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New middle Eocene radiolarian species (Rhizaria, Polycystinea) from Blake Nose, subtropical western North Atlantic Ocean

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Non-technical Summary.—Diverse and well-preserved radiolarians (siliceous planktonic microfossils) have been recovered from middle Eocene sediment cores drilled at Blake Nose, a submarine promontory in the western North Atlantic Ocean. In addition to known species, many unknown forms were observed in this material, including 21 new radiolarian taxa. The new species belong to 18 genera and 12 families. Information is provided on the position of each new species in the stratigraphic column. In addition, we have re-described and illustrated the morphological variability of the poorly known species *Pterocyrtidium zitteli* Bütschli, 1882.

Abstract.—Diverse and well-preserved radiolarian assemblages were recovered from the middle Eocene sedimentary sequences drilled at Ocean Drilling Program Site 1051 (Leg 171B; western subtropical Atlantic). In addition to biostratigraphically important species, several unknown morphotypes were observed in this material, leading to the description of three new spumellarian species and 18 new nassellarian species. Described herein are: *Periphaena petrushevskayae* n. sp. (Phacodiscidae), *Stylodictya oligodonta* n. sp. (Trematodiscidae), *Excentrosphaerella delicata* n. sp. (Heliodiscidae), *Eucyrtidium granatum* n. sp. (Eucyrtidiidae), *Dictyoprora echidna* n. sp., *Spirocyrtis matsuokai* n. sp. (Artostrobiidae), *Elaphospyris cordiformis* n. sp., *Elaphospyris quadricornis* n. sp. (Cephalospyrididae), *Ceratocyrtis oconnori* n. sp. (Lophophaenidae), *Botryocella*? *alectrida* n. sp., *Pylobotrys*? *bineti* n. sp. (Pylobotrydidae), *Lychnocanium cheni* n. sp., *Lychnocanium cingulatum* n. sp., *Lychnocanium croizoni* n. sp., *Lychnocanium forficula* n. sp. (Lithochytrididae), *Apoplanius hyalinus* n. sp., *Apoplanius cryptodirus* n. sp. (Lophocyrtiidae), *Albatrossidium messiaeni* n. sp., *Phormocyrtis microtesta* n. sp., *Cryptocarpium*? *judoka* n. sp. (Pterocorythidae), and *Thyrsocyrtis kamikuri* n. sp. (Theocotylidae). Biostratigraphic information is provided for each new species. In addition, we re-describe and illustrate the morphological variability of a remarkable *Pterocyrtidium* species formerly published by Bütschli (1882a).

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Introduction

Polycystine radiolarians are a large group of marine planktonic protozoans that secrete a morphologically complex skeleton made of opaline silica. Known since the early Cambrian (Obut and Iwata, 2000; Pouille et al., 2011), their extensive fossil record makes them valuable biostratigraphic markers and an ideal taxonomic group for paleoceanography and macroevolutionary studies (De Wever et al., 2001; Lazarus et al., 2021). However, despite their importance in fossil plankton assemblages, a substantial portion of the radiolarian diversity preserved in the fossil record remains undocumented, hindering the expression of their full biostratigraphic and paleoceanographic potential.

Eocene radiolarians were the first to receive sustained attention from micropaleontologists, with the description of several hundred species from siliceous-rich chalk beds cropping out on Barbados Island (Ehrenberg, 1839, 1846, 1847, 1874, 1876; Bütschli, 1882a, b; Haeckel, 1887). This body of early taxonomic work has constituted the core of the Paleogene radiolarian taxonomy for nearly a century, although some contributions were also made in the first half of the twentieth century (e.g., Clark and Campbell, 1942, 1945). The launch of scientific ocean drilling programs in the early 1970s marked a pivotal change in the history of Cenozoic radiolarian research, allowing extensive recoveries of radiolarian assemblages around the world and rekindling interest in describing their diversity (e.g., Riedel and Sanfilippo, 1970, 1971, 1978; Petrushevskaya and Kozlova, 1972; Foreman, 1973; Sanfilippo and Riedel, 1973, 1982, 1992; Nigrini, 1977; Sanfilippo and Caulet, 1998). However, most of these studies have focused on biostratigraphically important species, which represent only a minute fraction of the total radiolarian diversity. As a result, numerous rare morphotypes that are of no interest for biostratigraphic correlations, or those belonging to poorly defined genera and families, were not documented and remained undescribed until recently (i.e., Meunier and Danelian, 2023).

To contribute to our understanding of Paleogene radiolarian diversity, 21 new species distributed among 16 genera and 13 families are formally described from the middle Eocene sequences cored at Ocean Drilling Program Site 1051 (Leg 171B; western subtropical Atlantic). Most of these new taxa were previously illustrated by Kamikuri (2015) in an extensive monograph conducted at neighboring ODP Site 1052, but

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they were left in open nomenclature. Biostratigraphic information is provided here for each new species, and stratophenetic relationships to previously described species are suggested.

Materials and methods

Materials.—ODP Site 1051 (30°03′N, 76°21′W, modern water depth of ∼1983 m below sea level, mbsl) was drilled on the Blake Nose, a promontory situated on the edge of the Blake Plateau, in the western North Atlantic Ocean (Fig. 1). This site provided an expanded and nearly continuous upper Paleocene through lower upper Eocene sedimentary sequence, dominated by silica-bearing nannofossil oozes rich in radiolarians, diatoms, and sponge spicules (Norris et al., 1998). Paleo-water depth estimates based on benthic foraminifera indicate lower bathyal depths (1000–2000 mbsl) at this site during the Eocene (Norris et al., 1998), with a slightly more southerly paleolatitude of ∼25°N (Ogg and Bardot, 2001). The estimated sedimentation rate is ∼4 cm/ka (Norris et al., 1998; Edgar et al., 2010). The species described in the present paper come from 16 samples collected from the richest and most diverse radiolarian interval, which spans cores 2H to 18X (12.73–174.28 meters composite depth [mcd]) in Hole 1051A (Sanfilippo and Blome, 2001).

Methods.—Samples were treated according to the procedures described in Sanfilippo et al. (1985) and Tetard et al. (2020). About 2 cm^2 of untreated sediment were first soaked in a polypropylene beaker containing 30 mL of 30% hydrochloric acid (HCl) to dissolve calcium carbonate. At the end of

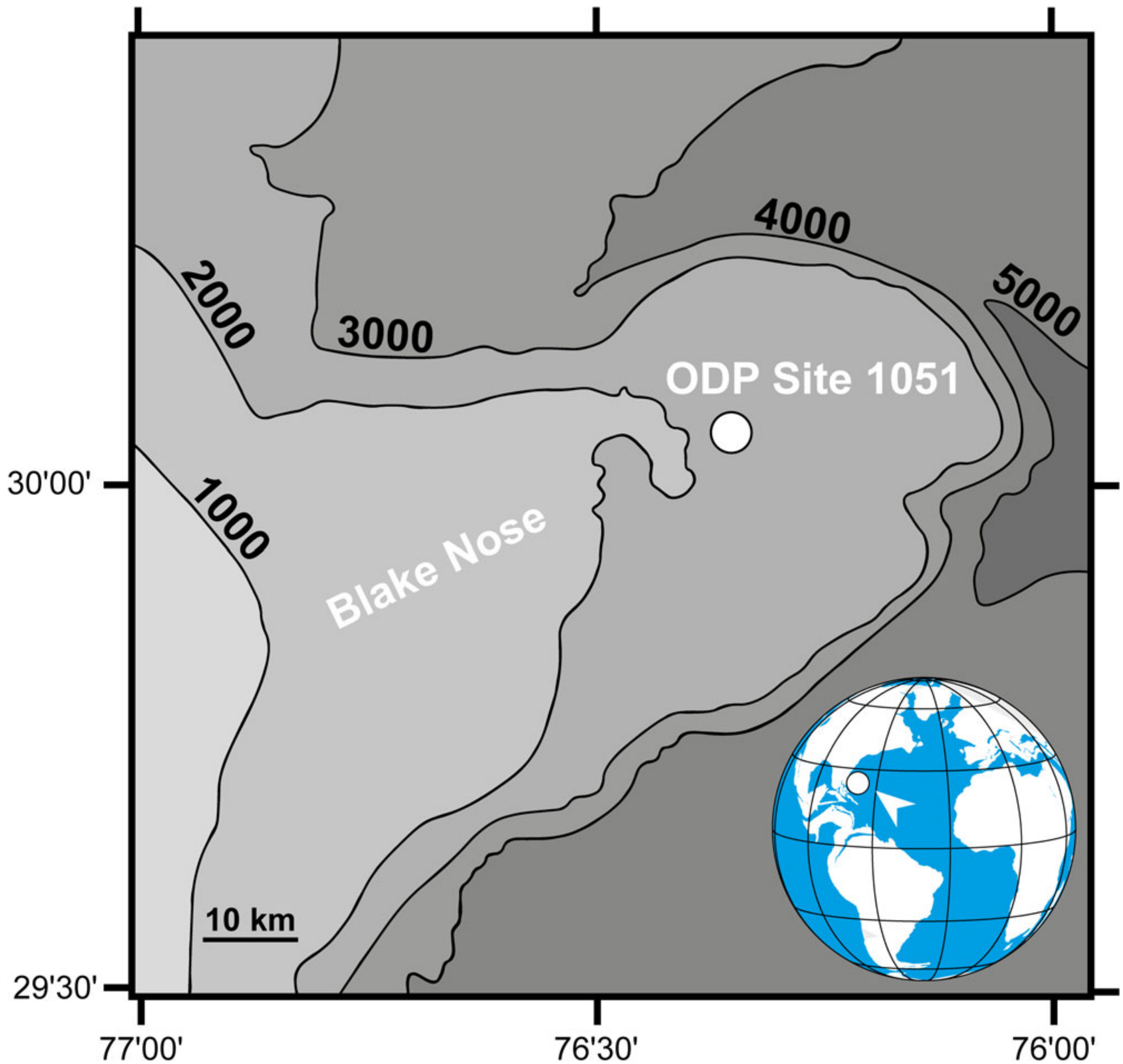

Figure 1. Location of Blake Nose in the western North Atlantic Ocean (modified from Land et al., 1999). The box shows the detailed location of ODP Site 1051 (Leg 171B) on a bathymetric map (modified from Norris et al., 1998). Bathymetry is in meters.

this stage, a few mL of HCl were added to ensure the end of the reaction. The resulting residues were then washed with distilled water and soaked in 30 mL of 10% hydrogen peroxide (H_2O_2) to remove organic material. Finally, the siliceous residues were sieved through a 45-µm mesh to remove small radiolarian fragments and clay. Three slides were prepared per sample using ~3 mg of dry residues randomly spread on a coverslip (Witkowski et al., 2012). Coverslips were mounted on standard glass slides using Eukitt® mounting medium (refractive index = 1.49).

Observation and identification of radiolarians were performed using a Zeiss Axio Imager. A2 transmitted light microscope at 20× magnification. Images were captured using a Zeiss AxioCam ERc5s digital camera. To create a fully focused composite image of a single specimen, a set of ~5 images was taken at different f-stops and stacked using Helicon Focus v.7.6.6 (HeliconSoft).

All measurements provided in the systematic paleontology section were performed on specimen images using the image analysis software ImageJ (Schneider et al., 2012). The stratigraphic occurrences of the new species are shown in Fig. 2, and the associated bioevents are summarized in Table 1.

Repository and institutional abbreviation.—All holotypes and figured specimens (Figs. 3–8) are deposited in the public paleontological collection of the University of Lille (USTL), France. Specimens are located according to hole number, core number, section number, interval depth, and England Finder coordinates.

Systematic paleontology

The higher-level classification adopted here is based on the most recent and integrative radiolarian classification of Suzuki et al. (2021). Genus assignments of the new species are consistent with the diagnosis provided by O'Dogherty et al. (2021).

The morphological terminology used in the text to designate different parts of the fundamental nassellarian spicule

