=*Psilomelissa* Haeckel, 1881; = *Micromelissa* Haeckel, 1887; = *Dimelissa* Campbell, 1951)

Type species: *Peromelissa phalacra* Haeckel, 1887

**Description.** Lophophaenidae with two segments, and constriction between cephalis and thorax, above the median bar. The apical spine runs along the outside of the cephalis rather than existing free within it (as in *Lithomelissa*). The cephalis may have similar pore structure to the thorax, or be hyaline toward the top (as in *Peromelissa phalacra* Haeckel 1887). The apical spine may protrude out the top of the cephalis, or end on along the cephalic wall. The dorsal, left lateral, and right lateral spines extend outside the shell at approximately the same angle. These spines are typically as strong, or stronger, than the apical spine.

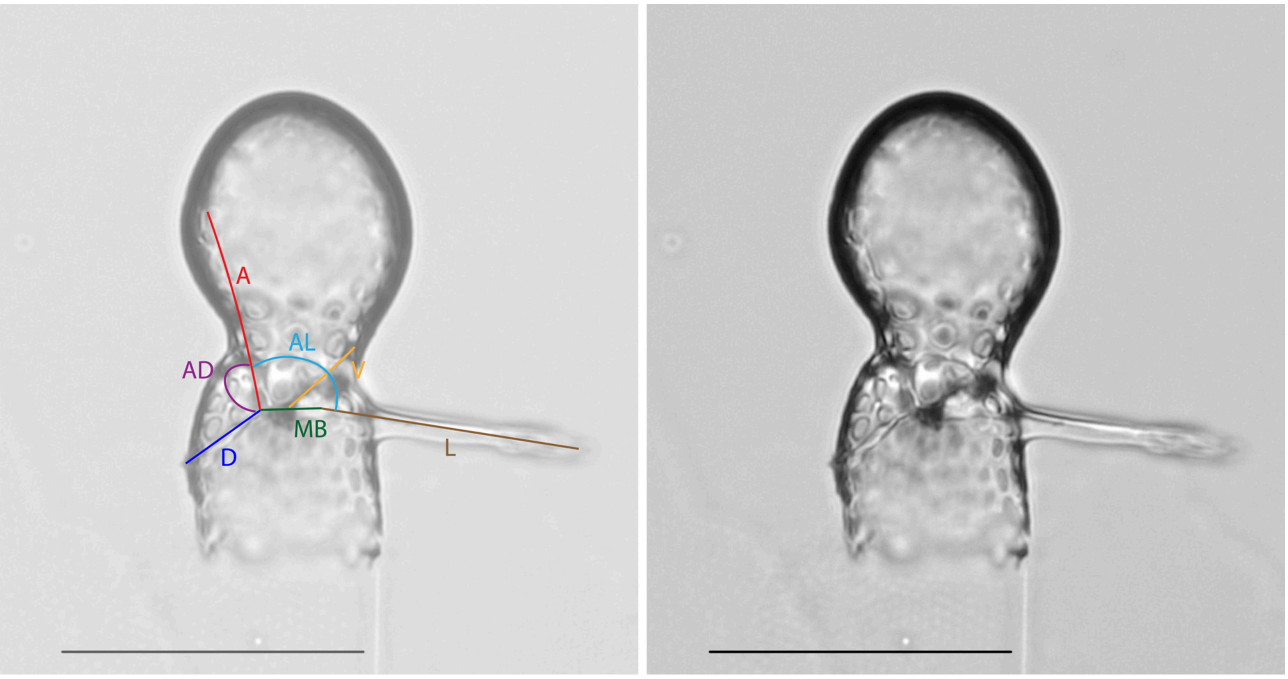

**FIGURE 15.** Internal skeletal structure of *Peromelissa phalacra* (Haeckel) Petrushevskaya.

**Remarks.** This genus was first described vaguely by Haeckel (1882) as a two-segmented skeleton with a smooth cephalis, and a rounded thorax with three lateral spines. No species were placed into this genus until Haeckel (1887). In 1887, Haeckel added that *Peromelissa* does not have a cephalic horn; however, subsequent observations (i.e., Petrushevskaya 1971) have shown that *Peromelissa* does indeed have a cephalic horn, though it can vary greatly in size and strength. The type species was designated as *Peromelissa phalacra* Haeckel, 1887 by Campbell (1954). In Petrushevskaya (1971)'s analysis of the internal skeletal structure of the type species, she observed that *Peromelissa phalacra* Haeckel, 1887 does have an apical horn, and also emended the genus definition to include forms with an open thorax, which were originally excluded from Haeckel's 1882 and 1887 diagnoses. Petrushevskaya's emendation thus nullified the differences between *Peromelissa* Haeckel, 1881, *Psilomelissa* Haeckel, 1881, *Micromelissa* Haeckel, 1887, and *Dimelissa* Campbell, 1951. She suggested that all of these names should be united under *Peromelissa* Haeckel 1881, which was adopted and further clarified by Matsuzaki *et al.* (2015). Here we follow Matsuzaki *et al.* (2015)'s description, and agree with these authors' statement that *Peromelissa* differs from *Lithomelissa* in that the apical spine is not free within the cephalis. However, neither Petrushevskaya (1971) nor Matsuzaki *et al.* (2015) explicitly state why *Peromelissa* conflicts with *Lophophaena*. It is our opinion that the species currently in *Peromelissa* are as similar to *Lophophaena* species as they are to each other, and there is no specific characteristic that separates them. For the sake of avoiding further confusion, we retain the genus *Peromelissa* for the described species observed during this study, but do not place any of our new species in this problematic genus.

In this study we observed the following valid species of *Peromelissa*: *Peromelissa phalacra* Haeckel, 1887 and *Peromelissa thoracites* (Haeckel) Matsuzaki *et al.,* 2015. Although it was not observed in this study, *Micromelissa apis* Haeckel, 1887 should likely be transferred to *Peromelissa*, due to the genus-level synonymizations of Petrushevskaya (1971) and Matsuzaki *et al.* (2015). We do not include *Peromelissa crassa* Tan, 1927, because the illustration does not appear to depict a lophophaenid. *Peromelissa psilocrana* Haeckel, 1887 was only briefly described but not illustrated, and to our knowledge has never been subsequently used by other authors, making it likely a *nomen oblitum*. *Peromelissa capito* (Ehrenberg) Haeckel, 1887 was transferred from *Lithomelissa*, but as no justification was given by the author and the existing illustrations are vague, we do not follow this transfer here.

**Range.** ?Late Miocene–Recent

### *Peromelissa phalacra* (Haeckel 1887) Petrushevskaya, 1971

Plate 38, Figs. 3A–6.

*Psilomelissa phalacra* n. sp., Haeckel, 1887, p. 1208–1209 [not figured].
*Peromelissa phalacra* n. sp., Haeckel, 1887, pl. 57, fig. 11.
*Psilomelissa longispina* n. sp., Cleve, 1900, pl. 4, fig. 4.
*Psilomelissa phalacra* Haeckel, Popofsky, 1908, pl. 34, fig. 4.
*Psilomelissa phalacra* Haeckel, Popofsky, 1913, text-fig. 48.
*Lithomelissa monoceras* n. sp., Popofsky, 1913, pl. 32, fig. 7, text-fig. 43.
*Lithomelissa thoracites* Haeckel, Benson, 1966, pl. 24, fig. 13 (non figs. 11–12).
*Peromelissa phalacra* Haeckel, Petrushevskaya, 1971, pl. 46, fig. 14; pl. 59, figs. 1–2; pl. 72, figs. 14–17.
*Peromelissa phalacra* (Haeckel) Petrushevskaya, Renz, 1974, pl. 18, fig. 7.
*Lithomelissa monoceras* Popofsky, Tan and Tchang, 1976, text-fig. 49.
*Peromelissa phalacra* Haeckel, Boltovskoy and Riedel, 1980, pl. 5, fig. 3.
*Peromelissa phalacra* Haeckel, Takahashi and Honjo, 1981, pl. 7, figs. 4–5 (non fig. 3).
*Peromelissa phalacra* Haeckel, Nishimura and Yamauchi, 1984, pl. 32, fig. 12 (non fig. 1).
non *Peromelissa phalacra* Haeckel, Boltovskoy and Jankilevich, 1985, pl. 4, fig. 8.
*Peromelissa phalacra* Haeckel, Boltovskoy and Riedel, 1987, pl. 4, fig. 14.
*Peromelissa phalacra* Haeckel, Fujioka, 1990, pl. 45, fig. 9.
*Peromelissa phalacra* Haeckel, Takahashi, 1991, pl. 25, figs. 11–15.
*Peromelissa thoracites* forma *phalacra*, Van de Paverd, 1995, pl. 66, figs. 11–14.
*Lithomelissa monoceras* Popofsky, Tan and Su, 2003, text-fig. 106.
*Peromelissa phalacra* Haeckel, Okazaki *et al.,* 2005, fig. 12.16.
*Peromelissa phalacra* Haeckel, Itaki *et al.,* 2010, fig. 6.19.
*Peromelissa phalacra* Haeckel, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** *Peromelissa phalacra* was originally described by Haeckel (1887) as having a closed thorax, differentiating it from *Psilomelissa phalacra* Haeckel (1887). However, *Psilomelissa phalacra* was not figured by Haeckel, and subsequent observations by Petrushevskaya (1971) and the present study suggest that the thorax can be on a gradient between open and closed, and thus probably attributable to intraspecific and/or ontogenetic variation. Following Petrushevskaya (1971), we consider *Psilomelissa phalacra* and *Peromelissa phalacra* to be the same species. *Psilomelissa longispina* (Cleve, 1900) and some mentions of *Lithomelissa monoceras* (Popofsky, 1913), including Popofsky's original illustrations, are also listed in our synonymy, following Petrushevskaya (1971). *Peromelissa phalacra* Haeckel is differentiated from *Peromelissa thoracites* (Haeckel) Matsuzaki *et al.,* 2015 in having a weaker apical spine, narrower thorax, and a slightly elongated cephalis with significantly smaller pores than the thorax, which becomes increasingly hyaline toward the top.

**Range.** Pliocene– Recent, EEP (Table 1).

### *Peromelissa thoracites* (Haeckel) Matsuzaki *et al.,* 2015

Plate 38, Figs. 7A–10.

*Lithomelissa thoracites* n. sp., Haeckel, 1862, pl. 6, figs. 2–8.
*Lithomelissa thoracites* Haeckel, Hertwig, 1879, pl. 8, fig. 1.

*Psilomelissa tricuspidata* n. sp., Popofsky, 1908, p. 284, pl. 32, fig. 9; pl. 33, fig. 8.
*Lithomelissa thoracites* Haeckel, Popofsky, 1913, text-figs. 44–47.
*Lithomelissa thoracites* Haeckel, Schröder, 1914, text-figs. 61–62.
*Lithomelissa thoracites* Haeckel, Benson, 1966, pl. 24, figs 10–12 (non fig. 13).
*Dimelissa thoracites* Haeckel, Petrushevskaya, 1971, pl. 69, figs. 7–8.
? *Dimelissa* cf. *thoracites* Haeckel, Petrushevskaya, 1971, pl. 69, figs. 5–6.
*Lithomelissa monoceras* Popofsky, Casey, 1971, pl. 23.2, fig. 16.
*Lithomelissa monoceras* Popofsky, Renz, 1974, pl. 18, fig. 14.
*Lithomelissa monoceras* Popofsky, Renz, 1976, pl. 8, fig. 12.
*Peromelissa phalacra* Haeckel, Takahashi and Honjo, 1981, pl. 7, fig. 3 (non figs. 4–5).
*Lithomelissa thoracites* Haeckel, Molina-Cruz, 1982, pl. 4, figs. 12–13.
*Peromelissa phalacra* Haeckel, Nishimura and Yamauchi, 1984, pl. 32, fig. 1 (non fig. 12).
*Lithomelissa thoracites* Haeckel, Nishimura and Yamauchi, 1984, pl. 32, figs. 2–3.
non *Lithomelissa* cf. *thoracites* Haeckel, Nishimura and Yamauchi, 1984, pl. 32, fig. 4.
*Lithomelissa thoracites* Haeckel, Boltovskoy and Riedel, 1987, pl. 4, fig. 7.
*Peromelissa thoracites* forma *thoracites,* Van de Paverd, 1995, pl. 66, figs. 9–10.
*Peromelissa thoracites* forma *scaphopdium*, Van de Paverd, 1995, pl. 65, figs. 17–21.
non *Peromelissa thoracites?*, Van de Paverd, 1995, pl. 65, figs. 12–14, 16.
non *Lithomelissa thoracites* Haeckel, Chen and Tan, 1996, pl. 28, figs. 1–4
*Lithomelissa monoceras* Popofsky, Chen and Tan, 1996, pl. 28, fig. 5 (?fig. 6).
*Peromelissa phalacra* Haeckel, Sashida and Kurihara, 1999, fig. 7.12.
*Lithomelissa monoceras* Popofsky, Tan and Su, 2003, text-fig. 105.
non *Dimelissa thoracites* Haeckel group, Okazaki *et al.,* 2005, fig. 12.15.
non *Dimelissa thoracites* Haeckel, Itaki, 2009, pl. 15, figs. 1–8.
*Dimelissa* aff. *thoracites* Haeckel, Itaki, 2009, pl. 15, figs. 14–16.
? *Lithomelissa thoracites* Haeckel, Sono *et al.,* 2009, pl. 3, fig. 3.
*Dimelissa thoracites* Haeckel, Itaki *et al.,* 2010, fig. 6.9–6.10.
*Dimelissa monoceras* Popofsky, Matsuzaki *et al.,* 2014, pl. 3, fig. 5.
*Peromelissa thoracites* Haeckel, Matsuzaki *et al.,* 2015, fig. 7.16.
*Peromelissa tricuspidata* Popofsky, Matsuzaki *et al.,* 2015, fig. 7.17.
non *Lithomelissa thoracites* Haeckel, Chen *et al.*, 2017, figs. 9–10, 12–13 (?figs. 11, 14).
*Lithomelissa thoracites* Haeckel, Trubovitz *et al.,* 2020, supplementary data 7.
*Lithomelissa* cf. *thoracites* Haeckel, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** *Lithomelissa thoracites* (Haeckel) was designated the type species of *Dimelissa* (Campbell, 1951) by Petrushevskaya (1971). However, Matsuzaki *et al.* (2015) considered *Dimelissa* as a junior synonym of *Peromelissa* (Haeckel 1881) and thus transferred *L. thoracites* Haeckel to the genus *Peromelissa.* Van de Paverd (1995) also suggested that this species should be considered *Peromelissa*, but the transfer was not formalized. Here we agree with Matsuzaki *et al.* (2015) that *Dimelissa* and *Peromelissa* should not be separate genera, and adopt their transfer here. However, the reason this species does not fit the definition of *Lophophaena* is not clear. *Peromelissa thoracites* (Haeckel) Matsuzaki *et al.* has often been confused with *Peromelissa phalacra* Haeckel in the literature. Like *Peromelissa phalacra,* this species has also sometimes been called *Lithomelissa monoceras* Popofsky. However, *Lithomelissa monoceras* as originally described and illustrated by Popofsky (1913) is a junior synonym of *Peromelissa phalacra* Haeckel. Subsequent authors (i.e., Casey, 1971, Renz, 1974, 1976) have illustrated specimens under the name *Lithomelissa monoceras* Popofsky that have a strong apical spine embedded in the cephalis wall, relatively large pores on the cephalis, and a relatively broad thorax, which are more characteristic of *Peromelissa thoracites* Haeckel than *Peromelissa phalacra* Haeckel, and are thus included in our synonymy.

**Range.** Late Upper Miocene—Recent (Table 1).

## Genus *Pelagomanes* n. gen.

urn:lsid:zoobank.org:act:43256F4F-DF95-4C62-B43F-F12AC0F62E2A

Type species: *Lithomelissa? kozoi* Renaudie and Lazarus, 2013a

**Description.** *Pelagomanes* has a small cephalis in proportion to the thorax, compared to most other lophophaenid genera. The apical spine runs along the wall of the cephalis and extends upward as a horn with a slight curve at its base, before the spine reaches the apex of the cephalis. Although not present in every species of *Pelagomanes*, a very prominent—and sometimes forked—apical horn is typical. The ventral spine is thornlike in appearance; it tends to be broader at its base, giving it a triangular shape. The thorax is always wider and longer than the cephalis. Shoulders and ridges between them develop on the upper part of the thorax, and typically extend downwards as ribs that terminate as three feet or many teeth at the base of the thorax. Species in this genus do not have an axobate.

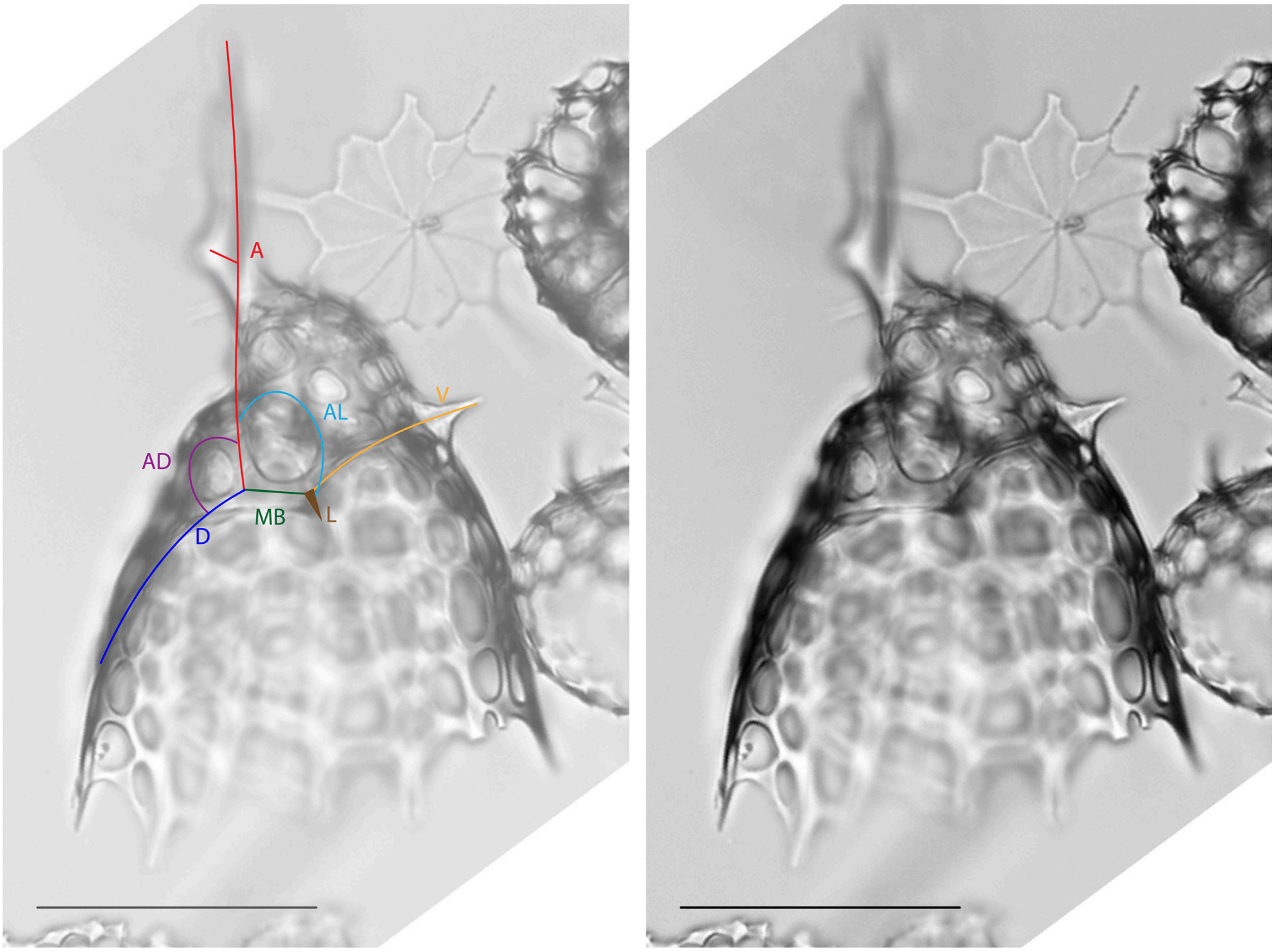

**FIGURE 16.** Internal skeletal structure of *Pelagomanes cantharoides* (Sugiyama and Furutani, 1992) n. comb.

**Remarks.** Here we have identified a complex of related species, which have been assigned (often questionably by their authors) to various genera within Lophophaenidae. The new genus *Pelagomanes* is similar to *Ceratocyrtis* in the proportions of cephalis and thorax, short median bar, and downward-angled dorsal spine. However, the lack of a dendritic axobate differentiates *Pelagomanes* from *Ceratocyrtis*. This genus differs from *Lophophaena* in the structure of ribs along the length of the thorax (usually terminating as feet) and relatively small cephalis compared to the size of the thorax. It differs from *Lithomelissa* in that the apical spine runs along the side of the cephalic wall rather than passing freely through it. The shape and proportions of the cephalis and thorax differentiate this genus from *Amphiplecta*, *Arachnocorallium*, *Arachnocorys*, *Botryopera*, and *Peromelissa*. The boundary between *Pelagomanes* and *Pseudodictyophimus* is problematic, as the latter genus is in need of a revision. At present, we consider *Pseudodictyophimus* to be different due to its shorter thorax and relatively longer feet. *Pseudodictyophimus* is limited to three feet in total, whereas *Pelagomanes* can have more, or have feet in addition to teeth at the base of the thorax. The strong apical spine with a hook-like curved base is also typical of *Pelagomanes* but not *Pseudodictyophimus*. The genus *Cephaluspinus* Alvira-Martìn, 1971 was regarded as a junior synonym of *Lophophaena* by Petrushevskaya (1981); *Pelagomanes* differs from both of these generic concepts in that the cephalis is relatively smaller, compared to the breadth of the thorax.

We consider the following species to be included in *Pelagomanes*:

*Pelagomanes cantharoides* (Sugiyama and Furutani, 1992) n. comb., *Pelagomanes ibburi* n. sp., *Pelagomanes* *kozoi* (Renaudie and Lazarus, 2013a) n. comb., *Pelagomanes morawanensis* (Funakawa, 1995b) n. comb., *Pelagomanes? piperata* (Renaudie and Lazarus, 2015) n. comb., *Pelagomanes stigi* (Bjørklund, 1976) partim. (pl. 15, fig. 15a–b, 13, non figs. 12, 14, 16–17) n. comb., *Pelagomanes tekopua* (O'Connor, 1997) n. comb., *Pelagomanes thaumasia* (Caulet, 1991) n. comb.

**Etymology.** Latin for "the ghost from the sea" (masc. noun).

**Range.** Oligocene—Recent, so far as known.

### *Pelagomanes cantharoides* **(Sugiyama and Furutani, 1992) n. comb.**

Plate 40, Figs. 1–3, 7–8, 10, 14.

*Ceratocyrtis? cantharoides* n. sp., Sugiyama and Furutani, 1992, pl. 13, figs. 1–2; pl. 20, figs. 1–2b.
*Ceratocyrtis* sp. aff. *C. cucullaris* (Ehrenberg), Tsoy and Shastina, 1999, pl. 35, fig. 6.
*Ceratocyrtis? cantharoides* Sugiyama and Furutani, Renaudie, 2014, pl. 22, fig. 3.
*Ceratocyrtis cantharoides* Sugiyama and Furutani, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** Sugiyama and Furutani (1992) only tentatively placed this species in *Ceratocyrtis* because it lacks the well-developed, dendritic axobate that is typical of *Ceratocyrtis* species. The authors state that the apical horn has 1–2 branches on the dorsal side. It is this forked apical horn that separates *P. cantharoides* from similar taxa (i.e., *P. morawanensis* and *P. tekopua*). However, it is unclear whether this character alone should justify the separation of this species from *P. morawanensis* (Funakawa). Plate 40 demonstrates that specimens sharing the character of a forked apical horn often have as many differences between one another as with specimens without a forked horn. This suggests that a forked horn may not be a reliable distinguishing character, and these two species concepts may require revision. Here we provisionally accept these two concepts as separate species, but acknowledge that further study may show they are the same.

**Range.** Middle Miocene in the EEP, though the range in our material is not well constrained (Table 1). Sugiyama and Furutani (1992) described this species from the Middle Miocene of Japan. Renaudie (2014) reported it from the Early–Middle Miocene of the Southern Ocean.

### *Pelagomanes ibburi* **n. sp.**

Plate 41, Figs. 1A–6B.

urn:lsid:zoobank.org:act:3F89A23A-6C54-4E59-8FA0-71B62A21F316
*Lithomelissa kozoi* cf sp 1, Trubovitz *et al.* 2020, supplementary data 7.

**Diagnosis.** *Pelagomanes* with a cephalis that ranges from having few, small pores to being entirely hyaline, has a relatively weak hooklike apical horn, and an elongated thorax with very strong shoulders at the top and three feet in addition to small teeth at the base.

**Description.** The cephalis of this species has small pores and is often hyaline (i.e., figs. 1 and 2). The apical horn extends from the dorsal side of the cephalis before reaching the apex, and is slightly curved at its base. The thorax is approximately twice the length of the cephalis, and slightly wider than it. Pores on the thorax get larger toward the base, and have the tendency to become more elongated in shape. Prominent shoulders exhibit at the top of the thorax, and the furrows between them extend downwards as ribs along the thorax and finally as bladed feet at the base of the skeleton. The base of the thorax may be enclosed in some specimens (i.e., fig. 3), and fully-preserved individuals show small teeth at the base of the thorax between the three feet.

**Remarks.** This species differs from *Pelagomanes kozoi* Renaudie and Lazarus, 2013a (Pl. 39, Figs. 1–6) in that the shoulders are usually stronger, and the teeth at the base of the thorax are shorter and have more contrast with the three feet. In addition, the thorax of this species tends to be longer than in *P. kozoi*, and the cephalis is often more hyaline. This species differs from *Pseudodictyophimus gracilipes* in that the thorax is narrower and more elongated. The apical and ventral horns show variable development, but are never as strong as those of *P. thaumasia* (Pl. 39, Figs. 10A–11), *P. morawanensis* (Pl. 40, Figs. 4A–6, 9, 11–12), or *P. tekopua* (Pl. 40, Fig. 13).

**Material examined.** 78 specimens observed from samples 321-1337A-35X-1, 106–108cm (Middle Miocene), 321-1337A-31X-6, 4–6cm (Middle Miocene), 321-1337D-30H-3, 103–104cm (Middle Miocene), 321-1337D-

26H-3, 142–144cm (Late Miocene), 321-1337D-23H-6, 134–137cm (Late Miocene), 321-1337A-18H-6, 77–80cm (Late Miocene), 321-1337A-16H-6, 121–124cm (Late Miocene), 321-1337A-14H-7, 39–42cm (Late Miocene), 321-1337A-12H-5, 23–26cm (Late Miocene), 321-1337A-10H-2, 91–94cm (Early Pliocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), 321-1337A-6H-3, 29–32cm (Late Pliocene), 321-1337A-4H-6, 115–118cm (Early Pleistocene), 321-1337A-4H-2, 16–19cm (Middle Pleistocene), 321-1337A-3H-2, 103–106cm (Middle Pleistocene), 321-1337A-2H-3, 76–79cm (Late Pleistocene), and 321-1337D-1H-1, 0–3cm (Recent).

**Holotype.** Pl. 41, Figs. 2A–B; sample 321-1337A-16H-6, 121–124cm; ECO-141; Z12-4.

**Paratypes.** (1) Pl. 41, figs. 1A–B; sample 321-1337A-16H-6, 121–124cm; ECO-143; K12-3. (2) Pl. 41, figs. 4A–B; sample 321-1337D-23H-6, 134–137cm; ECO-145; N15-1. (3) Pl. 41, figs. 3A–B; sample 321-1337D-23H-6, 134–137cm; ECO-145; G17-2. (4) Pl. 41, figs. 6A–B; sample 321-1337A-14H-7, 39–42cm; ECO-138; V9-2. (5) Pl. 41, figs. 5A–B; sample 321-1337A-16H-6, 121–124cm; ECO-143; J18-2.

**Measurements.** Cephalis height 30–37 (34)μm, cephalis width 26–31 (29)μm, thorax length (not including feet) 45–59 (49)μm, width at shoulders 38–47 (42)μm. Based on 8 specimens.

**Etymology.** Named for ibbur in Jewish folklore, a type of benevolent spirit possession intended to help people succeed.

**Range.** Middle Miocene—Recent, EEP (Table 1).

### *Pelagomanes morawanensis* (Funakawa, 1995b) n. comb.

Plate 40, Figs. 4A–6, 9, 11–12.

*Ceratocyrtis morawanensis* n. sp., Funakawa, 1995b, pl. 1, figs. 4–5.
*Ceratocyrtis? morawanensis* Funakawa, Renaudie, 2014, pl. 22, fig. 2.
*Lophophaena tekopua* O'Connor, Kamikuri, 2019, pl. 14, fig. 13 (non fig. 14).
*Lophophaena tekopua* O'Connor, Trubovitz *et al.*, 2020, supplementary data 7.

**Remarks.** Funakawa (1995b) gives no differential diagnosis between this species and *Pelagomanes cantharoides* (Sugiyama and Furutani, 1992), pl. 40, figs. 1–3, 7–8, 10, 14. The main difference we understand from the written descriptions of these species is the presence of a forked apical horn in *P. cantharoides* but not in *P. morawanensis*. As mentioned above, this character alone may not justify separate species. Until a more focused study can be done on these taxa, we retain the separate species concepts with some doubts. Funakawa (1995b) notes that this species is different from *P. thaumasia* (Caulet) (Pl. 39, Figs. 10A–11) in having longer apical and ventral horns, as well as being large overall. We would add that *P. thaumasia* tends to have more poorly developed ribs on the thorax than *P. morawanensis*.

**Range.** Middle Miocene in the EEP (Table 1). One broken specimen was observed in the Pliocene, but it is unclear whether this individual was reworked. Funakawa (1995) described this species from Upper Oligocene material in Japan. Renaudie (2014) reported this species from the Middle Miocene of the Southern Ocean.

### *Pelagomanes kozoi* (Renaudie and Lazarus, 2013a) n. comb.

Plate 39, Figs. 1–6.

*Lithomelissa setosa* Jørgensen, Takahashi, 1987, pl. 5, fig. E.
? *Ceratocyrtis?* sp. aff. *C. stigi* (Bjørklund), Sugiyama and Furutani, 1992, pl. 13, fig. 13.
*Lithomelissa* sp. D, Itaki *et al.,* 2008a, pl. 1, fig. 6.
*Lithomelissa* sp. D, Itaki *et al.,* 2009, pl. 17, figs. 15–23.
*Lithomelissa*? *kozoi* n. sp., Renaudie and Lazarus, 2013a, pl. 5, figs. 10a–11, 13a–b; pl. 8, fig. 5.
*Lithomelissa*? *kozoi* Renaudie and Lazarus, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** In our plates we provide images of *Pelagomanes kozoi* from both the EEP and the SO, where it was originally described. Figures 1–4B are of specimens observed during this study in the EEP. Specimen 6 is the holotype and specimen 5 is another specimen that was figured by Renaudie and Lazarus 2013a in their description. Both specimens are from the Late Pliocene Southern Ocean. Among the SO and EEP specimens there are some variations in overall size and shoulder development. This species differs from *Pelagomanes ibburi* n. sp. (Pl. 41, Figs. 1A–6B) in that it has multiple teeth of approximately equal strength, rather than three feet stronger than the rest. It differs from *P. stigi* (Bjørklund) (Pl. 39, Figs. 7–9) in having relatively smaller pores throughout the cephalis and thorax, more distinct shoulders and ribs, and usually a less prominent apical horn. *P. kozoi* is smaller than *P. thaumasia* (Pl. 39, Figs. 10A–11), has more shoulder development, is usually not as heavily silicified, and has more prominent teeth at the base of the thorax. This species differs from *P. cantharoides* (Pl. 40, Figs. 1–3, 7–8, 10, 14) in that the apical horn is not as strong, and it does not have any additional branching on the dorsal side. *P. kozoi* is smaller than both *P. cantharoides* and *P. morawanensis* (Pl. 40, Figs. 4A–6, 9, 11–12). Based on our understanding of *P. tekopua* (O'Connor 1997) (pl. 40, Fig. 13)*, P. kozoi* differs in having a relatively smaller cephalis:thorax ratio and lacks bladed apical and ventral horns.

**Range.** Lower Late Miocene—Latest Miocene, EEP (Table 1). Observed from the Late Miocene– Early Pleistocene in the Southern Ocean by Renaudie and Lazarus (2013a).

### *Pelagomanes*? *piperata* (Renaudie and Lazarus, 2015) n. comb.

Plate 42, Figs. 6–8.

*Botryopera piperata* n. sp., Renaudie and Lazarus, 2015, pl. 7, figs. 6–9B.

**Remarks.** This species was not observed in the EEP, but it is the authors' opinion that it fits the definition of *Pelagomanes* better than *Botryopera*, and thus is tentatively included here. The specimens on Pl. 42, Figs. 6–8 are from the Early Miocene Southern Ocean; photographs are reproduced from Renaudie and Lazarus (2015). *Pelagomanes*? *piperata* has a distinct upward-curving hooklike apical horn, a strong triangular ventral horn, shoulders, ribs, and teeth on the thorax, which are all typical of *Pelagomanes*. In addition, this species has the unusual character of a plate covering the aperture of the thorax. A similar feature was present on some specimens of *Pelagomanes ibburi* n. sp. (Pl. 41, Figs. 1A–6B), as well as one specimen of *Pelagomanes?* sp. B (Pl. 42, Fig. 2) and all specimens of *Pelagomanes?* sp. C (Pl. 42, Figs. 4A–5B).

**Range.** Late Oligocene—Pleistocene in the SO (reported by Renaudie and Lazarus, 2015).

### *Pelagomanes stigi* (Bjørklund, 1976) n. comb.

Plate 39, Figs. 7–9.

*Lithomelissa* sp., Chen, 1975, pl. 11, fig. 4 (non fig. 3).
*Lithomelissa stigi* n. sp., Bjørklund, 1976, partim. pl. 15, fig. 15A–B (non figs. 12–14, 16–17).
non *Ceratocyrtis stigi* (Bjørklund), Nigrini and Lombari, 1984, pl. 15, fig. 7.
? *Ceratocyrtis stigi* (Bjørklund) Nigrini and Lombari, Abelmann, 1990, pl. 4, fig. 12.
*Lithomelissa* cf. *stigi*, Vigour and Lazarus, 2002, pl. 3, figs. 11–13 (?fig. 10; non figs. 8–9).
non *Lithomelissa stigi*?, Vigour and Lazarus, 2002, pl. 3, fig. 14.
*Lithomelissa? stigi* Bjørklund, Renaudie, 2014, pl. 22, fig. 1.

**Remarks.** Some of the specimens figured in Bjørklund (1976) were transferred to *Ceratocyrtis panicula* by Petrushevskaya and Kozlova (1979). These include the specimens on Bjørklund (1976)'s pl. 15, figs. 12–14, and 17. In addition to these transferred specimens, we do not consider the specimen in fig. 16 to be conspecific with what we consider *Pelagomanes stigi* on Bjørklund (1976)'s pl. 15, fig. 15A–B (fig. 15 was designated as the holotype by Bjørklund 1976). Nigrini and Lombari (1984) transferred *Lithomelissa stigi* (Bjørklund) to *Ceratocyrtis*, and noted that they considered all specimens illustrated by Bjørklund (1976) to be conspecific. We agree that the specimen figured by Nigrini and Lombari (1984) belongs in *Ceratocyrtis*, but in our opinion it differs from *Lithomelissa stigi* Bjørklund (1976) pl. 15, figs. 15A–B. The concept of *Pelagomanes (Lithomelissa) stigi* has been inconsistently used in the literature, likely due in part to the morphological variation (and possibly different genera) included in the original species description and illustrations. Although no specimens of this species were observed in the EEP, we include illustrations of specimens from the Southern Ocean, sites 1138A (fig. 7), 751A (fig. 8), and 747A (fig. 9) to help clarify our concept. *Pelagomanes stigi* (Bjørklund) is identifiable for having relatively large pores on the cephalis, an apical horn that is thick at the base and curves upward in a hooklike fashion, and the absence of strong ribs and feet on the thorax.

*Pelagomanes tekopua* **(O'Connor, 1997) n. comb.**
Plate 40, Fig. 13.

*Pseudodictyophimus* sp. B, O'Connor, 1993, pl. 6, figs. 14–15.
*Lophophaena tekopua* n. sp., O'Connor, 1997, pl. 2, figs. 11–14, pl. 7, figs. 7–10.
*Lophophaena tekopua* O'Connor, Kamikuri, 2019, pl. 14, fig. 14 (non fig. 13).

**Remarks.** This species is very similar to *Pelagomanes cantharoides* (Pl. 40, Figs. 1–3, 7–8, 10, 14) *and P. morawanensis* (Pl. 40, Figs. 4A–6, 9, 11–12), and O'Connor (1997) provided no differential diagnosis between any of these species. The type material of this species appears to indicate a relatively larger cephalis:thorax ratio than either *Pelagomanes cantharoides* or *P. morawanensis*. However, the range of variability is not clear and we are not certain that this is indeed a separate species. Renaudie 2014 considered *Lophophaena tekopua* O'Connor along with *Pseudodictyophimus* sp. B O'Connor to be conspecific with *P. morawanensis* (Funakawa). Kamikuri (2019) identified two specimens as *Lophophaena tekopua* O'Connor; one of these is almost identical to the type material illustrated by O'Connor, and the other appears to more closely match the original illustrations of *P. morawanensis*. It is not evident to us whether these are two endpoints on a morphological continuum, or two distinct morphotypes that should be considered separate species. The group of taxa including *P. cantharoides*, *P. morawanensis,* and *P. tekopua* will require further work to determine the consistent differences between species, if there are any. For the purposes of this manuscript, we are tentatively retaining the three separate species concepts until more material can be examined.

**Range.** Middle Miocene, EEP (Table 1). Range poorly constrained.

*Pelagomanes thaumasia* **(Caulet, 1991) n. comb.**
Plate 39, Figs. 10A–11.

*Lophophaena? thaumasia* n. sp., Caulet, 1991, pl. 2, figs. 5–6.
*Lophophaena? thaumasia* Caulet, Renaudie, 2014, pl. 33, fig. 4.
*Lithomelissa? kozoi* cf sp 4 (partim), Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** *P. thaumasia* has a strong tribladed apical horn, which differentiates it from *P. kozoi* (Pl. 39, Figs. 1–6) and *P. stigi* (Pl. 39, Figs. 7–9). It has randomly arranged pores on the thorax, which do not align along ribs, as in *P. morawanensis* (Pl. 40, Figs. 4A–6, 9, 11–12) and *P. cantharoides* (Pl. 40, Figs. 1–3, 7–8, 10, 14). This species lacks strong ribs and prominent teeth at the base of the thorax. The specimens observed in the EEP appear to have a slightly more narrow thorax than those observed by Renaudie in the Southern Ocean, and those figured by Caulet (1991).

**Range.** Middle Miocene—Pleistocene in the EEP (Table 1).

*Pelagomanes* **sp. A**
Plate 41, Figs. 7A–8B.

*Lithomelissa kozoi* cf sp 2, Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species is distinct for its small and tilted cephalis, and relatively large pores on thorax. It differs from *P. stigi* (Pl. 39, Figs. 7–9) in having smaller and more numerous pores on the cephalis, but is otherwise quite similar.

**Material examined.** 7 specimens observed from samples 321-1337A-12H-5, 23–26cm (Late Miocene), 321-1337A-10H-2, 91–94cm (Early Pliocene), 321-1337A-7H-6, 104–107cm (Early Pliocene), 321-1337A-5H-5, 11–14cm (Late Pliocene), and 321-1337A-4H-2, 16–19cm (Middle Pleistocene).

**Range.** Latest Miocene—Pleistocene, EEP (Table 1).

### *Pelagomanes*? sp. B

Plate 42, Figs. 1A–3.

**Remarks.** It is not clear to us whether all of these specimens are conspecific, or that they should certainly be included in *Pelagomanes*. These specimens are small, and have a relatively large and rounded cephalis, with usually more numerous pores compared to the other taxa included in this genus. The thorax is very short, only slightly longer than the height of the cephalis, and terminates with at least size strong, sometimes bladed feet. There is a distinct hyaline zone near the base of the thorax, where the pores stop and the feet begin. One specimen (fig. 2) has an enclosed base.

**Material examined.** 4 specimens observed from samples 321-1337D-30H-3, 103–104cm (Middle Miocene) and 321-1337D-26H-3W, 142–144cm (Late Miocene).

**Range.** Middle–Late Miocene in the EEP, range not well constrained (Table 1).

### *Pelagomanes*? sp. C

Plate 42, Figs. 4A–5B.

unknown plagonid group C sp 60, partim., Trubovitz *et al.,* 2020, supplementary data 7.

**Remarks.** This species has a small, rounded thorax that is enclosed on the bottom, differentiating it from the other described *Pelagomanes* taxa, but making it similar to one specimen of *Pelagomanes?* sp. B (Pl. 42, Fig. 2). At least six feet protrude from the thorax, just above its base, which is a characteristic shared with *Pelagomanes kozoi* as well as *Pelagomanes?* sp. B. It resembles *Pseudodictyophimus gracilipes bicornis* Petrushevskaya,1967 except that it always has more than three feet, which excludes it from being in *Pseudodictyophimus*.

**Material examined.** 4 specimens observed from sample 321-1337A-31X-6, 4–6cm (Middle Miocene).

**Range.** Middle Miocene in the EEP, range not well constrained (Table 1).

## DISCUSSION

This study confirms the presence of a highly diversified lophophaenid assemblage in the EEP from the Miocene–Recent. Trubovitz *et al.* (2020) documented a total of 129 lophophaenid taxa that we consider to belong to the same lophophaenid genera treated in this manuscript. Out of these 129 species, 84 lophophaenid species concepts presented in Trubovitz *et al.* (2020) correspond directly to individual species concepts discussed and illustrated in this manuscript. There are an additional 7 taxa in Trubovitz *et al.* (2020) that are only partially synonymous with taxonomic concepts presented here; some of these have been combined (partim.) under other names. Three species in Trubovitz *et al.* (2020) were completely subsumed under other species names, as we determined them to be synonymous. Twenty-five open-nomenclature species categories in Trubovitz *et al.* (2020) were excluded here due to currently inadequate documentation and/or poorly-constrained concepts, but will likely prove to be distinct species once additional material can be examined. We found 8 problematic taxonomic concepts in Trubovitz *et al.* (2020) that are likely to be either synonyms or deformed specimens of other taxa, and thus are unlikely to be classified as distinct new species following additional investigation. Upon re-examination of the material used by Trubovitz *et al.* (2020), we identified 8 new taxonomic concepts that were not previously recognized and had formerly been lumped under other categories. While we have revised a significant portion of the lophophaenid species concepts introduced in Trubovitz *et al.* (2020), the majority of them (84) have remained the same (albeit with updated names), and the overall diversity estimates of EEP lophophaenids from the Late Miocene–Recent are similar between the two studies. Trubovitz *et al.* (2020) estimated there to be a total of 129 species belonging to our selected set of lophophaenid genera, and here we document 101 taxa within the same scope, with an additional 25 taxa likely definable with further study. If we assume that the results of this more detailed study of one clade is representative, we conclude that the provisional taxonomic framework used in Trubovitz *et al.* (2020) for all late Neogene tropical polycystine Radiolaria is robust, and the conclusions of that study will not be significantly affected by further taxonomic research. However, the necessity to clarify and better document numerous existing name concepts and formally describe numerous new species suggests that while we have made some progress toward quantifying and describing Late Neogene radiolarian diversity in the EEP, there is still much work to be done.

Of note, lophophaenids were found to have comparably high relative abundances and species richness in Southern Ocean assemblages (Renaudie and Lazarus, 2013b, 2016) to their EEP counterparts. Like the taxa discussed here, a large portion of SO lophophaenids had not been named or described prior to the work of Renaudie and Lazarus (2013a, 2014, 2015, 2016). This indicates that lophophaenid diversity is a vital component of total radiolarian diversity on a global scale, and is in need of greater attention by radiolarian workers. In modern oceans, molecular research also shows that Plagiacanthoidea (which includes Lophophaenidae) is extremely diverse; plagonids made up most of the sequences in the environmental DNA analyzed by Sandin *et al.* (2019). Plagiacanthoidea was also shown to be diverse in modern plankton assemblages across latitudes (Boltovskoy *et al.,* 2010) and water depths (Boltovskoy, 2017). Our research thus confirms that lophophaenids are a highly speciose group, based on the EEP material we examined. The sheer multitude of species makes this a challenging group to study—a difficulty that is compounded by species' complex morphologic structures, typically small size, sometimes incomplete preservation of specimens, and substantial gaps in the existing taxonomic framework. Nonetheless, we expect that future work on this clade will be highly productive and informative to estimates of global biodiversity; many undescribed species were too rare to be properly treated in this study. Both paleontological study of fossil forms and molecular sequencing of modern taxa have great potential to lead to a better understanding of past and present lophophaenid diversity, as well as marine plankton diversity more broadly.

**TABLE 1. Occurrence chart of Late Neogene–Recent lophophaenids in the EEP.**

Extremely rare (ER) = <0.1%; Rare (R) = 0.1–0.5%; Common (C) = 0.5–1%; Abundant (A) = >1%. Samples that were not enumerated are marked with asterisks and show abundance as X (= 1–2 specimens in the sample) or XX (= 3+ specimens in the sample).

| **Site** | | **1337D** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** |
|---|---|---|---|---|---|---|---|---|
| **Species-level specimens** | | **3569** | **3368** | **2355** | **2190** | **2165** | **2534** | **2144** |
| **Sample** | | **321-1337D-1H-1, 0-3cm** | **321-1337A-2H-3, 76-79cm** | **321-1337A-3H-2, 103-106cm** | **321-1337A-4H-2, 16-19cm** | **321-1337A-4H-6, 115-118cm** | **321-1337A-5H-5, 11-14cm** | **321-1337A-6H-3, 29-32cm** |
| **Depth (mbsf)** | | **0.02** | **8.78** | **17.55** | **26.18** | **33.16** | **40.13** | **46.81** |
| **Age (Ma)** | *** = not counted** | **0** | **0.7** | **1.2** | **1.7** | **2.3** | **2.7** | **3.1** |
| **Stage name** | | **Recent** | **Late Pleistocene** | **Middle Pleistocene** | **Middle Pleistocene** | **Early Pleistocene** | **Late Pliocene** | **Late Pliocene** |
| **Species** | **Author** | - | - | - | - | - | - | - |
| *Amphiplecta acrostoma* | Haeckel 1887 | ER | R | | ER | ER | ER | ER |
| *Amphiplecta cylindrocephala*? | Dumitrica 1973 | | | | | | | |
| *Amphiplecta tripleura?* | Funakawa 1995 | | | | | | | |
| *Amphiplecta kikimorae* n. sp. | | | | | | | | |
| *Amphiplecta* cf. *kikimora*e | open nomenclature | ER | | | | | | |
| *Arachnocorallium calvata* | (Haeckel 1887) Petrushevskaya 1971 | R | R | C | R | R | R | R |

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**TABLE 1.** (Continued)

| **Site** | | **1337D** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** |
|---|---|---|---|---|---|---|---|---|
| **Species-level specimens** | | **3569** | **3368** | **2355** | **2190** | **2165** | **2534** | **2144** |
| **Sample** | | **321-1337D-1H-1, 0-3cm** | **321-1337A-2H-3, 76-79cm** | **321-1337A-3H-2, 103-106cm** | **321-1337A-4H-2, 16-19cm** | **321-1337A-4H-6, 115-118cm** | **321-1337A-5H-5, 11-14cm** | **321-1337A-6H-3, 29-32cm** |
| **Depth (mbsf)** | | **0.02** | **8.78** | **17.55** | **26.18** | **33.16** | **40.13** | **46.81** |
| **Age (Ma)** | *** = not counted** | **0** | **0.7** | **1.2** | **1.7** | **2.3** | **2.7** | **3.1** |
| **Stage name** | | **Recent** | **Late Pleistocene** | **Middle Pleistocene** | **Middle Pleistocene** | **Early Pleistocene** | **Late Pliocene** | **Late Pliocene** |
| **Species** | **Author** | - | - | - | - | - | - | - |
| *Arachnocorallium* cf. *calvata*? | Petrushevskaya 1971 | R | R | | R | ER | | |
| *Arachnocorallium stilla* | Renaudie & Lazarus 2015 | | | | ER | | | |
| *Arachnocorys circumtexta* | (Haeckel 1862) Petrushevskaya 1971 | R | R | R | R | ER | R | |
| *Arachnocorys pentacantha* | (Popofsky 1913) Petrushevskaya 1971 | A | A | C | R | R | ER | |
| *Arachnocorys pentacantha wanii* | n. subsp. | R | R | C | C | R | R | R |
| *Arachnocorys spinosissima* | (Tan and Tchang 1976) n. comb. | | ER | ER | ER | | ER | |
| *Arachnocorys umbellifera* | (Haeckel 1862) Petrushevskaya 1971 | R | ER | ER | R | ER | R | R |
| *Arachnocorys jorogumoae* | n. sp. | | | | | | | |
| *Arachnocorys*? sp. | open nomenclature | ER | ER | ER | ER | | | |
| *Botryopera? daleki* | Renaudie and Lazarus 2013 | | | | | | | |
| *Botryopera setosa* | (Jørgensen 1900) Kruglikova 1989 | | R | | ER | | ER | |
| *Botryopera amabie* | n. sp. | | | | | | | |
| *Botryopera babayagae* | n. sp. | C | C | R | R | R | A | C |
| *Botryopera bolotniki* | n. sp. | | | | | | | |
| *Botryopera* sp. A | open nomenclature | | | | | | | |
| *Botryopera* sp. B | open nomenclature | | | | | | | |

*...... Continued on the next page*

**TABLE 1. (**Continued)

| **Site** | | **1337D** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** |
|---|---|---|---|---|---|---|---|---|
| **Species-level specimens** | | **3569** | **3368** | **2355** | **2190** | **2165** | **2534** | **2144** |
| **Sample** | | **321-1337D-1H-1, 0-3cm** | **321-1337A-2H-3, 76-79cm** | **321-1337A-3H-2, 103-106cm** | **321-1337A-4H-2, 16-19cm** | **321-1337A-4H-6, 115-118cm** | **321-1337A-5H-5, 11-14cm** | **321-1337A-6H-3, 29-32cm** |
| **Depth (mbsf)** | | **0.02** | **8.78** | **17.55** | **26.18** | **33.16** | **40.13** | **46.81** |
| **Age (Ma)** | *** = not counted** | **0** | **0.7** | **1.2** | **1.7** | **2.3** | **2.7** | **3.1** |
| **Stage name** | | **Recent** | **Late Pleistocene** | **Middle Pleistocene** | **Middle Pleistocene** | **Early Pleistocene** | **Late Pliocene** | **Late Pliocene** |
| **Species** | **Author** | - | - | - | - | - | - | - |
| *Ceratocyrtis cucullaris* | (Ehrenberg) Petrushevskaya 1971 | | | R | | | | |
| *Ceratocyrtis histricosa* | (Jørgensen 1905) Petrushevskaya 1971 | | R | ER | ER | R | R | ER |
| *Ceratocyrtis spinosiretis* | (Takahashi 1991) Matsuzaki et al 2015 | | | ER | R | R | | ER |
| *Ceratocyrtis*? *chimii* | n. sp. | | | | | | | |
| *Ceratocyrtis vila* | n. sp. | | | | | | | |
| *Ceratocyrtis* sp. A | open nomenclature | R | R | C | C | R | R | R |
| *Ceratocyrtis* sp. B | open nomenclature | ER | | | ER | ER | ER | ER |
| *Ceratocyrtis* sp. C | open nomenclature | | | | | ER | | ER |
| *Ceratocyrtis* sp. D | open nomenclature | | | | | | ER | ER |
| *Ceratocyrtis* sp. E | open nomenclature | | | | | | ER | |
| *Ceratocyrtis* sp. F | open nomenclature | | | | | | R | |
| *Ceratocyrtis* sp. G | open nomenclature | | | | | | | |
| *Ceratocyrtis* sp. H | open nomenclature | | | | | | | |
| *Ceratocyrtis* sp. I group | open nomenclature | | | | | | | |
| *Lithomelissa celsagula* | Renaudie and Lazarus 2015 | | | | | | | |
| *Lithomelissa cheni* | Caulet 1991 | | | | | | | |
| *Lithomelissa ehrenbergi* | Bütschli 1882 | ER | ER | R | R | R | R | R |

...... *Continued on the next page*

**TABLE 1.** (Continued)

| **Site** | | **1337D** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** |
|---|---|---|---|---|---|---|---|---|
| **Species-level specimens** | | **3569** | **3368** | **2355** | **2190** | **2165** | **2534** | **2144** |
| **Sample** | | **321-1337D-1H-1, 0-3cm** | **321-1337A-2H-3, 76-79cm** | **321-1337A-3H-2, 103-106cm** | **321-1337A-4H-2, 16-19cm** | **321-1337A-4H-6, 115-118cm** | **321-1337A-5H-5, 11-14cm** | **321-1337A-6H-3, 29-32cm** |
| **Depth (mbsf)** | | **0.02** | **8.78** | **17.55** | **26.18** | **33.16** | **40.13** | **46.81** |
| **Age (Ma)** | *** = not counted** | **0** | **0.7** | **1.2** | **1.7** | **2.3** | **2.7** | **3.1** |
| **Stage name** | | **Recent** | **Late Pleistocene** | **Middle Pleistocene** | **Middle Pleistocene** | **Early Pleistocene** | **Late Pliocene** | **Late Pliocene** |
| **Species** | **Author** | - | - | - | - | - | - | - |
| *Lithomelissa* cf. *ehrenbergi* | open nomenclature | | | | | | ER | |
| *Lithomelissa mitra* | Bütschli 1882 | | | | | | C | |
| *Lithomelissa alkonost* | n. sp. | | | ER | | R | | ER |
| *Lithomelissa babai* | n. sp. | ER | | R | ER | | C | ER |
| *Lithomelissa dybbuk* | n. sp. | | R | R | C | R | A | R |
| *Lithomelissa sirina* | n. sp. | | | R | A | A | C | A |
| *Lithomelissa* sp. A | open nomenclature | | | ER | | ER | R | ER |
| *Lithomelissa* sp. B | open nomenclature | R | ER | ER | | | ER | |
| *Lithomelissa* sp. C | open nomenclature | | | | | | | |
| *Lithomelissa* sp. D | open nomenclature | | ER | ER | ER | | | ER |
| *Lophophaena amictoria* | Renaudie and Lazarus 2015 | | ER | | | ER | | |
| *Lophophaena buetschlii* | (Haeckel 1887) Petrushevskaya 1971 | A | A | R | R | R | C | C |
| *Lophophaena cylindrica* | (Cleve 1900) Petrushevskaya 1971 | A | R | C | R | C | A | A |
| *Lophophaena hispida* | (Ehrenberg 1862) Petrushevskaya 1971 | A | A | A | C | A | A | ER |
| *Lophophaena laticeps* | (Jørgensen 1905) Kunihara and Matsuoka 2010 | | | | | | | |
| *Lophophaena? leberu* | Renaudie and Lazarus 2012 | | | | | | | |

...... *Continued on the next page*

**TABLE 1.** (Continued)

| **Site** | | **1337D** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** |
|---|---|---|---|---|---|---|---|---|
| **Species-level specimens** | | **3569** | **3368** | **2355** | **2190** | **2165** | **2534** | **2144** |
| **Sample** | | **321-1337D-1H-1, 0-3cm** | **321-1337A-2H-3, 76-79cm** | **321-1337A-3H-2, 103-106cm** | **321-1337A-4H-2, 16-19cm** | **321-1337A-4H-6, 115-118cm** | **321-1337A-5H-5, 11-14cm** | **321-1337A-6H-3, 29-32cm** |
| **Depth (mbsf)** | | **0.02** | **8.78** | **17.55** | **26.18** | **33.16** | **40.13** | **46.81** |
| **Age (Ma)** | *** = not counted** | **0** | **0.7** | **1.2** | **1.7** | **2.3** | **2.7** | **3.1** |
| **Stage name** | | **Recent** | **Late Pleistocene** | **Middle Pleistocene** | **Middle Pleistocene** | **Early Pleistocene** | **Late Pliocene** | **Late Pliocene** |
| **Species** | **Author** | - | - | - | - | - | - | - |
| *Lophophaena macrencephala* | Clark and Campbell 1945 partim. | | | | | | | |
| *Lophophaena nadezdae* | Petrushevskaya 1971 | C | A | C | A | C | A | C |
| *Lophophaena rhopalica* | Renaudie and Lazarus 2016 | | | | | | | |
| *Lophophaena simplex* | Funakawa 1994 | | | | | | | |
| *Lophophaena undulatum* | (Popofsky 1913) nov. comb. | ER | ER | R | ER | | | |
| *Lophophaena variabilis* | (Popofsky 1913) Petrushevskaya 1971 | R | | ER | | | | |
| *Lophophaena witjazii* | (Petrushevskaya 1971) nov. comb. | C | ER | R | | R | ER | R |
| *Trisulcus testudus?* | Petrushevskaya 1971 (group) | ER | | | | | ER | |
| *Lophophaena arie* | n. sp. | | ER | ER | R | ER | ER | ER |
| *Lophophaena casperi* | n. sp. | | | | | | | |
| *Lophophaena domovoi* | n. sp. | | | | | | | |
| *Lophophaena gozui* | n. sp. | | | | | | | |
| *Lophophaena ikiryo* | n. sp. | | | | | | | |
| *Lophophaena ikota* | n. sp. | | | | | | | ER |
| *Lophophaena kaonashii* | n. sp. | | | | | | | |
| *Lophophaena leshii* | n. sp. | | | | | | | |
| *Lophophaena rusalkae* | n. sp. | | | | | | | ER |
| *Lophophaena shishigae* | n. sp. | | | | | | | |

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**TABLE 1.** (Continued)

| **Site** | | **1337D** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** |
|---|---|---|---|---|---|---|---|---|
| **Species-level specimens** | | **3569** | **3368** | **2355** | **2190** | **2165** | **2534** | **2144** |
| **Sample** | | **321-1337D-1H-1, 0-3cm** | **321-1337A-2H-3, 76-79cm** | **321-1337A-3H-2, 103-106cm** | **321-1337A-4H-2, 16-19cm** | **321-1337A-4H-6, 115-118cm** | **321-1337A-5H-5, 11-14cm** | **321-1337A-6H-3, 29-32cm** |
| **Depth (mbsf)** | | **0.02** | **8.78** | **17.55** | **26.18** | **33.16** | **40.13** | **46.81** |
| **Age (Ma)** | *** = not counted** | **0** | **0.7** | **1.2** | **1.7** | **2.3** | **2.7** | **3.1** |
| **Stage name** | | **Recent** | **Late Pleistocene** | **Middle Pleistocene** | **Middle Pleistocene** | **Early Pleistocene** | **Late Pliocene** | **Late Pliocene** |
| **Species** | **Author** | - | - | - | - | - | - | - |
| *Lophophaena ushionii* | n. sp. | | | | | | | |
| *Lophophaena* cf. *decacantha* | open nomenclature | | | ER | | | | |
| *Lophophaena decacantha* group | (Haeckel 1887), sensu Takahashi (1991) | | R | R | R | ER | ER | ER |
| *Lophophaena* cf. *witjazii* | open nomenclature | ER | ER | ER | | R | | |
| *Lophophaena* sp. A | open nomenclature | | ER | | | | | |
| *Lophophaena* sp. B | open nomenclature | | | | | | | |
| *Lophophaena*? sp. C | open nomenclature | | ER | ER | ER | | ER | ER |
| *Lophophaena* sp. E group | open nomenclature | | | ER | | | | ER |
| *Lophophaena* sp. F | open nomenclature | A | A | A | C | C | R | C |
| *Lophophaena* sp. G | open nomenclature | | ER | R | ER | | ER | ER |
| *Lophophaena* sp. H | open nomenclature | | | | | | ER | |
| *Lophophaena* sp. I | open nomenclature | | | | ER | | ER | ER |
| *Lophophaena* sp. J | open nomenclature | | | | | | ER | |
| *Lophophaena* sp. L | open nomenclature | | | | | ER | | |
| *Lophophaena* sp. M | open nomenclature | | | | | | | |
| *Lophophaena* sp. N | open nomenclature | | | | | | | |
| *Lophophaena* sp. O | open nomenclature | ER | ER | ER | | | | |

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**TABLE 1. (**Continued)

| **Site** | | **1337D** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** |
|---|---|---|---|---|---|---|---|---|
| **Species-level specimens** | | **3569** | **3368** | **2355** | **2190** | **2165** | **2534** | **2144** |
| **Sample** | | **321-1337D-1H-1, 0-3cm** | **321-1337A-2H-3, 76-79cm** | **321-1337A-3H-2, 103-106cm** | **321-1337A-4H-2, 16-19cm** | **321-1337A-4H-6, 115-118cm** | **321-1337A-5H-5, 11-14cm** | **321-1337A-6H-3, 29-32cm** |
| **Depth (mbsf)** | | **0.02** | **8.78** | **17.55** | **26.18** | **33.16** | **40.13** | **46.81** |
| **Age (Ma)** | *** = not counted** | **0** | **0.7** | **1.2** | **1.7** | **2.3** | **2.7** | **3.1** |
| **Stage name** | | **Recent** | **Late Pleistocene** | **Middle Pleistocene** | **Middle Pleistocene** | **Early Pleistocene** | **Late Pliocene** | **Late Pliocene** |
| **Species** | **Author** | - | - | - | - | - | - | - |
| *Peromelissa phalacra* | (Haeckel 1887) Petrushevskaya 1971 | C | R | C | R | ER | ER | |
| *Peromelissa thoracites* | (Haeckel) Matsuzaki et al. 2015 | A | A | A | A | A | C | C |
| *Pelagomanes cantharoides* | Sugiyama and Furutani 1992 | | | | | | | |
| *Pelagomanes kozoi* | Renaudie and Lazarus 2013 | | | | | | | |
| *Pelagomanes morawanensis* | Funakawa 1995 | | | | | | | |
| *Pelagomanes tekopua* | O'Connor 1997 | | | | | | | |
| *Pelagomanes thaumasia* | Caulet 1991 | | | | ER | ER | | |
| *Pelagomanes ibburi* | n. sp. | ER | ER | ER | R | ER | | R |
| *Pelagomanes* sp. A | open nomenclature | | | | ER | | R | |
| *Pelagomanes*? sp. C | open nomenclature | | | | | | | |

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**TABLE 1.** (Continued)

| **Site** | | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** |
|---|---|---|---|---|---|---|---|---|
| **Species-level specimens** | | **2226** | **2177** | **2248** | **2518** | **2327** | **2649** | **NA** |
| **Sample** | | **321-1337A-7H-6, 104-107cm** | **321-1337A-10H-2, 91-94cm** | **321-1337A-12H-5, 23-26cm** | **321-1337A-14H-7, 39-42cm** | **321-1337A-16H-6, 121-124cm** | **321-1337A-18H-6,77-80cm** | **321-1337A-21H-1, 33-35cm** |
| **Depth (mbsf)** | | **61.55** | **83.93** | **106.74** | **128.91** | **147.22** | **165.79** | **186.35** |
| **Age (Ma)** | *** = not counted** | **3.8** | **4.8** | **5.8** | **6.7** | **7.4** | **8.2** | **9.4*** |
| **Stage name** | | **Early Pliocene** | **Early Pliocene** | **Late Miocene** | **Late Miocene** | **Late Miocene** | **Late Miocene** | **Late Miocene** |
| **Species** | **Author** | - | - | - | - | - | - | - |
| *Amphiplecta acrostoma* | Haeckel 1887 | R | R | R | ER | | | |
| *Amphiplecta cylindrocephala*? | Dumitrica 1973 | | ER | | | | | |
| *Amphiplecta tripleura?* | Funakawa 1995 | | | | | | ER | |
| *Amphiplecta kikimorae* n. sp. | | R | | | | | | |
| *Amphiplecta* cf. *kikimora*e | open nomenclature | ER | | | | | | |
| *Arachnocorallium calvata* | (Haeckel 1887) Petrushevskaya 1971 | ER | R | ER | R | R | R | |
| *Arachnocorallium* cf. *calvata*? | Petrushevskaya 1971 | | | | | | | |
| *Arachnocorallium stilla* | Renaudie & Lazarus 2015 | | | ER | | | | |
| *Arachnocorys circumtexta* | (Haeckel 1862) Petrushevskaya 1971 | ER | | ER | ER | | | |
| *Arachnocorys pentacantha* | (Popofsky 1913) Petrushevskaya 1971 | | | | | | | |
| *Arachnocorys pentacantha wanii* | n. subsp. | | | | | | | |
| *Arachnocorys spinosissima* | (Tan and Tchang 1976) n. comb. | | R | R | R | | | |
| *Arachnocorys umbellifera* | (Haeckel 1862) Petrushevskaya 1971 | C | C | A | C | C | R | |
| *Arachnocorys jorogumoae* | n. sp. | | | | C | C | | X |
| *Arachnocorys*? sp. | open nomenclature | ER | | | | | | |

*.....Continued on the next page*

**TABLE 1.** (Continued)

| **Site** | | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** |
|---|---|---|---|---|---|---|---|---|
| **Species-level specimens** | | **2226** | **2177** | **2248** | **2518** | **2327** | **2649** | **NA** |
| **Sample** | | **321-1337A-7H-6, 104-107cm** | **321-1337A-10H-2, 91-94cm** | **321-1337A-12H-5, 23-26cm** | **321-1337A-14H-7, 39-42cm** | **321-1337A-16H-6, 121-124cm** | **321-1337A-18H-6,77-80cm** | **321-1337A-21H-1, 33-35cm** |
| **Depth (mbsf)** | | **61.55** | **83.93** | **106.74** | **128.91** | **147.22** | **165.79** | **186.35** |
| **Age (Ma)** | *** = not counted** | **3.8** | **4.8** | **5.8** | **6.7** | **7.4** | **8.2** | **9.4*** |
| **Stage name** | | **Early Pliocene** | **Early Pliocene** | **Late Miocene** | **Late Miocene** | **Late Miocene** | **Late Miocene** | **Late Miocene** |
| **Species** | **Author** | - | - | - | - | - | - | - |
| *Botryopera? daleki* | Renaudie and Lazarus 2013 | | | | R | | ER | |
| *Botryopera setosa* | (Jørgensen 1900) Kruglikova 1989 | R | | | | | | |
| *Botryopera amabie* | n. sp. | | | | | | | |
| *Botryopera babayagae* | n. sp. | R | C | R | | ER | | |
| *Botryopera bolotniki* | n. sp. | | ER | | R | ER | | |
| *Botryopera* sp. A | open nomenclature | | | | | | | |
| *Botryopera* sp. B | open nomenclature | | | | | | | |
| *Ceratocyrtis cucullaris* | (Ehrenberg) Petrushevskaya 1971 | | | | | | | |
| *Ceratocyrtis histricosa* | (Jørgensen 1905) Petrushevskaya 1971 | | | ER | | R | | |
| *Ceratocyrtis spinosiretis* | (Takahashi 1991) Matsuzaki et al 2015 | | | | R | ER | ER | |
| *Ceratocyrtis? chimii* | n. sp. | | | | | | | XX |
| *Ceratocyrtis vila* | n. sp. | | C | R | C | R | C | X |
| *Ceratocyrtis* sp. A | open nomenclature | R | R | ER | R | R | | |
| *Ceratocyrtis* sp. B | open nomenclature | | | ER | ER | ER | | |
| *Ceratocyrtis* sp. C | open nomenclature | | | | | | | |

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**TABLE 1.** (Continued)

| **Site** | | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** |
|---|---|---|---|---|---|---|---|---|
| **Species-level specimens** | | **2226** | **2177** | **2248** | **2518** | **2327** | **2649** | **NA** |
| **Sample** | | **321-1337A-7H-6, 104-107cm** | **321-1337A-10H-2, 91-94cm** | **321-1337A-12H-5, 23-26cm** | **321-1337A-14H-7, 39-42cm** | **321-1337A-16H-6, 121-124cm** | **321-1337A-18H-6,77-80cm** | **321-1337A-21H-1, 33-35cm** |
| **Depth (mbsf)** | | **61.55** | **83.93** | **106.74** | **128.91** | **147.22** | **165.79** | **186.35** |
| **Age (Ma)** | *** = not counted** | **3.8** | **4.8** | **5.8** | **6.7** | **7.4** | **8.2** | **9.4*** |
| **Stage name** | | **Early Pliocene** | **Early Pliocene** | **Late Miocene** | **Late Miocene** | **Late Miocene** | **Late Miocene** | **Late Miocene** |
| **Species** | **Author** | - | - | - | - | - | - | - |
| *Ceratocyrtis* sp. D | open nomenclature | ER | ER | | | | ER | |
| *Ceratocyrtis* sp. E | open nomenclature | | R | | R | | R | |
| *Ceratocyrtis* sp. F | open nomenclature | | | R | ER | R | C | |
| *Ceratocyrtis* sp. G | open nomenclature | | | | | | ER | |
| *Ceratocyrtis* sp. H | open nomenclature | | | | | | | |
| *Ceratocyrtis* sp. I group | open nomenclature | | | | | R | R | |
| *Lithomelissa celsagula* | Renaudie and Lazarus 2015 | | | | | ER | ER | |
| *Lithomelissa cheni* | Caulet 1991 | | | | | ER | | |
| *Lithomelissa ehrenbergi* | Bütschli 1882 | R | ER | | | ER | | |
| *Lithomelissa* cf. *ehrenbergi* | open nomenclature | A | C | R | | R | | |
| *Lithomelissa mitra* | Bütschli 1882 | C | C | ER | | ER | | |
| *Lithomelissa alkonost* | n. sp. | R | ER | R | C | A | R | |
| *Lithomelissa babai* | n. sp. | R | R | | | | | |
| *Lithomelissa dybbuk* | n. sp. | ER | ER | ER | ER | | | |
| *Lithomelissa sirina* | n. sp. | C | A | A | A | A | A | |
| *Lithomelissa* sp. A | open nomenclature | R | | ER | | | | |
| *Lithomelissa* sp. B | open nomenclature | ER | ER | ER | | | ER | |
| *Lithomelissa* sp. C | open nomenclature | | | | | | ER | |
| *Lithomelissa* sp. D | open nomenclature | R | R | | | ER | | |
| *Lophophaena amictoria* | Renaudie and Lazarus 2015 | | ER | | | | | |

*.....Continued on the next page*

**TABLE 1.** (Continued)

| **Site** | | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** |
|---|---|---|---|---|---|---|---|---|
| **Species-level specimens** | | **2226** | **2177** | **2248** | **2518** | **2327** | **2649** | **NA** |
| **Sample** | | **321-1337A-7H-6, 104-107cm** | **321-1337A-10H-2, 91-94cm** | **321-1337A-12H-5, 23-26cm** | **321-1337A-14H-7, 39-42cm** | **321-1337A-16H-6, 121-124cm** | **321-1337A-18H-6,77-80cm** | **321-1337A-21H-1, 33-35cm** |
| **Depth (mbsf)** | | **61.55** | **83.93** | **106.74** | **128.91** | **147.22** | **165.79** | **186.35** |
| **Age (Ma)** | *** = not counted** | **3.8** | **4.8** | **5.8** | **6.7** | **7.4** | **8.2** | **9.4*** |
| **Stage name** | | **Early Pliocene** | **Early Pliocene** | **Late Miocene** | **Late Miocene** | **Late Miocene** | **Late Miocene** | **Late Miocene** |
| **Species** | **Author** | - | - | - | - | - | - | - |
| *Lophophaena buetschlii* | (Haeckel 1887) Petrushevskaya 1971 | R | R | ER | ER | | | |
| *Lophophaena cylindrica* | (Cleve 1900) Petrushevskaya 1971 | A | A | A | R | | | |
| *Lophophaena hispida* | (Ehrenberg 1862) Petrushevskaya 1971 | | | | | | | |
| *Lophophaena laticeps* | (Jørgensen 1905) Kunihara and Matsuoka 2010 | ER | R | | | | | |
| *Lophophaena? leberu* | Renaudie and Lazarus 2012 | | ER | | | | | |
| *Lophophaena macrencephala* | Clark and Campbell 1945 partim. | | | ER | | ER | ER | |
| *Lophophaena nadezdae* | Petrushevskaya 1971 | R | C | R | R | | ER | |
| *Lophophaena rhopalica* | Renaudie and Lazarus 2016 | | | | | | | |
| *Lophophaena simplex* | Funakawa 1994 | | | | | | | |
| *Lophophaena undulatum* | (Popofsky 1913) nov. comb. | R | R | ER | | | | |
| *Lophophaena variabilis* | (Popofsky 1913) Petrushevskaya 1971 | | | | | | | |
| *Lophophaena witjazii* | (Petrushevskaya 1971) nov. comb. | R | R | R | R | R | ER | |
| *Trisulcus testudus?* | Petrushevskaya 1971 (group) | | | | | | | |
| *Lophophaena arie* | n. sp. | ER | | ER | | ER | | |