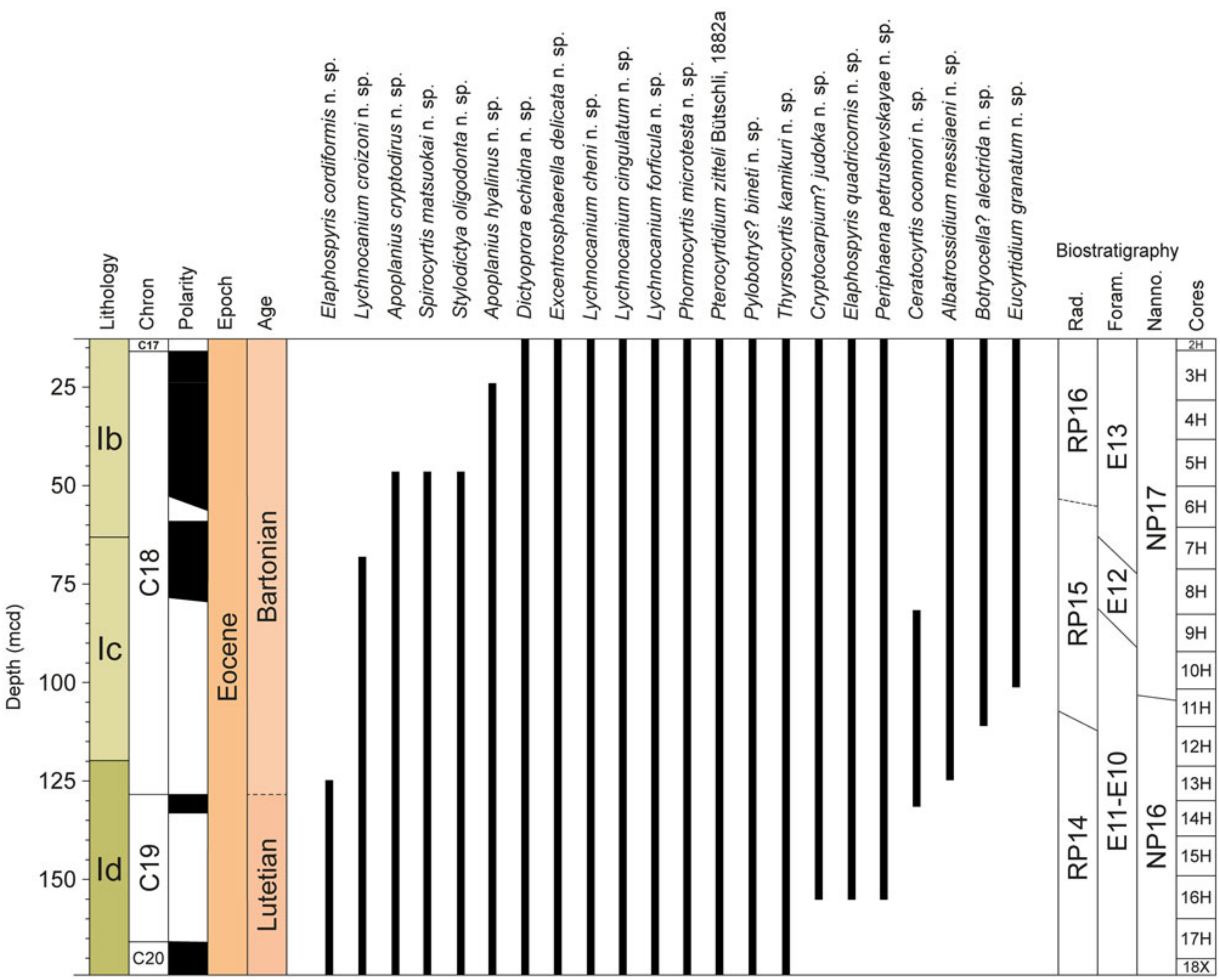

Figure 2. Range chart of the 21 new radiolarian species from the late middle Eocene of ODP Site 1051 (Blake Nose, western subtropical Atlantic). Lithology column based on data from Norris et al. (1998). Geomagnetic timescale after calibration of Ogg and Bardot (2001). Radiolarian biostratigraphy after Sanfilippo and Blome (2001), planktonic foraminiferal biostratigraphy after Norris et al. (1998) and Edgar et al. (2010), and calcareous nannofossil biostratigraphy after Mita (2001). Black = normal-polarity intervals; white = reversed-polarity intervals; 1b = nannofossil ooze with siliceous microfossils to siliceous nannofossil ooze; 1c = nannofossil ooze with siliceous microfossils to siliceous nannofossil ooze; 1d = siliceous nannofossil chalk to nannofossil chalk with siliceous microfossils; mcd = meters composite depth.

Table 1. Summary of first occurrences (FO) and last occurrences (LO) at ODP Site 1051, drilled on the Blake Plateau (western North Atlantic). Abbreviations: mbsf, meters below seafloor; mcd, meters composite depth.

ODP Site 1051		Depth (m)	
Radiolarian bioevents	Core-section, interval (cm) Base/top	mbsf Base/top	mcd Base/top
LO *Apoplanius hyalinus* n. sp.	4H-5W, 56–58/2R-5W, 55–57	31.36/12.35	35.31/12.73
LO *Apoplanius cryptodirus* n. sp.	6R-5W, 53–55/4R-5W, 56–58	50.33/31.36	57.58/35.31
LO *Spirocyrtis matsuokai* n. sp.	6R-5W, 53–55/4R-5W, 56–58	50.33/31.36	57.58/35.31
LO *Stylodictya oligodonta* n. sp.	6R-5W, 53–55/4R-5W, 56–58	50.33/31.36	57.58/35.31
LO *Lychnocanium croizoni* n. sp.	8H-5W, 61–63/6H-5W, 53–55	68.20/50.33	78.56/57.58
LO *Ceratocyrtis oconnori* n. sp.	9H-2W, 53–55/8H-5W, 61–63	74.33/68.20	84.69/78.56
FO *Eucyrtidium granatum* n. sp.	11H-2W, 62–64/10H-5W, 52–54	93.42/88.32	103.78/98.68
FO *Botryocella*? *alectrida* n. sp.	12H-2W, 55–57/11H-5W, 59–61	102.85/97.89	113.78/108.25
FO *Albatrossidium messiaeni* n. sp.	13H-5W, 58–60/13H-2W, 52–54	116.88/112.32	127.06/122.50
LO *Elaphospyris cordiformis* n. sp.	13H-5W, 58–60/13H-2W, 52–54	116.88/112.32	127.06/122.50
FO *Ceratocyrtis oconnori* n. sp.	14H-5W, 52–53/13H-5W, 58–60	126.32/116.88	136/127.06
FO *Cryptocarpium*? *judoka* n. sp.	18X-5W, 54–56/14H-5W, 52–53	164.74/126.32	174.28/136
FO *Elaphospyris quadricornis* n. sp.	18X-5W, 54–56/14H-5W, 52–53	164.74/126.32	174.28/136
FO *Periphaena petrushevskayae* n. sp.	18X-5W, 54–56/14H-5W, 52–53	164.74/126.32	174.28/136

follows that of Petrushevskaya (1984). The reader is also invited to see Goll (1968, p. 1413, text-figure 6) for features specific to the family Cephalospyrididae, and Sanfilippo and Caulet (1998, p. 6, text-figure 2) for the family Lophocyrtiidae.

Infrakingdom Rhizaria Cavalier-Smith, 2002, emend. Cavalier-Smith, 2003
Phylum Retaria Cavalier-Smith, 1999
Class Polycystinea Ehrenberg, 1839
Order Spumellaria Ehrenberg, 1876
Superfamily Lithocyclioidea Ehrenberg, 1846
Family Phacodiscidae Haeckel, 1882
Genus *Periphaena* Ehrenberg, 1874

Type species.—*Periphaena decora* Ehrenberg, 1874, p. 246 (unfigured); Ehrenberg, 1876, p. 80, pl. 28, fig. 6; by monotypy.

Periphaena petrushevskayae new species
Figure 3.1–3.4

1972 *Periphaena* sp.; Petrushevskaya and Kozlova, p. 523, pl. 14, figs. 4, 5.

Holotype.—Figure 3.1; collection number USTL 4525-1; coordinates K55/2; sample ODP 171B-1051A-9R-2W, 53–55 cm; upper part of the *Podocyrtis* (*L.*) *chalara* Zone (RP15; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.—Phacodiscid species with a thick equatorial hyaline girdle bearing 6–10 triangular spines of variable lengths.

Occurrence.—*Periphaena petrushevskayae* n. sp. occurs throughout the studied interval, from the upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14) to the lower part of the *Podocyrtis* (*L.*) *goetheana* Zone (RP15).

Description.—Shell lenticular, externally smooth, with a phacodiscid center and a well-developed equatorial hyaline girdle. Six to 10 triangular equatorial spines of variable length arise from the girdle as extensions. Cortical shell about three times the diameter of the medullary shell, perforated by numerous small cylindrical pores that are uniform in size and shape (~10 pores in a radius). Medullary shell double, globular, attached to the cortical shell by a few thick rods.

Etymology.—The specific epithet honors Dr. Maria G. Petrushevskaya, who was the first to illustrate this radiolarian taxon in the fauna of DSDP Site 144.

Dimensions.—Based on 19 specimens (mean): shell diameter: 133–183 µm (160 µm), length of equatorial spines: 34–156 µm (76 µm).

Remarks.—The new species differs from *Periphaena contiguum* (Ehrenberg, 1874), *P. delta* Sanfilippo and Riedel, 1973, *P. heliasteriscus* (Clark and Campbell, 1942), *P. humboldti* (Ehrenberg, 1847), and *P. umbonatum* (Ehrenberg, 1874) in having an equatorial hyaline girdle, and from *P. decora* Ehrenberg, 1874, in having well-developed equatorial spines. Finally, *P. petrushevskayae* n. sp. is distinguished from *P. cingillum* (Haeckel, 1887) in having fewer than 10 equatorial spines.

In many aspects, *P. petrushevskayae* n. sp. resembles *P. decora*, from which it probably evolved by modification of the equatorial girdle.

Superfamily Trematodiscoidea Haeckel, 1862, emend. Suzuki in Suzuki et al., 2021
Family Trematodiscidae Haeckel, 1862, emend. Suzuki in Suzuki et al., 2021
Genus *Stylodictya* Ehrenberg, 1846

Type species.—*Stylodictya gracilis* Ehrenberg, 1854, pl. 36, fig. 28; by monotypy.

Stylodictya oligodonta new species
Figure 3.5–3.8

Holotype.—Figure 3.5; collection number USTL 4536-2; coordinates R52/1; sample ODP 171B-1051A-11H-2W, 62–

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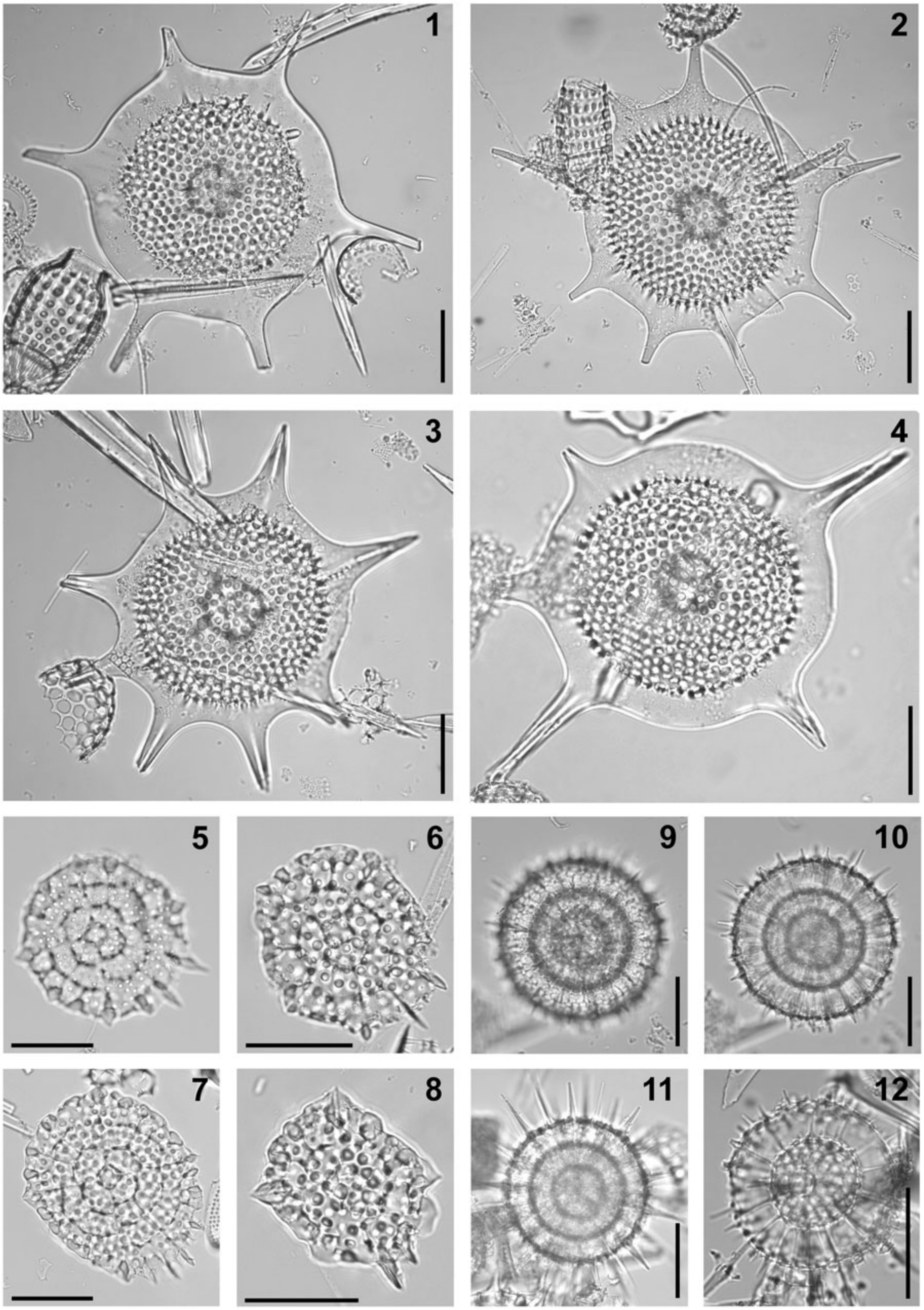

Figure 3. Composite light micrographs of new radiolarian species from ODP Site 1051 (Blake Nose, western subtropical Atlantic). (**1–4**) *Periphaena petrushevskayae* n. sp.: (**1**) holotype, ODP 171B-1051A-9R-2W, 53–55 cm, USTL 4525-1, K55/2; (**2**) ODP 171B-1051A-9H-2W, 53–55 cm, USTL 4524-2, S55/3; (**3**) ODP 171B-1051A-9H-2W, 53–55 cm, USTL 4524-3, U55/1; (**4**) ODP 171B-1051A-9H-5W, 53–55 cm, USTL 4529-2, K44/2. (**5–8**) *Stylodictya oligodonta* n. sp.: (**5**) holotype, ODP 171B-1051A-11H-2W, 62–64 cm, USTL 4536-2, R52/1; (**6**) ODP 171B-1051A-9H-2W, 53–55 cm, USTL 4526-3, R46/3; (**7**) ODP 171B-1051A-9H-2W, 53–55 cm, USTL 4525-3, T41/3; (**8**) poorly developed form, ODP 171B-1051A-9H-2W, 53–55 cm, USTL 4525-2, V64/1. (**9–12**) *Excentrosphaerella delicata* n. sp.: (**9**) holotype, cortical shell, ODP 171B-1051A-9H-2W, 53–55 cm, USTL 4524-6, F73/1; (**10**) holotype, inner structure; (**11**) ODP 171B-1051A-9H-2W, 53–55 cm, USTL 4526-2, V49/1; (**12**) inner structure, ODP 171B-1051A-9H-2W, 53–55 cm, USTL 4524-4, O65/3. All scale bars equal 50 μm.

64 cm; *Podocyrtis* (*L.*) *chalara* Zone (RP15; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.—Small trematodiscid species with fewer than four annular rings, and a few short equatorial spines.

Occurrence.—This species is found throughout the studied interval, from the upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14) to the lower part of the *Podocyrtis* (*L.*) *goetheana* Zone (RP16).

Description.—Shell as a subcircular flat disc, tending to be angular in outline in some specimens. Disc concentrically chambered, with a decussate microsphere surrounded by one (Fig. 3.8) to three (Fig. 3.7) annular rings. Margin of the disc bearing many small, triangular to rounded spines of various lengths. Four longer spines are usually present, representing extensions of the cylindrical primary radial rays from the inner disc. Pores subcircular, scattered over the surface, and usually more widely spaced spaced and less numerous on the marginal ring.

Etymology.—The specific epithet means ‘few teeth’ in Greek, in allusion to the sparse marginal spines of the new species.

Dimensions.—Based on 11 specimens (mean): shell diameter: 72–119 µm (89 µm), spine lengths: 4–20 µm (10 µm).

Remarks.—The new species is is placed in the genus *Stylodictya* because it had a decussate microsphere surrounded by several narrow concentric rings and from which four primary and many secondary equatorial spines extend. The small size of *Stylodictya oligodonta* n. sp. (shell diameter < 120 µm), as well as its short triangular to rounded spines, allow it to be distinguished from all other middle Eocene flattened spumellarian species with a decussate microsphere.

Superfamily Haliommoidea Ehrenberg, 1846
Family Heliodiscidae Haeckel, 1882, emend. Dumitrică, 1984
Genus *Excentrosphaerella* Dumitrică, 1978

Type species.—*Excentrosphaerella sphaeroconcha* Dumitrică, 1978, p. 238, pl. 5, fig. 22; subsequent designation by O’Dogherty et al., 2021.

Excentrosphaerella delicata new species
Figure 3.9–3.12

Holotype.—Figure 3.9, 3.10; collection number USTL 4524-6; coordinates F73/1; sample ODP 171B-1051A-9H-2W, 53–55 cm; *Podocyrtis* (*L.*) *chalara* Zone (RP15; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.—Relatively small *Excentrosphaerella* species with a shell ratio of 1:2:3.

Occurrence.—*Excentrosphaerella delicata* n. sp. occurs sporadically throughout the studied interval, from the upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14) to the lower part of the *Podocyrtis* (*L.*) *goetheana* Zone (RP16).

Description.—Delicate four-shelled test with a small eccentric microsphere embedded in a subspherical inner medullary shell. Outer medullary shell surrounded by two concentric spherical shells connected by numerous filamentous radial beams that protrude out of the cortical shell as long conical spines. Third shell and cortical shell perforated by numerous small, randomly arranged, subcircular pores.

Etymology.—The name is derived from the Latin *delicatus*, meaning ‘soft, delicate’, for the thin-walled cortical shell of the new species.

Dimensions.—Based on five specimens (mean): diameter of microsphere: 12–15 µm (13 µm), diameter of outer medullary shell: 38–44 µm (41 µm), diameter of third shell: 61–73 µm (67 µm), diameter of cortical shell: 102–118 µm (108 µm), length of cortical spines: 15–46 µm (23 µm).

Remarks.—*Excentrosphaerella delicata* n. sp. differs from *E. sphaeroconcha* Dumitrică, 1978, and *Actinomma capillaceum* Haeckel, 1887, in being two times smaller and in having an inner medullary shell to cortical shell ratio of 1:3 instead of a ratio of 1:4 (Dumitrică, 1978, pl. 5, fig. 22), 1:5 (Dumitrică, 2019, fig. 11a, b), or 1:7 (Haeckel, 1887, pl. 29, fig. 2). The new species is also distinguished from the middle Miocene specimens illustrated as *E. sphaeroconcha* by Sugiyama and Furutani (1992, pl. 12, figs. 1, 2, pl. 16, fig. 3) in having a spherical outer medullary shell.

Order Nassellaria Ehrenberg, 1876
Superfamily Eucyrtidioidea Ehrenberg, 1846, emend. Suzuki et al., 2021
Family Eucyrtidiidae Ehrenberg, 1846, emend. Suzuki et al., 2021
Genus *Eucyrtidium* Ehrenberg, 1846

Type species.—*Lithocampe acuminata* Ehrenberg, 1844, p. 84 (unfigured); Ehrenberg, 1854, pl. 22, fig. 27; subsequent designation by Frizzell and Middour, 1951, p. 33.

Eucyrtidium granatum new species
Figure 4.1–4.4

2015 *Eucyrtidium* sp. A; Kamikuri, pl. 9, fig. 6a, b.

Holotype.—Figure 4.1; collection number USTL 4513-1; coordinates M69/3; sample ODP 171B-1051A-2H-5W, 55–57 cm; lower part of the *Podocyrtis* (*L.*) *goetheana* Zone (RP16; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.—*Eucyrtidium* species with an abdominal segment that is more than twice as high as the thorax and is perforated by numerous small, closely spaced pores.

Occurrence.—This rare species occurs sporadically from the upper part of the *Podocyrtis* (*P.*) *chalara* Zone (RP15) to the lower part of the *Podocyrtis* (*L.*) *goetheana* Zone (RP16).

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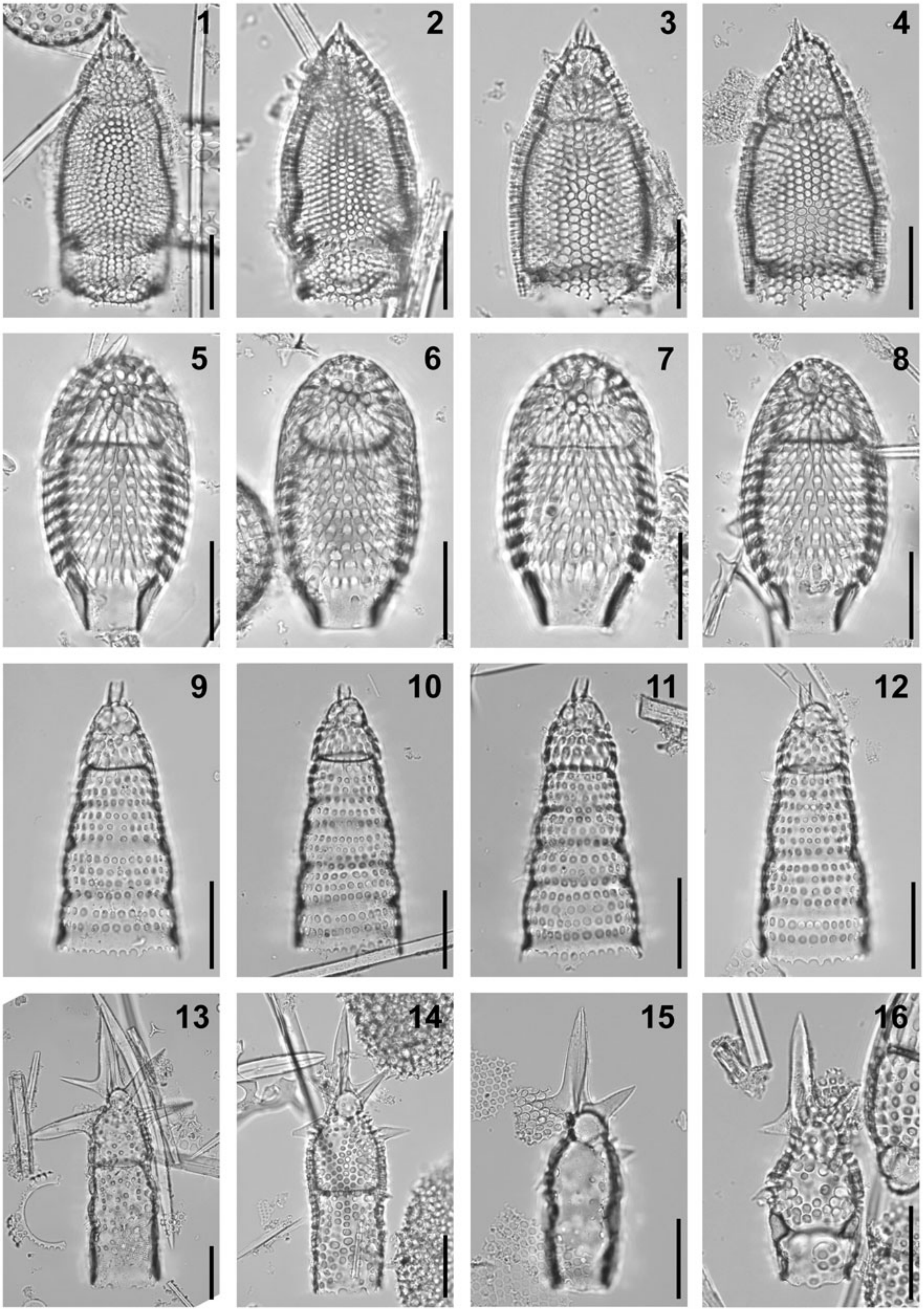

Figure 4. Composite light micrographs of new radiolarian species from ODP Site 1051 (Blake Nose, western subtropical Atlantic). (**1–4**) *Eucyrtidium granatum* n. sp.: (**1**) holotype, ODP 171B-1051A-2H-5W, 55–57 cm, USTL 4513-1, M69/3; (**2**) ODP 171B-1051A-4H-5W, 56–58 cm, USTL 4517-1, V48/3; (**3**) ODP 171B-1051A-4H-5W, 56–58 cm, USTL 4515-4, T70/2; (**4**) ODP 171B-1051A-4H-5W, 56–58 cm, USTL 4515-3, T49/4. (**5–8**) *Dictyoprora echidna* n. sp.: (**5**) holotype, ODP 171B-1051A-6H-5W, 53–55 cm, USTL 4518-1, M41/3; (**6**) ODP 171B-1051A-6H-5W, 53–55 cm, USTL 4519-1, M47/1; (**7**) ventral view, ODP 171B-1051A-2H-5W, 55–57 cm, USTL 4512-1, N63/3; (**8**) ventral view, ODP 171B-1051A-6H-5W, 53–55 cm, USTL 4518-2, H64/2. (**9–12**) *Spirocyrtis matsuokai* n. sp.: (**9**) holotype, ODP 171B-1051A-14H-5W, 52–54 cm, USTL 4554-1, S69/2; (**10**) ODP 171B-1051A-14H-5W, 52–54 cm, USTL 4554-2, H48/3; (**11**) ODP 171B-1051A-9H-2W, 53–55 cm, USTL 4524-1, N41/2; (**12**) ODP 171B-1051A-14H-5W, 52–54 cm, USTL 4554-3, M38/2. (**13–16**) *Pterocyrtidium zitteli* Bütschli, 1882a: (**13**) ODP 171B-1051A-4H-5W, 56–58 cm, USTL 4515-2, K40/4; (**14**) ODP 171B-1051A-9H-2W, 53–55 cm, USTL 4526-1, Q53/1; (**15**) hyaline form, ODP 171B-1051A-18X-5W, 54–56 cm, USTL 4562-2, X63/1; (**16**) poorly developed form, ODP 171B-1051A-18X-5W, 54–56 cm, USTL 4562-1, P51/2. All scale bars equal 50 μm.

Description.—Shell multi-segmented, subcylindrical, and very thick-walled. Cephalis relatively small, hemispherical to subspherical, perforated by a few small subcircular pores, bearing a short apical horn. Collar stricture marked by a slight constriction. Thorax campanulate to truncate conical, thick-walled, with subcircular pores scattered over the surface. Lumbar stricture marked by a moderate constriction and by a thin internal ridge that appears externally as a dark line. Abdomen subcylindrical, elongated and thick-walled, perforated by numerous, small subcircular pores, which are closely spaced and weakly arranged in longitudinal rows (18–23 in a row). Post-lumbar stricture almost invisible from the outside, marked only by a thin dark line. Fourth segment cylindrical, as broad as the abdomen but always shorter. Abdominal termination open, and invariably ragged along a row of pores.

Etymology.—The name is derived from the Latin *granatus*, meaning 'having many seeds or grains', for the shell ornamentation of the new species.

Dimensions.—Based on 5 specimens (mean): total length without the apical horn: 143–179 µm (162 µm), length of apical horn: 12–17 µm (15 µm), length of cephalothorax without the apical horn: 41–48 µm (44 µm), length of abdomen: 86–116 µm (96 µm), length of first post-abdominal segment: 31–45 µm (38 µm).

Remarks.—*Eucyrtidium granatum* n. sp. differs from all other species of the genus *Eucyrtidium* in having a thick-walled shell with a characteristic ornamentation consisting of many small, closely spaced pores.

Superfamily Artostrobioidea Riedel, 1967
Family Artostrobiidae Riedel, 1967, sensu Sugiyama, 1998
Genus *Dictyoprora* Haeckel, 1887

Type species.—*Dictyocephalus amphora* Haeckel, 1887, p. 1305, pl. 62, fig. 4; subsequent designation by Campbell, 1953, p. 296.

Dictyoprora echidna new species
Figure 4.5–4.8

1973 *Theocampe amphora* (Haeckel) group; Foreman, p. 431, pl. 9, fig. 8 (part).
2015 *Dictyoprora* sp. E; Kamikuri, pl. 12, figs. 11a, b.

Holotype.—Figure 4.5; collection number USTL 4518-1; coordinates M41/3; sample ODP 171B-1051A-6H-5W, 53–55 cm; upper part of the *Podocyrtis* (*L.*) *chalara* Zone (RP15; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.—*Dictyoprora* species with a general ovoid outline and an abdominal segment perforated by 8 to ten closely spaced rows of pores.

Occurrence.—*Dictyoprora echidna* n. sp. is abundant from the uppermost part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14) to the lowermost part of the *Podocyrtis* (*L.*) *goetheana* Zone (RP16).

Description.—Shell three-segmented, ovoid, and smooth externally. Cephalis subspherical to hemispherical, unarmed, deeply embedded in the thorax. Cephalic pores circular and closely spaced. Ventral pore relatively large, circular to ovoid (Fig. 4.7, 4.8). Ventral tube not developed. Collar stricture indistinct. Thorax short, trapezoidal to slightly inflated, with downwardly directed subcircular pores arranged in two or three transverse rows. Lumbar stricture marked by a thin obscure band. Abdomen barrel-shaped, thick-walled, and perforated by 8–10 closely spaced rows of downward directed subcircular pores. Shell tapers distally, ending in a hyaline, inverted-truncated conical peristome with a smooth margin.

Etymology.—The specific epithet refers to the Latin name of the spiny anteaters (echidna), for the shell ornamentation of the new species, which evokes the texture of the back of these animals covered by spines.

Dimensions.—Based on 26 specimens (mean): total length: 113–159 µm (135 µm), length of cephalothorax: 40–54 µm (47 µm), length of abdomen: 72–107 µm (89 µm), length of hyaline peristome: 13–23 µm (19 µm).