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**TABLE 1.** (Continued)

| **Site** | | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** |
|---|---|---|---|---|---|---|---|---|
| **Species-level specimens** | | **2226** | **2177** | **2248** | **2518** | **2327** | **2649** | **NA** |
| **Sample** | | **321-1337A-7H-6, 104-107cm** | **321-1337A-10H-2, 91-94cm** | **321-1337A-12H-5, 23-26cm** | **321-1337A-14H-7, 39-42cm** | **321-1337A-16H-6, 121-124cm** | **321-1337A-18H-6,77-80cm** | **321-1337A-21H-1, 33-35cm** |
| **Depth (mbsf)** | | **61.55** | **83.93** | **106.74** | **128.91** | **147.22** | **165.79** | **186.35** |
| **Age (Ma)** | *** = not counted** | **3.8** | **4.8** | **5.8** | **6.7** | **7.4** | **8.2** | **9.4*** |
| **Stage name** | | **Early Pliocene** | **Early Pliocene** | **Late Miocene** | **Late Miocene** | **Late Miocene** | **Late Miocene** | **Late Miocene** |
| **Species** | **Author** | - | - | - | - | - | - | - |
| *Lophophaena casperi* | n. sp. | | | | C | A | A | XX |
| *Lophophaena domovoi* | n. sp. | | | | | | | |
| *Lophophaena gozui* | n. sp. | | | | | | | |
| *Lophophaena ikiryo* | n. sp. | | R | R | C | C | | |
| *Lophophaena ikota* | n. sp. | ER | ER | ER | | | | |
| *Lophophaena kaonashii* | n. sp. | | | | | | | |
| *Lophophaena leshii* | n. sp. | | | | | | | |
| *Lophophaena rusalkae* | n. sp. | R | | ER | C | | R | |
| *Lophophaena shishigae* | n. sp. | | | | | | | X |
| *Lophophaena ushionii* | n. sp. | | | | | | | |
| *Lophophaena* cf. *decacantha* | open nomenclature | | | | | | | |
| *Lophophaena decacantha* group | (Haeckel 1887), sensu Takahashi (1991) | ER | ER | ER | | | | |
| *Lophophaena* cf. *witjazii* | open nomenclature | | | | ER | ER | | |
| *Lophophaena* sp. A | open nomenclature | | | | | | | |
| *Lophophaena* sp. B | open nomenclature | | | ER | | | | |
| *Lophophaena*? sp. C | open nomenclature | | ER | ER | | | | |
| *Lophophaena* sp. E group | open nomenclature | | ER | | | | | |
| *Lophophaena* sp. F | open nomenclature | R | R | R | | | | |
| *Lophophaena* sp. G | open nomenclature | ER | | | | | | |

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**TABLE 1.** (Continued)

| **Site** | | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** |
|---|---|---|---|---|---|---|---|---|
| **Species-level specimens** | | **2226** | **2177** | **2248** | **2518** | **2327** | **2649** | **NA** |
| **Sample** | | **321-1337A-7H-6, 104-107cm** | **321-1337A-10H-2, 91-94cm** | **321-1337A-12H-5, 23-26cm** | **321-1337A-14H-7, 39-42cm** | **321-1337A-16H-6, 121-124cm** | **321-1337A-18H-6,77-80cm** | **321-1337A-21H-1, 33-35cm** |
| **Depth (mbsf)** | | **61.55** | **83.93** | **106.74** | **128.91** | **147.22** | **165.79** | **186.35** |
| **Age (Ma)** | *** = not counted** | **3.8** | **4.8** | **5.8** | **6.7** | **7.4** | **8.2** | **9.4*** |
| **Stage name** | | **Early Pliocene** | **Early Pliocene** | **Late Miocene** | **Late Miocene** | **Late Miocene** | **Late Miocene** | **Late Miocene** |
| **Species** | **Author** | - | - | - | - | - | - | - |
| *Lophophaena* sp. H | open nomenclature | ER | | ER | ER | | | |
| *Lophophaena* sp. I | open nomenclature | ER | ER | ER | ER | R | | |
| *Lophophaena* sp. J | open nomenclature | ER | | | R | R | ER | |
| *Lophophaena* sp. L | open nomenclature | ER | ER | | | | | |
| *Lophophaena* sp. M | open nomenclature | | ER | | | | | |
| *Lophophaena* sp. N | open nomenclature | | ER | | | | | |
| *Lophophaena* sp. O | open nomenclature | | | ER | | | | |
| *Peromelissa phalacra* | (Haeckel 1887) Petrushevskaya 1971 | | ER | | | | | |
| *Peromelissa thoracites* | (Haeckel) Matsuzaki et al. 2015 | R | R | ER | R | | | |
| *Pelagomanes cantharoides* | Sugiyama and Furutani 1992 | | | | | | | |
| *Pelagomanes kozoi* | Renaudie and Lazarus 2013 | | | ER | ER | ER | | |
| *Pelagomanes morawanensis* | Funakawa 1995 | | | | | | | |
| *Pelagomanes tekopua* | O'Connor 1997 | | | | | | | |
| *Pelagomanes thaumasia* | Caulet 1991 | | | | | | R | |
| *Pelagomanes ibburi* | n. sp. | ER | ER | R | C | C | R | |
| *Pelagomanes* sp. A | open nomenclature | ER | ER | ER | | | | |
| *Pelagomanes*? sp. B | open nomenclature | | | | | | | |
| *Pelagomanes*? sp. C | open nomenclature | | | | | | | |

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**TABLE 1.** (Continued)

| **Site** | | **1337D** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** |
|---|---|---|---|---|---|---|---|
| **Species-level specimens** | | **2841** | **NA** | **NA** | **NA** | **NA** | **NA** |
| **Sample** | | **321-1337D-23H-6,134-137cm** | **321-1337D-26H-3, 142-144cm** | **321-1337D-30H-3, 103-104cm** | **321-1337A-31X-6, 4-6cm** | **321-1337A-34X-2, 40-42cm** | **321-1337A-35X-1, 106-108cm** |
| **Depth (mbsf)** | | **208.45** | **232.53** | **261.37** | **288.06** | **311.30** | **320.23** |
| **Age (Ma)** | *** = not counted** | **10.3** | **11.2 (12)*** | **12.2 (13)*** | **~14*** | **~15*** | **~15.5*** |
| **Stage name** | | **Late Miocene** | **Late Miocene** | **Middle Miocene** | **Middle Miocene** | **Middle Miocene** | **Middle Miocene** |
| **Species** | **Author** | - | - | - | - | - | - |
| *Amphiplecta acrostoma* | Haeckel 1887 | ER | | | | | |
| *Amphiplecta cylindrocephala*? | Dumitrica 1973 | | | | | | |
| *Amphiplecta tripleura?* | Funakawa 1995 | ER | X | XX | | X | |
| *Amphiplecta kikimorae* n. sp. | | | | | | | |
| *Amphiplecta* cf. *kikimora*e | open nomenclature | | | | | | |
| *Arachnocorallium calvata* | (Haeckel 1887) Petrushevskaya 1971 | ER | | | | | |
| *Arachnocorallium* cf. *calvata*? | Petrushevskaya 1971 | | | | | | |
| *Arachnocorallium stilla* | Renaudie & Lazarus 2015 | | | | | | |
| *Arachnocorys circumtexta* | (Haeckel 1862) Petrushevskaya 1971 | | | | | | |
| *Arachnocorys pentacantha* | (Popofsky 1913) Petrushevskaya 1971 | | | | | | |
| *Arachnocorys pentacantha wanii* | n. subsp. | | | | | | |
| *Arachnocorys spinosissima* | (Tan and Tchang 1976) n. comb. | | | | | | |
| *Arachnocorys umbellifera* | (Haeckel 1862) Petrushevskaya 1971 | | | | | | |
| *Arachnocorys jorogumoae* | n. sp. | | | X | | | |
| *Arachnocorys*? sp. | open nomenclature | | | | | | |
| *Botryopera? daleki* | Renaudie and Lazarus 2013 | ER | X | XX | XX | X | |
| *Botryopera setosa* | (Jørgensen 1900) Kruglikova 1989 | ER | | | X | | X |
| *Botryopera amabie* | n. sp. | | X | XX | XX | | XX |
| *Botryopera babayagae* | n. sp. | | | | | | |
| *Botryopera bolotniki* | n. sp. | ER | | | | | |
| *Botryopera* sp. A | open nomenclature | | X | X | X | | |
| *Botryopera* sp. B | open nomenclature | | X | X | | | |
| *Ceratocyrtis cucullaris* | (Ehrenberg) Petrushevskaya 1971 | | | | | | |

*.....Continued on the next page*

**TABLE 1.** (Continued)

| **Site** | | **1337D** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** |
|---|---|---|---|---|---|---|---|
| **Species-level specimens** | | **2841** | **NA** | **NA** | **NA** | **NA** | **NA** |
| **Sample** | | **321-1337D-23H-6,134-137cm** | **321-1337D-26H-3, 142-144cm** | **321-1337D-30H-3, 103-104cm** | **321-1337A-31X-6, 4-6cm** | **321-1337A-34X-2, 40-42cm** | **321-1337A-35X-1, 106-108cm** |
| **Depth (mbsf)** | | **208.45** | **232.53** | **261.37** | **288.06** | **311.30** | **320.23** |
| **Age (Ma)** | *** = not counted** | **10.3** | **11.2 (12)*** | **12.2 (13)*** | **~14*** | **~15*** | **~15.5*** |
| **Stage name** | | **Late Miocene** | **Late Miocene** | **Middle Miocene** | **Middle Miocene** | **Middle Miocene** | **Middle Miocene** |
| **Species** | **Author** | - | - | - | - | - | - |
| *Ceratocyrtis histricosa* | (Jørgensen 1905) Petrushevskaya 1971 | ER | | | | | |
| *Ceratocyrtis spinosiretis* | (Takahashi 1991) Matsuzaki et al 2015 | ER | | | | | |
| *Ceratocyrtis*? *chimii* | n. sp. | C | X | | | | |
| *Ceratocyrtis vila* | n. sp. | R | | | | | X |
| *Ceratocyrtis* sp. A | open nomenclature | | | | | | |
| *Ceratocyrtis* sp. B | open nomenclature | ER | | | | | |
| *Ceratocyrtis* sp. C | open nomenclature | | | | | | |
| *Ceratocyrtis* sp. D | open nomenclature | R | | | | | |
| *Ceratocyrtis* sp. E | open nomenclature | ER | | | | | |
| *Ceratocyrtis* sp. F | open nomenclature | C | | | | | |
| *Ceratocyrtis* sp. G | open nomenclature | | | | | | |
| *Ceratocyrtis* sp. H | open nomenclature | R | X | | | | |
| *Ceratocyrtis* sp. I group | open nomenclature | R | | | | | |
| *Lithomelissa celsagula* | Renaudie and Lazarus 2015 | | | | | | |
| *Lithomelissa cheni* | Caulet 1991 | R | | | | | |
| *Lithomelissa ehrenbergi* | Bütschli 1882 | | | | | | |
| *Lithomelissa* cf. *ehrenbergi* | open nomenclature | | | | | | |
| *Lithomelissa mitra* | Bütschli 1882 | | | | | | |
| *Lithomelissa alkonost* | n. sp. | R | | | | | |
| *Lithomelissa babai* | n. sp. | | | | | | |
| *Lithomelissa dybbuk* | n. sp. | | | | | | |
| *Lithomelissa sirina* | n. sp. | A | | | | | |
| *Lithomelissa* sp. A | open nomenclature | | | | | | |
| *Lithomelissa* sp. B | open nomenclature | | | | | | |
| *Lithomelissa* sp. C | open nomenclature | ER | | | | | |
| *Lithomelissa* sp. D | open nomenclature | | | | | | |
| *Lophophaena amictoria* | Renaudie and Lazarus 2015 | | | X | | | |

*.....Continued on the next page*

**TABLE 1.** (Continued)

| **Site** | | **1337D** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** |
|---|---|---|---|---|---|---|---|
| **Species-level specimens** | | **2841** | **NA** | **NA** | **NA** | **NA** | **NA** |
| **Sample** | | **321-1337D-23H-6,134-137cm** | **321-1337D-26H-3, 142-144cm** | **321-1337D-30H-3, 103-104cm** | **321-1337A-31X-6, 4-6cm** | **321-1337A-34X-2, 40-42cm** | **321-1337A-35X-1, 106-108cm** |
| **Depth (mbsf)** | | **208.45** | **232.53** | **261.37** | **288.06** | **311.30** | **320.23** |
| **Age (Ma)** | *** = not counted** | **10.3** | **11.2 (12)*** | **12.2 (13)*** | **~14*** | **~15*** | **~15.5*** |
| **Stage name** | | **Late Miocene** | **Late Miocene** | **Middle Miocene** | **Middle Miocene** | **Middle Miocene** | **Middle Miocene** |
| **Species** | **Author** | - | - | - | - | - | - |
| *Lophophaena buetschlii* | (Haeckel 1887) Petrushevskaya 1971 | | | | | | |
| *Lophophaena cylindrica* | (Cleve 1900) Petrushevskaya 1971 | | | | | | |
| *Lophophaena hispida* | (Ehrenberg 1862) Petrushevskaya 1971 | | | | | | |
| *Lophophaena laticeps* | (Jørgensen 1905) Kunihara and Matsuoka 2010 | | | | | | |
| *Lophophaena? leberu* | Renaudie and Lazarus 2012 | | | | | | |
| *Lophophaena macrencephala* | Clark and Campbell 1945 partim. | | | | | | |
| *Lophophaena nadezdae* | Petrushevskaya 1971 | | | | | | |
| *Lophophaena rhopalica* | Renaudie and Lazarus 2016 | ER | XX | XX | X | | X |
| *Lophophaena simplex* | Funakawa 1994 | | X | X | | | |
| *Lophophaena undulatum* | (Popofsky 1913) nov. comb. | R | | | | | |
| *Lophophaena variabilis* | (Popofsky 1913) Petrushevskaya 1971 | | | | | | |
| *Lophophaena witjazii* | (Petrushevskaya 1971) nov. comb. | | | | | | |
| *Trisulcus testudus?* | Petrushevskaya 1971 (group) | | | | | | |
| *Lophophaena arie* | n. sp. | | | | | | |
| *Lophophaena casperi* | n. sp. | | | | | | |
| *Lophophaena domovoi* | n. sp. | C | | | X | | |
| *Lophophaena gozui* | n. sp. | R | XX | | XX | | |
| *Lophophaena ikiryo* | n. sp. | | | | | | |
| *Lophophaena ikota* | n. sp. | R | XX | | | | |
| *Lophophaena kaonashii* | n. sp. | ER | XX | X | XX | | |
| *Lophophaena leshii* | n. sp. | C | | | | | |
| *Lophophaena rusalkae* | n. sp. | ER | | | | | |
| *Lophophaena shishigae* | n. sp. | R | | | | | |
| *Lophophaena ushionii* | n. sp. | | X | | XX | | |
| *Lophophaena* cf. *decacantha* | open nomenclature | | | | | | |

*.....Continued on the next page*

**TABLE 1.** (Continued)

| **Site** | | **1337D** | **1337A** | **1337A** | **1337A** | **1337A** | **1337A** |
|---|---|---|---|---|---|---|---|
| **Species-level specimens** | | **2841** | **NA** | **NA** | **NA** | **NA** | **NA** |
| **Sample** | | **321-1337D-23H-6,134-137cm** | **321-1337D-26H-3, 142-144cm** | **321-1337D-30H-3, 103-104cm** | **321-1337A-31X-6, 4-6cm** | **321-1337A-34X-2, 40-42cm** | **321-1337A-35X-1, 106-108cm** |
| **Depth (mbsf)** | | **208.45** | **232.53** | **261.37** | **288.06** | **311.30** | **320.23** |
| **Age (Ma)** | *** = not counted** | **10.3** | **11.2 (12)*** | **12.2 (13)*** | **~14*** | **~15*** | **~15.5*** |
| **Stage name** | | **Late Miocene** | **Late Miocene** | **Middle Miocene** | **Middle Miocene** | **Middle Miocene** | **Middle Miocene** |
| **Species** | **Author** | - | - | - | - | - | - |
| *Lophophaena decacantha* group | (Haeckel 1887), sensu Takahashi (1991) | | | | | | |
| *Lophophaena* cf. *witjazii* | open nomenclature | | | | | | |
| *Lophophaena* sp. A | open nomenclature | | | | | | |
| *Lophophaena* sp. B | open nomenclature | ER | | | | | |
| *Lophophaena*? sp. C | open nomenclature | | | | | | |
| *Lophophaena* sp. E group | open nomenclature | | | | | | |
| *Lophophaena* sp. F | open nomenclature | | | | | | |
| *Lophophaena* sp. G | open nomenclature | | | | | | |
| *Lophophaena* sp. H | open nomenclature | | | | | | |
| *Lophophaena* sp. I | open nomenclature | | | | | | |
| *Lophophaena* sp. J | open nomenclature | | | | | | |
| *Lophophaena* sp. L | open nomenclature | ER | | | | | |
| *Lophophaena* sp. M | open nomenclature | ER | | | | | |
| *Lophophaena* sp. N | open nomenclature | | | | | | |
| *Lophophaena* sp. O | open nomenclature | | | | | | |
| *Peromelissa phalacra* | (Haeckel 1887) Petrushevskaya 1971 | | | | | | |
| *Peromelissa thoracites* | (Haeckel) Matsuzaki et al. 2015 | | | | | | |
| *Pelagomanes cantharoides* | Sugiyama and Furutani 1992 | | XX | X | XX | | X |
| *Pelagomanes kozoi* | Renaudie and Lazarus 2013 | R | XX | | | | |
| *Pelagomanes morawanensis* | Funakawa 1995 | R | XX | X | XX | | |
| *Pelagomanes tekopua* | O'Connor 1997 | | | | X | | |
| *Pelagomanes thaumasia* | Caulet 1991 | ER | XX | XX | XX | | X |
| *Pelagomanes ibburi* | n. sp. | R | X | X | X | | XX |
| *Pelagomanes* sp. A | open nomenclature | | | | | | |
| *Pelagomanes*? sp. B | open nomenclature | | X | XX | | | |
| *Pelagomanes*? sp. C | open nomenclature | | | | XX | | |

## ACKNOWLEDGMENTS

We thank the International Ocean Discovery Program (IODP) for providing sediment samples; the U.S. Science Support Program (Schlanger Fellowship), Geological Society of America, Paleontological Society, Cushman Foundation, German Academic Exchange Service (DAAD), and Make Our Planet Great Again—German Research Initiative (MOPGRA-GRI) for funding this work; and Fr. Sylvia Salzmann (Museum für Naturkunde) for sample preparation.

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## SUPPLEMENTARY TABLE 1.

Holotype and paratype specimens, designated by sample #, slide #, museum #, England Finder coordinates, and plate citation in this manuscript. Part A indicates the museum number of each slide containing type material. Part B lists the holotype and all paratypes of each new species and subspecies.

**Part A: List of museum numbers for each slide.**

| Sample | Slide # | Museum # |
|---|---|---|
| 321-1337A-3H-2, 103-106cm | slide 1 | **ECO-126** |
| 321-1337A-4H-2, 16-19cm | slide 1 | **ECO-127** |
| 321-1337A-4H-2, 16-19cm | slide 2 | **ECO-128** |
| 321-1337A-4H-2, 16-19cm | slide 3 | **ECO-129** |
| 321-1337A-4H-6, 115-118cm | slide 1 | **ECO-130** |
| 321-1337A-4H-6, 115-118cm | slide 2 | **ECO-131** |
| 321-1337A-4H-6, 115-118cm | slide 3 | **ECO-132** |
| 321-1337A-7H-6, 104-107cm | slide 1 | **ECO-133** |
| 321-1337A-7H-6, 104-107cm | slide 2 | **ECO-134** |
| 321-1337A-7H-6, 104-107cm | slide 3 | **ECO-135** |
| 321-1337A-12H-5, 23-26cm | slide 1 | **ECO-136** |
| 321-1337A-12H-5, 23-26cm | slide 2 | **ECO-137** |
| 321-1337A-14H-7, 39-42cm | slide 1 | **ECO-138** |
| 321-1337A-14H-7, 39-42cm | slide 2 | **ECO-139** |
| 321-1337A-14H-7, 39-42cm | slide 3 | **ECO-140** |
| 321-1337A-16H-6, 121-124cm | slide 1 | **ECO-141** |
| 321-1337A-16H-6, 121-124cm | slide 2 | **ECO-142** |
| 321-1337A-16H-6, 121-124cm | slide 3 | **ECO-143** |
| 321-1337A-21H-1, 33-35cm | slide 2 | **ECO-144** |
| 321-1337D-23H-6,134-137cm | slide 1 | **ECO-145** |
| 321-1337D-23H-6,134-137cm | slide 2 | **ECO-146** |
| 321-1337D-23H-6,134-137cm | slide 3 | **ECO-147** |
| 321-1337D-26H-3, 142-144cm | slide 3 | **ECO-148** |
| 321-1337D-30H-3, 103-104cm | slide 1 | **ECO-149** |
| 321-1337D-30H-3, 103-104cm | slide 3 | **ECO-150** |
| 321-1337A-31X-6, 4-6cm | slide 2 | **ECO-151** |

**Part B. Type material of each new species.**

| Species | *Amphiplecta kikimorae* | *Arachnocorys jorogumoae* | *Arachnocorys pentacantha wanii* | *Botryopera amabie* | *Botryopera babayagae* |
|---|---|---|---|---|---|
| **Holotype** | 321-1337A-7H-6, 104-107cm; slide #2; L4-1; ECO-134 | 321-1337A-14H-7, 39-42cm; slide #1; X12-1; ECO-138 | 321-1337A-4H-2, 16-19cm; slide #1; P21-1; ECO-127 | 321-1337D-30H-3, 103-104cm, slide #3; O43-4; ECO-150 | 321-1337A-3H-2, 103-106cm; slide #1; E35-2; ECO-126 |
| **Holotype citation** | Pl. 2, Figs. 1A-C | Pl. 4, Figs. 2A-B | Pl. 5, Figs. 1A-C | Pl. 7, Figs. 4A-B | Pl. 9, Figs. 2A-B |
| **Paratype 1** | 321-1337A-7H-6, 104-107cm; slide #2; S32-2; ECO-134 | 321-1337A-16H-6, 121-124cm; slide #1; L11-3; ECO-141 | 321-1337A-3H-2, 103-106cm; slide #1; G2-2; ECO-126 | 321-1337D-30H-3, 103-104cm, slide #1; O36-2; ECO-149 | 321-1337A-3H-2, 103-106cm; slide #1; E35-2; ECO-126 |
| **Paratype 1 citation** | Pl. 2, Figs. 2A-B | Pl. 4, Figs. 1A-B | Pl. 5, Figs. 3A-B | not figured | Pl. 9, Figs. 1A-B |
| **Paratype 2** | 321-1337A-7H-6, 104-107cm; slide #3; K5-1; ECO-135 | 321-1337A-14H-7, 39-42cm; slide #1; Q20-3; ECO-138 | 321-1337A-3H-2, 103-106cm; slide #1; J42-3; ECO-126 | 321-1337D-30H-3, 103-104cm, slide #1; D4-3; ECO-149 | 321-1337A-4H-6, 115-118cm, slide #1, S19-4; ECO-130 |
| **Paratype 2 citation** | Pl. 2, Figs. 3A-B | Pl. 4, Fig. 3 | Pl. 5, Figs. 6A-B | Pl. 7, Fig. 5 | Pl. 9, Figs. 6A-B |
| **Paratype 3** | 321-1337A-7H-6, 104-107cm; slide #3; R6-2; ECO-135 | 321-1337A-21H-1, 33-35cm; slide #2; E18-4; ECO-144 | 321-1337A-3H-2, 103-106cm; slide #1; Y4-3; ECO-126 | | 321-1337A-4H-2, 16-19cm; slide #1; P21-1; ECO-127 |
| **Paratype 3 citation** | Pl. 2, Fig. 4 | Pl. 4, Figs. 4A-B | Pl. 5, Figs. 7A-B | | Pl. 9, Figs. 5A-B |
| **Paratype 4** | 321-1337A-7H-6, 104-107cm; slide #2; Q17-1; ECO-134 | 321-1337A-16H-6, 121-124cm; slide #1; K29-1; ECO-141 | 321-1337A-4H-2, 16-19cm; slide #1; P19-3; ECO-127 | | 321-1337A-3H-2, 103-106cm; slide #1; K30-1; ECO-126 |
| **Paratype 4 citation** | Pl. 2, Figs. 5A-B | Pl. 4, Fig. 8 | Pl. 5, Fig. 5 | | Pl. 9, Fig. 7 |
| **Paratype 5** | 321-1337A-7H-6, 104-107cm; slide #3;U31-4; ECO-135 | 321-1337A-16H-6, 121-124cm; slide #2; N34-3; ECO-142 | 321-1337A-3H-2, 103-106cm; slide #1; D37-3; ECO-126 | | |
| **Paratype 5 citation** | not figured | Pl. 4, Fig. 9 | Pl. 5, Figs. 2A-B | | |
| **Paratype 6** | | 321-1337A-16H-6, 121-124cm; slide #3; W5-1; ECO-143 | | | |
| **Paratype 6 citation** | | Pl. 4, Fig. 7 | | | |

......*Continued on the next page*

**Part B (continued)**

| Species | *Botryopera bolotniki* | *Ceratocyrtis? chimii* | *Ceratocyrtis vila* | *Lithomelissa alkonost* | *Lithomelissa babai* |
|---|---|---|---|---|---|
| **Holotype** | 321-1337A-14H-7, 39-42cm; slide #1; F36-4; ECO-138 | 321-1337A-21H-1, 33-35cm; slide #2 custom; X28-2; ECO-144 | 321-1337D-23H-6,134-137cm; slide #2; R41-3; ECO-146 | 321-1337A-14H-7, 39-42cm; slide #1; U15-3; ECO-138 | 321-1337A-7H-6, 104-107cm; slide #2; C26-3; ECO-134 |
| **Holotype citation** | Pl. 8, Figs. 1A-B | Pl. 11, Figs. 5A-C | Pl. 12, Figs. 1A-B | Pl. 16, Figs. 1A-B | Pl. 18, Figs. 1A-C |
| **Paratype 1** | 321-1337A-14H-7, 39-42cm; slide #1; D30-1; ECO-138 | 321-1337A-21H-1, 33-35cm; slide #2 custom; W7-1; ECO-144 | 321-1337A-21H-1, 33-35cm; slide #2; P12-1; ECO-144 | 321-1337A-16H-6, 121-124cm; slide #1; Q26-3; ECO-141 | 321-1337A-7H-6, 104-107cm; slide #2; U30-1; ECO-134 |
| **Paratype 1 citation** | Pl. 8, Figs. 2A-B | Pl. 11, Fig. 8 | Pl. 12, Fig. 7 | Pl. 16, Figs. 3A-B | Pl. 18, Fig. 2 |
| **Paratype 2** | 321-1337A-14H-7, 39-42cm; slide #3; M12-3; ECO-140 | 321-1337A-21H-1, 33-35cm; slide #2 custom; D34-1; ECO-144 | 321-1337A-21H-1, 33-35cm; slide #2; Y23-1; ECO-144 | 321-1337A-16H-6, 121-124cm; slide #3; P14-2; ECO-143 | 321-1337A-7H-6, 104-107cm; slide #1; G15-3; ECO-133 |
| **Paratype 2 citation** | Pl. 8, Figs. 3A-B | Pl. 11, Fig. 4 | Pl. 12, Fig. 4 | Pl. 16, Figs. 4A-B | Pl. 18, Figs. 3A-B |
| **Paratype 3** | 321-1337A-14H-7, 39-42cm; slide #3; T27-2; ECO-140 | 321-1337D-23H-6,134-137cm; slide #1; G31-4; ECO-145 | 321-1337D-23H-6,134-137cm; slide #1; O6-4; ECO-145 | 321-1337A-16H-6, 121-124cm; slide #3; M3-2; ECO-143 | 321-1337A-7H-6, 104-107cm; slide #2; G27-1; ECO-134 |
| **Paratype 3 citation** | Pl. 8, Figs. 6A-B | Pl. 11, Figs. 6A-B | Pl. 12, Figs. 3A-B | Pl. 16, Fig. 5 | not figured |
| **Paratype 4** | 321-1337A-14H-7, 39-42cm; slide #2; Y34-3; ECO-139 | 321-1337D-23H-6,134-137cm; slide #1; K6-1; ECO-145 | 321-1337D-23H-6,134-137cm; slide #1; H13-2; ECO-145 | 321-1337A-16H-6, 121-124cm; slide #3; C17-2; ECO-143 | 321-1337A-7H-6, 104-107cm; slide #1; X24-4; ECO-133 |
| **Paratype 4 citation** | Pl. 9, Figs. 4A-B | Pl. 11, Fig. 9 | Pl. 12, Figs. 2A-B | Pl. 16, Fig. 6 | Pl. 18, Figs. 4A-B |
| **Paratype 5** | 321-1337A-14H-7, 39-42cm; slide #3; Z14-4; ECO-140 | 321-1337D-23H-6,134-137cm; slide #1; O27-2; ECO-145 | 321-1337D-23H-6,134-137cm; slide #2; V16-2; ECO-146 | 321-1337A-16H-6, 121-124cm; slide #1; K17-2; ECO-141 | 321-1337A-7H-6, 104-107cm; slide #2; K38-2; ECO-134 |
| **Paratype 5 citation** | not figured | Pl. 11, Fig. 7 | Pl. 12, Fig. 5 | Pl. 16, Figs. 7A-B | Pl. 18, Figs. 5A-B |
| **Paratype 6** | 321-1337A-14H-7, 39-42cm; slide #1; S33-3; ECO-138 | 321-1337D-23H-6,134-137cm; slide #2; V40-3; ECO-146 | 321-1337D-23H-6,134-137cm; slide #2; P16-3; ECO-146 | 321-1337A-16H-6, 121-124cm; slide #3; Q5-2; ECO-143 | 321-1337A-7H-6, 104-107cm; slide #3; F37-4; ECO-135 |
| **Paratype 6 citation** | Pl. 8, Figs. 5A-B (deformed) | Pl. 11, Figs. 1A-C | Pl. 12, Fig. 6 | Pl. 16, Figs. 2A-B | not figured |
| **Paratype 7** | 321-1337A-14H-7, 39-42cm; slide #1; N10-4; ECO-138 | 321-1337D-23H-6,134-137cm; slide #2; O31-2; ECO-146 | 321-1337A-16H-6, 121-124cm; slide #1; G35-4; ECO-141 | 321-1337A-16H-6, 121-124cm; slide #2; X34-3; ECO-142 | |
| **Paratype 7 citation** | not figured | Pl. 11, Figs. 2A-C | not figured | not figured | |
| **Paratype 8** | | 321-1337D-23H-6,134-137cm; slide #2; K30-1; ECO-146 | | | |
| **Paratype 8 citation** | | Pl. 11, Fig. 3 | | | |

*......Continued on the next page*

**Part B (continued)**

| Species | *Lithomelissa dybbuki* | *Lithomelissa sirin* | *Lophophaena arie* | *Lophophaena casperi* | *Lophophaena domovoi* |
|---|---|---|---|---|---|
| **Holotype** | 321-1337A-4H-6, 115-118cm, slide #3, C25-1; ECO-132 | 321-1337A-16H-6, 121-124cm; slide #1; X39-2; ECO-141 | 321-1337A-3H-2, 103-106cm; slide #1; H11-1; ECO-126 | 321-1337A-21H-1, 33-35cm; slide #2 custom; G3-1; ECO-144 | 321-1337D-23H-6,134-137cm; slide #3; K30-4; ECO-147 |
| **Holotype citation** | Pl. 19, Figs. 5A-B | Pl. 17, Fig. 1 | Pl. 26, Fig. 1A-B | Pl. 28, Figs. 1A-B | Pl. 30, Figs. 1A-C |
| **Paratype 1** | 321-1337A-4H-6, 115-118cm, slide #2, C38-2; ECO-131 | 321-1337A-16H-6, 121-124cm; slide #2; M3-3; ECO-142 | 321-1337A-4H-2, 16-19cm; slide #2; D11-4; ECO-128 | 321-1337A-21H-1, 33-35cm; slide #2 custom; S16-2; ECO-144 | 321-1337D-23H-6,134-137cm; slide #3; F8-1; ECO-147 |
| **Paratype 1 citation** | Pl. 19, Fig. 3 | Pl. 17, Fig. 2 | Pl. 26, Figs. 2A-B | Pl. 28, Figs. 4A-B | Pl. 30, Fig. 2 |
| **Paratype 2** | 321-1337A-4H-6, 115-118cm, slide #2, O34-1; ECO-131 | 321-1337A-16H-6, 121-124cm; slide #3; Y10-4; ECO-143 | 321-1337A-4H-2, 16-19cm; slide #3; L12-2; ECO-129 | 321-1337A-14H-7, 39-42cm; slide# 2; W39-4; ECO-139 | 321-1337D-23H-6,134-137cm; slide #2; T35-1; ECO-146 |
| **Paratype 2 citation** | Pl. 19, Fig. 1 | Pl. 17, Figs. 4A-B | Pl. 26, Figs. 4A-B | Pl. 28, Fig. 2 | Pl. 30, Figs. 3A-B |
| **Paratype 3** | 321-1337A-4H-2, 16-19cm; slide #1; X18-3; ECO-127 | 321-1337A-16H-6, 121-124cm; slide #3; O8-3; ECO-143 | 321-1337A-7H-6, 104-107cm; slide #2; T26-1; ECO-134 | 321-1337A-14H-7, 39-42cm; slide# 1; Q30-1; ECO-138 | 321-1337D-23H-6,134-137cm; slide #1; K25-2; ECO-145 |
| **Paratype 3 citation** | Pl. 19, Figs. 4A-B | Pl. 17, Fig. 7 | Pl. 26, Figs. 3A-B | Pl. 28, Figs. 8A-B | Pl. 30, Figs. 7A-B |
| **Paratype 4** | 321-1337A-4H-6, 115-118cm, slide #3, Y35-2; ECO-132 | 321-1337A-14H-7, 39-42cm; slide #1; P17-2; ECO-138 | 321-1337A-4H-2, 16-19cm; slide #2; U13-3; ECO-128 | 321-1337A-16H-6, 121-124cm; slide #1; W22-1; ECO-141 | 321-1337D-23H-6,134-137cm; slide #2; M9-1; ECO-146 |
| **Paratype 4 citation** | Pl. 19, Figs. 6A-B | Pl. 17, Figs. 3A-B | Pl. 26, Figs. 5A-B | Pl. 28, Figs. 7A-B | Pl. 30, Fig. 5 |
| **Paratype 5** | 321-1337A-4H-2, 16-19cm; slide #2; E20-4; ECO-128 | 321-1337A-14H-7, 39-42cm; slide #3; M17-2; ECO-140 | 321-1337A-7H-6, 104-107cm; slide #2; R36-4; ECO-134 | 321-1337A-16H-6, 121-124cm; slide #2; M17-1; ECO-142 | 321-1337D-23H-6,134-137cm; slide #2; N37-3; ECO-146 |
| **Paratype 5 citation** | not figured | Pl. 17, Figs. 11A-B | not figured | Pl. 28, Figs. 5A-B | not figured |
| **Paratype 6** | 321-1337A-4H-2, 16-19cm; slide #1; F21-1; ECO-127 | 321-1337A-14H-7, 39-42cm; slide #3; R37-4; ECO-140 | | 321-1337A-16H-6, 121-124cm; slide #1; J15-4; ECO-141 | |
| **Paratype 6 citation** | not figured | Pl. 17, Figs. 8A-B | | Pl. 28, Fig. 3 | |
| **Paratype 7** | | | | 321-1337A-16H-6, 121-124cm; slide #1; H39-4; ECO-141 | |
| **Paratype 7 citation** | | | | Pl. 28, Figs. 6A-B | |
| **Paratype 8** | | | | 321-1337A-16H-6, 121-124cm; slide #1; C2-2; ECO-141 | |
| **Paratype 8 citation** | | | | not figured | |

*......Continued on the next page*

**Part B (continued)**

| **Species** | ***Lophophaena gozui*** | ***Lophophaena ikiryo*** | ***Lophophaena ikota*** | ***Lophophaena kaonashii*** | ***Lophophaena leshii*** |
|---|---|---|---|---|---|
| **Holotype** | 321-1337D-23H-6,134-137cm; slide #3; O22-1; ECO-147 | 321-1337A-14H-7, 39-42cm; slide #1; E37-1; ECO-138 | 321-1337D-23H-6,134-137cm; slide #1; W7-3; ECO-145 | 321-1337D-23H-6,134-137cm; slide #3; W22-4; ECO-147 | 321-1337D-23H-6,134-137cm; slide #3; D9-2; ECO-147 |
| **Holotype citation** | Pl. 31, Figs. 1A-B | Pl. 32, Figs. 4A-B | Pl. 33, Figs. 2A-B | Pl. 34, Figs. 5A-B | Pl. 24, Fig. 4 |
| **Paratype 1** | 321-1337D-23H-6,134-137cm; slide #1; Z26-1; ECO-145 | 321-1337A-12H-5, 230-26cm; slide #2; C3-3; ECO-137 | 321-1337D-23H-6,134-137cm; slide #1; P30-1; ECO-145 | 321-1337D-26H-3, 142-144cm; slide #3; G8-4; ECO-148 | 321-1337D-23H-6,134-137cm; slide #1; H34-2; ECO-145 |
| **Paratype 1 citation** | Pl. 31, Fig. 2 | Pl. 32, Fig. 9 | Pl. 33, Figs. 3A-B | Pl. 34, Figs. 9A-B | Pl. 24, Figs. 3A-C |
| **Paratype 2** | 321-1337D-23H-6,134-137cm; slide #1; U8-3; ECO-145 | 321-1337A-14H-7, 39-42cm; slide #3; L33-4; ECO-140 | 321-1337D-23H-6,134-137cm; slide #3; U11-1; ECO-147 | 321-1337A-31X-6, 4-6cm; slide #2; O11-4; ECO-151 | 321-1337D-23H-6,134-137cm; slide #3; K27-2; ECO-147 |
| **Paratype 2 citation** | Pl. 31, Fig. 5 | Pl. 32, Figs. 1A-B | Pl. 33, Fig. 4 | Pl. 34, Figs. 4A-B | Pl. 24, Figs. 5A-B |
| **Paratype 3** | 321-1337D-26H-3, 142-144cm; slide #3; Y41-1; ECO-148 | 321-1337A-16H-6, 121-124cm; slide #2; K4-2; ECO-142 | 321-1337D-23H-6,134-137cm; slide #2; Z20-4; ECO-146 | 321-1337A-31X-6, 4-6cm; slide #2; T25-1; ECO-151 | 321-1337D-23H-6,134-137cm; slide #1; H5-4; ECO-145 |
| **Paratype 3 citation** | Pl. 31, Figs. 4A-B | Pl. 32, Figs. 3A-B | Pl. 33, Fig. 5 | Pl. 34, Figs. 8A-B | Pl. 24, Figs. 7A-B |
| **Paratype 4** | 321-1337D-26H-3, 142-144cm; slide #3; U32-1; ECO-148 | 321-1337A-16H-6, 121-124cm; slide #3; S7-1; ECO-143 | 321-1337D-23H-6,134-137cm; slide #2; N33-3; ECO-146 | 321-1337A-31X-6, 4-6cm; slide #2; U32-3; ECO-151 | 321-1337D-23H-6,134-137cm; slide #1; L7-3; ECO-145 |
| **Paratype 4 citation** | Pl. 31, Fig. 6 | Pl. 32, Figs. 6A-B | Pl. 33, Figs. 7A-B | Pl. 34, Fig. 7 | Pl. 24, Fig. 8 |
| **Paratype 5** | 321-1337D-23H-6,134-137cm; slide #1; H13-3; ECO-145 | 321-1337A-16H-6, 121-124cm; slide #3; R27-2; ECO-143 | 321-1337D-23H-6,134-137cm; slide #1; M28-1; ECO-145 | 321-1337D-26H-3, 142-144cm; slide #3; Z8-1; ECO-148 | 321-1337D-23H-6,134-137cm; slide #1; P15-2; ECO-145 |
| **Paratype 5 citation** | not figured | Pl. 32, Fig. 8 | not figured | not figured | Pl. 24, Fig. 9 |
| **Paratype 6** | | 321-1337A-16H-6, 121-124cm; slide #3; F33-1; ECO-143 | 321-1337D-23H-6,134-137cm; slide #2; Q39-2; ECO-146 | | 321-1337D-23H-6,134-137cm; slide #1; O14-4; ECO-145 |
| **Paratype 6 citation** | | Pl. 32, Figs. 5A-B | not figured | | Pl. 24, Figs. 6A-B |
| **Paratype 7** | | 321-1337A-14H-7, 39-42cm; slide #1; J41-1; ECO-138 | | | 321-1337D-23H-6,134-137cm; slide #2; Q37-1; ECO-146 |
| **Paratype 7 citation** | | Pl. 32, Figs. 7A-B | | | not figured |
| **Paratype 8** | | | | | 321-1337D-23H-6,134-137cm; slide #2; J9-3; ECO-146 |
| **Paratype 8 citation** | | | | | not figured |

*......Continued on the next page*

**Part B5 (continued)**

| **Species** | ***Lophophaena rusalkae*** | ***Lophophaena shishigae*** | ***Lophophaena ushionii*** | ***Pelagomanes ibburi*** |
|---|---|---|---|---|
| **Holotype** | 321-1337A-14H-7, 39-42cm; slide #1; N20-4; ECO-138 | 321-1337D-23H-6,134-137cm; slide #2; W4-2; ECO-146 | 321-1337A-31X-6, 4-6cm; slide #2; T6-1; ECO-151 | 321-1337A-16H-6, 121-124cm; slide #1; Z12-4; ECO-141 |
| **Holotype citation** | Pl. 29, Fig. 4 | Pl. 35, Fig. 1 | Pl. 31, Figs. 7A-B | Pl. 41, Figs. 2A-B |
| **Paratype 1** | 321-1337A-12H-5, 230-26cm; slide #1; X10-2; ECO-136 | 321-1337D-23H-6,134-137cm; slide #2; W37-1; ECO-146 | 321-1337A-31X-6, 4-6cm; slide #2; O40-3; ECO-151 | 321-1337A-16H-6, 121-124cm; slide #3; K12-3; ECO-143 |
| **Paratype 1 citation** | Pl. 29, Figs. 5A-B | Pl. 35, Figs. 2A-B | Pl. 31, Fig. 10 | Pl. 41, Figs. 1A-B |
| **Paratype 2** | 321-1337A-14H-7, 39-42cm; slide #3; Z14-2; ECO-140 | 321-1337A-21H-1, 33-35cm; slide #2; V2-2; ECO-144 | 321-1337A-31X-6, 4-6cm; slide #2; U26-4; ECO-151 | 321-1337D-23H-6,134-137cm; slide #1; N15-1; ECO-145 |
| **Paratype 2 citation** | Pl. 29, Figs. 2A-B | Pl. 35, Fig. 3 | not figured | Pl. 41, Figs. 4A-B |
| **Paratype 3** | 321-1337A-14H-7, 39-42cm; slide #2; Y39-3; ECO-139 | 321-1337D-23H-6,134-137cm; slide #3; W30-4; ECO-147 | | 321-1337D-23H-6,134-137cm; slide #1; G17-2; ECO-145 |
| **Paratype 3 citation** | Pl. 29, Figs. 1A-B | Pl. 35, Fig. 4 | | Pl. 41, Figs. 3A-B |
| **Paratype 4** | 321-1337A-14H-7, 39-42cm; slide #2; X7-2; ECO-139 | 321-1337D-23H-6,134-137cm; slide #2; Y6-1; ECO-146 | | 321-1337A-14H-7, 39-42cm; slide #1; V9-2; ECO-138 |
| **Paratype 4 citation** | Pl. 29, Figs. 2A-B | Pl. 35, Fig. 5 | | Pl. 41, Figs. 6A-B |
| **Paratype 5** | 321-1337A-12H-5, 230-26cm; slide #1; Z5-4; ECO-136 | 321-1337D-23H-6,134-137cm; slide #2; A34-4; ECO-146 | | 321-1337A-16H-6, 121-124cm; slide #3; J18-2; ECO-143 |
| **Paratype 5 citation** | Pl. 29, Fig. 3 | Pl. 35, Figs. 6A-B | | Pl. 41, Figs. 5A-B |
| **Paratype 6** | 321-1337A-14H-7, 39-42cm; slide #2; O25-3; ECO-139 | | | |
| **Paratype 6 citation** | Pl. 29, Fig. 6 | | | |
| **Paratype 7** | 321-1337A-14H-7, 39-42cm; slide #1; C25-4; ECO-138 | | | |
| **Paratype 7 citation** | not figured | | | |

## PLATES 1–42

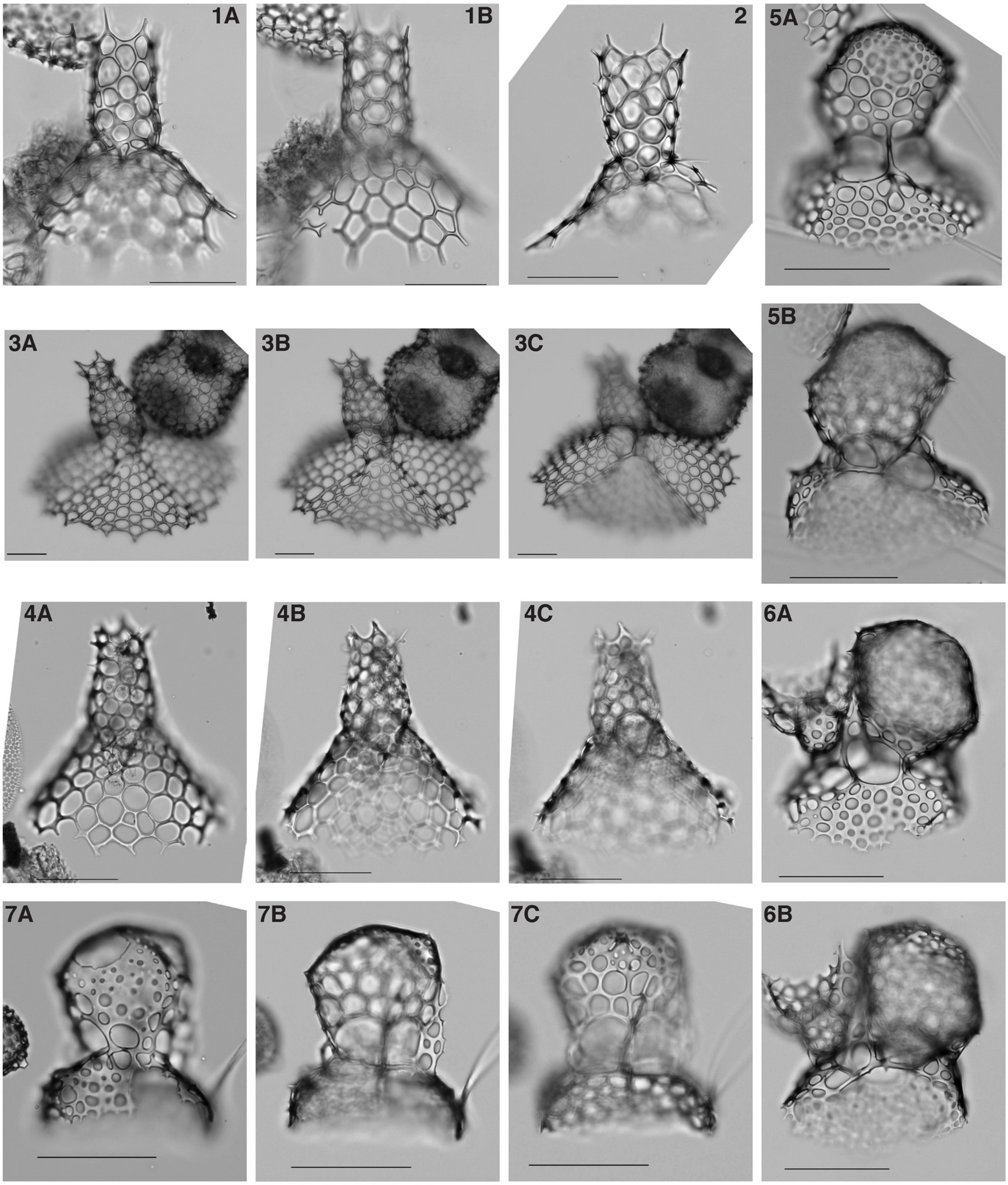

**PLATE 1.**
1A–2: *Amphiplecta acrostoma* Haeckel 1887 (sample 321-1337A-3H-2, 103–106cm)
3A–4C: *Amphiplecta cylindrocephala*? Dumitrica 1973 (sample 321-1337A-10H-2, 91–94cm)
5A–7C: *Amphiplecta tripleura?* Funakawa 1995 (sample 321-1337D-30H-3, 103–104cm)

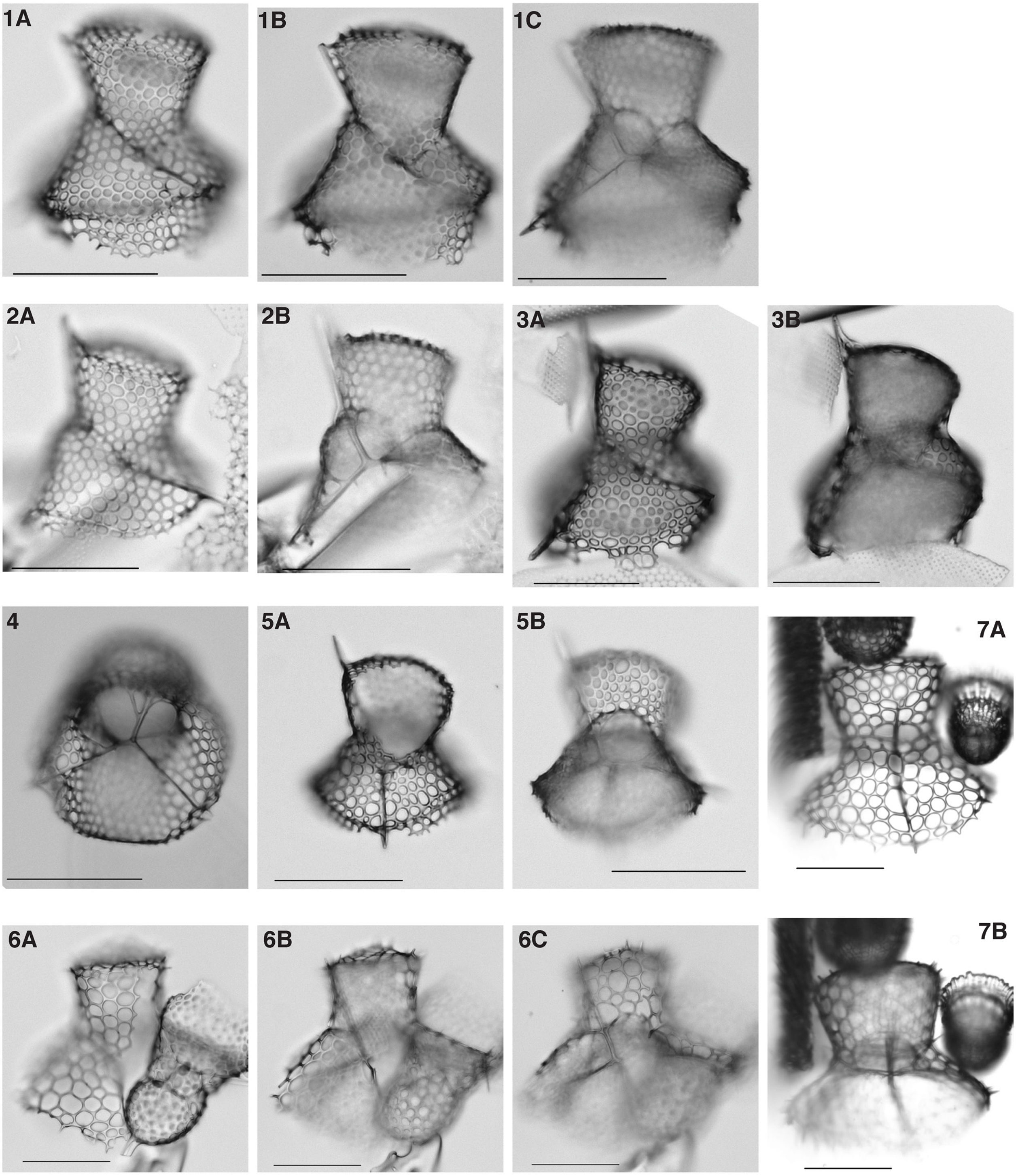

**PLATE 2.**

1A–5B: *Amphiplecta kikimorae* n. sp. (sample 321-1337A-7H-6, 104–107cm)

6A–7B: *Amphiplecta* sp. cf. *A. kikimorae* (6—sample 321-1337A-7H-6, 104–107cm; 7—sample 321-1337D-1H-1, 0–3cm)

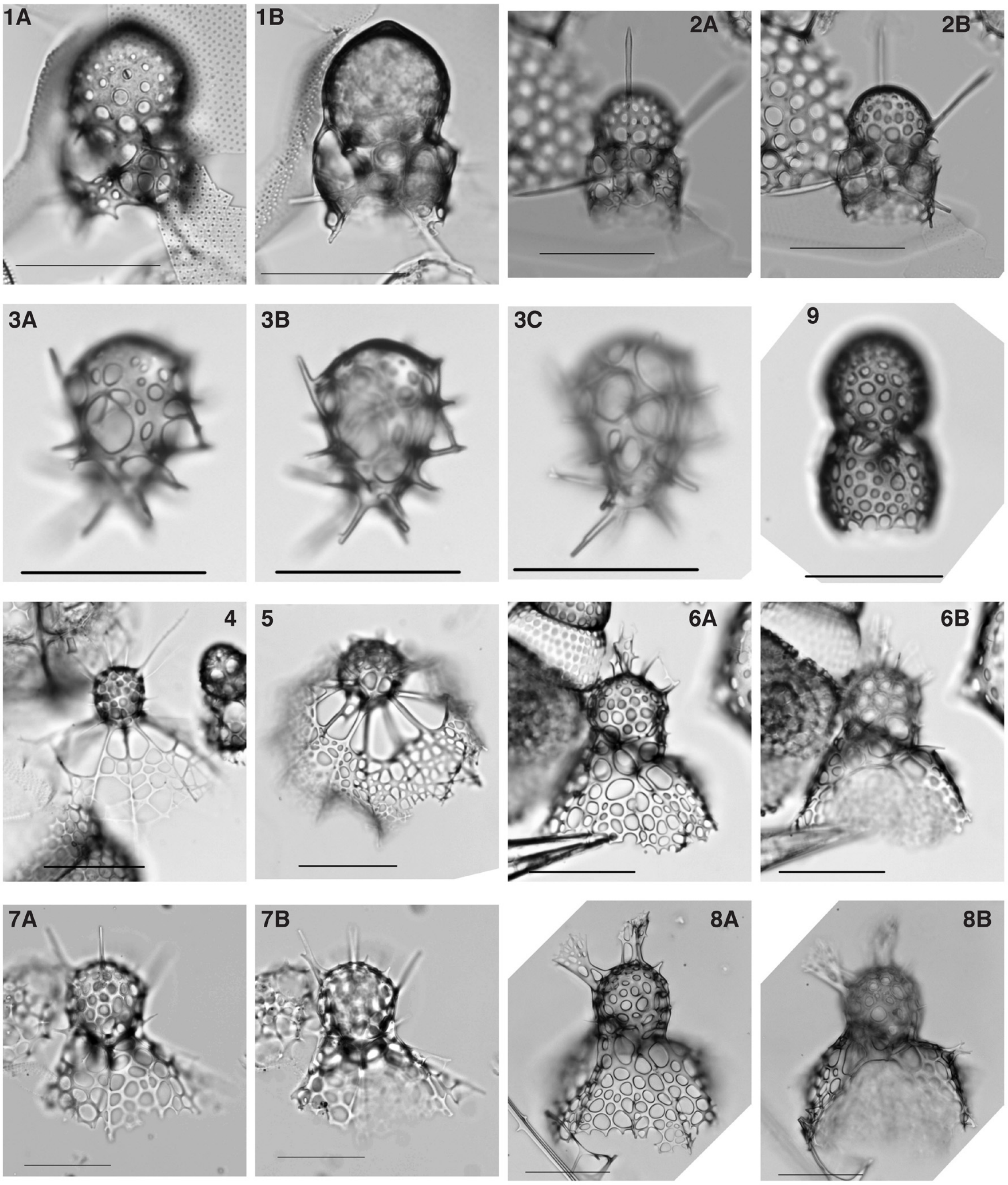

**PLATE 3.**
1A–B: *Arachnocorallium calvata* (Haeckel 1887) Petrushevskaya 1971 (sample 321-1337A-10H-2, 91–94cm)
2A–B: *Arachnocorallium calvata?* (Haeckel 1887) Petrushevskaya 1971 (sample 321-1337A-3H-2, 103–106cm)
3A–C: *Arachnocorallium stilla* Renaudie and Lazarus 2015 (sample 321-1337A-4H-2, 16–19cm)
4–5: *Arachnocorys circumtexta* (Haeckel 1862) Petrushevskaya 1971 (4—sample 321-1337D-1H-1, 0–3cm; 5—sample 321-1337A-4H-2, 16–19cm)
6A–8B: *Arachnocorys umbellifera* (Haeckel 1862) Petrushevskaya 1971 (6—sample 321-1337A-10H-2, 91–94cm; 7—sample 321-1337D-1H-1, 0–3cm; 8—sample 321-1337A-14H-7, 39–42cm)
9: *Arachnocorys?* sp. (sample 321-1337A-4H-2, 16–19cm)

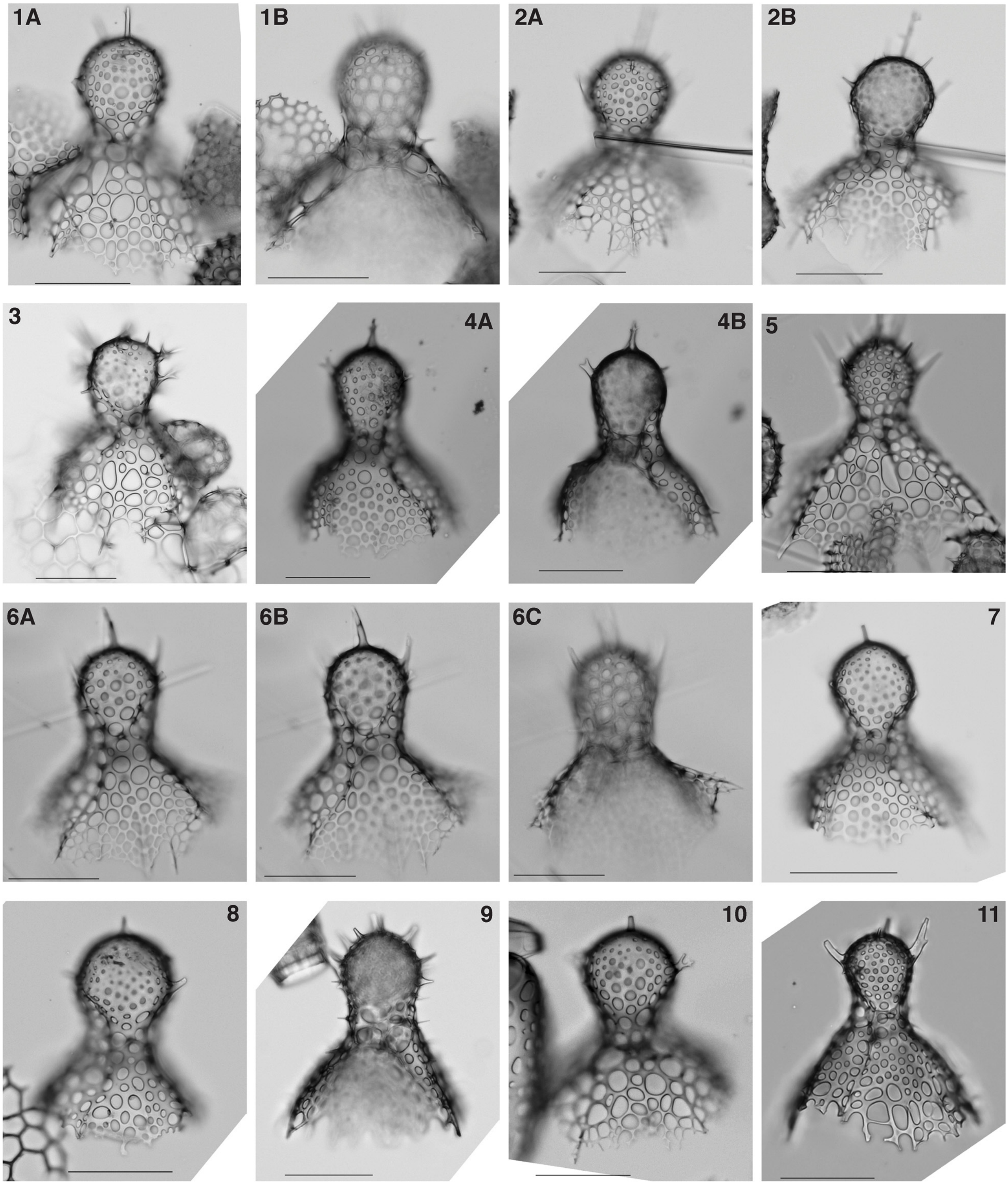

**PLATE 4.**

1A–10: *Arachnocorys jorogumoae* n. sp. (1, 7–9—sample 321-1337A-16H-6, 121–124cm; 2–3, 5–6, 10—sample 321-1337A-14H-7, 39–42cm; 4—sample 321-1337A-21H-1, 33–35cm; 11—sample 321-1337D-30H-3, 103–104cm)

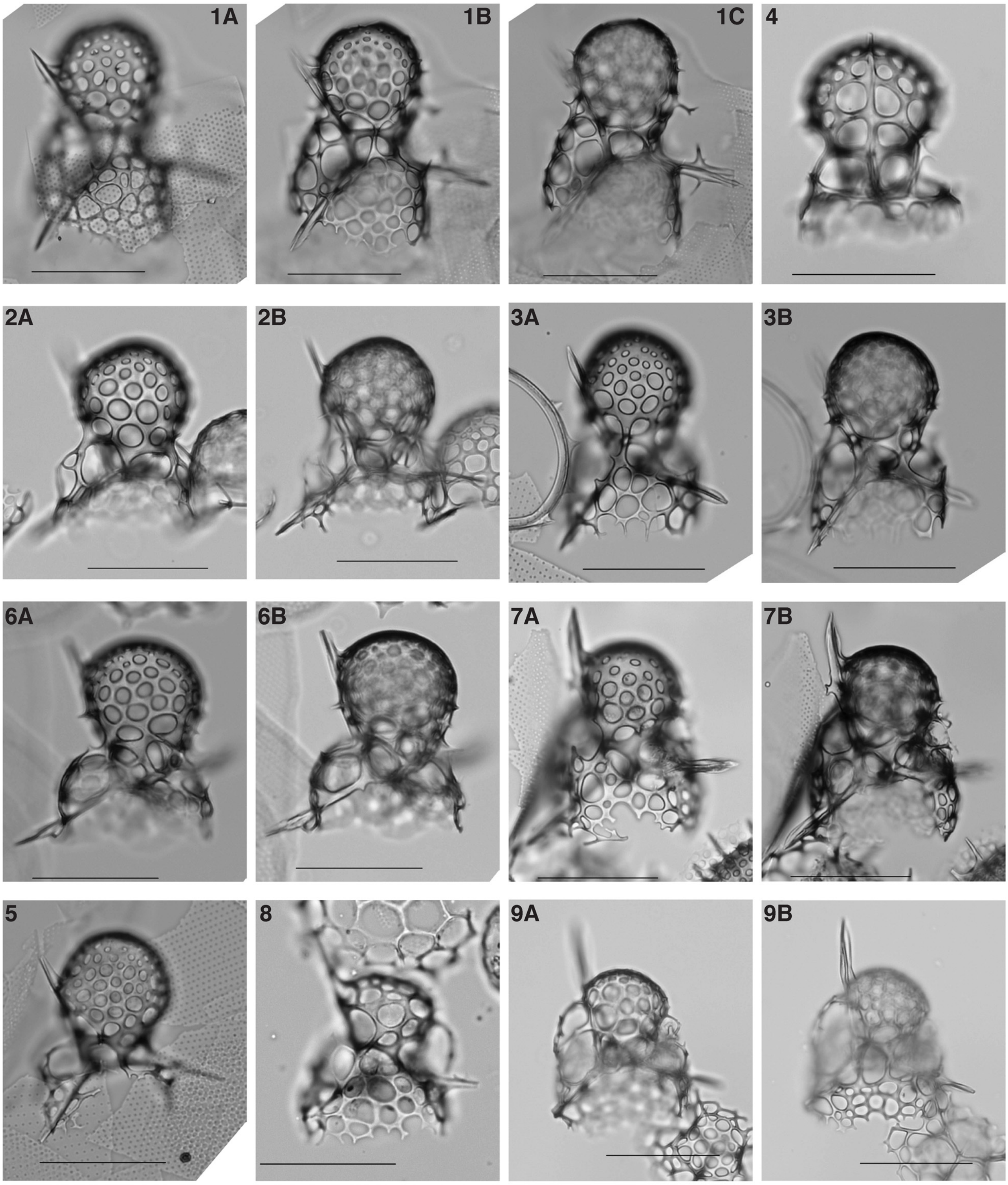

**PLATE 5.**

1A–7B: *Arachnocorys pentacantha wanii* n. subsp. (1, 5—sample 321-1337A-4H-2, 16–19cm; 2–4, 6–7—sample 321-1337A-3H-2, 103–106cm)

8–9B: *Arachnocorys pentacantha* (Popofsky 1913) Petrushevskaya 1971 (8—sample 321-1337D-1H-1, 0–3cm; 9—sample 321-1337A-3H-2, 103–106cm)

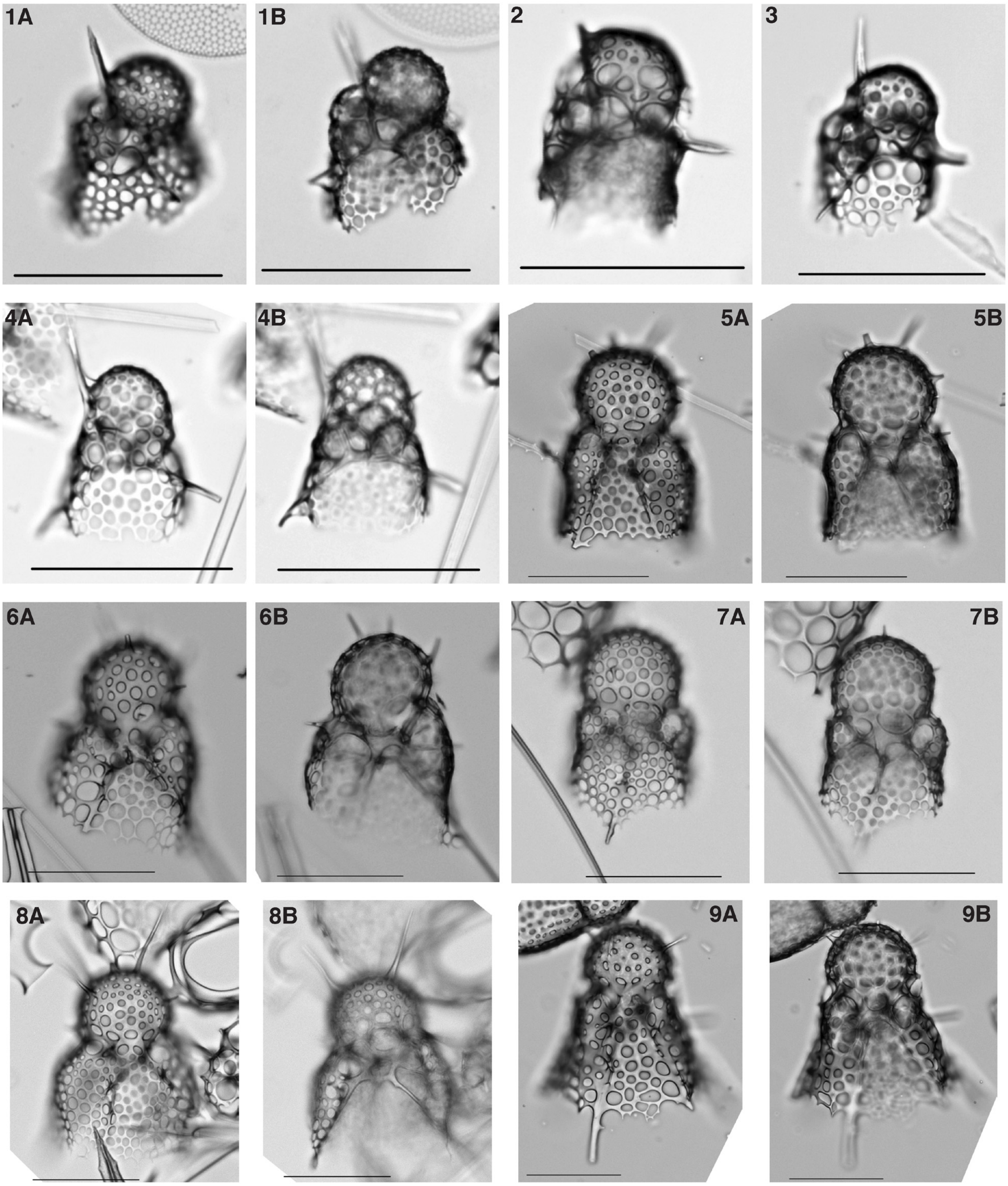

**PLATE 6.**

1A–4B: *Arachnocorys spinosissima* Tan and Tchang 1976 (1– sample 321-1337A-12H-5, 23–26cm; 2–3—sample 321-1337A-10H-2, 91–94cm; 4—sample 321-1337A-14H-7, 39–42cm)

5A–8B: *Botryopera? daleki* Renaudie and Lazarus 2013 (5—sample 321-1337D-30H-3, 103–104cm; 6–7—sample 321-1337A-14H-7, 39–42cm; 8—sample 321-1337D-26H-3, 142–144cm)

9A–B: *Botryopera?* cf. *daleki* Renaudie and Lazarus 2013 (sample 321-1337A-31X-6, 4–6cm)

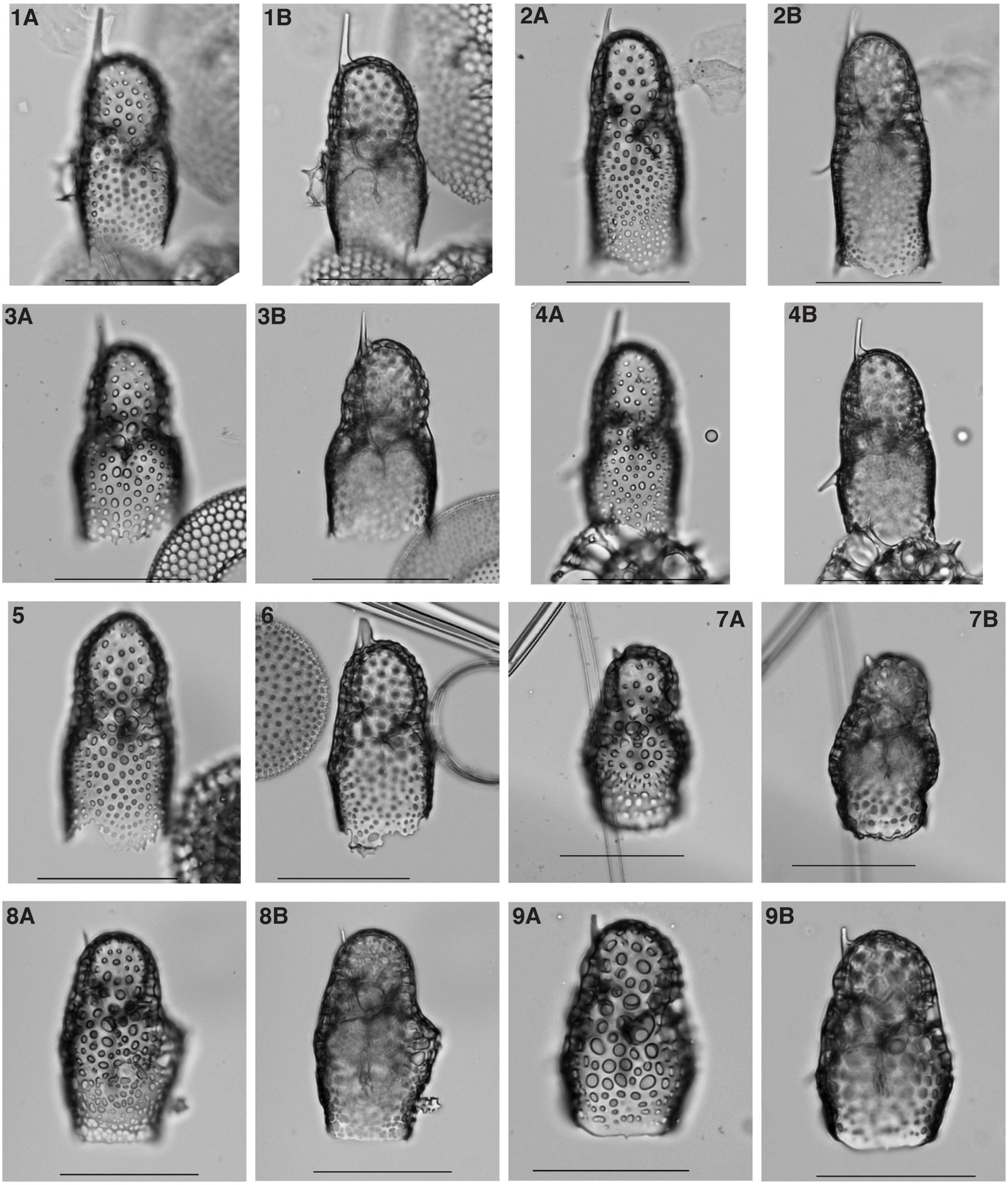

**PLATE 7.**

1A–6: *Botryopera amabie* n. sp. (1, 6—sample 321-1337A-35X-1, 106–108cm; 2–3—sample 321-1337A-31X-6, 4–6cm; 4–5—sample 321-1337D-30H-3, 103–104cm)

7A–9B: *Botryopera* sp. A (7, 9—sample 321-1337A-31X-6, 4–6cm; 8—sample 321-1337D-30H-3, 103–104cm)