Remarks.—*Dictyoprora echidna* n. sp. differs from other *Dictyoprora* species in having a large cephalis, which is deeply embedded in the thoracic segment, and no lumbar constriction, giving the shell an overall ovoid shape. It also differs from *Phormostichoartus ashbyi* Renaudie and Lazarus, 2015, in having a trisegmented shell.

A few specimens exhibiting an intermediate morphology between *D. mongolfieri* (Ehrenberg, 1854) and *D. echidna* n. sp. were observed at ODP Site 1051 (~136 mcd), suggesting that the latter is an offshoot of *D. mongolfieri*. This intermediate morphotype is characterized by a high number of abdominal pores, which are longitudinally aligned.

Genus *Spirocyrtis* Haeckel, 1882, emend. Nigrini, 1977

Type species.—*Spirocyrtis scalaris* Haeckel, 1887, p. 1509, pl. 76, fig. 14; subsequent designation by Campbell, 1954, p. D142.

Spirocyrtis matsuokai new species
Figure 4.9–4.12

Holotype.—Figure 4.9; collection number USTL 4554-1; coordinates S69/2; sample ODP 171B-1051A-14H-5W, 52–54 cm; upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.—*Spirocyrtis* species with a reduced ventral tube, whose shell is subcylindrical in shape, with slight post-thoracic constrictions.

Occurrence.—This species is found in almost all the studied samples, from the lowermost part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14) to the lower part of the *Podocyrtis* (*L.*) *goetheana* Zone (RP16).

Description.—Shell multisegmented, smooth, relatively thin-walled, subcylindrical in overall shape. Cephalis

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hemispherical, poreless, bearing a long straight apical tube and lacking a well-developed ventral tube. Collar stricture almost indistinct. Thorax truncate conical to cylindrical, only slightly longer than the cephalis, and penetrated by downwardly directed subcircular pores. Lumbar stricture marked by a thin dark band. Abdomen and post-abdominal segments barrel-shaped and rounded, the second post-abdominal segment being generally the widest. Each segment is perforated by subcircular pores arranged in three to four transverse rows, except for the third post-abdominal segment, which generally has only two rows of pores. Lumbar and post-lumbar strictures marked by a hyaline band. Last segment ragged along row of pores in all the observed specimens.

Etymology.—This species is named in honor of Dr. Atsushi Matsuoka (Niigata University, Japan) for his contribution to the study of recent and fossil radiolarians.

Dimensions.—Based on 13 specimens (mean): total length without the apical tube: 143–202 µm (164 µm), length of cephalothorax: 38–43 µm (40 µm), length of apical tube: 8–23 µm (14 µm), length of abdomen: 20–35 µm (27 µm); length of all post-abdominal segments: 77–133 µm (98 µm); maximum breadth of shell: 56–69 µm (63 µm).

Remarks.—*Spirocyrtis matsuokai* n. sp. differs from *Spirocyrtis cornutella* Haeckel, 1887, in having lumbar and post-lumbar strictures marked by a poreless band; from *S. gyroscalaris* Nigrini, 1977, *S. scalaris* Petrushevskaya and Kozlova, 1972, and *S. subscalaris* Nigrini, 1977, in having a maximum of four transverse rows of pores on the post-abdominal segments, and a less prominent ventral tube; from *S. proboscis* O'Connor, 1994, in having a smaller apical tube and a more cylindrical shell; from *S. scalaris* Haeckel, 1887, in having fewer than five post-abdominal segments, the constrictions of which are rounded rather than sharply angular; from *S. subtilis* Petrushevskaya and Kozlova, 1972, in having less-developed constrictions between segments, conferring the shell a smoother outline; from *S.*? *hollisi* Renaudie and Lazarus, 2012, and *S.*? *renaudiei* Meunier and Danelian, 2023, in having a subcylindrical shell rather than a conical or a pupoid shell.

Family Rhopalosyringiidae Empson-Morin, 1981
Genus *Pterocyrtidium* Bütschli, 1882

Type species.—*Pterocanium barbadense* Ehrenberg, 1874, p. 254 (unfigured); Ehrenberg, 1876, p. 82, pl. 17, fig. 6; subsequent designation by Petrushevskaya and Kozlova, 1972, p. 552.

Pterocyrtidium zitteli Bütschli, 1882
Figure 4.13–4.16

1882a *Pterocyrtidium Zitteli* [sic] Bütschli, p. 531, pl. 33, fig. 28a, b.
2015 *Pterocyrtidium zitteli* Bütschli; Kamikuri, pl. 9, fig. 8.

Diagnosis.—*Pterocyrtidium* species with a dichotomous apical horn, and a sparsely pored thorax and abdomen.

Occurrence.—This species occurs sporadically throughout the studied interval, from the upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14) to the lower part of the *Podocyrtis* (*L.*) *goetheana* Zone (RP16).

Description.—Shell composed of three segments, cylindrical, and thick-walled. Cephalis subspherical to globular, poreless, or perforated by a few small circular pores. Apical spine protruding as a stout, dichotomous, bladed apical horn. The main branch of the apical horn lies on the axis of the shell, the second branch extends from the cephalic wall or the proximal part of the main branch at an angle of 45–90°. Ventral spine is protruding as a pointed vertical spine, which is always shorter than the apical horn. Collar stricture slightly expressed. Thorax thick-walled, subcylindrical to ovoid-elongated. Thoracic pores vary in number and size. They may be scattered over the surface or quincuncially arranged. In the larger specimens, the primary lateral spines and the dorsal spine usually extend into the upper thorax as long, bladed, pointed wings. Thorax and abdomen separated by an internal ridge that appears externally as a thin dark band. Abdomen subcylindrical, longer than the thorax, pierced by subcircular pores that may be either longitudinally aligned or randomly arranged. Abdomen terminates in an undifferentiated margin, usually ragged along a row of pores.

Dimensions.—Based on 19 specimens (mean): length of main branch of the apical horn: 32–81 µm (64 µm), length of secondary branch of the apical horn (when present): 14–51 µm (32 µm), length of ventral horn (when present): 18–55 µm (33 µm), length of wings (when present): 13–67 µm (36 µm), total length without the apical horn: 87–192 µm (127 µm), length of cephalothorax without the apical horn: 57–88 µm (76 µm), length of abdomen: 31–114 µm (60 µm).

Remarks.—*Pterocyrtidium zitteli* differs from all other species of the genus *Pterocyrtidium* by its distinctive dichotomous apical horn. This species shows a great morphological variability in terms of size, number of thoracic wings, and number of thoracic and abdominal pores. Several small, stunted, aberrant morphotypes were found in the material examined, possibly represeting juvenile specimens or aberrant forms.

Superfamily Acanthodesmioidea Haeckel, 1862
Family Cephalospyrididae Haeckel, 1882
Genus *Elaphospyris* Haeckel, 1882

Type species.—*Ceratospyris heptaceros* Ehrenberg, 1874, p. 219 (unfigured); Ehrenberg, 1876, p. 66, pl. 20, fig. 2; subsequent designation by Chediya, 1959, p. 180.

Elaphospyris cordiformis new species
Figure 5.1–5.4

Holotype.—Figure 5.1; collection number USTL 4562-4; coordinates N51/2; sample ODP 171B-1051A-18X-5W, 54–56 cm; upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14; Sanfilippo and Blome, 2001); middle Eocene.

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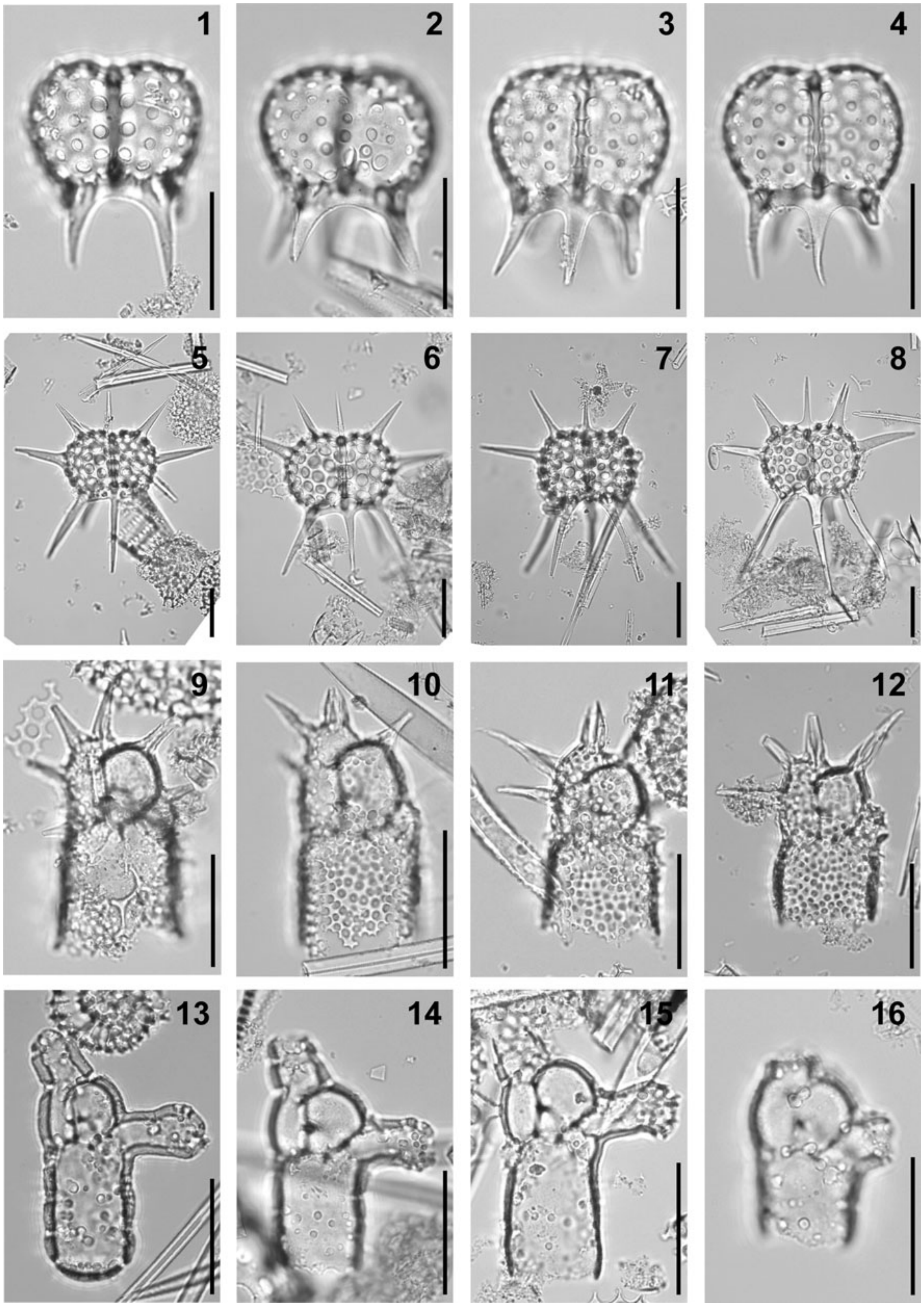

Figure 5. Composite light micrographs of new radiolarian species from ODP Site 1051 (Blake Nose, western subtropical Atlantic). (**1–4**) *Elaphospyris cordiformis* n. sp.: (**1**) holotype, ODP 171B-1051A-18X-5W, 54–56 cm, USTL 4562-4, N51/2; (**2**) ODP 171B-1051A-18X-5W, 54–56 cm, USTL 4561-3, R70/1; (**3**) ODP 171B-1051A-18X-5W, 54–56 cm, USTL 4562-3, U42/3; (**4**) ODP 171B-1051A-18X-5W, 54–56 cm, USTL 4560-3, W52/3. (**5–8**) *Elaphospyris quadricornis* n. sp.: (**5**) holotype, ODP 171B-1051A-4H-5W, 56–58 cm, USTL 4517-2, T47/2; (**6**) ODP 171B-1051A-2H-5W, 55–57 cm, USTL 4513-3, Q66/4; (**7**) ODP 171B-1051A-4H-5W, 56–58 cm, USTL 4516-2, G58/1; (**8**) ODP 171B-1051A-2H-5W, 55–57 cm, USTL 4513-4, D47/3. (**9–12**) *Botryocella*? *alectrida* n. sp.: (**9**) holotype, ODP 171B-1051A-4H-5W, 56–58 cm, USTL 4516-1, Z61/1; (**10**) ODP 171B-1051A-14H-5W, 52–54 cm, USTL 4554-4, E43/1; (**11**) ODP 171B-1051A-14H-5W, 52–54 cm, USTL 4554-5, G44/4; (**12**) ODP 171B-1051A-9H-2W, 53–55 cm, USTL 4524-4, H60/4. (**13–16**) *Pylobotrys*? *bineti* n. sp.: (**13**) holotype, ODP 171B-1051A-10H-2W, 53–55 cm, USTL 4530-1, J41/2; (**14**) ODP 171B-1051A-11H-5W, 59–61 cm, USTL 4539-1, L48/3; (**15**) ODP 171B-1051A-10H-5W, 55–57 cm, USTL 4533-2, K46/2; (**16**) ODP 171B-1051A-11H-2W, 62–64 cm, USTL 4536-1, L71/2. All scale bars equal 50 μm.

Diagnosis.—Cephalospyridid species with a smooth-surfaced shell perforated by small subcircular pores, and a pair of very short lateral cephalic spines.

Occurrence.—Only the end of the stratigraphic range of the species is documented here. This corresponds to the upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14).

Description.—Lattice shell quadrate to cordiform, smooth-surfaced, with a slight sagittal constriction. The sagittal ring appears by transparency as a thick opaque band. Cephalis bearing a short apical horn and two reduced lateral horns. Ventral side of the cephalis perforated by four elongated unpaired sagittal-lattice pores. Other cephalic pores small, subcircular, and quincuncially arranged. Five conical feet, straight and slightly divergent, arise from the basal ring.

Etymology.—Derived from the Latin *cordi* meaning 'heart' and *forma* meaning 'shape'.

Dimensions.—Based on 21 specimens (mean): length of cephalis: 43–57 µm (50 µm), maximum breadth of cephalis: 65–86 µm (76 µm), length of apical horn (when present): 4–12 µm (8 µm), length of lateral cephalic horns (when present): 3–6 µm (4 µm), length of feet: 27–60 µm (38 µm).