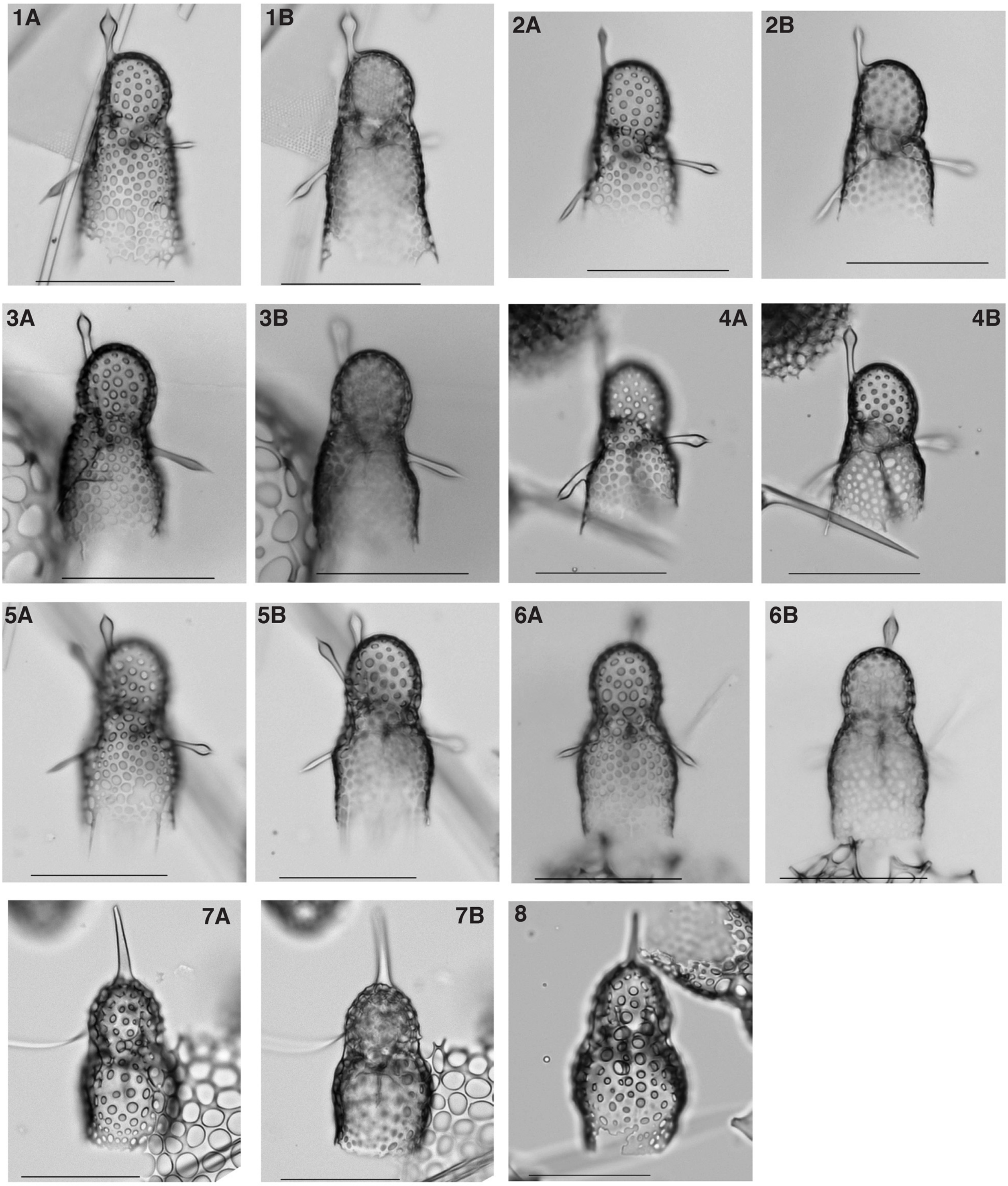

**PLATE 8.**

1A–6B: *Botryopera bolotniki* n. sp. (sample 321-1337A-14H-7, 39–42cm)

7A–8: *Botryopera* sp. B (7– sample 321-1337D-26H-3, 142–144cm; 8—sample 321-1337D-30H-3, 103–104cm)

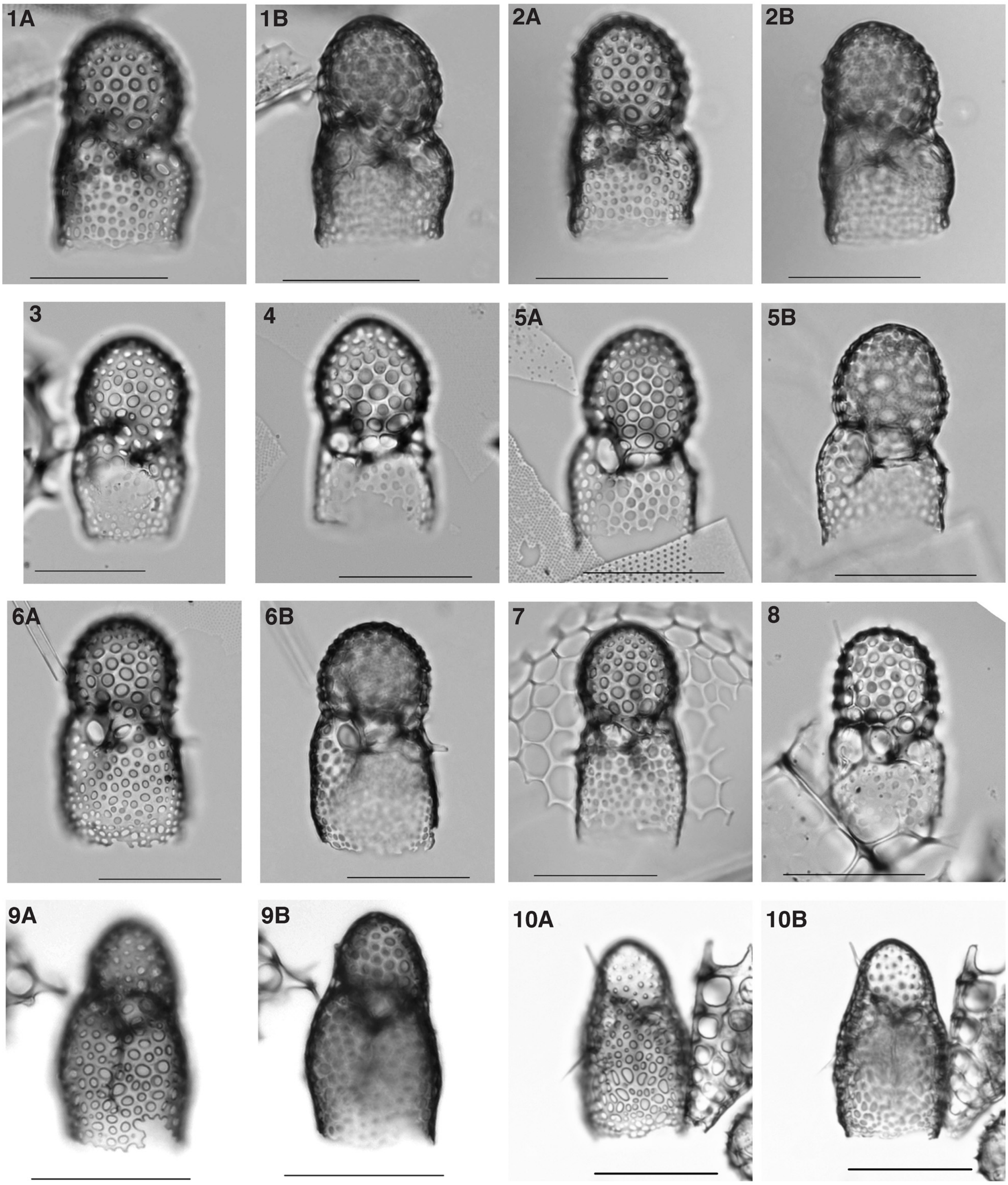

**PLATE 9.**

1A–8: *Botryopera babayagae* n. sp. (1–2, 7—sample 321-1337A-3H-2, 103–106cm; 3–4, 8—sample 321-1337D-1H-1, 0–3cm; 5– sample 321-1337A-4H-2, 16–19cm; 6– sample 321-1337A-4H-6, 115–118cm)

9A–10B: *Botryopera setosa* (Jørgensen 1900) Kruglikova 1989 (9—sample 321-1337A-2H-3, 76–79cm; 10—sample 321-1337D-23H-6, 134–137cm)

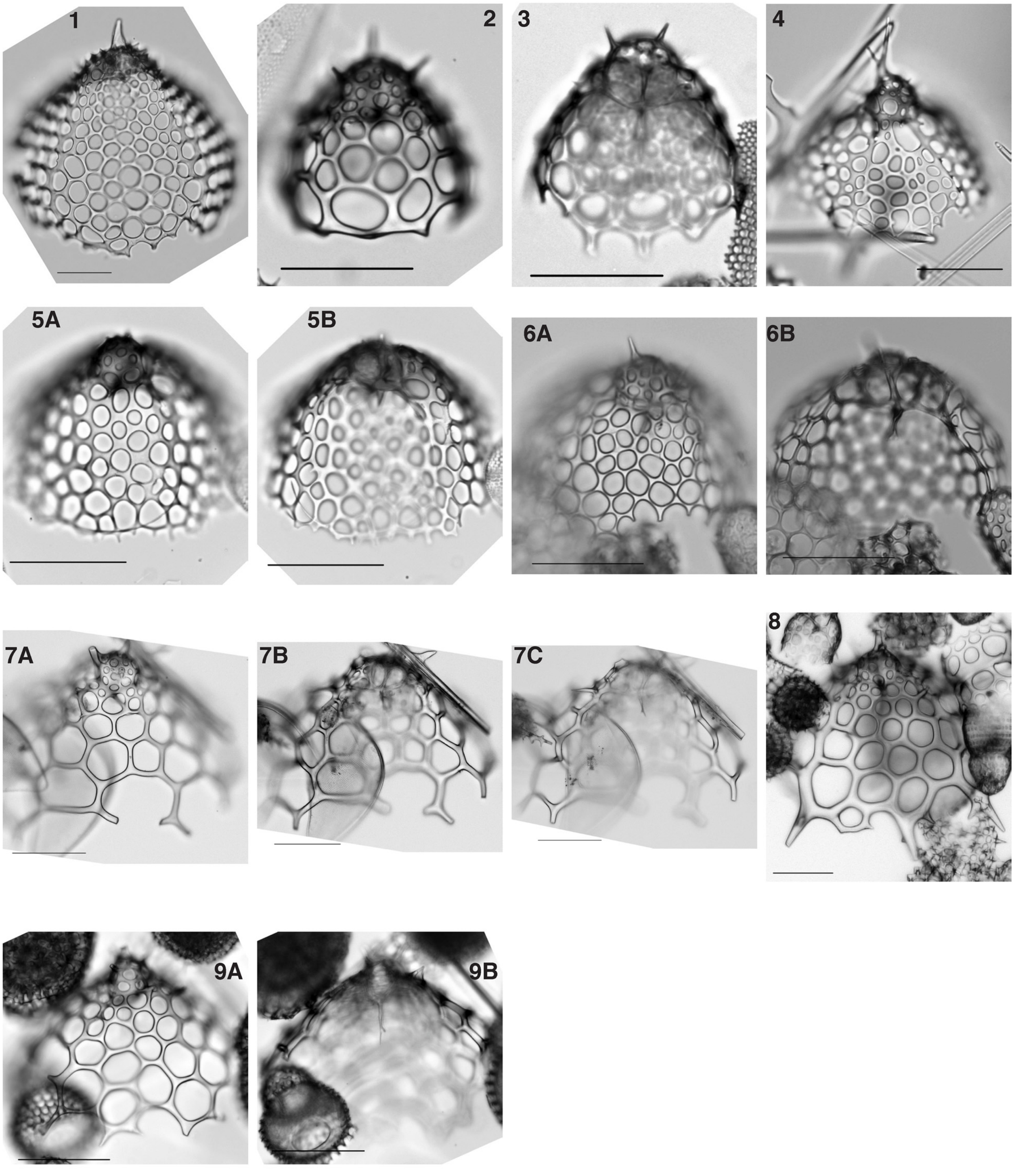

**PLATE 10.**

1: *Ceratocyrtis cucullaris* (Ehrenberg) Petrushevskaya 1971 (sample 321-1337A-3H-2, 103–106cm)

2–3: *Ceratocyrtis histricosa* (Jørgensen 1905) Petrushevskaya 1971 (2– sample 321-1337A-4H-6, 115–118cm; 3– sample 321-1337A-16H-6, 121–124cm)

4: *Ceratocyrtis spinosiretis* (Takahashi 1991) Matsuzaki *et al* 2015 (sample 321-1337A-14H-7, 39–42cm)

5A–6B: Ceratocyrtis sp. A (5– sample 321-1337A-10H-2, 91–94cm; 6– sample 321-1337A-3H-2, 103–106cm)

7A–9B: Ceratocyrtis sp. B (7—sample 321-1337A-12H-5, 23–26cm; 8—sample 321-1337A-16H-6, 121–124cm; 9—sample 321-1337D-23H-6, 134–137cm)

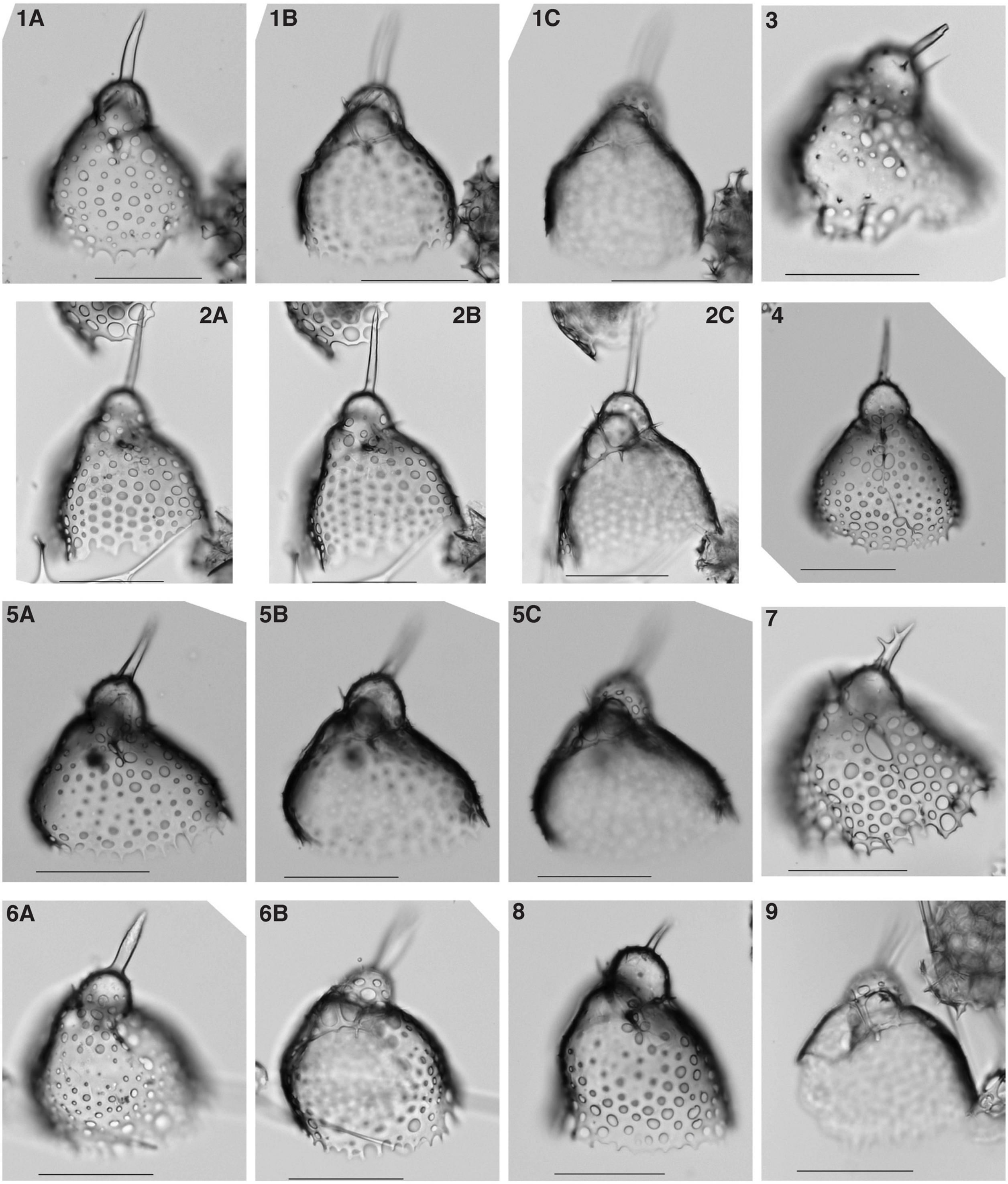

**PLATE 11.**
1A–9: *Ceratocyrtis? chimii* n. sp. (1–2, 6–7—sample 321-1337D-23H-6, 134–137cm; 4–5, 8–9—sample 321-1337A-21H-1, 33–35cm)

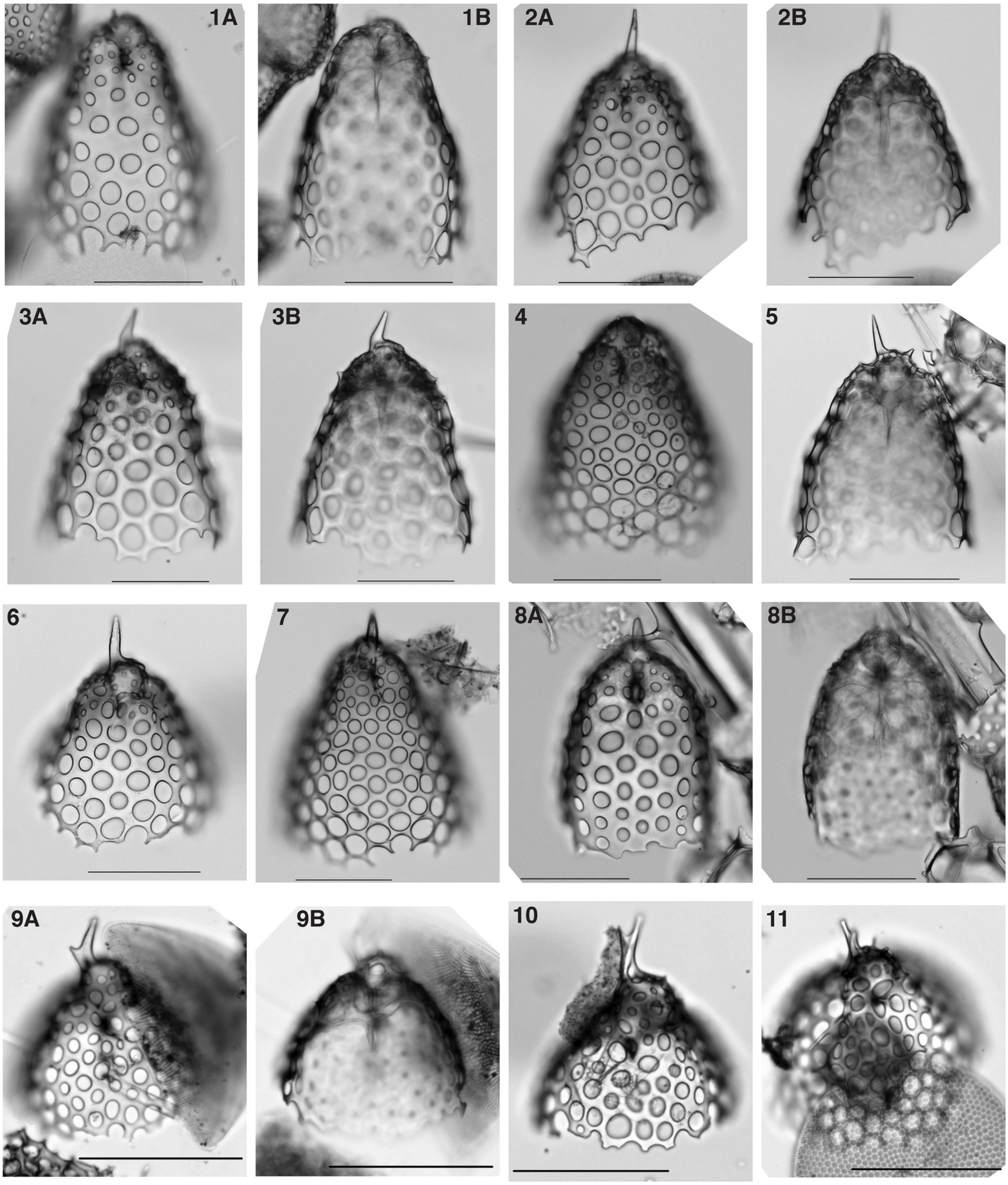

**PLATE 12.**

1A–8B: *Ceratocyrtis vila* n. sp. (1–3, 5–6—sample 321-1337D-23H-6, 134–137cm; 4, 7—sample 321-1337A-21H-1, 33–35cm; 8—sample 321-1337A-35X-1, 106–108cm)

9A–11: *Ceratocyrtis* sp. F (9—sample 321-1337A-18H-6, 77–80cm; 10—sample 321-1337A-5H-5, 11–14cm; 11– sample 321-1337A-16H-6, 121–124cm)

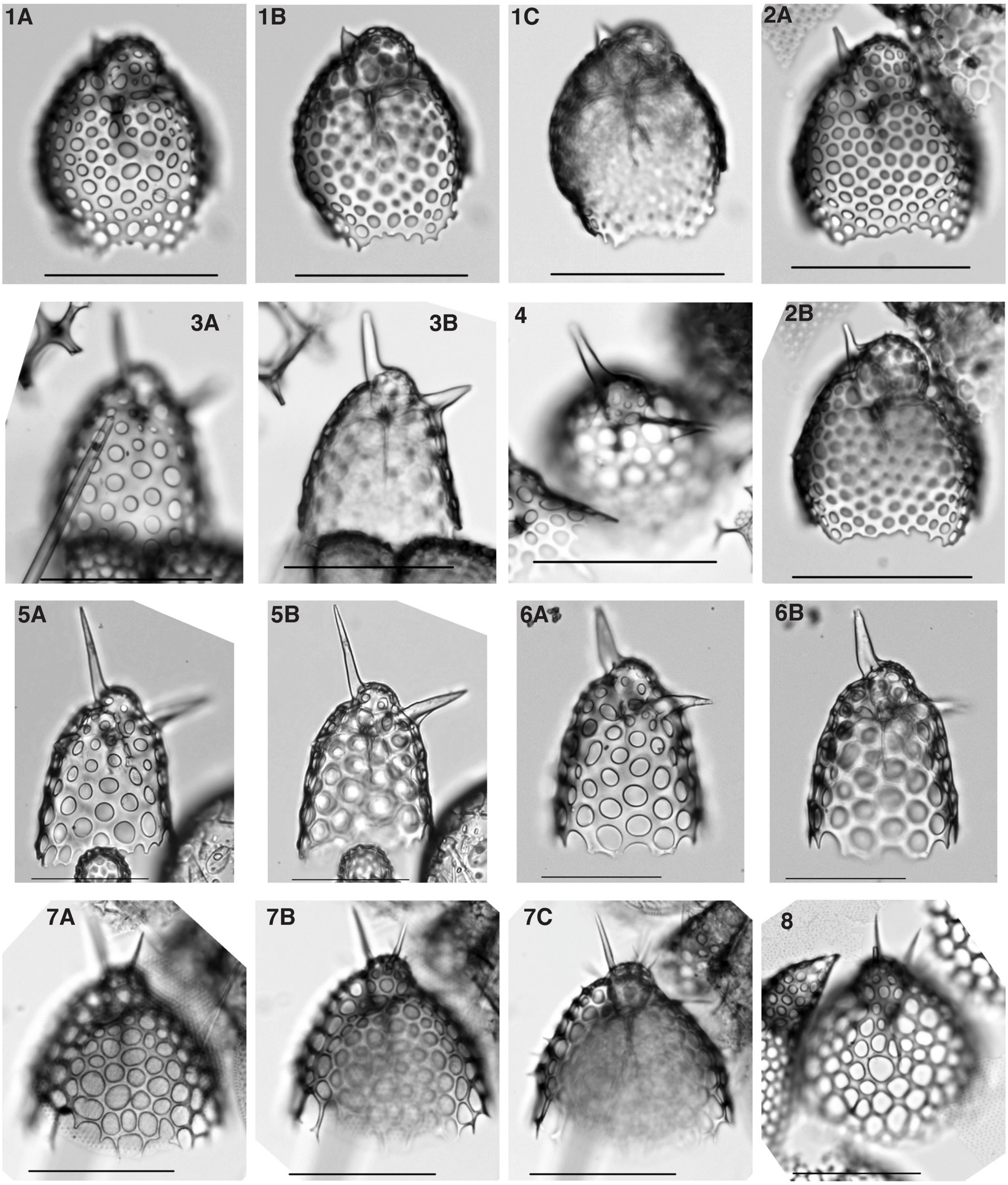

**PLATE 13.**

1A–2B: *Ceratocyrtis* sp. C (sample 321-1337A-4H-6, 115–118cm)

3A–6B: *Ceratocyrtis* sp. H (3–5—sample 321-1337D-23H-6, 134–137cm; 6—sample 321-1337D-26H-3, 142–144cm)

7A–8: *Ceratocyrtis* sp. E (sample 321-1337A-10H-2, 91–94cm)

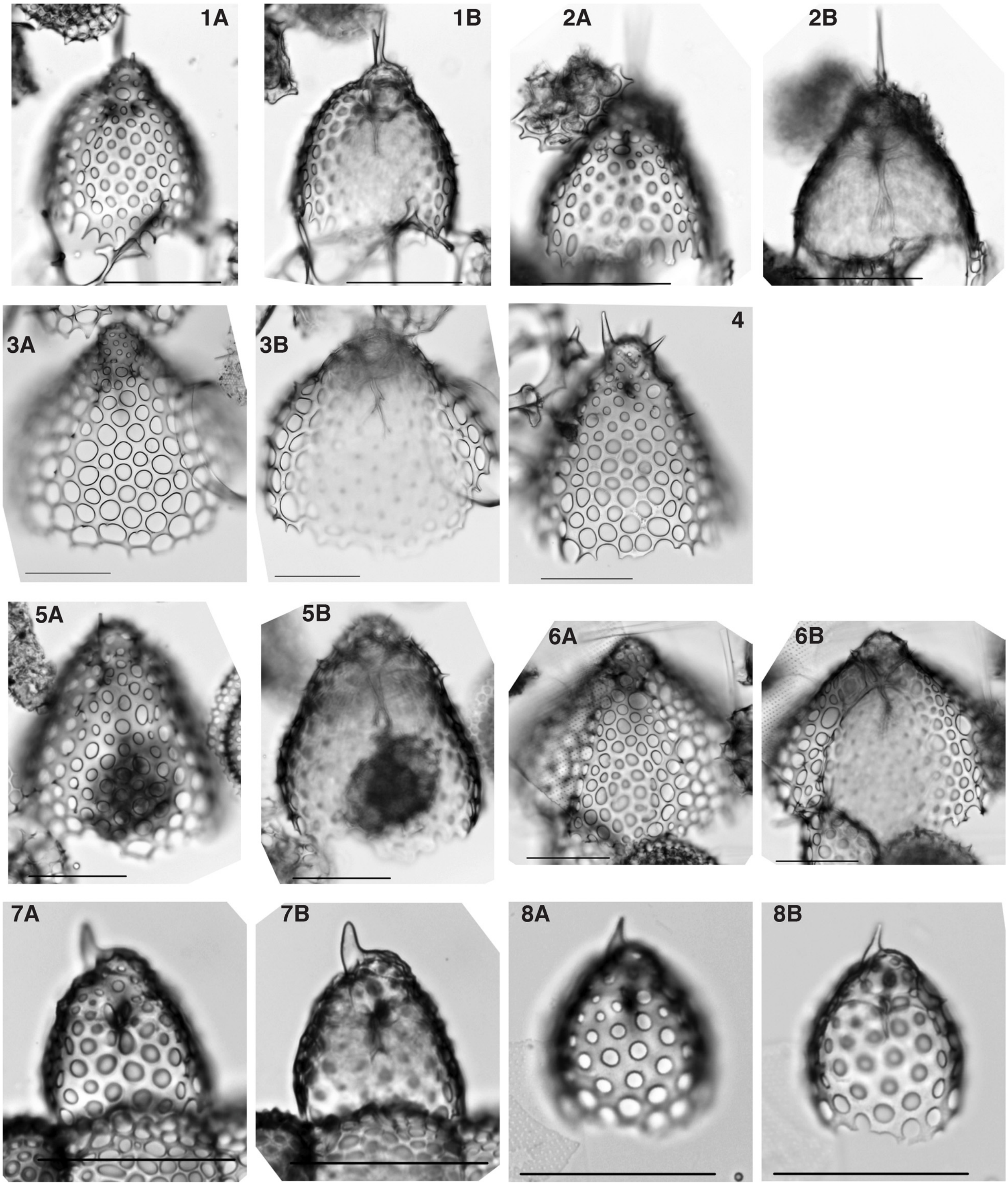

**PLATE 14.**

1A–2B: *Ceratocyrtis* sp. G (sample 321-1337A-18H-6, 77–80cm)

3A–6B: *Ceratocyrtis* sp. I group (3—sample 321-1337A-16H-6, 121–124cm; 4–6—sample 321-1337D-23H-6, 134–137cm)

7A–8B: *Ceratocyrtis* sp. D (sample 321-1337A-6H-3, 29–32cm)

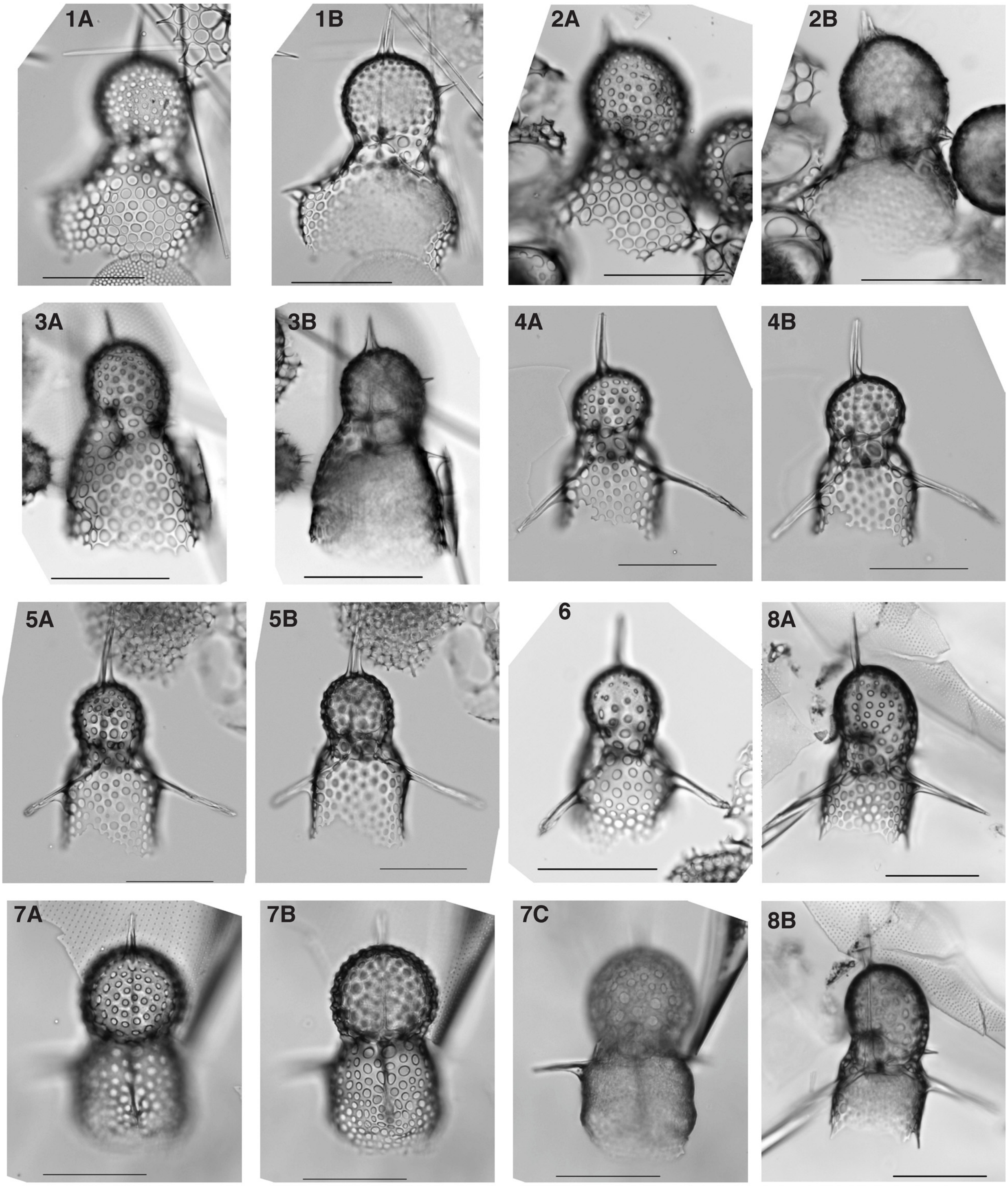

**PLATE 15.**

1A–2B: *Lithomelissa celsagula* Renaudie and Lazarus 2015 (1—sample 321-1337A-14H-7, 39–42cm; 2—sample 321-1337A-18H-6, 77–80cm)

3A–B: *Lithomelissa cheni* Caulet 1991 (sample 321-1337D-23H-6, 134–137cm)

4A–6: *Lithomelissa mitra* Bütschli 1882 (4–5—sample 321-1337A-4H-6, 115–118cm; 6—sample 321-1337A-5H-5, 11–14cm)

7A–C: *Lithomelissa ehrenbergi* Bütschli 1882 (sample 321-1337A-3H-2, 103–106cm)

8A–B: *Lithomelissa* sp. cf. *L. ehrenbergi* Bütschli 1882 (sample 321-1337A-7H-6, 104–107cm)

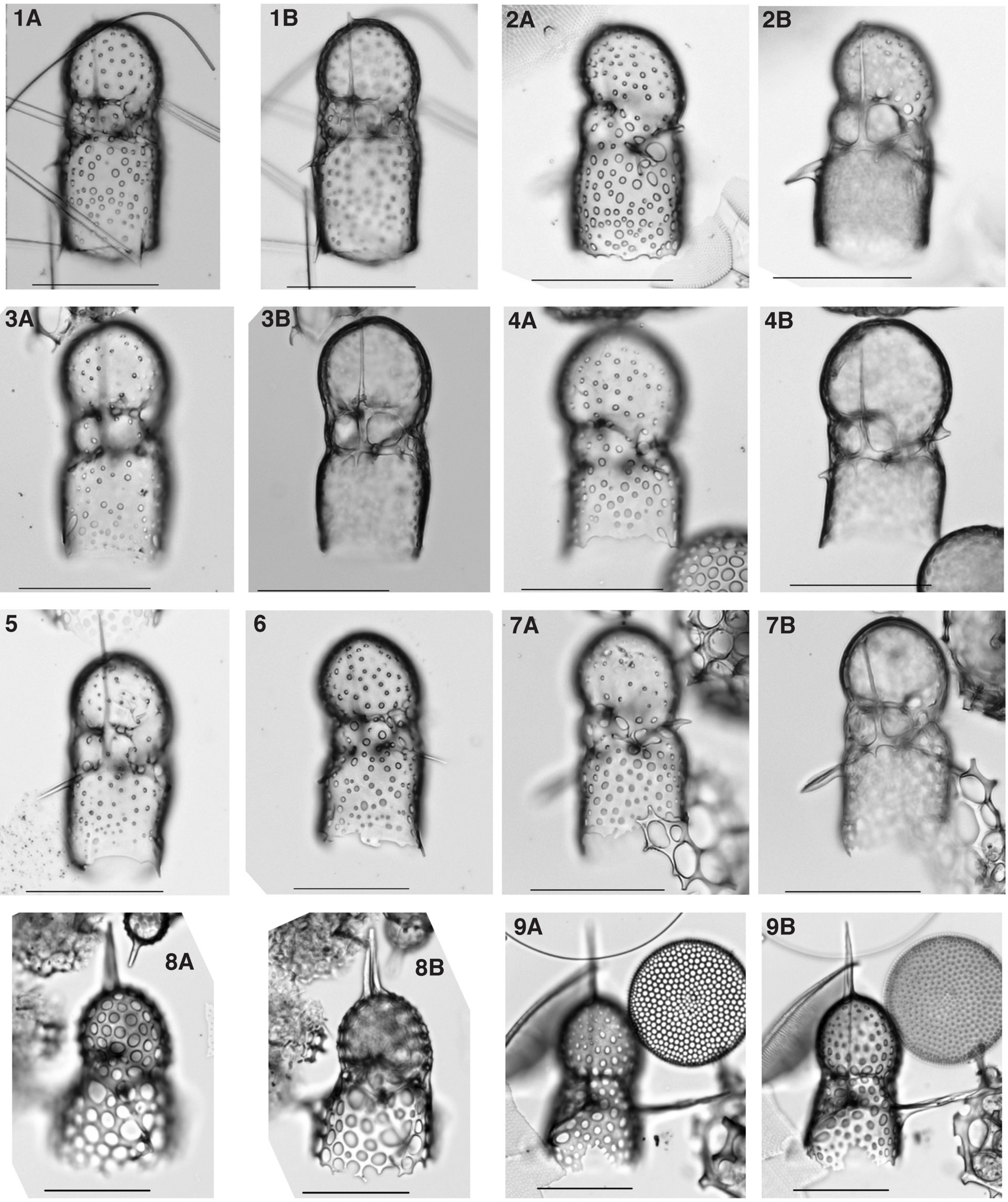

**PLATE 16.**

1A–7B: *Lithomelissa alkonost* n. sp. (1—sample 321-1337A-14H-7, 39–42cm; 2–7—sample 321-1337A-16H-6, 121–124cm)

8A–B: *Lithomelissa* sp. D (sample 321-1337A-6H-3, 29–32cm)

9A–B: *Lithomelissa* cf. *L. ehrenbergi* Bütschli 1882 (sample 321-1337A-7H-6, 104–107cm)

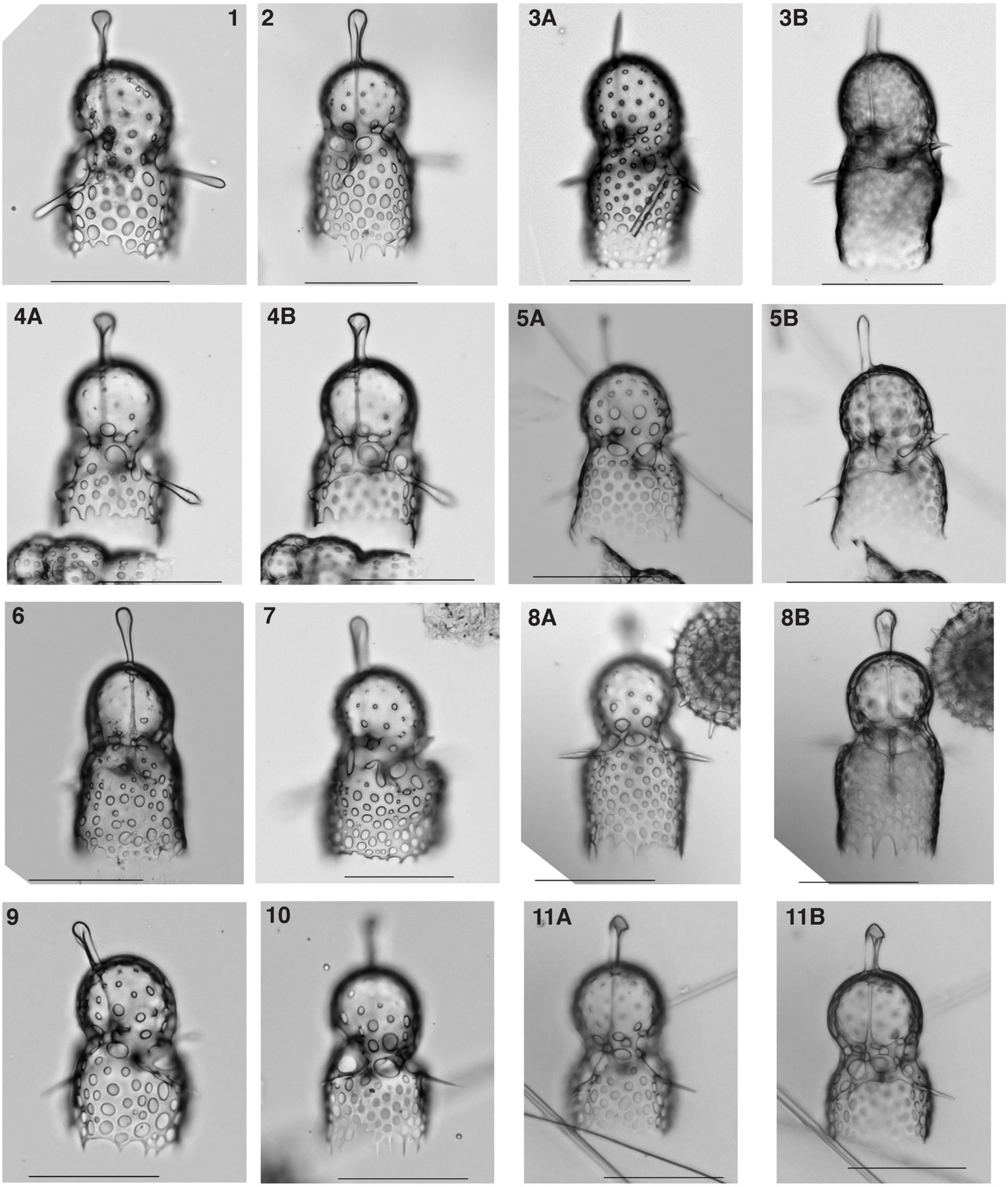

**PLATE 17.**

1–11B: *Lithomelissa sirin* n. sp. (1–2, 4, 7—sample 321-1337A-16H-6, 121–124cm; 3, 5, 8-11—sample 321-1337A-14H-7, 39–42cm)

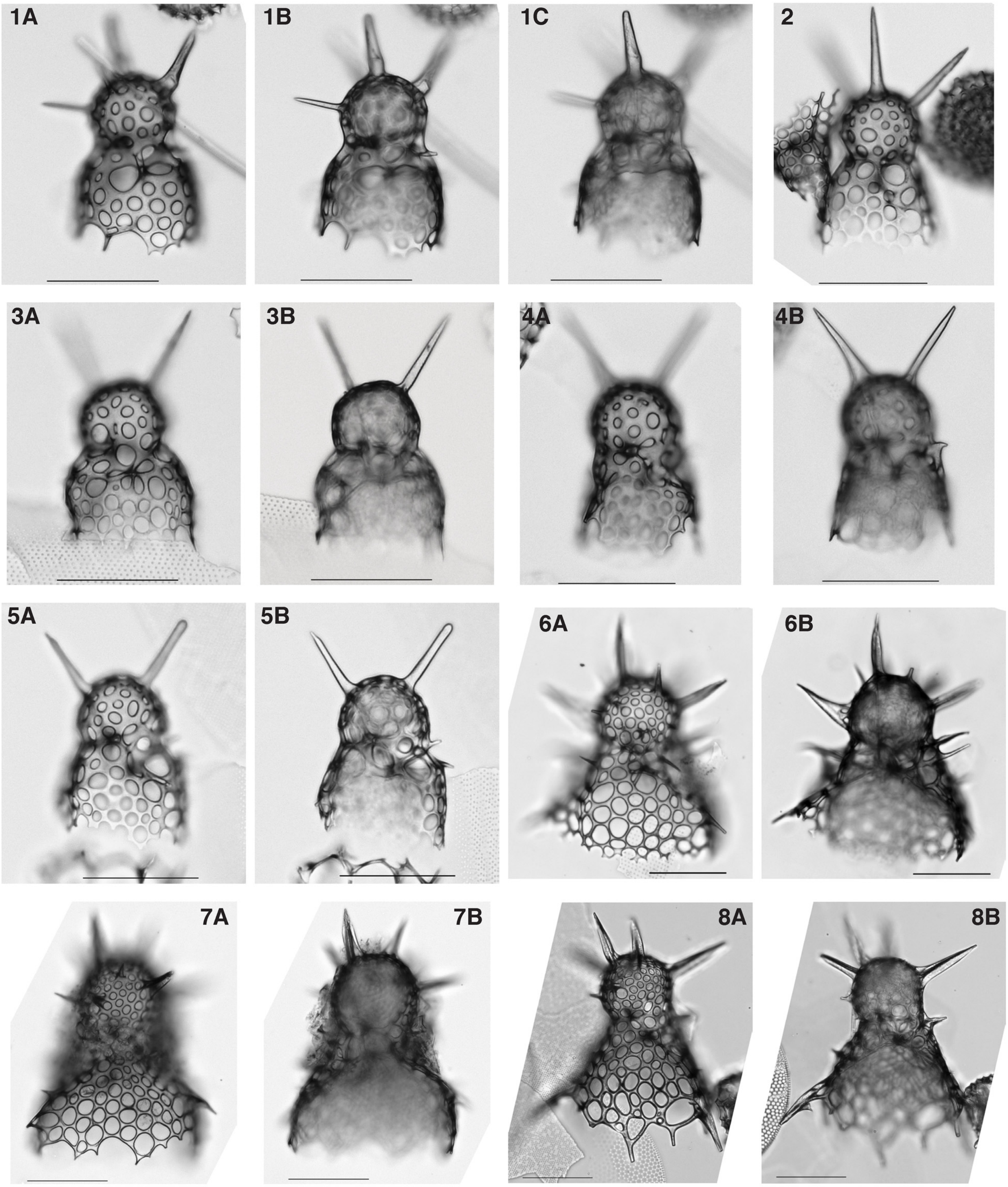

**PLATE 18.**

1A–5B: *Lithomelissa babai* n. sp. (sample 321-1337A-7H-6, 104–107cm)

6A–8B: *Lithomelissa* sp. B (6– sample 321-1337A-5H-5, 11–14cm; 7– 321-1337A-12H-5, 23–26cm; 8—321-1337A-10H-2, 91–94cm)

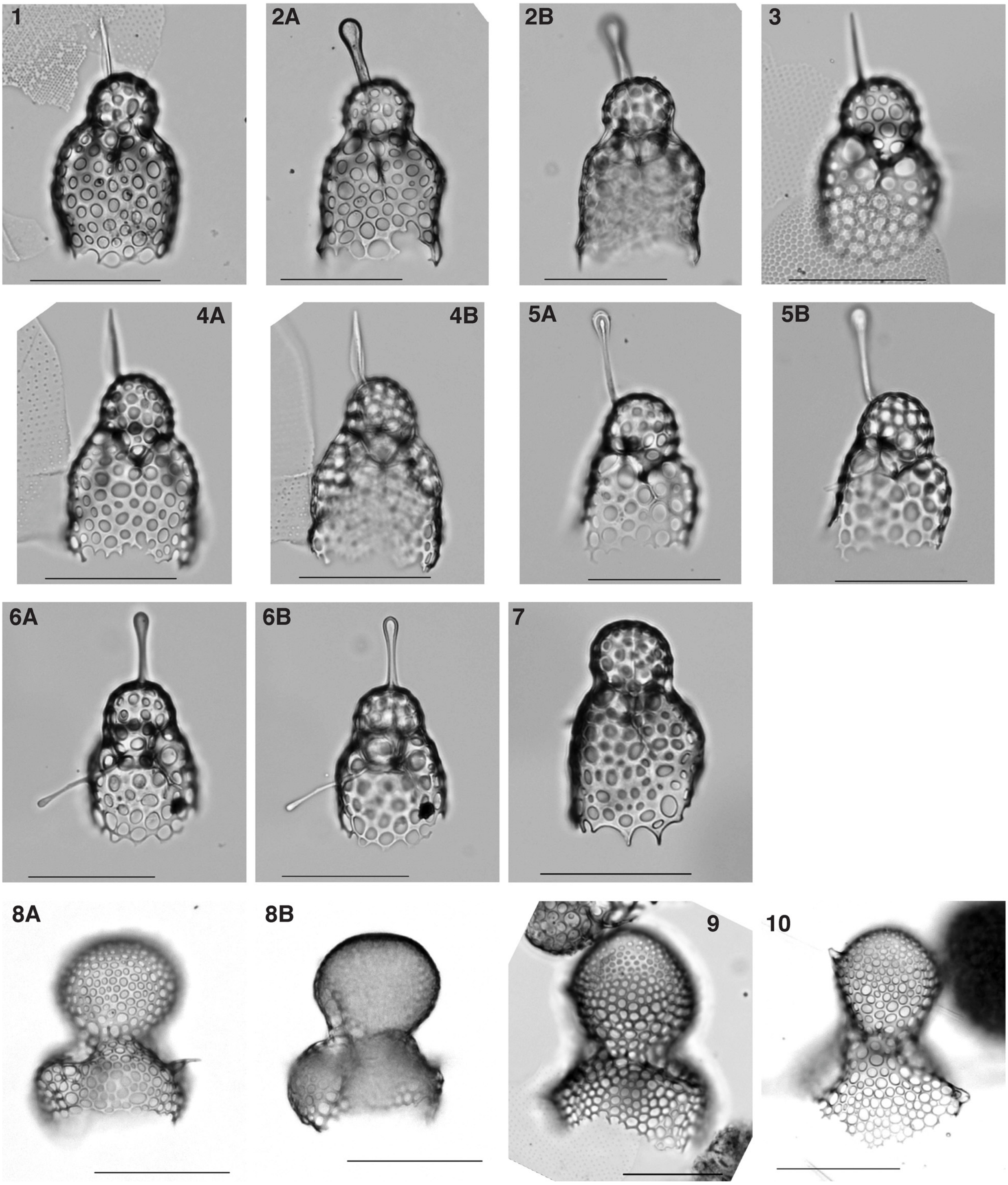

**PLATE 19.**
1–7: *Lithomelissa dybbuki* n. sp. (1–3, 5–7—sample 321-1337A-4H-6, 115–118cm; 4– sample 321-1337A-4H-2, 16–19cm)
8A–10: *Lithomelissa* sp. I (8—sample 321-1337A-7H-6, 104–107cm; 9—sample 321-1337A-5H-5, 11–14cm; 10– sample 321-1337A-14H-7, 39–42cm)

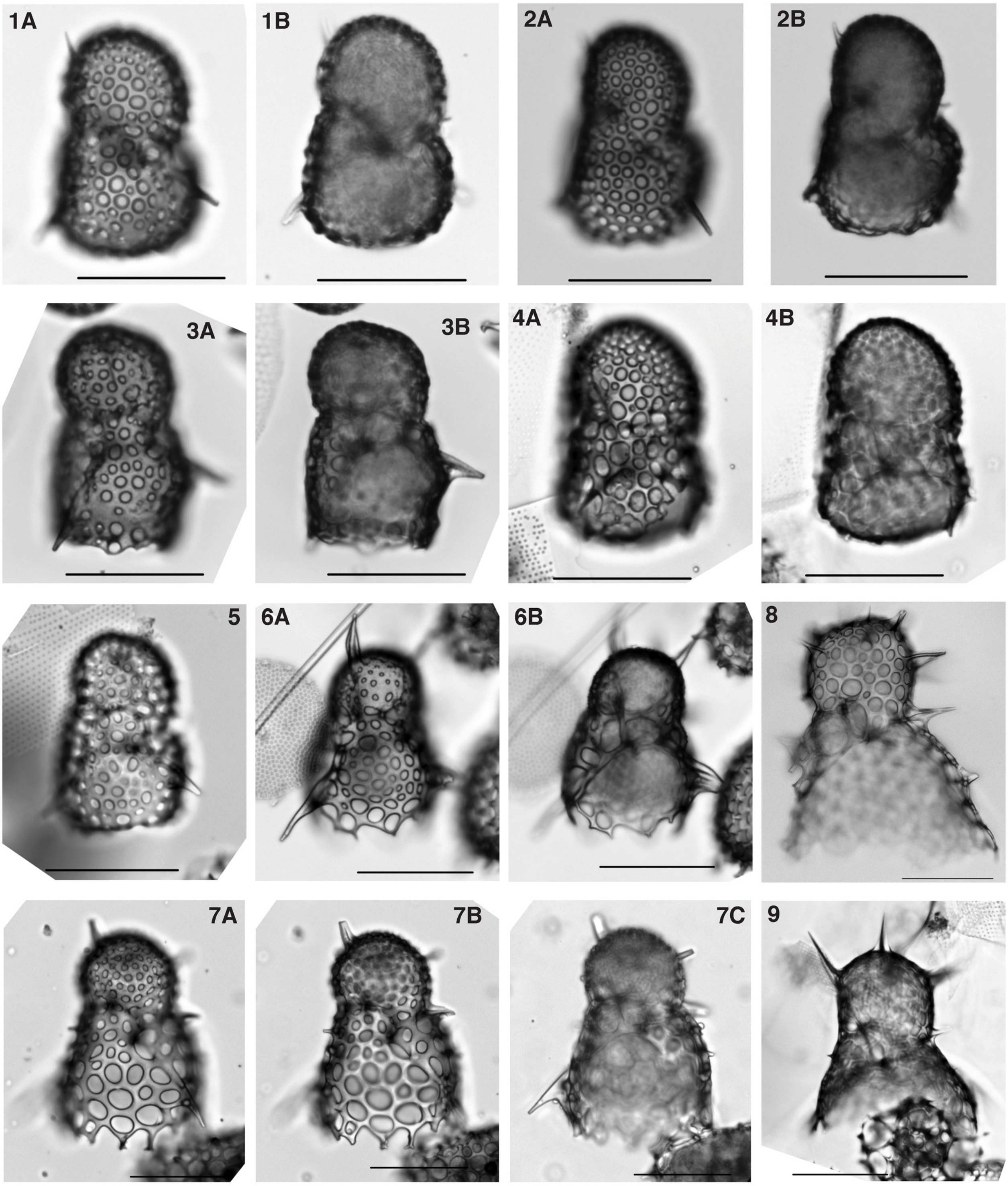

**PLATE 20.**

1A–5: *Lithomelissa* sp. A (1–2, 4—sample 321-1337A-5H-5, 11–14cm; 3—sample 321-1337A-7H-6, 104–107cm; 5—sample 321-1337A-6H-3, 29–32cm)

6A–7C: *Lithomelissa* sp. C (6—sample 321-1337D-23H-6, 134–137cm; 7—sample 321-1337A-16H-6, 121–124cm)

8–9: *Lithomelissa* sp. B (8– sample 321-1337A-14H-7, 39–42cm; 9—sample 321-1337A-4H-2, 16–19cm)

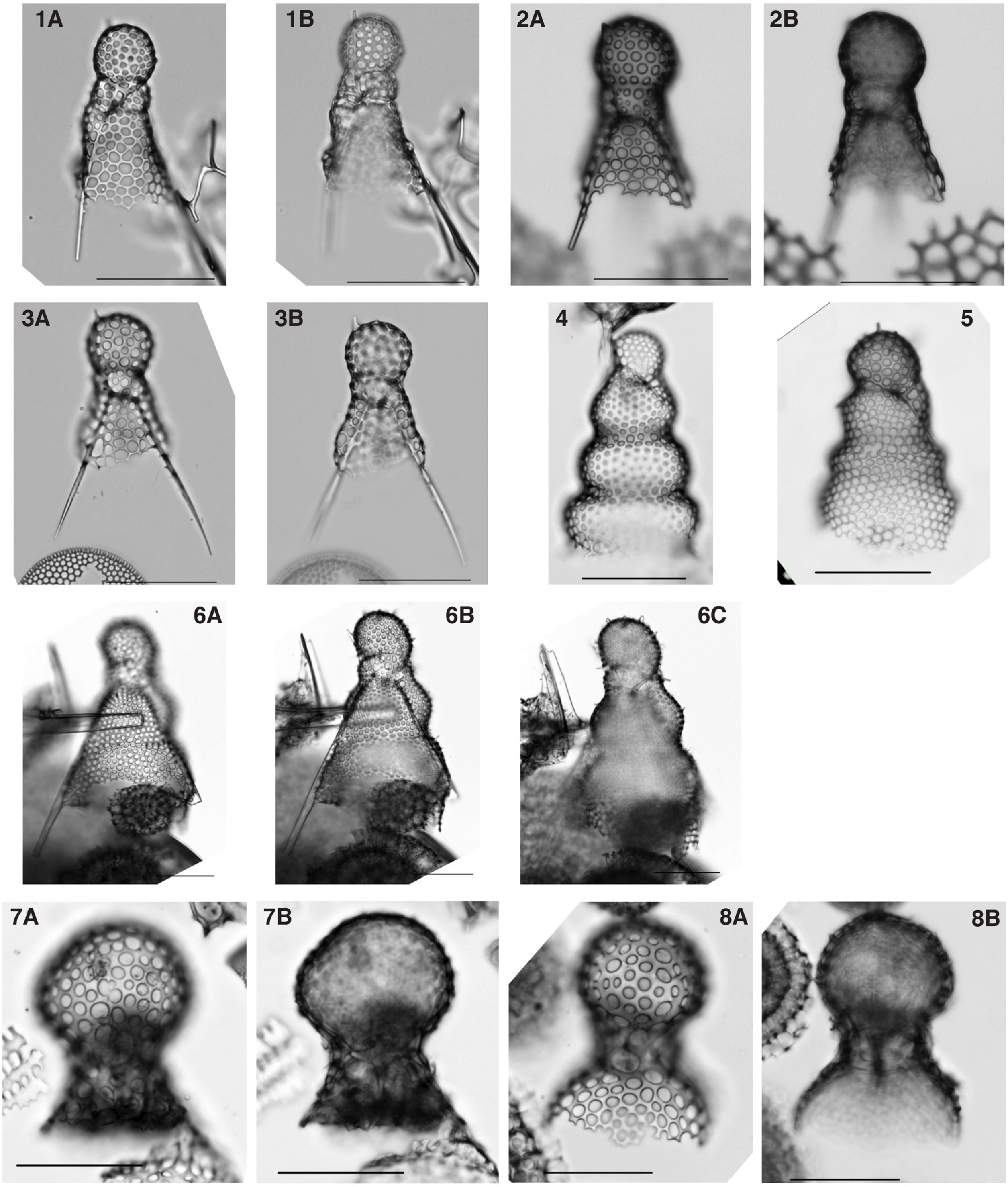

**PLATE 21.**

1A–3B: *Lophophaena amictoria* Renaudie and Lazarus 2015 (1—sample 321-1337D-30H-3, 103–104cm; 2—321-1337A-2H-3, 76–79cm; 3—321-1337A-4H-6, 115–118cm)

4–5: *Lophophanea undulatum* (Popofsky 1913) nov. comb. (4—sample 321-1337A-3H-2, 103–106cm; 5—sample 321-1337D-1H-1, 0–3cm)

6A–C: *Lophophaena* sp. M (sample 321-1337D-23H-6, 134–137cm)

7A–8B: *Lophophaena macrencephala* Clark and Campbell 1945 partim. (sample 321-1337A-18H-6, 77–80cm)

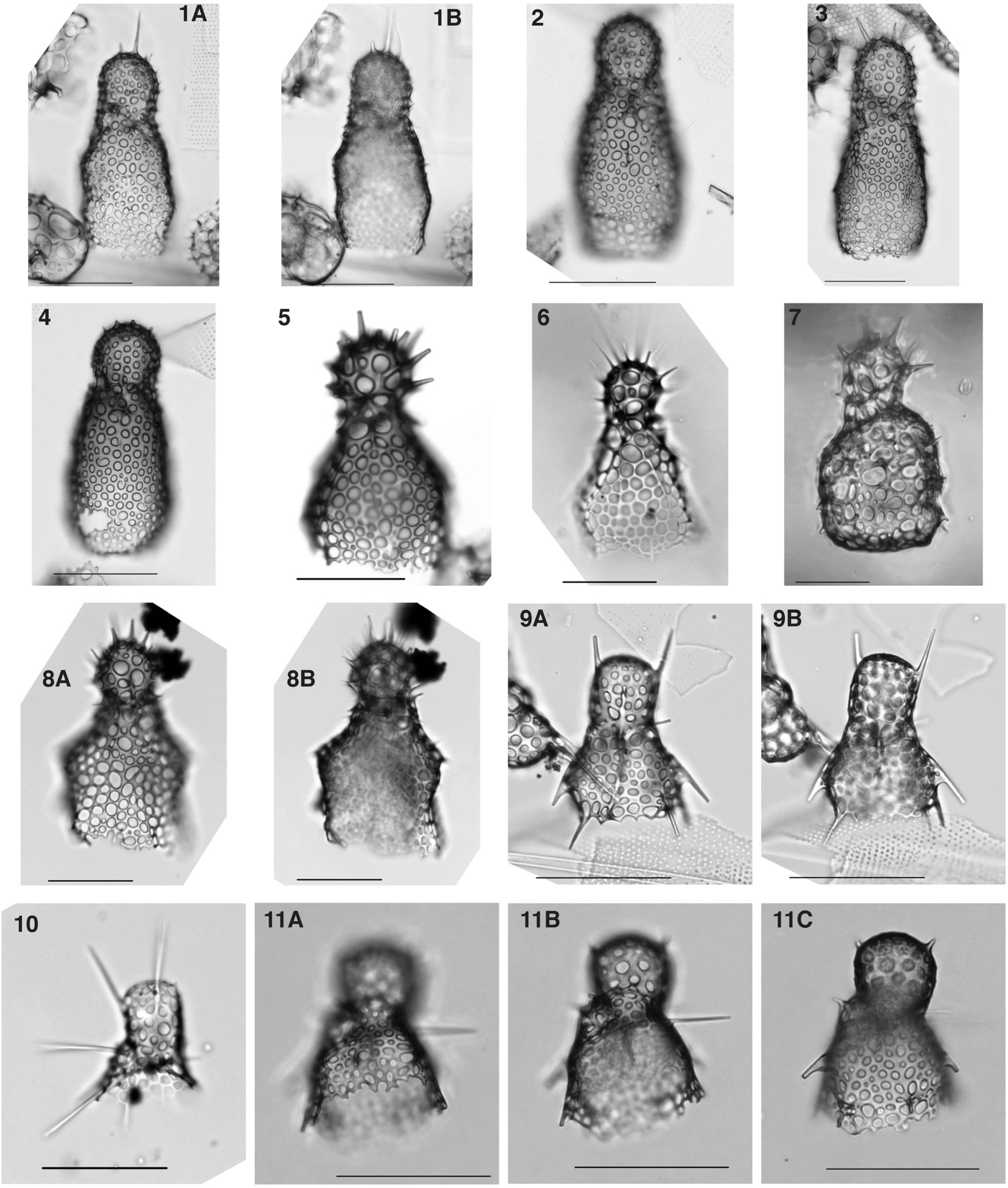

**PLATE 22.**

1A–4: *Lophophaena cylindrica* (Cleve 1900) Petrushevskaya 1971 (sample 321-1337A-7H-6, 104–107cm)

5–8B: *Lophophaena hispida* (Ehrenberg 1862) Petrushevskaya 1971 (5–6—sample 321-1337D-1H-1, 0–3cm; 7– sample 321-1337A-3H-2, 103–106cm; 8—sample 321-1337A-4H-6, 115–118cm)

9A–11C: *Lophophaena variabilis* (Popofsky 1913) Petrushevskaya 1971 (9, 11—sample 321-1337A-3H-2, 103–106cm; 10—sample 321-1337D-1H-1, 0–3cm)

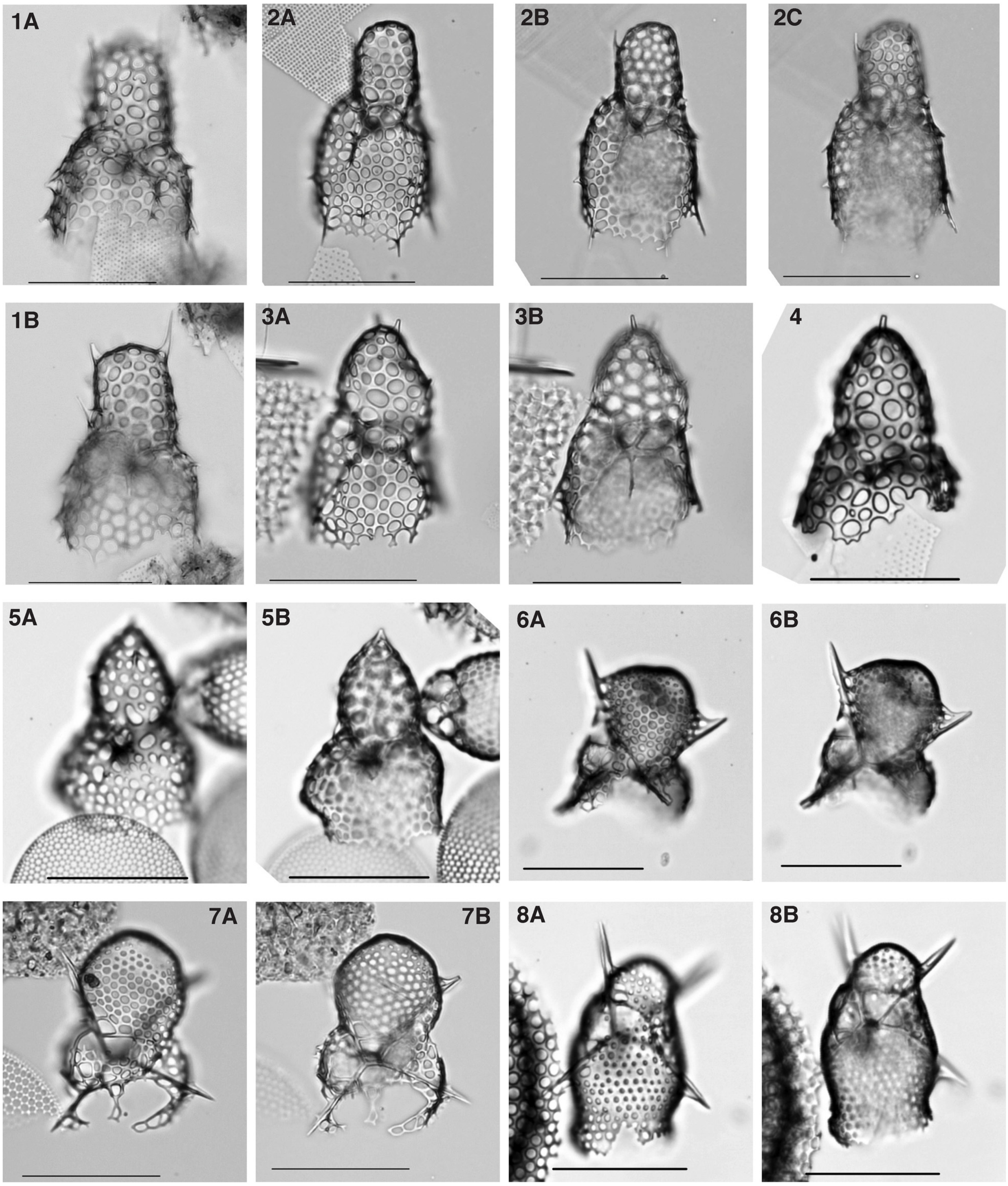

**PLATE 23.**

1A–2C: *Lophophaena nadezdae* Petrushevskaya 1971 (1—sample 321-1337A-3H-2, 103–106cm; 2—sample 321-1337A-4H-2, 16–19cm)

3A–5B: *Lophophaena* sp. C (3—sample 321-1337A-4H-2, 16–19cm; 4—sample 321-1337A-6H-3, 29–32cm; 5—sample 321-1337A-12H-5, 23–26cm)

6A– 7B: *Lophophaena laticeps* (Jørgensen 1905) Kunihara and Matsuoka 2010 (sample 321-1337A-10H-2, 91–94cm)

8A–B: *Stichopilium bicorne* Haeckel 1887 (sample 321-1337D-23H-6, 134–137cm)

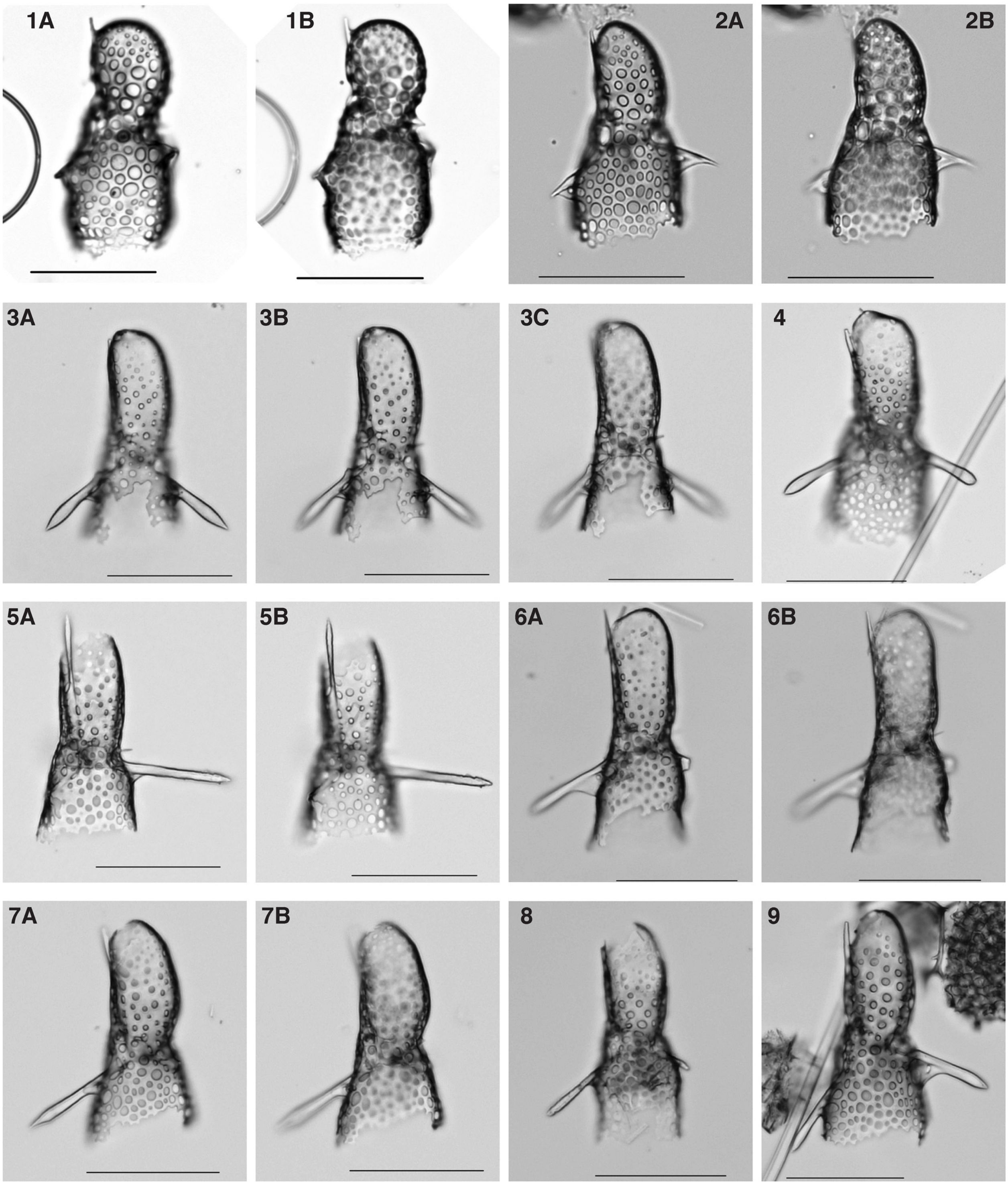

**PLATE 24.**

1A–2B: *Lophophaena buetschlii* (Haeckel 1887) Petrushevskaya 1971 (1—sample 321-1337A-5H-5, 11–14cm; 2—sample 321-1337A-10H-2, 91–94cm)

3A–9: *Lophophaena leshii* n. sp. (sample 321-1337D-23H-6, 134–137cm)