Remarks.—This species is assigned to the genus *Elaphospyris* because of its very short apical horn, its pair of lateral cephalic horns, and its five divergent basal feet. *E. cordiformis* n. sp. is distinguished from other species of *Elaphospyris* by its smooth cephalis, which is perforated by relatively small pores and bears three very short spines. The presence of conical feet allows this species to be easily distinguished from cordiform, smooth-surfaced species of the genus Desmospyris such as *Desmospyris acuta* (Goll, 1968) or *D. lata* (Goll, 1969).

Elaphospyris quadricornis new species
Figure 5.5–5.8

2015 *Dendrospyris* sp. F; Kamikuri, pl. 13, figs. 3, 4.

Holotype.—Figure 5.5; collection number USTL 4517-2; coordinates T47/2; sample ODP 171B-1051A-4H-5W, 56–58 cm; lowermost part of the *Podocyrtis* (*L.*) *goetheana* Zone (RP16; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.—Cephalospyridid species with a latticed shell and two pairs of lateral cephalic spines.

Occurrence.—*Elaphospyris quadricornis* n. sp. occurs sporadically throughout the studied interval, from the upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14) to the lower part of the *Podocyrtis* (*L.*) *goetheana* Zone (RP16).

Description.—Shell unisegmented, thick-walled, and weakly tuberculate. Sagittal ring D-shaped, dividing the cephalis into two lobes. Cephalis bearing a needle-shaped apical horn, and two pairs of straight, pointed, lateral horns. First pair of lateral horns of about the same length as the apical horn, forming an angle of ∼30° with the sagittal ring; second pair of lateral horns usually longer and stronger, forming an angle of ∼90° with the sagittal ring. Ventral side of the cephalis pierced by four large, unpaired sagittal-lattice pores, while the dorsal side has no sagittal-lattice pores. Other cephalic pores subcircular, hexagonally framed, and arranged in symmetry with respect to the sagittal constriction. Five straight, pointed, and slightly divergent feet arise from the basal ring.

Etymology.—The specific epithet means four-horned in Latin.

Dimensions.—Based on 12 specimens (mean): length of cephalis: 45–103 µm (74 µm), maximum breadth of cephalis: 58–99 µm (80 µm), length of apical horn: 6–49 µm (25 µm), length of first pair of lateral cephalic horns: 8–50 µm (33 µm), length of second pair of lateral cephalic horns: 19–58 µm (39 µm), length of feet: 27–116 µm (69 µm).

Remarks.—*Elaphospyris quadricornis* n. sp. is assigned to the genus *Elaphospyris* because of the general morphology of its shell, which is similar to that of *E. didiceros* (Ehrenberg, 1874). *Elaphospyris quadricornis* n. sp. differs from all other species of the genus *Elaphospyris* in having two pairs of well-developed lateral cephalic horns and five long basal feet.

Superfamily Plagiacanthoidea Hertwig, 1879, emend. Sandin et al., 2019
Family Lophophaenidae Haeckel, 1882, sensu Petrushevskaya, 1971
Genus *Ceratocyrtis* Bütschli, 1882, emend Sugiyama, 1993

Type species.—*Cornutella*? *cucullaris* Ehrenberg, 1874, p. 221 (unfigured); 1876, p. 68, pl. 2, fig. 7; subsequent designation by Petrushevskaya, 1971, p. 98.

Ceratocyrtis oconnori new species
Figure 6.1–6.4

Holotype.—Figure 6.1; collection number USTL 4526-4; coordinates R49/4; sample ODP 171B-1051A-9H-2W, 53–55 cm; *Podocyrtis* (*L.*) *chalara* Zone (RP15; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.—*Ceratocyrtis* species with a large, thorny cephalis that is deeply embedded in the thoracic segment.

Occurrence.—This relatively rare species occurs sporadically throughout the studied interval, from the upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14) to the *Podocyrtis* (*L.*) *chalara* Zone (RP15).

Description.—Shell composed of two segments, relatively thick-walled and conical to inflated in general shape. Cephalis deeply embedded in the thoracic segment, perforated by subcircular pores, and bearing multiple horns. Delineating the cephalis from the thorax is difficult because there is no clear expression of the collar stricture. Thorax conically truncated to inflated ovate, and may have an irregular surface that is

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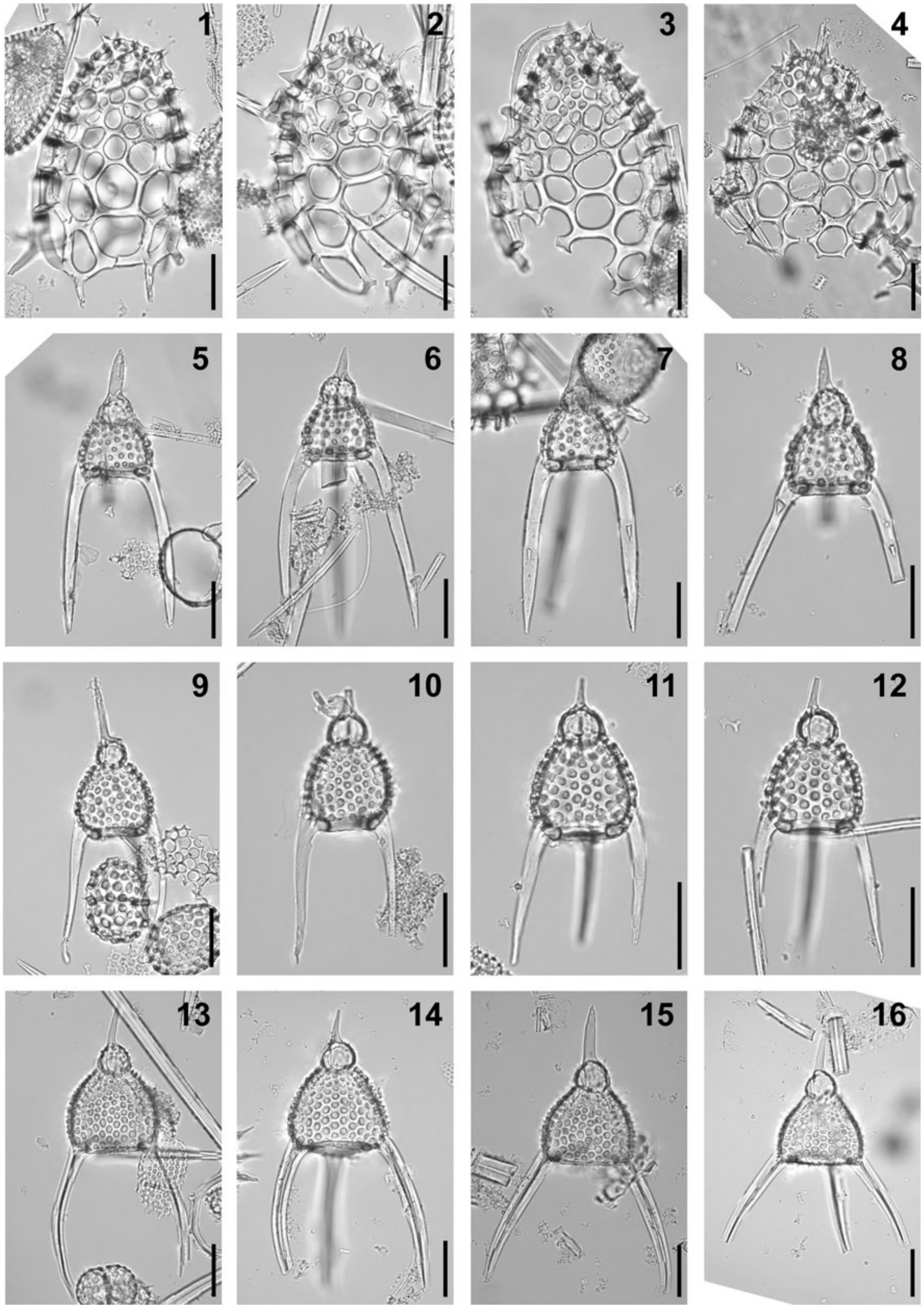

Figure 6. Composite light micrographs of new radiolarian species from ODP Site 1051 (Blake Nose, western subtropical Atlantic). (**1–4**) *Ceratocyrtis oconnori* n. sp.: (**1**) holotype, ODP 171B-1051A-9H-2W, 53–55 cm, USTL 4526-4, R49/4; (**2**) ODP 171B-1051A-9H-2W, 53–55 cm, USTL 4526-5, Q55/2; (**3**) ODP 171B-1051A-9H-5W, 53–55 cm, USTL 4566-1, G57/4; (**4**) ODP 171B-1051A-9H-2W, 53–55 cm, USTL 4525-5, S38/4. (**5–8**) *Lychnocanium cheni* n. sp.: (**5**) holotype, ODP 171B-1051A-18X-5W, 54–56 cm, USTL 4562-5, O41/3; (**6**) ODP 171B-1051A-18X-5W, 54–56 cm, USTL 4561-4, P70/3; (**7**) ODP 171B-1051A-18X-5W, 54–56 cm, USTL 4562-6, D52/3; (**8**) ODP 171B-1051A-18X-5W, 54–56 cm, USTL 4562-7, F60/3. (**9–12**) *Lychnocanium cingulatum* n. sp.: (**9**) holotype, ODP 171B-1051A-18X-5W, 54–56 cm, USTL 4561-1, X70/2; (**10**) ODP 171B-1051A-18X-5W, 55–56 cm, USTL 4560-1, C56/1; (**11**) ODP 171B-1051A-18X-5W, 54–56 cm, USTL 4561-5, O69/4; (**12**) ODP 171B-1051A-18X-5W, 54–56 cm, USTL 4560-2, T55/2. (**13–16**) *Lychnocanium forficula* n. sp.: (**13**) holotype, ODP 171B-1051A-18X-5W, 54–56 cm, USTL 4561-2, J55/3; (**14**) ODP 171B-1051A-11H-2W, 62–64 cm, USTL 4536-1, Q70/4; (**15**) holotype, ODP 171B-1051A-2H-5W, 55–57 cm, USTL 4513-2, H48/1; (**16**) ODP 171B-1051A-4H-5W, 56–58 cm, USTL 4515-5, W48/1. All scale bars equal 50 µm.

roughened by slender spines arising from the intervening pore bars (e.g., Fig. 6.2). Thoracic pores circular to elongated and randomly arranged. They are noticeably larger towards the oral end, although their size is not consistent. Distal part of the thorax ragged (Fig. 6.2–6.4) or flanked by a few long conical spines (Fig. 6.1). Aperture open wide.

Etymology.—The species is dedicated to Dr. Barry O'Connor (University of Auckland, New Zealand) in honor of his detailed taxonomic study of Cenozoic polycystine radiolarians.

Dimensions.—Based on seven specimens (mean): cephalothorax length without the apical horn: 121–227 µm (159 µm), length of apical horn: 8–41 µm (22 µm), maximum breadth of cephalothorax: 57–163 µm (93 µm).

Remarks.—The newly discovered species bears a close morphological resemblance to the middle Oligocene species *C. mashae* Bjorklund, 1976 and *C. robustus* Bjorklund, 1976, with which it shares a spiny shell and a relatively small cephalis that is partially embedded in the thorax. However, the two latter species are different from *C. oconnori* n. sp. because their cephalis is clearly distinguishable from the thorax, and their thorax is less tapered in its distal half. *Ceratocyrtis oconnori* n. sp. is also distinguished from similar-looking spumellarian species *Zealithapium mitra* (Ehrenberg, 1874) and *Z. oamaru* O'Connor, 1999 by its rounder overall shape and its more irregularly arranged thoracic pores.

Superfamily Pylobotrydoidea Haeckel, 1882
Family Pylobotrydidae Haeckel, 1882, sensu Sugiyama, 1998
Genus *Botryocella* Haeckel, 1887

Type species.—*Lithobotrys nucula* Ehrenberg, 1874, p. 238 (unfigured); Ehrenberg, 1876, p. 76, pl. 3, fig. 16; subsequent designation by Campbell, 1954, p. D144.

Botryocella? *alectrida* new species
Figure 5.9–5.12

Holotype.—Figure 5.9; collection number USTL 4516-1; coordinates Z61/1; sample ODP 171B-1051A-4H-5W, 56–58 cm; lower part of the *Podocyrtis* (*L.*) *goetheana* Zone (RP16; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.—Pylobotrydid species with a shell that is densely perforated and has a crest of long, bladed cephalic horns.

Occurrence.—This rare species occurs sporadically from the lower part of the *Podocyrtis* (*L.*) *chalara* Zone (RP15) to the lower part of the *Podocyrtis* (*L.*) *goetheana* Zone (RP16).

Description.—Shell two-segmented, laterally flattened, and relatively thick-walled. Cephalis trilobed, and perforated by numerous small, closely spaced pores, giving it a rough appearance. The anterior part of the eucephalic lobe is covered by a reniform to ovoid ante-cephalis lobe, which has three long-bladed horns (the third/posterior one corresponding to the apical spine). Absence of upper tube. Eucephalic lobe inflated, thick-walled, bearing a long, straight or curved horn. Post-cephalic lobe very reduced, and may have a short protruding horn (Fig. 5.9), which likely corresponds to the ventral spine. Collar stricture indistinct. Thorax subcylindrical, densely perforated by small, circular pores that are irregularly distributed on its surface. A small thoracic wing may develop from the dorsal spine (Fig. 5.9). Distal part of the thorax invariably ragged.

Etymology.—The specific epithet means 'rooster-like' in Greek, in allusion to the remarkable cephalic horns of the new species.

Dimensions.—Based on seven specimens (mean): length of cephalothorax without the cephalic spines: 97–78 µm (88 µm), length of eucephalic lobe: 28–33 µm (31 µm), length of ante-cephalic lobe: 36–40 µm (38 µm), length of cephalic spines: 13–39 µm (25 µm), length of thorax: 42–61 µm (51 µm).

Remarks.—The newly discovered species has been tentatively assigned to the genus *Botryocella* due to the fact that its eucephalic lobe is partially embedded into the shell and its collar stricture is not externally well-defined (Petrushevskaya, 1971). However, this classification is only provisional because the new species lacks a galea above the eucephalic lobe. Finally, *B. ? alectrida* n. sp. is distinguished from other middle Eocene pylobotrydid species by its remarkable crest of cephalic horns.