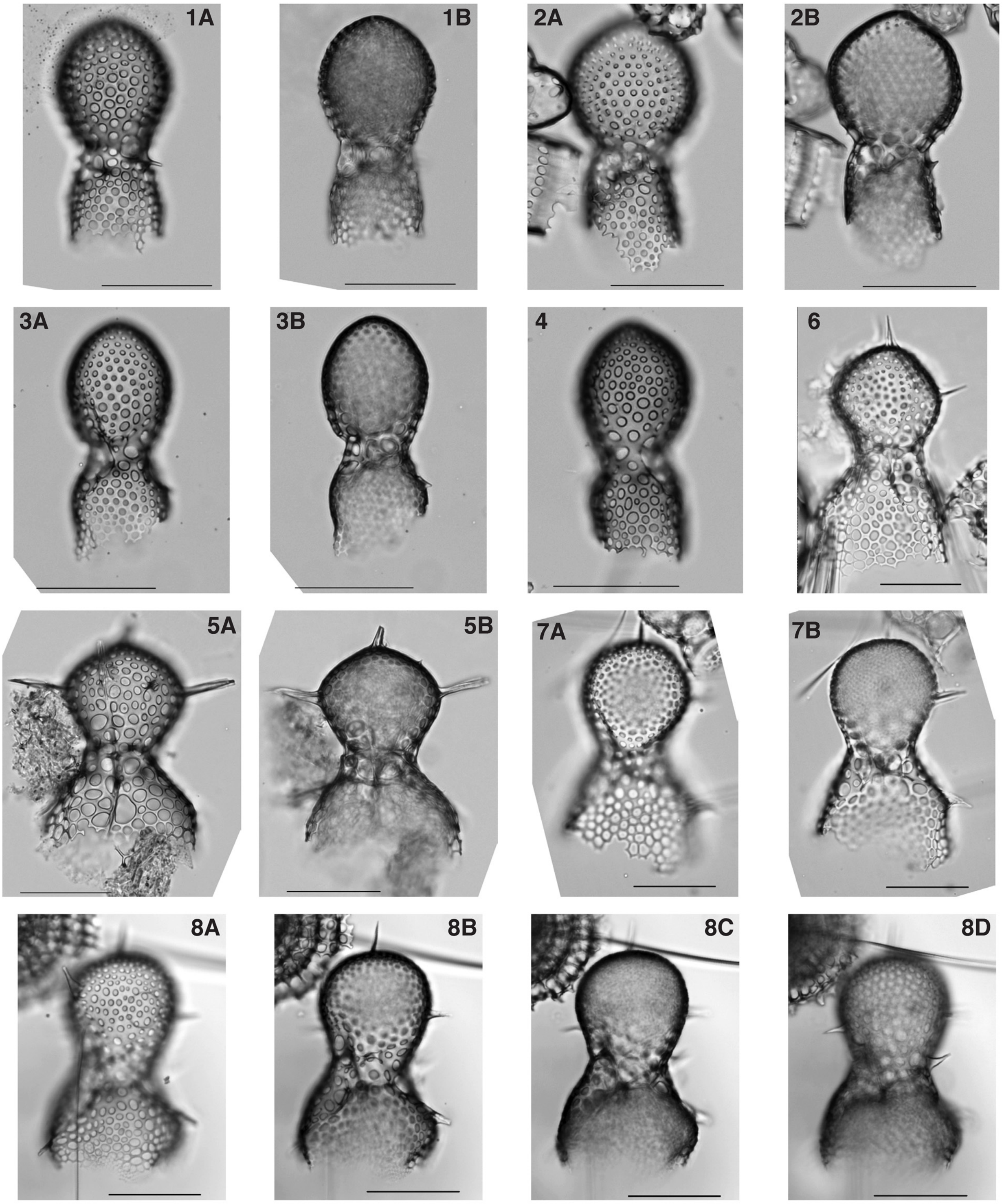

**PLATE 25.**

1A–4: *Lophophaena rhopalica* Renaudie and Lazarus 2016 (1,3—sample 321-1337D-30H-3, 103–104cm; 2—sample 321-1337A-35X-1, 106–108cm; 4—sample 321-1337A-31X-6, 4–6cm)

5A–B: *Lophophaena witjazii* (Petrushevskaya 1971) nov. comb. (sample 321-1337A-4H-6, 115–118cm)

6–8D: *Lophophaena* cf. *L. witjazii* (sample 321-1337A-14H-7, 39–42cm)

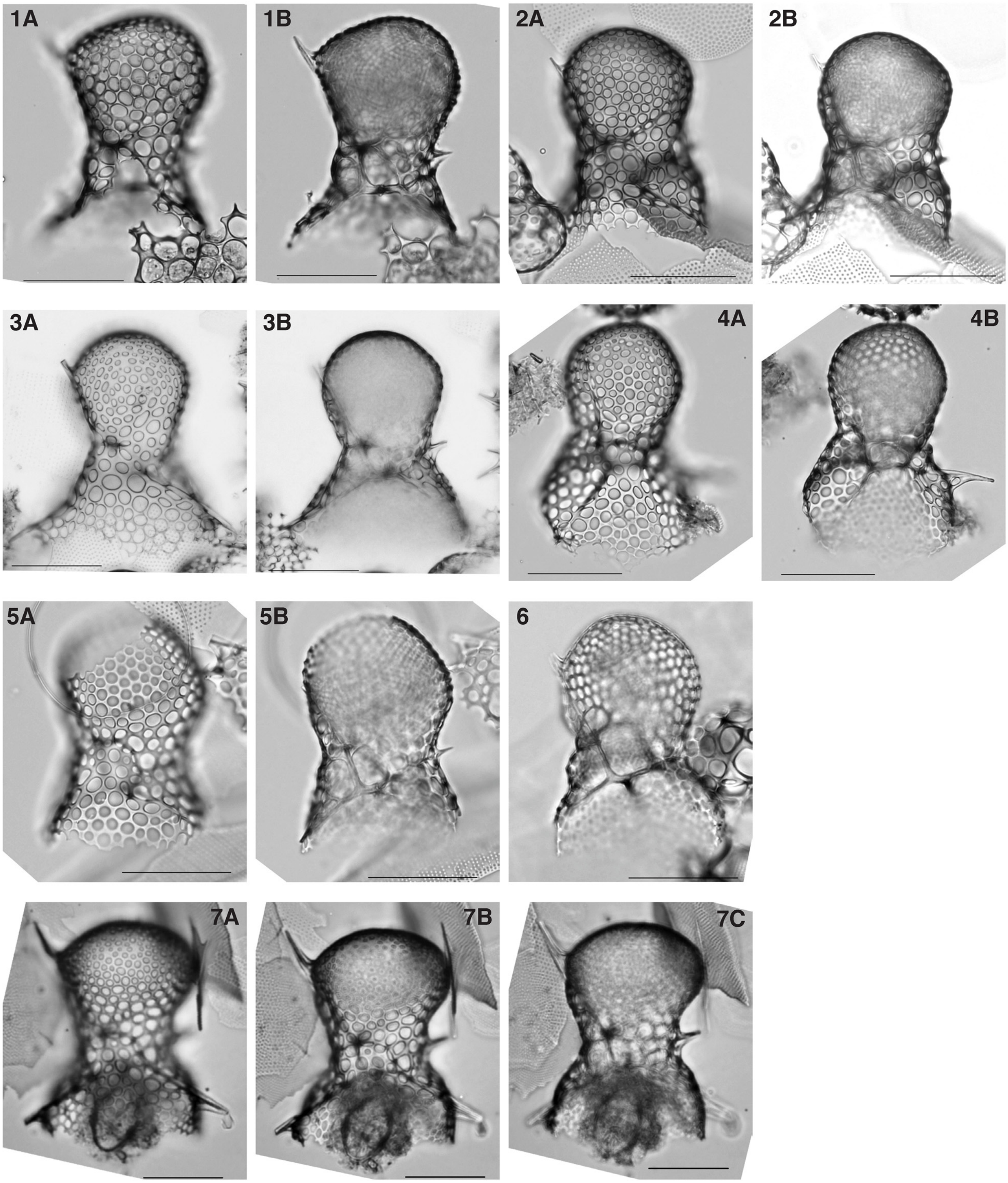

**PLATE 26.**

1A–6: *Lophophaena arie* n. sp. (1– sample 321-1337A-3H-2, 103–106cm; 2, 4–6—sample 321-1337A-4H-2, 16–19cm; 3—sample 321-1337A-7H-6, 104–107cm)

7A–C: *Lophophaena arie*? (sample 321-1337A-3H-2, 103–106cm)

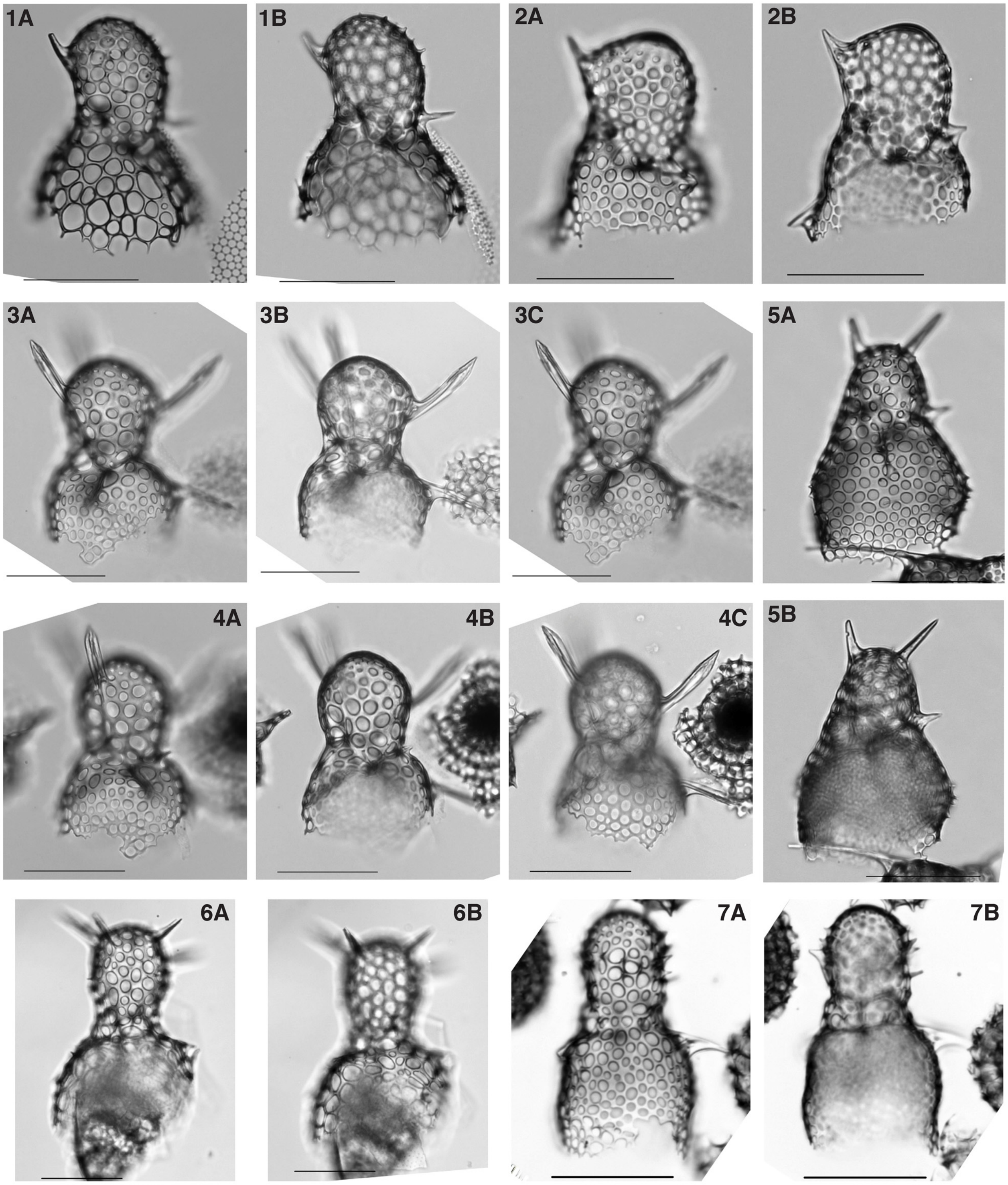

**PLATE 27.**

1A–2B: *Lophophaena decacantha* (Haeckel 1887) group sensu Takahashi 1991 (sample 321-1337A-4H-6, 115–118cm)

3A–4C: *Lophophaena* cf. *decacantha* (Haeckel 1887) Petrushevskaya 1971 (sample 321-1337A-3H-2, 103–106cm)

5A–B: *Lophophaena? leberu* Renaudie and Lazarus 2012 (sample 321-1337A-10H-2, 91–94cm)

6A–7B: *Lophophaena* sp. O (6—sample 321-1337A-3H-2, 103–106cm; 7—sample 321-1337A-12H-5, 23–26cm)

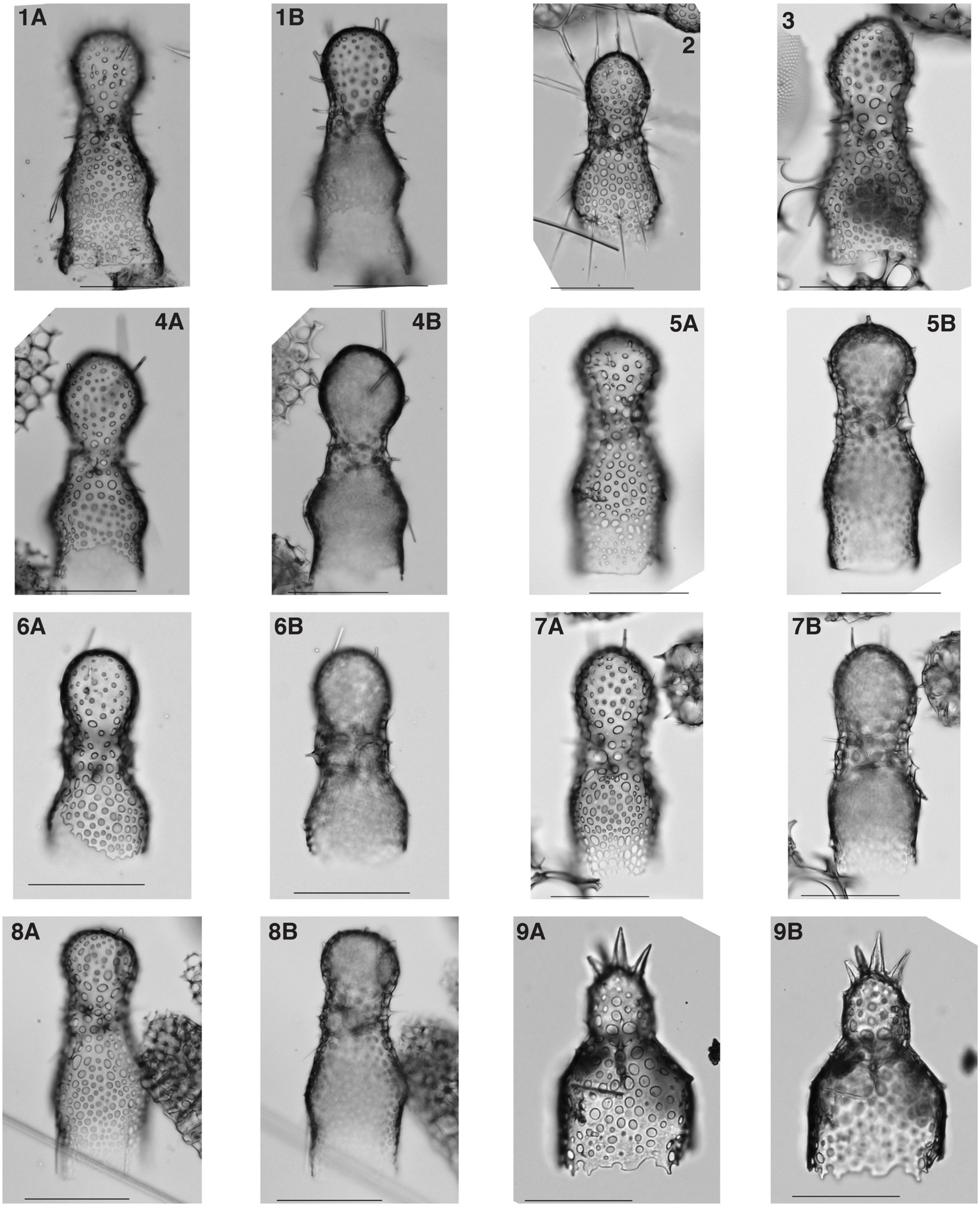

**PLATE 28.**

1A–8B: *Lophophaena casperi* n. sp. (1, 4—sample 321-1337A-21H-1, 33–35cm; 2, 8—sample 321-1337A-14H-7, 39–42cm; 3, 5–7—sample 321-1337A-16H-6, 121–124cm)

9A–B: *Lophophaena* sp. N (sample 321-1337A-10H-2, 91–94cm)

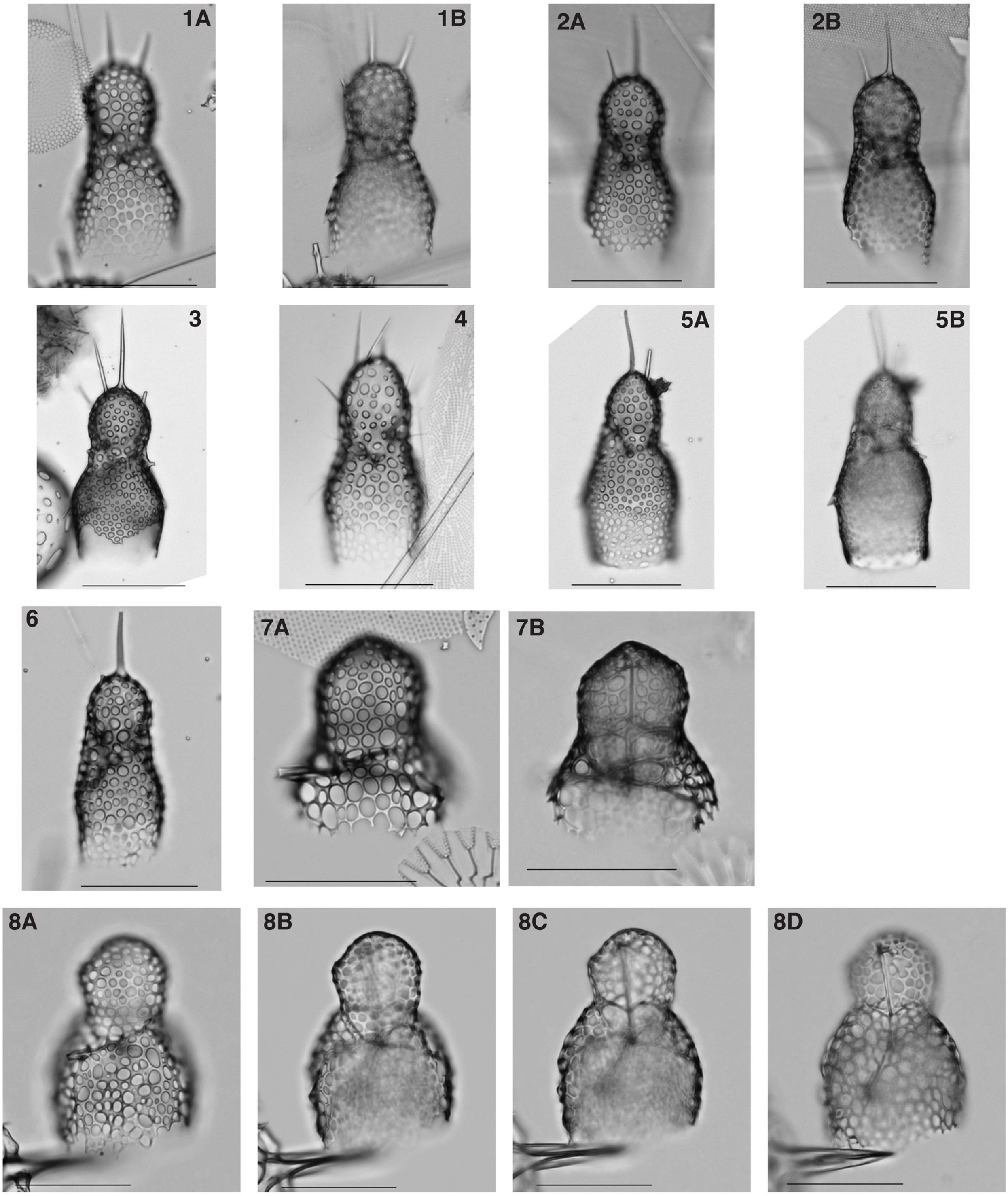

**PLATE 29.**

1A–6: *Lophophaena rusalkae* n. sp. (1–2, 4, 6—sample 321-1337A-14H-7, 39–42cm; 3, 5—sample 321-1337A-12H-5, 23–26cm)

7A–8D: *Lophophaena* sp. L (sample 321-1337A-4H-6, 115–118cm)

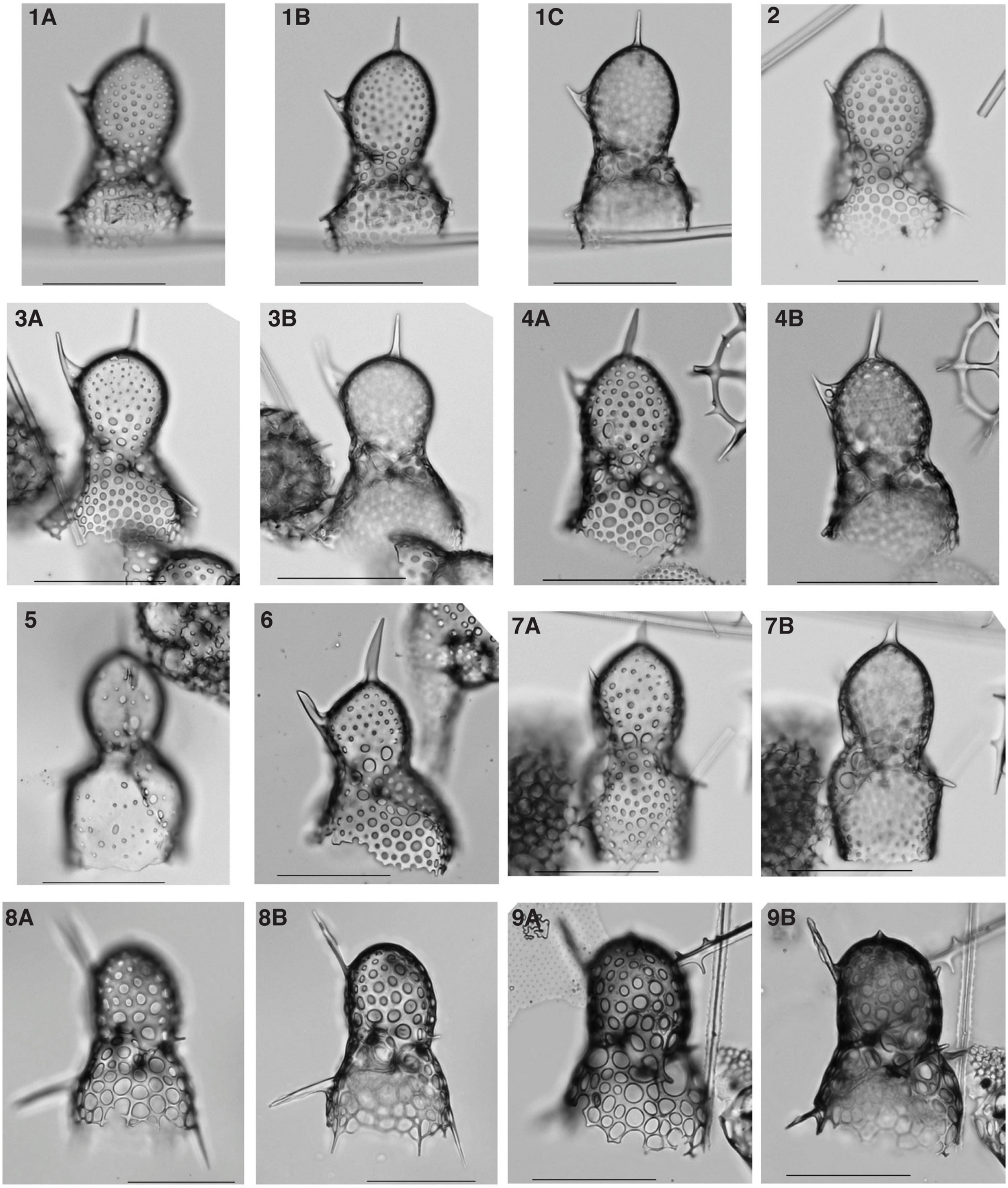

**PLATE 30.**

1A–7B: *Lophophaena domovoi* n. sp. (1–3, 5, 7—sample 321-1337D-23H-6, 134–137cm; 4, 6—sample 321-1337A-31X-6, 4–6cm)

8A–9B: *Lophophaena* sp. G (sample 321-1337A-3H-2, 103–106cm)

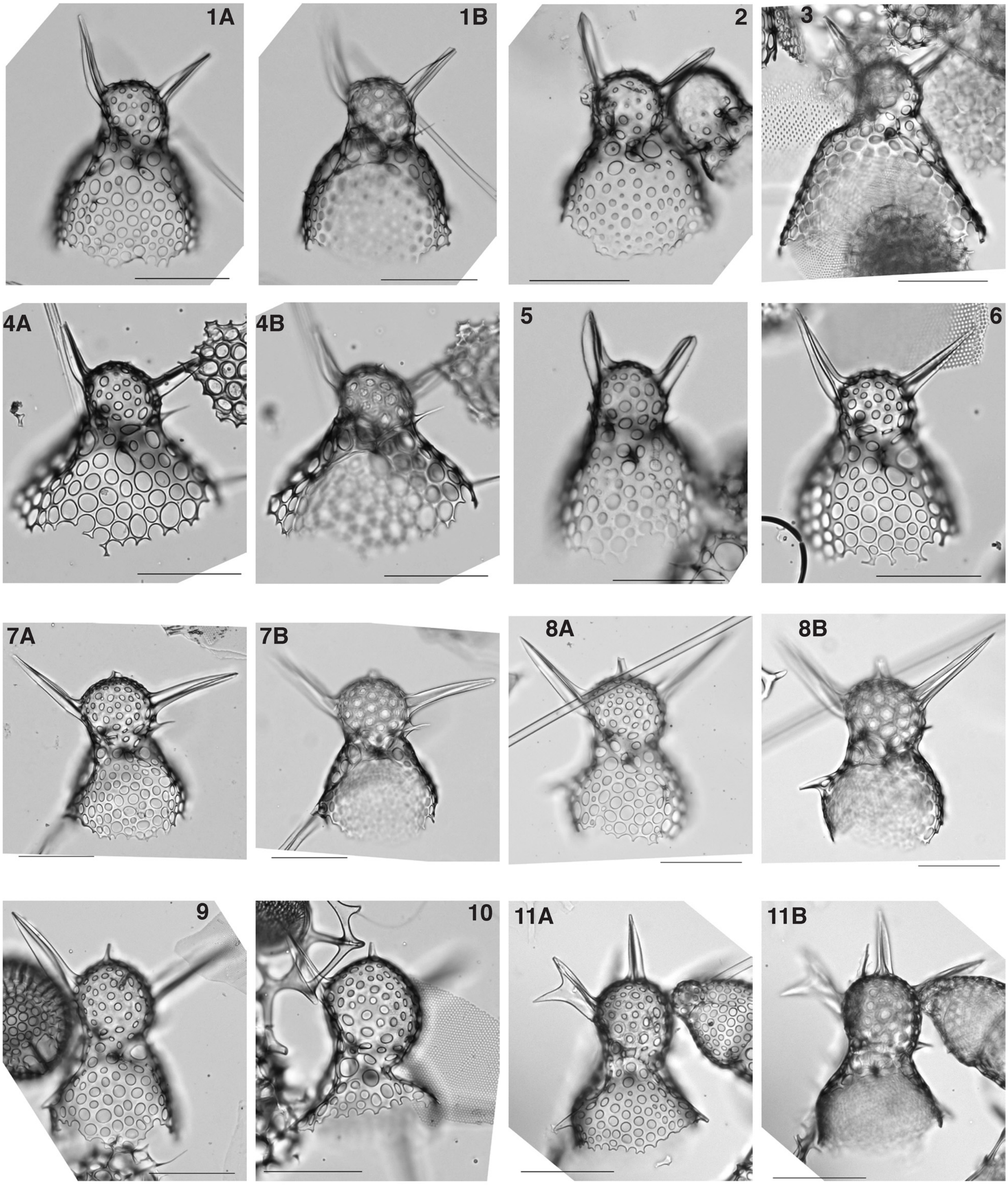

**PLATE 31.**

1A–6: *Lophophaena gozui* n. sp. (1–2, 5—sample 321-1337D-23H-6, 134–137cm; 3–4, 6– sample 321-1337D-26H-3, 142–144cm)

7A–11B: *Lophophaena ushionii* n. sp. (7–10—sample 321-1337A-31X-6, 4–6cm; 11—sample 321-1337D-26H-3, 142–144cm)

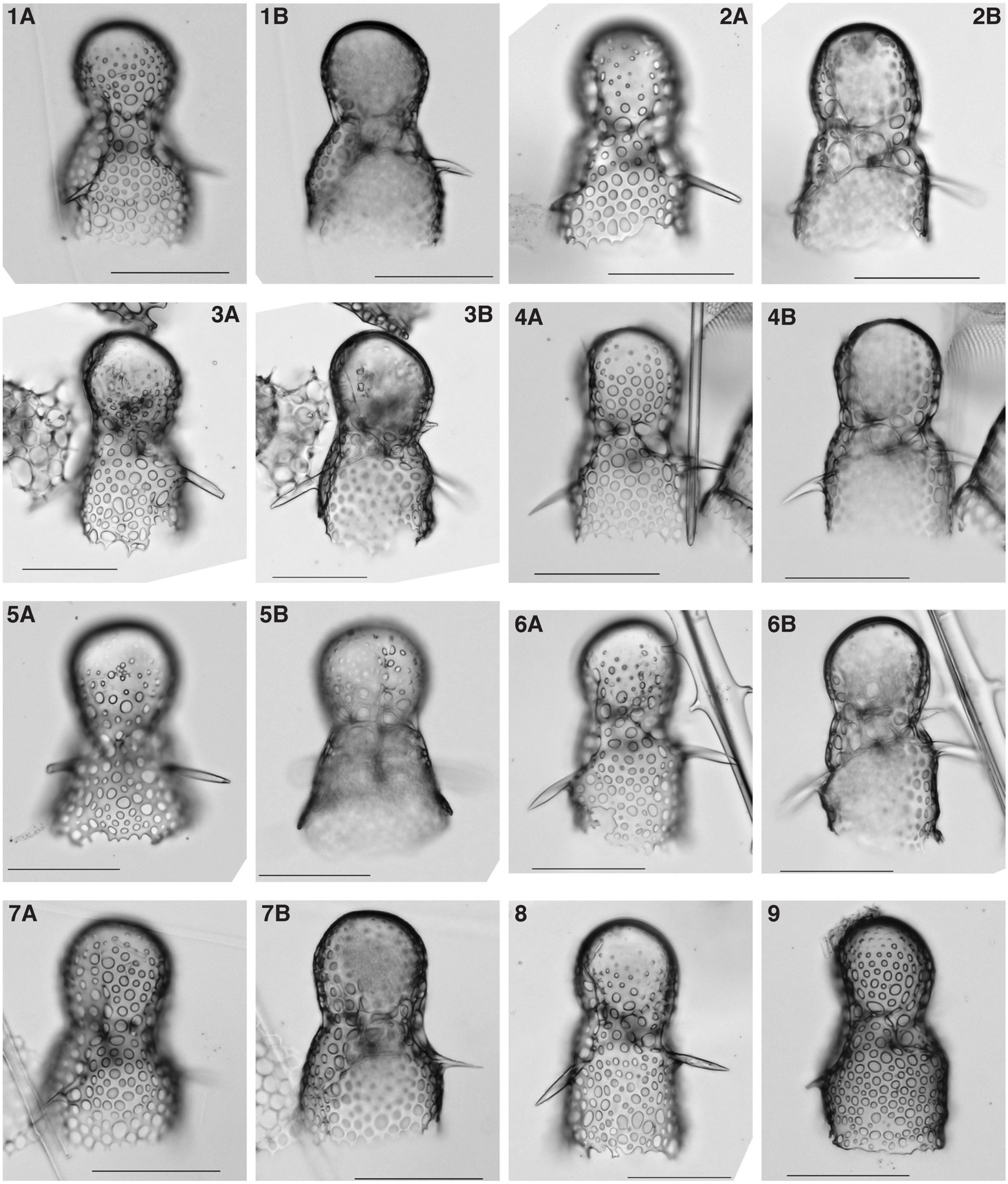

**PLATE 32.**

1A–9: *Lophophaena ikiryo* n. sp. (1, 4, 7—sample 321-1337A-14H-7, 39–42cm; 2–3, 5–6, 8—sample 321-1337A-16H-6, 121–124cm; 9—sample 321-1337A-12H-5, 23–26cm)

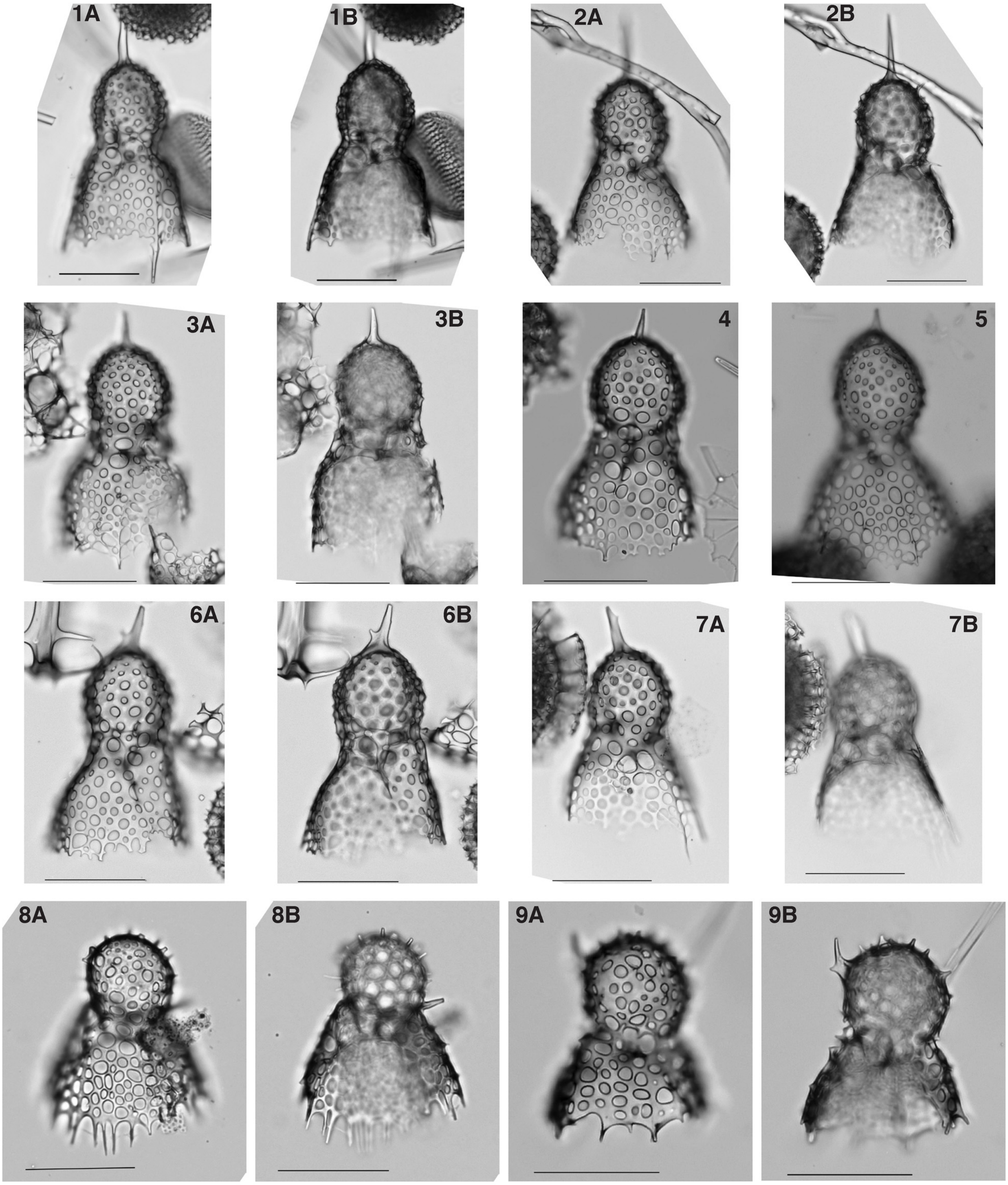

**PLATE 33.**

1A–7B: *Lophophaena ikota* n. sp. (1–5, 7—sample 321-1337D-23H-6, 134–137cm; 6—sample 321-1337D-26H-3, 142–144cm)

8A–9B: *Lophophaena simplex* Funakawa 1994 (8– sample 321-1337D-26H-3, 142–144cm; 9—sample 321-1337D-30H-3, 103–104cm)