Genus *Pylobotrys* Haeckel, 1882

Type species.—*Pylobotrys putealis* Haeckel, 1887, p. 1121, pl. 96, fig. 21; subsequent designation by Campbell, 1954, p. D144.

Pylobotrys? *bineti* new species
Figure 5.13–5.16

Holotype.—Figure 5.13; collection number USTL 4530-1; coordinates J41/2; sample ODP 171B-1051A-10H-2W, 53–55 cm; *Podocyrtis* (*L.*) *chalara* Zone (RP15; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.—Pylobotrydid species with an almost poreless thorax and two cephalic tubes protruding vertically and horizontally.

Occurrence.—This rare species is found throughout the investigated stratigraphic interval, from the upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14) to the lower part of the *Podocyrtis* (*L.*) *goetheana* Zone (RP16).

Description.—Shell composed of two segments and almost hyaline. Cephalis poreless and distinctly trilobed, with a small tubular post-cephalic lobe and a large globular eucephalic lobe partially embedded in a reniform ante-cephalic lobe. Ante- and post-cephalic lobes are extended into short, wide tubes that contain the apical and ventral spines. In some specimens, these tubes are open at the distal end. Thorax cylindrical, perforated by a few subcircular pores that are irregular in size and distribution. Aperture closed or undifferentiated.

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Etymology.—This species is named after the French architect and artist René Binet, who modeled the main entrance of the Paris Exposition Universelle of 1900 after Haeckel's drawing of Cenozoic radiolarians.

Dimensions.—Based on eight specimens (mean): height of eucephalic lobe: 23–30 µm (27 µm), height of antecephalic lobe without the apical tube: 20–26 µm (23 µm), length of apical tube: 8–33 µm (22 µm), length of ventral tube: 14–42 µm (29 µm), length of thorax: 33–60 µm (48 µm).

Remarks.—*Pylobotrys*? *bineti* is tentatively assigned to the genus *Pylobotrys* because of its distally closed, smooth-surfaced shell, and its two cephalic tubes, which include the apical and vertical spines. The new species is distinguished from *Acrobotrys disolenia* Haeckel, 1887 by its nearly hyaline shell and its smaller post-cephalic lobe, and from *A. tritubus* Riedel, 1957 in having only two cephalic tubes.

Superfamily Lithochytridoidea Ehrenberg, 1846
Family Lithochytrididae Ehrenberg, 1846, sensu Suzuki in Matsuzaki et al., 2015
Genus *Lychnocanium* Ehrenberg, 1846

Type species.—*Lychnocanium lucerna* Ehrenberg, 1847, p. 55, fig. 5; subsequent monotypy (Suzuki et al., 2021).

Lychnocanium cheni new species
Figure 6.5–6.8

1975 *Lychnocanium* sp.; Chen, p. 462, pl. 1, figs. 8, 9.
2020 *Lychnocanium tripodium* Ehrenberg; Hollis et al., pl. 14, figs. 8–10b.

Holotype.—Figure 6.5; collection number USTL 4562-5; coordinates O41/3; sample ODP 171B-1051A-18X-5W, 54–56 cm; upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.—Lithochytridid species with a thick-walled, hemispherical thorax and three straight, robust, and subparallel feet that are ovoid to rectangular in cross-section and longer than twice the length of the thorax.

Occurrence.—*Lychnocanium cheni* n. sp. occurs sporadically from the upper part of the *Podocyrtis* (*P.*) *mitra* Zone (RP14) to the lower part of the *Podocyrtis* (*L.*) *goetheana* Zone (RP16).

Description.—Shell composed of two segments. Cephalis thick-walled, globular, with a short and robust conical apical horn of approximately the same length. Cephalic pores subcircular, few in number and scattered. Collar stricture expressed externally as a slight change in the shell contour. Thorax hemispherical to truncate-conical, with a thick, rough wall. Thoracic pores subcircular and quincuncially arranged. Distal margin of the thorax constricted and marked by a relatively thick hyaline band. Feet straight, subparallel and ovoid to subrectangular in cross-section. They are more than twice as long as the thorax and extend from the peristome.

Etymology.—Named after Dr. Pei-Hsin Chen (Columbia University, New York), who was the first to illustrate it.

Dimensions.—Based on 12 specimens (mean): length of apical horn: 21–46 µm (32 µm), length of cephalis without the apical horn: 21–33 µm (27 µm), length of thorax: 45–72 µm (56 µm), length of feet: 131–256 µm (164 µm).

Remarks.—*Lychnocanium cheni* n. sp. differs from similar appearing lithochytridid species as follows: from *Lychnocanium babylonis* Clark and Campbell, 1942, group and *L. tribulus* Ehrenberg, 1874, in having longer, subparallel feet, and a hemispherical thorax, rather than a pyramidal to truncate conical thorax; from *L. nimrodi* Meunier and Danelian, 2023, by the absence of distally dilated apical horn and feet; from *L. falciferum* Ehrenberg, 1874, and *L. forficula* n. sp. by its straight feet; from *L. cypselus* Ehrenberg, 1874, in having longer, straighter feet and a hemispherical thorax, rather than an elongated, barrel-shaped thorax; from *L. tripodium* Ehrenberg, 1874, in having bigger thoracic pores and conical feet; from *L. trichopus* Ehrenberg, 1874, in having shorter and sturdier feet; from *L. alma* O'Connor, 1999, and *L. waiareka* O'Connor, 1999, in having conical feet and no vestigial abdomen. Finally, *L. cheni* n. sp. differs from *L. cingulatum* n. sp. in having three straight and robust feet, while those of *L. cingulatum* are slenderer and tend to become sinuous in their distal half. Additionally, *L. cheni* n. sp. has a shorter thorax, which is less than twice the height of the cephalis without the apical horn.

Lychnocanium cingulatum new species
Figure 6.9–6.12

1995 *Lychnocanium conicum* Clark and Campbell; Shilov, p. 126, pl. 2, fig. 1.

Holotype.—Figure 6.9; collection number USTL 4561-1; coordinates X70/2; sample ODP 171B-1051A-18X-5W, 54–56 cm; upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.—Lithochytridid species with a subspherical thorax terminating in a hyaline constricted peristome and three slender feet, the distal half of which is sinuous.

Occurrence.—*Lychnocanium cingulatum* n. sp. is quite abundant throughout the studied interval, from the upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14) to the lower part of the *Podocyrtis* (*L.*) *goetheana* Zone (RP16).

Description.—Shell composed of two segments, broadly conical in general shape. Cephalis subspherical, with small subcircular pores, bearing a slender conical apical horn, usually longer than the cephalis height. Collar stricture distinct. Thorax subspherical, penetrated by small subcircular pores quincuncially arranged. Peristome thick, poreless and constricted, with a smooth margin. Feet slender, downwardly directed, and slightly sinuous in their distal half, originating above the peristome. In some specimens, the feet are reduced to three short claws.

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Etymology.—The specific epithet *cingulatum* means 'with a girdle' in Latin and refers to the hyaline peristome of the new species.

Dimensions.—Based on 30 specimens (mean): length of apical horn: 16–73 µm (36 µm), length of cephalis without the apical horn: 19–30 µm (24 µm), length of thorax: 46–80 µm (61 µm), thickness of peristome: 5–12 µm (8 µm), length of feet: 44–121 µm (84 µm).

Remarks.—*Lychnocanium cingulatum* n. sp. differs from other middle Eocene lithochytridid species in that its feet originate above the peristome, which is marked by a thick hyaline band.

Lychnocanium croizoni new species
Figure 7.1–7.4

1973 Theoperid gen. et sp. indet., Sanfilippo and Riedel, pl. 35, fig. 6.

Holotype.—Figure 7.1; collection number USTL 4528-1; coordinates S67/2; sample ODP 171B-1051A-9H-5W, 53–55 cm; *Podocyrtis (L.) chalara* Zone (RP15; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.—Lithochytridid species whose feet are absent or reduced to three short claws.

Occurrence.—*Lychnocanium croizoni* n. sp. occurs throughout the studied interval, from the upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14) to the lower part of the *Podocyrtis* (*L.*) *goetheana* Zone (RP16).

Description.—Shell composed of two segments, thick-walled, and small. Cephalis globular, poreless, partially embedded in the thorax, and bearing a short conical apical horn. Thorax spindle-shaped to pyriform. Thoracic pores subcircular, and quincuncially arranged, but their arrangement tends to be less regular in the upper part of the thorax. Aperture open and bordered by a thick hyaline peristome with a smooth margin. Three inconspicuous conical feet originating just above the peristome are present in some specimens (Fig. 7.3).

Etymology.—This species is named after the French athlete Philippe Croizon, the first limbless person to swim across the English Channel.

Dimensions.—Based on 14 specimens (mean): length of cephalothorax without the apical horn: 101–123 µm (112 µm), length of cephalis without the apical horn: 19–26 µm (23 µm), length of apical horn: 7–23 µm (16 µm), length of thorax: 79–98 µm (89 µm), maximum breadth of thorax: 67–78 µm (73 µm), length of feet (when present): 10–12 µm (11 µm).

Remarks.—This remarkable species differs from all other lithochytridid species in being footless, or in having its feet reduced to three short claws. *Lychnocanium croizoni* n. sp. is distinguished from *Dictyophimus ceratium* Clark and Campbell, 1942, in having shorter feet and a more slender shell with no collar constriction. It also differs from *Plannapus hornibrooki* O'Connor, 1999, and *P. mauricei* O'Connor, 1999, in having a thicker cephalic wall, a stronger apical horn, and in lacking a vertical tube.

Lychnocanium forficula new species
Figure 6.13–6.16

Holotype.—Figure 6.13; collection number USTL 4561-2; coordinates J55/3; sample ODP 171B-1051A-18X-5W, 54–56 cm; upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.—Lithochytridid species with a thorax pierced by numerous closely spaced, quincuncially arranged pores and three bladed, inwardly curved feet.

Occurrence.—*Lychnocanium forficula* n. sp. is abundant throughout the investigated interval, from the upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14) to the lower part of the *Podocyrtis* (*L.*) *goetheana* Zone (RP16).

Description.—Shell conical, composed of two segments. Cephalis subspherical, perforated by numerous small subcircular pores, bearing a stout conical apical horn. Collar stricture marked by a sharp change in the contour of the shell. Thorax truncate conical to campanulate, with numerous closely spaced subcircular pores that are hexagonally framed and quincuncially arranged. Peristome slightly constricted and marked by a thin internal ridge. Feet three-bladed, longer than the thorax, and inwardly curved, extending from the thoracic margin. In some specimens, an inconspicuous row of reticulations has been observed on the distal margin of the thorax.

Etymology.—The specific epithet refers to the Latin genus name of the European earwig (*Forficula*), whose male forceps are curved like the feet of the new species.

Dimensions.—Based on 23 specimens (mean): length of cephalis without the apical horn: 22–34 µm (29 µm), length of apical horn: 21–53 µm (40 µm), length of thorax: 66–86 µm (76 µm), length of feet: 117–188 µm (145 µm).

Remarks.—*Lychnocanium forficula* n. sp. differs from the similar-looking species *L. cypselus* Ehrenberg, 1874, in having a truncate conical thorax rather than a barrel-shaped elongated thorax. It is also distinguished from *L. falciferum* Ehrenberg, 1854, *L. bellum* Clark and Campbell, 1942, and *L. trichopus* Ehrenberg, 1874 by its shorter, regularly arcuate feet, which are approximately as long as the cephalothorax (excluding the apical horn). *Lychnocanium forficula* n. sp. can be distinguished from *L. turgidum* Ehrenberg, 1874, by its longer feet and its longer apical horn; from *L. crassipes* Ehrenberg, 1874, and *L. conicum* Clark and Campbell, 1942, by the presence of bladed feet; from *L. tetrapodium* Ehrenberg, 1874, in having three convergent feet rather than four divergent feet; and from *L. cheni* n. sp., *L. cingulatum* n. sp., and *L. tripodium*

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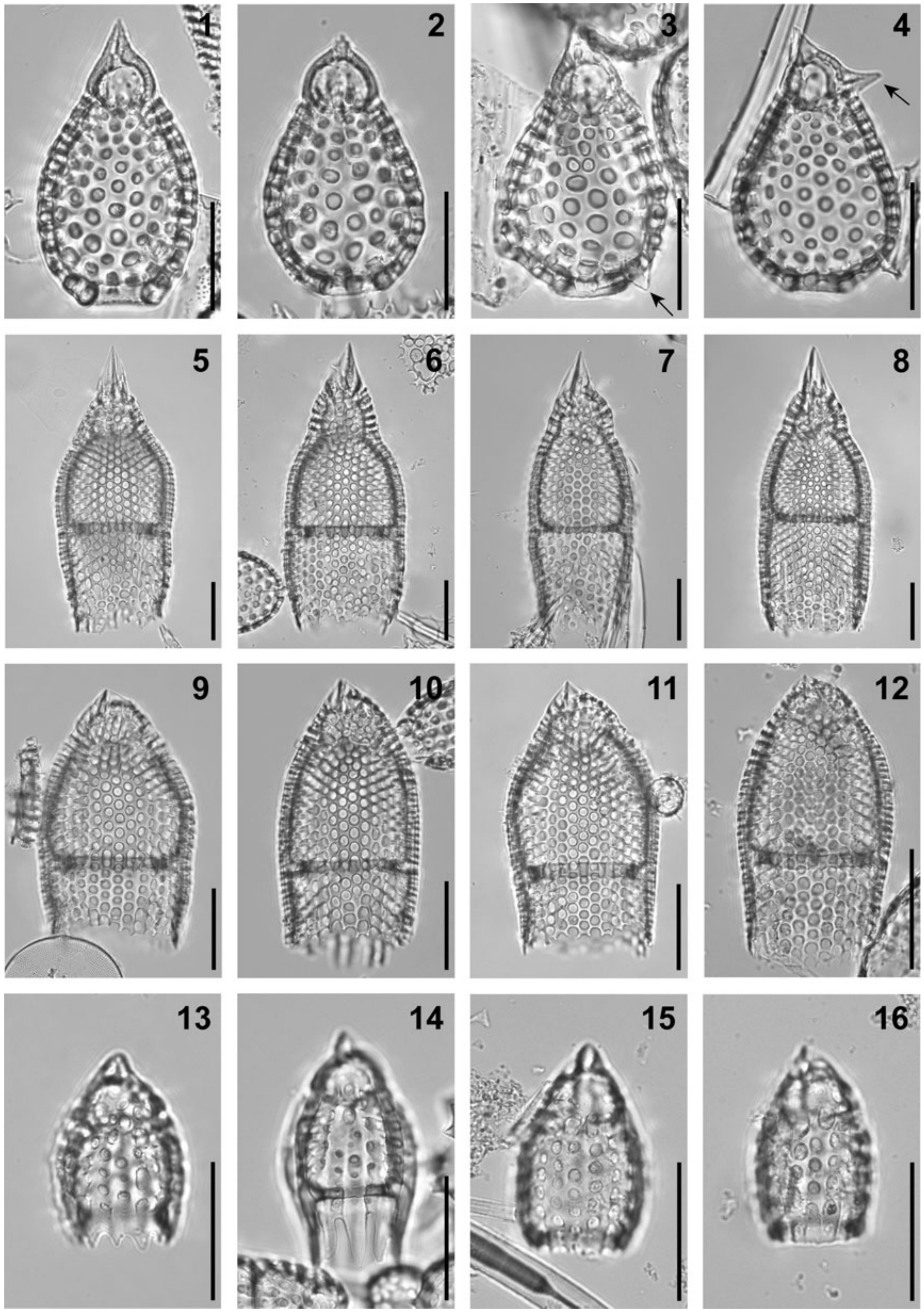

Figure 7. Composite light micrographs of new radiolarian species from ODP Site 1051 (Blake Nose, western subtropical Atlantic). (**1–4**) *Lychnocanium croizoni* n. sp.: (**1**) holotype, ODP 171B-1051A-9H-5W, 53–55 cm, USTL 4528-1, S67/2; (**2**) ODP 171B-1051A-10H-5W, 52–54 cm, USTL 4533-1, F53/3; (**3**) specimen showing short feet (arrow), ODP 171B-1051A-9H-5W, 53–55 cm, USTL 4528-4, V65/2; (**4**) specimen showing ventral horn (arrow), ODP 171B-1051A-10H-2W, 53–55 cm, USTL 4530-4, E60/4. (**5–8**) *Albatrossidium messiaeni* n. sp.: (**5**) holotype, ODP 171B-1051A-9H-5W, 53–55 cm, USTL 4529-1, X42/4; (**6**) ODP 171B-1051A-4H-5W, 56–58 cm, USTL 4515-1, X61/3; (**7**) ODP 171B-1051A-9H-2W, 53–55 cm, USTL 4524-5, F47/3; (**8**) ODP 171B-1051A-9H-5W, 53–55 cm, USTL 4529-3, W09/3. (**9–12**) *Cryptocarpium*? *judoka* n. sp.: (**9**) holotype, ODP 171B-1051A-13H-5W, 58–60 cm, USTL 4551-1, R40/2; (**10**) ODP 171B-1051A-10H-2W, 53–55 cm, USTL 4530-2, F43/2; (**11**) ODP 171B-1051A-9H-5W, 53–55 cm, USTL 4565-1, S48/4; (**12**) ODP 171B-1051A-9H-2W, 53–55 cm, USTL 4525-6, K69/1. (**13–16**) *Phormocyrtis microtesta* n. sp.: (**13**) holotype, ODP 171B-1051A-9H-5W, 53–55 cm, USTL 4529-4, W46/3; (**14**) ODP 171B-1051A-9H-5W, 53–55 cm, USTL 4528-3, P53/4; (**15**) ODP 171B-1051A-13H-2W, 52–54 cm, USTL 4549-1, W56/2; (**16**) ODP 171B-1051A-13H-2W, 52–54 cm, USTL 4550-1, H60/2. All scale bars equal 50 µm.

Ehrenberg, 1874, in having curved feet rather than straight, subparallel feet. The new species also differs from *L. carinatum* Ehrenberg, 1874, *L. continuum* Ehrenberg, 1874, *L. tridentatum* Ehrenberg, 1874, and *L. trifolium* Riedel and Sanfilippo, 1971, in having a porous thorax rather than a hyaline or partially hyaline thorax. Finally, the lack of sigmoid feet distinguishes the new species from *Lychnocanoma bajunensis* Renz, 1984.

Superfamily Pterocorythoidea Haeckel, 1882, emend. Suzuki et al., 2021
Family Pterocorythidae Haeckel, 1882
Genus *Albatrossidium* Sanfilippo and Riedel, 1992

Type species.—*Albatrossidium minzok* Sanfilippo and Riedel, 1992, p. 16, pl. 2, fig. 7; original designation.

Albatrossidium messiaeni new species
Figure 7.5–7.8

2015 *Eucyrtidium*? sp. D; Kamikuri, pl. 9, fig. 9a, b.

Holotype.—Figure 7.5; collection number USTL 4529-1; coordinates X42/4; sample ODP 171B-1051A-9H-5W, 53–55 cm; *Podocyrtis (L.) chalara* Zone (RP15; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.—*Albatrossidium* species with a thick-walled cephalis perforated by ovoid to elongated pores.

Occurrence.—This species is common from the upper part of the *Podocyrtis (L.) mitra* Zone (RP14) to the lower part of the *Podocyrtis (L.) goetheana* Zone (RP16).

Description.—Shell three-segmented, cylindrical, and thick-walled. Cephalis hemispherical, very thick-walled, and bearing a prominent, broad-based apical horn. Cephalic pores subcircular, except at the base of the horn where they are longitudinally elongated and form grooves in the proximal part of the horn. Lateral lobes of the cephalis indistinct. Collar stricture marked by a moderate change in the contour of the shell. Thorax hemispherical, elongated to subcylindrical. Thoracic pores circular and quincuncially arranged. Thorax and abdomen separated by an internal ridge, that appears externally as a thick dark band. Abdomen subcylindrical, approximately as long as the thorax, or slightly shorter. Abdominal pores less regular in size and shape compared to the thoracic ones, tending toward longitudinal arrangement. Abdomen terminates in an undifferentiated, ragged margin in all observed specimens.

Etymology.—Named after the French composer, organist, and ornithologist Olivier Messiaen.

Dimensions.—Based on 30 specimens (mean): total length without the apical horn: 161–207 μm (183 μm), length of apical horn: 18–51 μm (37 μm), length of cephalis without the apical horn: 23–47 μm (32 μm), length of thorax: 73–101 μm (83 μm), length of abdomen: 42–97 μm (70 μm).

Remarks.—*Albatrossidium messiaeni* n. sp. differs from *A. annikasanfilippoae* Meunier and Danelian, 2023 and *A. regis* Meunier and Danelian, 2023 in that it lacks a cephalic hole accessory cephalis spines. The new species is also distinguished from *A. minzok* Sanfilippo and Riedel, 1992, and *A. tenellum* (Foreman, 1973) by its very thick-walled cephalis, which is perforated by ovoid to elongated pores.

Genus *Cryptocarpium* Sanfilippo and Riedel, 1992

Type species.—*Cryptoprora ornata* Ehrenberg, 1874 (unfigured); 1876, p. 222, pl. 5, fig. 8; original designation.

Cryptocarpium? *judoka* new species
Figure 7.9–7.12

non 1973 *Cryptoprora ornata* Ehrenberg; Sanfilippo and Riedel, pl. 35, figs. 7, 8.
?1995 *Cryptocarpium*? *ornatum* (Ehrenberg); Strong et al., p. 208, pl. 11, figs. S, T.
1997 *Cryptocarpium ornatum* (Ehrenberg); Hollis et al., p. 66, pl. 6, figs. 24, 25 (part).
2012 *Cryptocarpium ornatum* (Ehrenberg); Moore and Kamikuri, p. 6, pl. P2, fig. 4 (part).

Holotype.—Figure 7.9; collection number USTL 4551-1; coordinates R40/2; sample ODP 171B-1051A-13H-5W, 58–60 cm; upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.—Pterocorythid species with a bullet-shaped shell and a short, broad-based apical horn.

Occurrence.—This species is present in all of the analyzed samples, from the upper part of the *Podocyrtis (L.) mitra* Zone (RP14) to the lower part of the *Podocyrtis (L.) goetheana* Zone (RP16).

Description.—Shell three-segmented, thick-walled, and bullet-shaped. Cephalis hemispherical and composed of three lobes: a large unpaired eucephalic lobe and two smaller lateral lobes (Figures 7.10, 7.11). The thickness of the shell and the poorly developed external furrows can make the cephalic lobes difficult to distinguish. The cephalis is also a slightly embedded in the thorax, giving the species the appearance of a carpocaniid. A short, broad-based apical horn is present in most observed specimens. Thorax campanulate to subcylindrical, thick-walled and pierced by small circular pores quincuncially arranged. Lumbar stricture defined by a thick internal septum that appears externally as a dark band. Abdomen subcylindrical, perforated by subcircular pores that are less regular in size and arrangement than those of the thorax. The end of the abdomen is ragged along a row of pores.

Etymology.—From the Japanese *judoka*, which designates the practitioner of the martial art of judo. The specific epithet refers to the large lumbar septum of the new species, which resembles the black belt of a judoka.

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Dimensions.—Based on 19 specimens (mean): total length without the apical horn: 109–168 µm (132 µm), length of apical horn: 6–10 µm (7 µm), length of cephalothorax without the apical horn: 20–31 µm (24 µm), length of abdomen: 28–78 µm (41 µm).

Remarks.—*Cryptocarpium*? *judoka* n. sp. is tentatively assigned to the genus *Cryptocarpium* because of its general "carpocaniid-like" morphology, *Cryptocarpium*? *judoka* n. sp. is tentatively assigned to the genus *Cryptocarpium* because of its general "carpocaniid-like" morphology, its very reduced apical horn, and its trilobed cephalic shield, which is partially embedded in the thoracic segment.

Cryptocarpium? *judoka* n. sp. differs from the lectotype of *Cr. ornatum* (Ehrenberg, 1874) designated by O'Dogherty et al. (2021) in having a symmetrical cephalis bearing a short apical horn rather than a hornless asymmetrically placed cephalis, and in having more thoracic pores (∼10 in a longitudinal row). *Cryptocarpium*? *judoka* n. sp. is also differs from *Cr*.? *azyx* (Sanfilippo and Riedel, 1973) by having a subcylindrical, three-segmented shell. In addition to the cephalis structure, the new species differs from the carpocaniid species *Carpocanopsis cingulata* Riedel and Sanfilippo, 1971, by having a subcylindrical thorax and abdomen, rather than an inflated thorax and a tapered abdomen, and from *Carpocanopsis bramlettei* Riedel and Sanfilippo, 1971, by having a porous abdomen. *Cryptocarpium*? *judoka* n. sp. also differs from the specimens illustrated as "pterocoryid gen. and sp. indet" by Sanfilippo and Riedel (1973, pl. 35, figs. 7, 8) in having a smaller apical horn and a cephalis that is more deeply embedded in the thoracic segment, and from the specimens illustrated as *Cr. ornatum* by Sanfilippo and Riedel (1992, pl. 2, figs. 18–20) in having a subcylindrical shell without a lumbar constriction.

Genus *Phormocyrtis* Haeckel, 1887

Type species.—*Phormocyrtis longicornis* Haeckel, 1887, p. 1370, pl. 69, fig. 15; subsequent designation by Campbell (1954), p. D134.

Phormocyrtis microtesta new species

Figures 7.13–7.16

Holotype.—Figure 7.13; collection number USTL 4529-4; coordinates W46/3; sample ODP 171B-1051A-9H-5W, 53–55 cm; *Podocyrtis (L.) chalara* Zone (RP15; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.—*Phormocyrtis* species with a small two-segmented shell.

Occurrence.—*Phormocyrtis microtesta* n. sp. is very abundant in almost all the studied samples, from the upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14) to the lower part of the *Podocyrtis* (*L.*) *goetheana* Zone (RP16).

Description.—Shell small, two-segmented, and thick-walled. Cephalis hemispherical, poreless or penetrated by a few subcircular pores, bearing a short, bladed apical horn. Collar stricture slightly expressed externally. Thorax barrel-shaped to subcylindrical, thick-walled, and twice as long as the cephalis. Thoracic pores subcircular, irregular in size, and weakly arranged in longitudinal rows. These rows contain three to six pores and are sometimes separated by inconspicuous longitudinal ridges. Distal margin of thorax undifferentiated (Fig. 7.15, 7.16) or surrounded by a few short, triangular, or rectangular spines (Fig. 7.13, 7.14).

Etymology.—The specific epithet means 'small shell' in Greek and refers to the relatively small size of the new species compared to other members of the genus *Phormocyrtis*.

Dimensions.—Based on 18 specimens (mean): length of apical horn: 7–16 µm (10 µm), length of cephalis without the apical horn: 16–29 µm (23 µm), length of thorax: 36–67 µm (51 µm), length of lamellar teeth: 11–30 µm (19 µm).

Remarks.—*Phormocyrtis microtesta* n. sp. is distinguished from other *Phormocyrtis* species by its two-segmented shell, which as an undifferentiated peristome, or a vestigial abdomen reduced to a crown of short spines.

Family Lophocyrtiidae Sanfilippo and Caulet in De Wever et al., 2001

Genus *Apoplanius* Sanfilippo and Caulet, 1998

Type species.—*Lophocyrtis* (*Apoplanius*) *klydus* Sanfilippo and Caulet, 1998, p. 12, pl. 5, fig. 5a; original designation.

Apoplanius cryptodirus new species

Figure 8.1–8.4

Holotype.—Figure 8.1; collection number USTL 4533-3; coordinates W52/3; sample ODP 171B-1051A-10H-5W, 52–54 cm; *Podocyrtis* (*L.*) *chalara* Zone (RP15; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.—*Apoplanius* species with a short hemispherical to inflated thorax that envelopes the lower part of the cephalis.

Occurrence.—*Apoplanius cryptodirus* n. sp. is common throughout the studied interval, from the upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14) to the lower part of the *Podocyrtis* (*L.*) *goetheana* Zone (RP16).