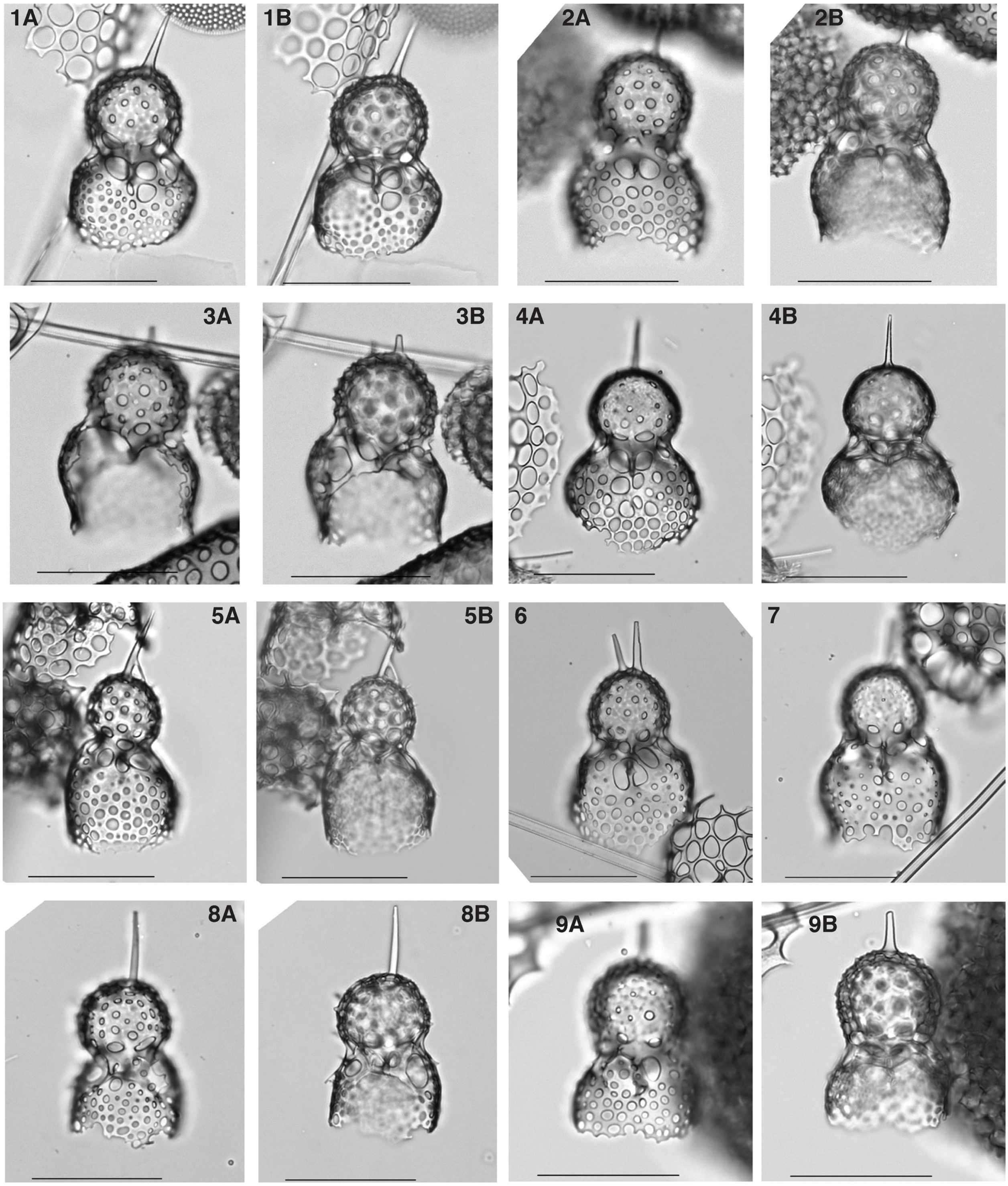

**PLATE 34.**

1–9B: *Lophophaena kaonashii* n. sp. (1–3, 9—sample 321-1337D-26H-3, 142–144cm; 4,7–8—sample 321-1337A-31X-6, 4–6cm; 5—sample 321-1337D-23H-6, 134–137cm; 6—sample 321-1337D-30H-3, 103–104cm)

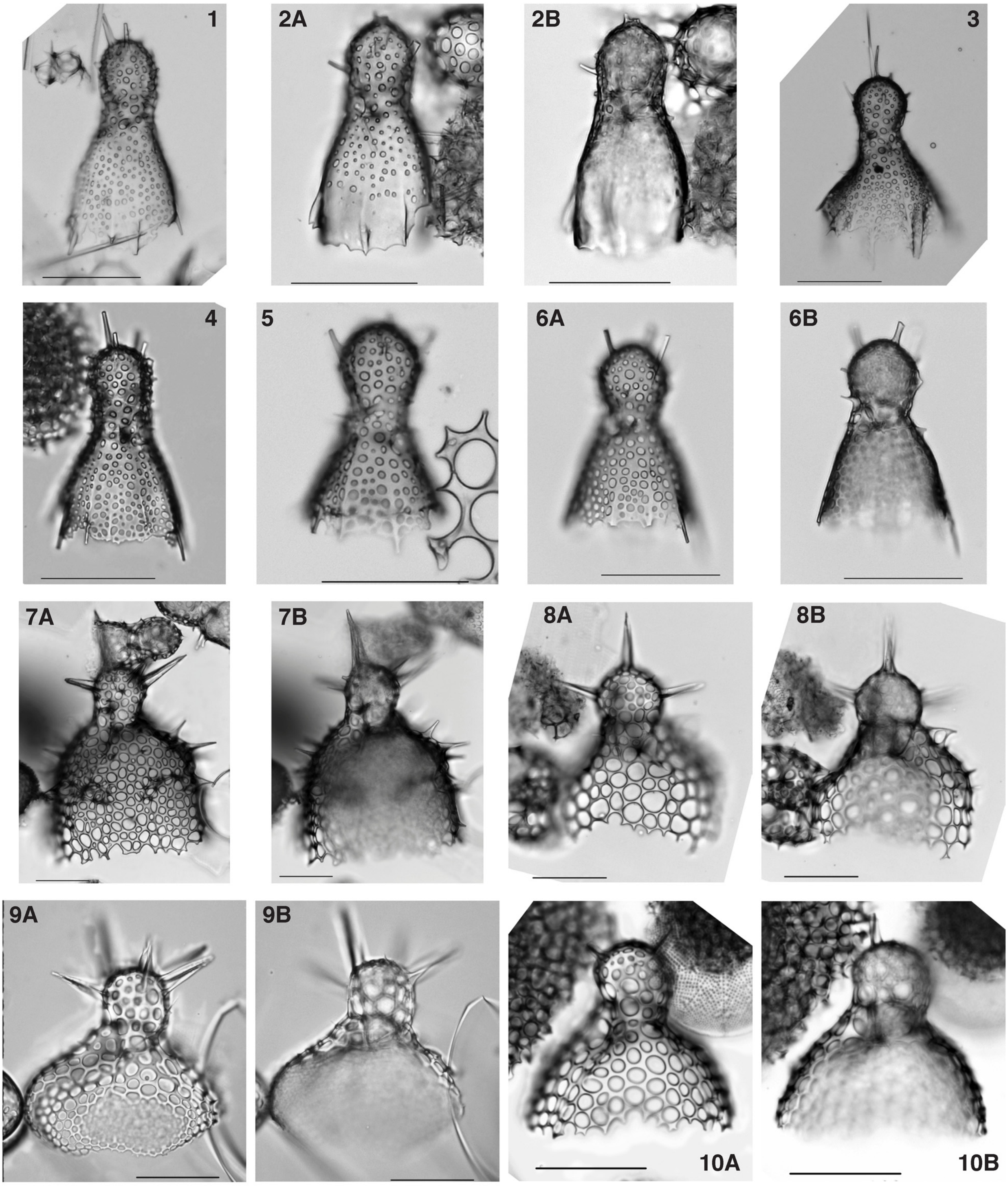

**PLATE 35.**

1–6B: *Lophophaena shishigae* n. sp. (1–2, 4–5—sample 321-1337D-23H-6, 134–137cm; 3—sample 321-1337A-21H-1, 33–35cm)

7A–10B: *Lophophaena* sp. H (7—sample 321-1337A-7H-6, 104–107cm; 8—sample 321-1337A-5H-5, 11–14cm; 9—sample 321-1337A-14H-7, 39–42cm; 10- sample 321-1337A-12H-5, 23–26cm)

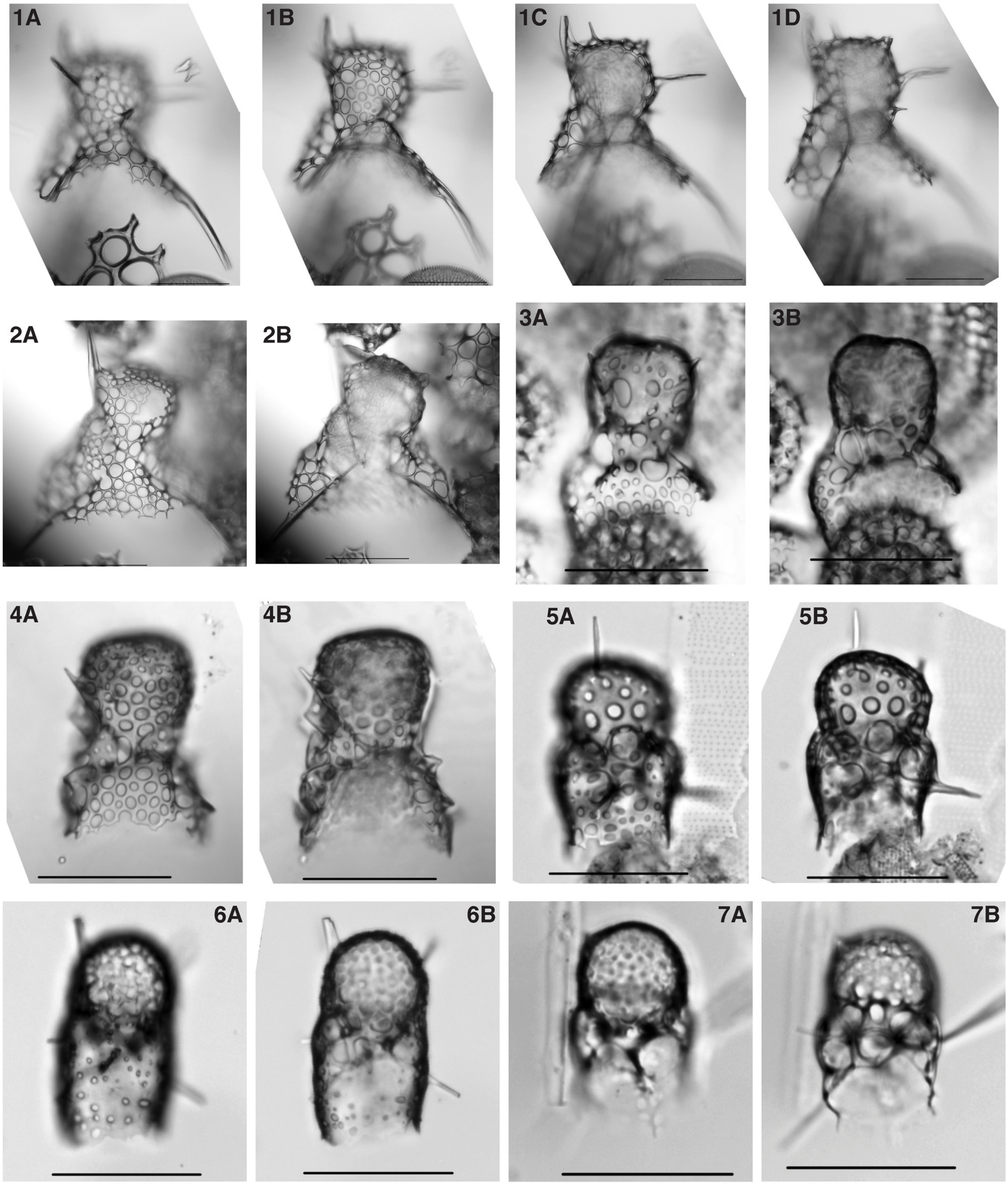

**PLATE 36.**

1A–2B: *Lophophaena* sp. A (sample 321-1337A-2H-3, 76–79cm)

3A–4B: *Lophophaena* sp. B (3—sample 321-1337D-23H-6, 134–137cm; 4—321-1337A-12H-5, 23–26cm)

5A–7B: Lophophaena sp. cf. *Trisulcus testudus* Petrushevskaya 1971 group (5–6—sample 321-1337A-5H-5, 11–14cm; 7—321-1337D-1H-1, 0–3cm)

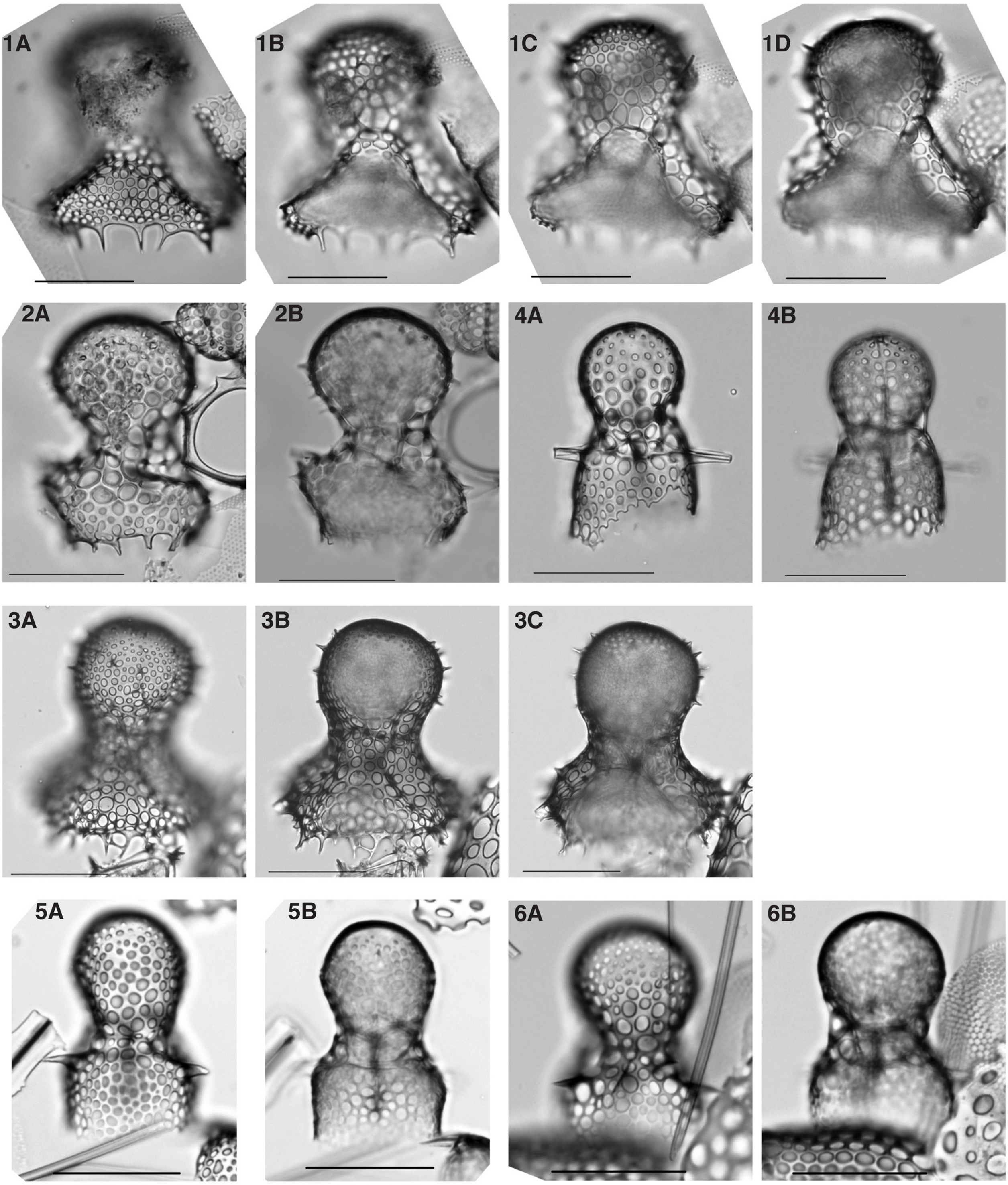

**PLATE 37.**

1A–3C: *Lophophaena* sp. E group (1—sample 321-1337A-6H-3, 29–32cm; 2—sample 321-1337A-3H-2, 103–106cm; 3—sample 321-1337A-10H-2, 91–94cm)

4A–6B: *Lophophaena* sp. J (4—sample 321-1337A-4H-6, 115–118cm; 5-6—sample 321-1337A-14H-7, 39–42cm)

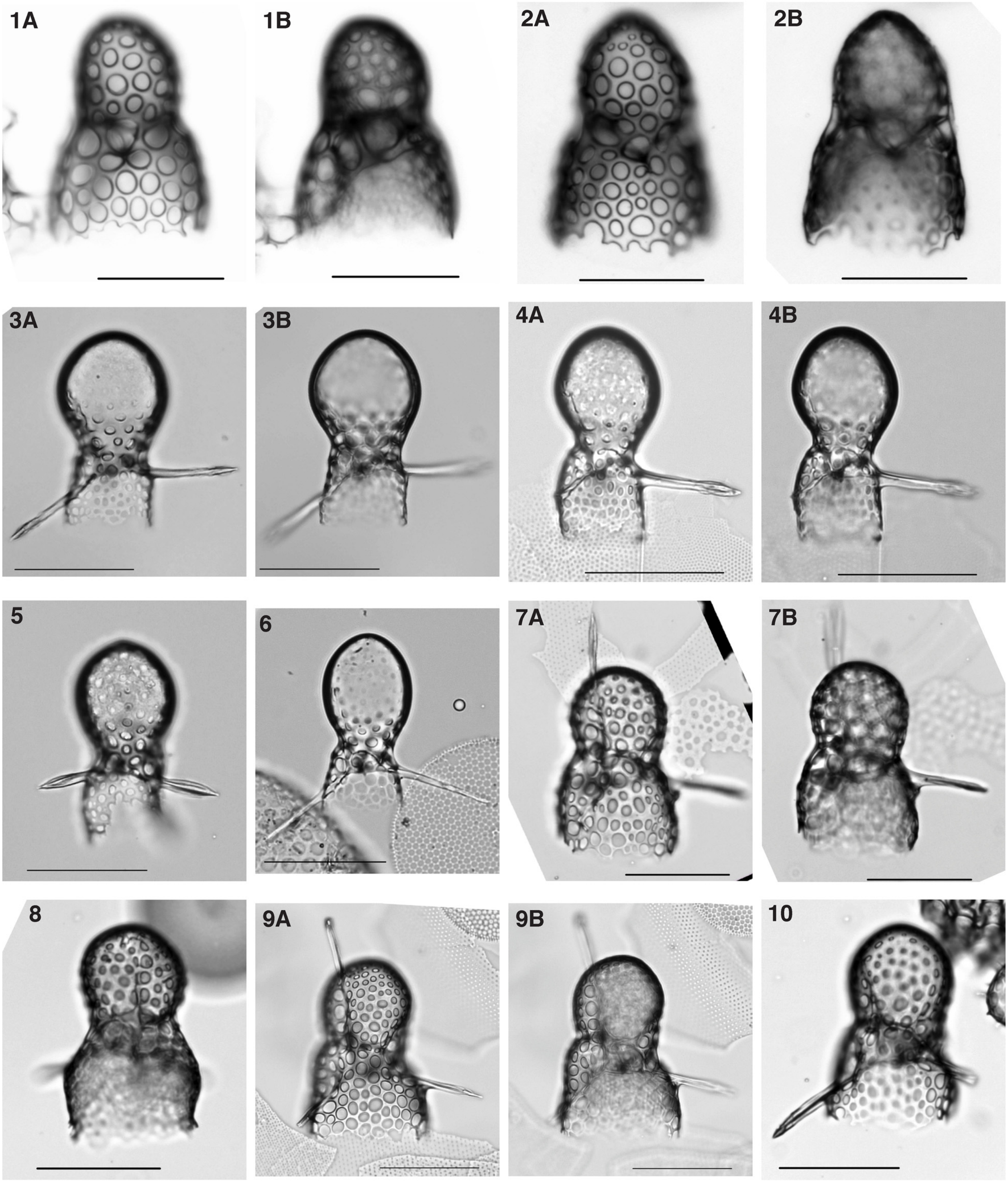

**PLATE 38.**

1A–2B: *Lophophaena* sp. F (sample 321-1337D-1H-1, 0–3cm)

3A–6: *Peromelissa phalacra* (Haeckel 1887) Petrushevskaya 1971 (3—sample 321-1337A-4H-6, 115–118cm; 4—sample 321-1337A-3H-2, 103–106cm; 5—sample 321-1337A-10H-2, 91–94cm; 6—sample 321-1337D-1H-1, 0–3cm)

7A–10: *Peromelissa thoracites* (Haeckel 1887) Matsuzaki et al. 2015 (7–8– sample 321-1337A-14H-7, 39–42cm; 9—sample 321-1337A-4H-2, 16–19cm; 10—sample 321-1337A-5H-5, 11–14cm)

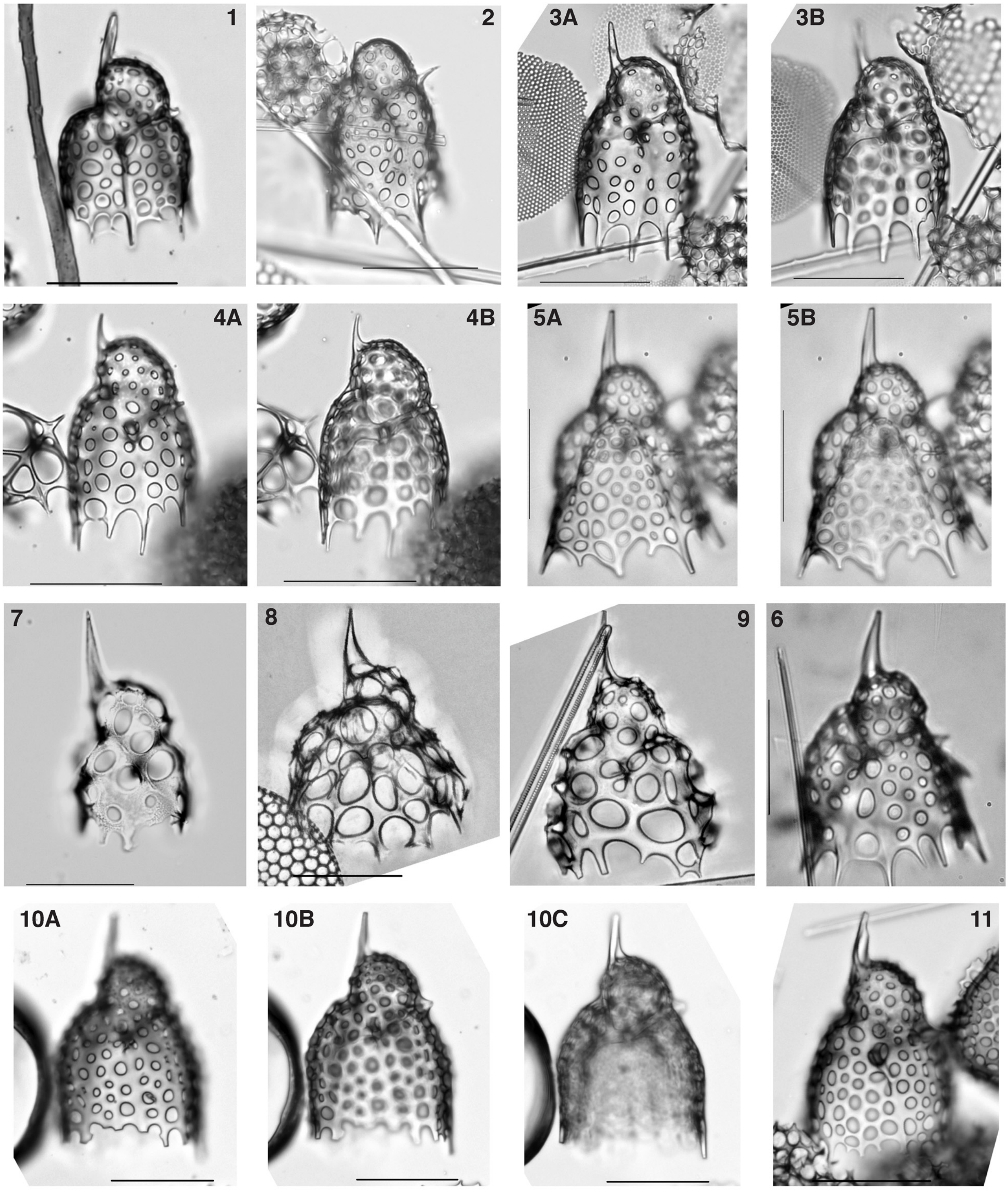

**PLATE 39.**

1–6: *Pelagomanes kozoi* (Renaudie and Lazarus 2013) nov. comb. (1–2—sample 321-1337A-16H-6, 121–124cm; 3–4—sample 321-1337D-26H-3, 142–144cm; 5—Late Pliocene Antarctic specimen from Renaudie and Lazarus 2013; 6—Holotype from Renaudie and Lazarus 2013)

7–9: *Pelagomanes stigi* (Bjørklund 1976) nov. comb. (specimens from the Southern Ocean, photographed in 2021 by D.B. Lazarus; 7—sample 1138A-13R-5W-30; 8—sample 751A-6H-6,48; 9—sample 747A-4H-7,45)

10A–11: *Pelagomanes thaumasia* (Caulet 1991) nov. comb. (10– sample 321-1337A-18H-6, 77–80cm; 11- sample 321-1337D-23H-6, 134–137cm)

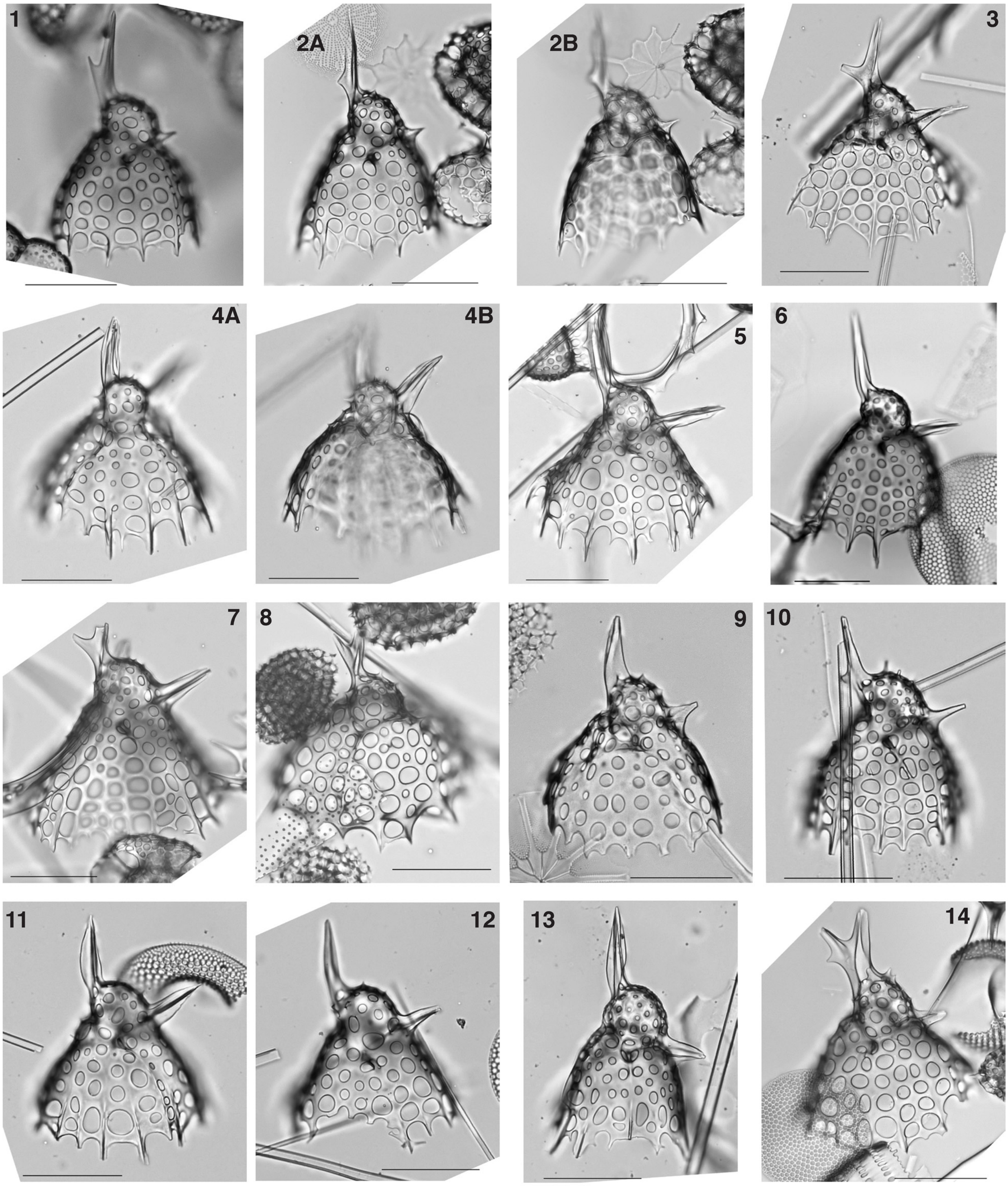

**PLATE 40.**

1–3, 7–8, 10, 14: *Pelagomanes cantharoides* (Sugiyama and Furutani 1992) nov. comb. (1–2 - sample 321-1337D-26H-3, 142–144cm; 3, 7, 10—sample 321-1337A-31X-6, 4–6cm; 8 - 321-1337D-30H-3, 103–104cm; 14—sample 321-1337A-35X-1, 106–108cm)

4A-6, 9, 11–12: *Pelagomanes morawanensis* (Funakawa 1995) nov. comb. (4–5, 11–12—sample 321-1337A-31X-6, 4–6cm; 6—sample 321-1337A-7H-6, 104–107cm; 9– sample 321-1337D-26H-3, 142–144cm)

13: *Pelagomanes tekopua* (O'Connor 1997) nov. comb. (sample 321-1337A-31X-6, 4–6cm)

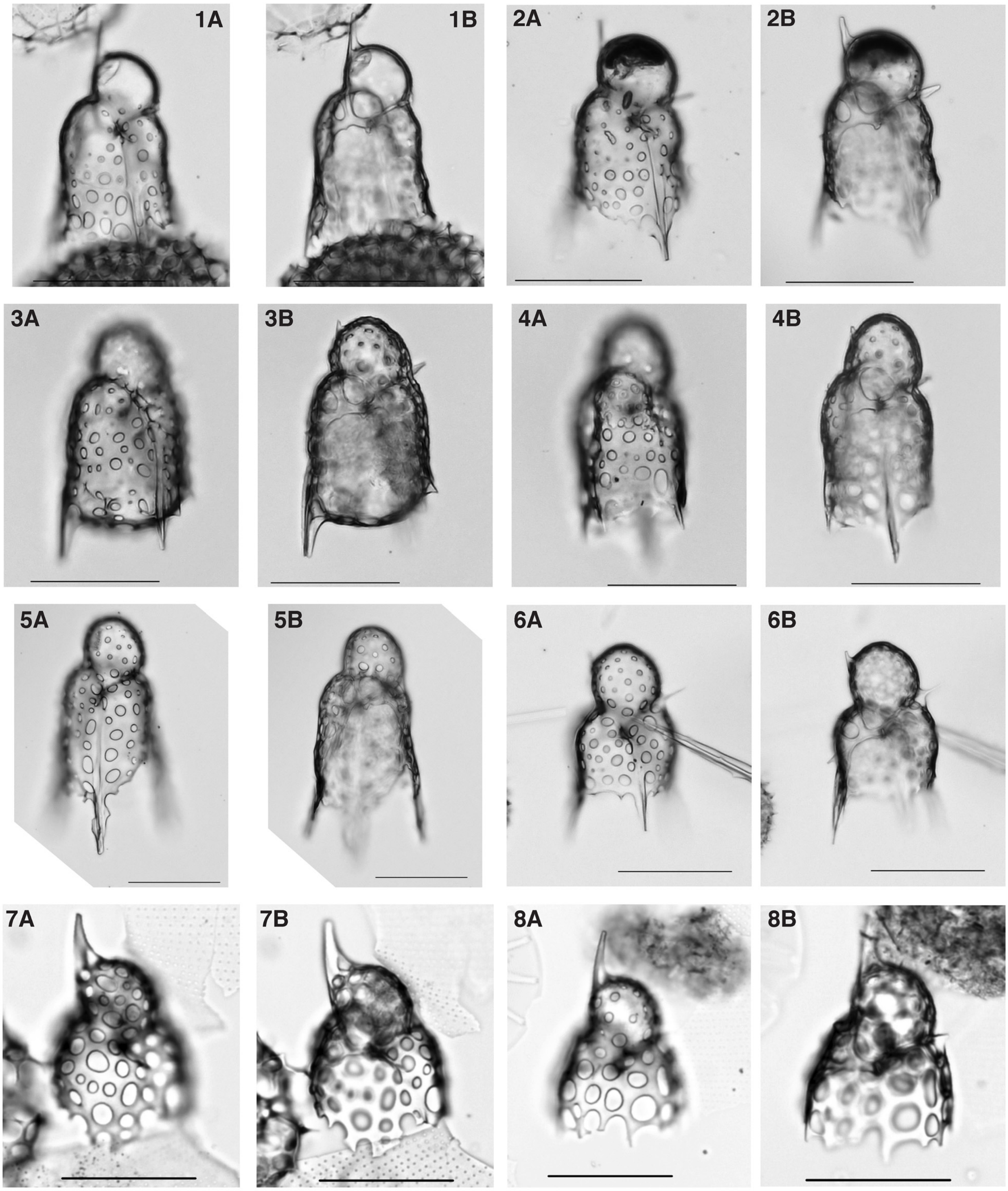

**PLATE 41.**

1A–6B: *Pelagomanes ibburi* n. sp. (1–2, 5—sample 321-1337A-16H-6, 121–124cm; 3–4– sample 321-1337D-23H-6, 134–137cm; 6—sample 321-1337A-14H-7, 39–42cm)

7A–8B: *Pelagomanes* sp. A (sample 321-1337A-5H-5, 11–14cm)

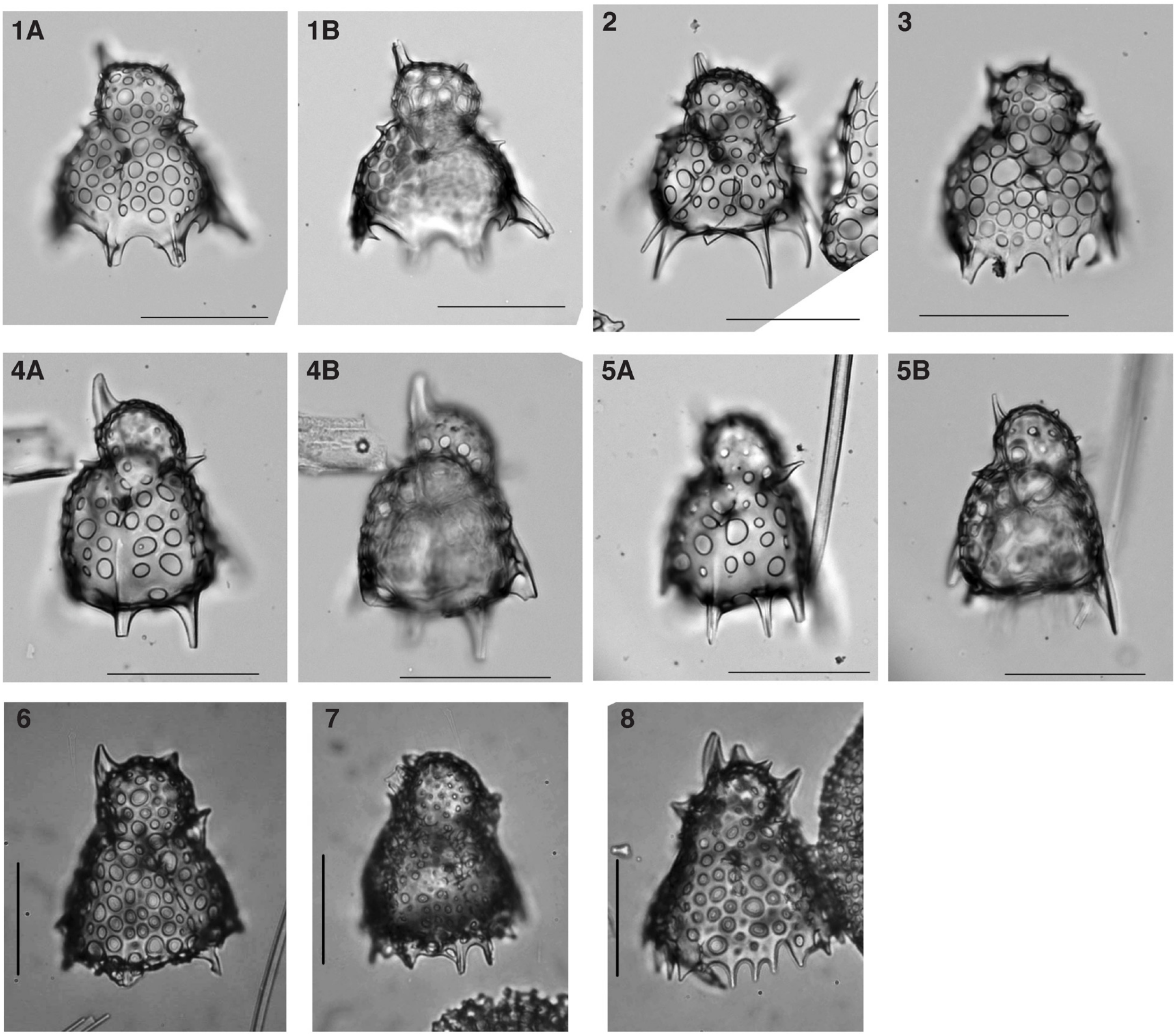

**PLATE 42.**

1A–3: *Pelagomanes?* sp. B (sample 321-1337D-30H-3, 103–104cm)

4A–5B: *Pelagomanes?* sp. C (sample 321-1337A-31X-6, 4–6cm)

6–8: *Pelagomanes? piperata* (Renaudie and Lazarus 2015) nov. comb. (Specimens are from the Early Miocene Southern Ocean; photographs are reproduced from Renaudie and Lazarus (2015)