Description.—Shell three-segmented, robust, and broadly cylindrical. Cephalis globular, poreless, very thick-walled, and partially embedded in a loose lattice of spines that originate from the upper margin of the thorax. Apical spine merges with the cephalic wall and is extended outward by a short conical apical horn. A secondary horn may develop on the dorsal side of the cephalis (Fig. 8.1, 8.2). Mitral arches depart from the apical spine in the middle of the cephalis and diverge quickly at a great angle (Fig. 8.4). The collar stricture is indicated by a change in the contour of the shell. Thorax hemispherical to inflated, penetrated by subcircular

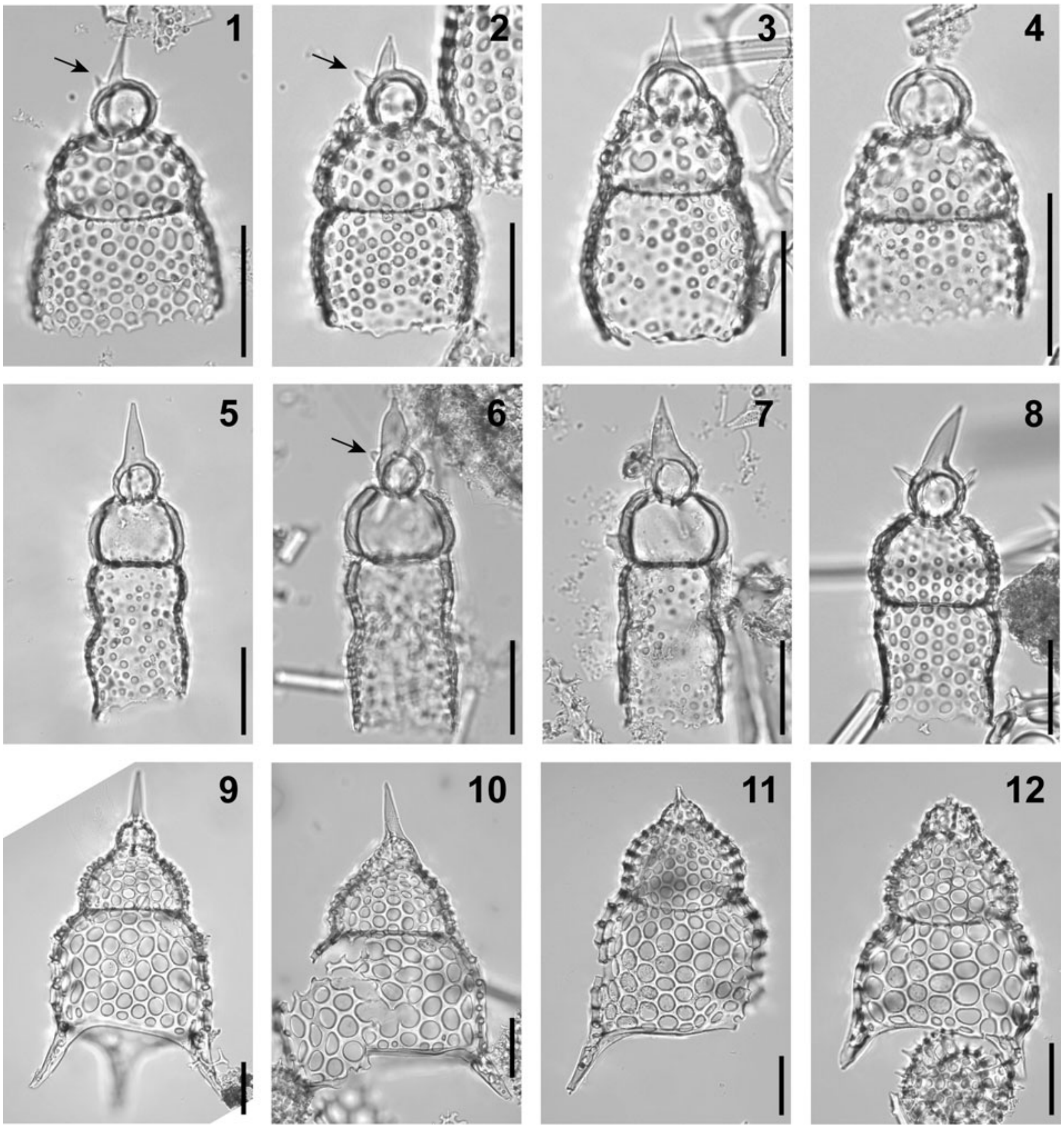

Figure 8. Composite light micrographs of new radiolarian species from ODP Site 1051 (Blake Nose, western subtropical Atlantic). (**1–4**) *Apoplanius cryptodirus* n. sp.: (**1**) holotype, showing dorsal horn (arrow), ODP 171B-1051A-10H-5W, 52–54 cm, USTL 4533-3, W52/3; (**2**) specimen showing dorsal horn (arrow), ODP 171B-1051A-14H-5W, 52–54 cm, USTL 4554-6, H58/4; (**3**) ODP 171B-1051A-9H-5W, 53–55 cm, USTL 4528-2, D64/1; (**4**) specimen showing mitral arches, ODP 171B-1051A-18X-5W, 54–56 cm, USTL 4562-8, O40/4; (**5–7**) *Apoplanius hyalinus* n. sp.: (**5**) holotype, ODP 171B-1051A-9H-5W, 53–55 cm, USTL 4566-2, S37/2; (**6**) specimen showing dorsal horn (arrow), ODP 171B-1051A-8H-5W, 53–55 cm, USTL 4521-1, S55/3; (**7**) ODP 171B-1051A-8H-5W, 53–55 cm, USTL 4522-1, N61/4; (**8**) *Apoplanius kerasperus* (Sanfilippo and Caulet, 1998): ODP 171B-1051A-10H-2W, 53–55 cm, USTL 4530-3, K60/2; (**9–12**) *Thyrsocyrtis kamikuri* n. sp.: (**9**) holotype, ODP 171B-1051A-9H-2W, 53–55 cm, USTL 4563-1, B34/3; (**10**) ODP 171B-1051A-9H-5W, 53–55 cm, USTL 4529-5, J44/1; (**11**) ODP 171B-1051A-9H-2W, 53–55 cm, USTL 4563-2, P37/1; (**12**) ODP 171B-1051A-9H-2W, 53–55 cm, USTL 4563-3, D46/3. All scale bars equal 50 μm.

pores that are irregular in size and and arranged in a weak quincuncial pattern. Lumbar stricture marked by an external constriction that is underlined by a thin dark band. Abdomen subcylindrical to inflated campanulate, with subcircular pores smaller than the thoracic ones. Abdominal end ragged along a row of pores or surrounded by a crown of small spines.

Etymology.—The specific epithet means 'hidden neck' in Greek.

Dimensions.—Based on 17 specimens (mean): total length without the apical horn: 77–115 μm (103 μm), length of cephalis without the apical horn: 17–25 μm (14 μm), length of apical horn: 7–18 μm (14 μm), length of ventral horn (when

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present): 4–10 µm (7 µm), length of thorax: 27–40 µm (32 µm), maximum breadth of thorax: 47–60 µm (56 µm), length of abdomen: 33–60 µm (49 µm), maximum breadth of abdomen: 62–81 µm (68 µm).

Remarks.—Apoplanius cryptodirus n. sp. is assigned to the genus *Apoplanius* based on its simple, short apical horn without three proximal openings, and its apical spine that is partially embedded in the cephalic wall (Sanfilippo and Caulet, 1998; O'Dogherty et al., 2021). *Apoplanius cryptodirus* n. sp. differs from *A. asperus* (Ehrenberg, 1874) and *A. nomas* (Sanfilippo and Caulet, 1998) in having a less inflated thorax, which is always narrower than the abdomen; from *A. kerasperus* (Sanfilippo and Caulet, 1998) in having a smaller apical horn and no auxiliary horns on the cephalis; from *A. klydus* (Sanfilippo and Caulet, 1998) in having a subcylindrical abdomen rather than a wavy abdomen, no thoracic wings, and no holes at the base of the apical horn. Finally, *A. cryptodirus* n. sp. is distinguished from *Theocorys minuta* Takemura and Ling, 1998, *T. perforalvus* O'Connor, 1997, and *T. saginata* Takemura and Ling, 1998, in having a horned cephalis that is partially embedded in the thorax.

Apoplanius hyalinus new species
Figure 8.5–8.7

Holotype.—Figure 8.5; collection number USTL 4566-2; coordinates S37/2; sample ODP 171B-1051A-9H-5W, 53–55 cm; *Podocyrtis (L.) chalara* Zone (RP15; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.—Apoplanius species with a thick-walled hyaline thorax.

Occurrence.—Apoplanius hyalinus n. sp. occurs sporadically throughout the studied interval, from the upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14) to the lower part of the *Podocyrtis* (*L.*) *chalara* Zone (RP15), and it becomes very abundant from the upper part of the *Podocyrtis* (*L.*) *chalara* Zone to the lower part of the *Podocyrtis (L.) goetheana* Zone (RP16).

Description.—Shell composed of three segments, cylindrical, and almost hyaline. Cephalis globular, thick-walled, and poreless, bearing a stout conical apical horn and sometimes a reduced dorsal horn (Fig. 8.6). Apical spine incorporated into the cephalic wall before dividing into two mitral arches near the top of the cephalis. Collar stricture well defined externally by a sharp change in the shell contour. Thorax short, globular flattened to inflated, thick-walled, and hyaline. The maximum thickness of the thoracic wall is reached in the middle part of the thorax, giving the thoracic wall a crescent appearance when viewed under a light microscope. Lumbar stricture marked by a slight constriction. Abdomen subcylindrical, sinuous and twice as long as the thorax. Abdominal pores subcircular, ariable in shape and size, scattered over the surface, or weakly aligned in longitudinal rows. Abdomen terminating in an undifferentiated margin.

Etymology.—From the Greek *hualinos*, meaning 'hyaline, transparent'.

Dimensions.—Based on 24 specimens (mean): total length without the apical horn: 112–159 µm (133 µm), length of cephalis without the apical horn: 19–26 µm (22 µm), length of apical horn: 32–47 µm (37 µm), length of thorax: 32–47 µm (37 µm), maximum breadth of thorax: 47–72 µm (54 µm), length of abdomen: 55–90 µm (74 µm).

Remarks.—The generic assignment of *Apoplanius hyalinus* n. sp. is based on its short, conical apical horn without three proximal arches, and its apical spine, which partially extends into the cephalic cavity as a columella (Sanfilippo and Caulet, 1998; O'Dogherty et al., 2021). *Apoplanius hyalinus* n. sp. differs from all other documented lophocyrtiid species in having a thick-walled hyaline thorax. *Apoplanius hyalinus* n. sp. shares many characteristics with *A. kerasperus* (Sanfilippo and Caulet, 1998) (Fig. 8.8), especially regarding the initial spicule, suggesting that the two species are closely related. The occurrence of relatively small and nearly poreless forms is recurrent in several Paleogene naselarian families. These hyaline species appear to be particularly abundant during the middle Eocene. They include the following taxa: *Lychnocanium trifolium* Riedel and Sanfilippo, 1971, and *L. continuum* Ehrenberg, 1874 (Lithochytrididae), *Calocyclas aphradia* Sanfilippo and Blome, 2001 (Theoperidae), *Theocorys anapographa* var. A Riedel and Sanfilippo, 1970 (Theocotylidae) and *Dendrospyris fragoides* Sanfilippo and Riedel, 1973 (Cephalospyrididae). Some of these species may be juveniles or aberrant forms belonging to species with a perforated skeleton; see, for example, *T. anapographa* var. A, which always occurs with typical *T. anapographa* (e.g., Sanfilippo and Blome, 2001; Meunier and Danelian, 2022).

Family Theocotylidae Petrushevskaya, 1981
Genus *Thyrsocyrtis* Ehrenberg, 1847

Type species.—Thyrsocyrtis rhizodon Ehrenberg, 1874, p. 262 (unfigured); Ehrenberg, 1876, p. 84, pl. 12, fig. 1; subsequent designation by Campbell, 1954, p. D130.

Thyrsocyrtis kamikuri new species
Figure 8.9–8.12

2015 *Thyrsocyrtis* sp. D; Kamikuri, pl. 5, figs. 1a–2b.
2020 *Thyrsocyrtis* sp. D; Hollis et al., pl. 11, fig. 22a–c.

Holotype.—Figure 8.9; collection number USTL 4563-1; coordinates B34/3; sample ODP 171B-1051A-9H-2W, 53–55 cm; *Podocyrtis* (*L.*) *chalara* Zone (RP15; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.—Thyrsocyrtis species with an inflated abdomen perforated by pores of the same diameter as those of the thorax, and three short, perforated feet.

Occurrence.—*Thyrsocyrtis kamikuri* n. sp. occurs sporadically throughout the studied interval, from the upper part of the *Podocyrtis* (*L.*) *mitra* Zone (RP14) to the lower part of the *Podocyrtis* (*L.*) *goetheana* Zone (RP16).

Description.—Shell composed of three segments, conical to campanulate. Cephalis small, hemispherical, sparsely perforated, and bearing a stout, bladed apical horn. Collar stricture moderately expressed. Thorax campanulate, perforated by subcircular pores of variable sizes, the largest being in the middle part of the segment. Thoracic surface sometimes slightly thorny. Lumbar stricture marked externally by a constriction and a thin internal ridge. Abdomen inflated to truncate conical, wider and longer than the thorax, with 8–10 pores on half-circumference. Abdominal pores subcircular to ovoid, of variable size but usually twice as wide as the thoracic ones. Thoracic and abdominal pores quincuncially arranged, and usually hexagonally framed. Peristome differentiated, widely open. Three short feet arising above the peristome, subparallel to divergent, and perforated by small subcircular pores.

Etymology.—*Thyrsocyrtis kamikuri* n. sp. is named in honor of Dr. Shin-ichi Kamikuri (Ibaraki University, Japan) who first illustrated this species.

Dimensions.—Based on 17 specimens (mean): total length without the apical horn: 161–228 µm (194 µm), length of apical horn: 13–55 µm (45 µm), length of cephalis without the apical horn: 20–29 µm (24 µm), length of thorax: 41–75 µm (63 µm), maximum breadth of thorax: 90–125 µm (102 µm), length of abdomen: 76–138 µm (106 µm), maximum breadth of abdomen: 114–193 µm (153 µm), length of feet: 34–70 µm (56 µm).

Remarks.—*Thyrsocyrtis kamikuri* n. sp. differs from *T. lochites* (Sanfilippo and Riedel, 1982), *T. orthotenes* Nigrini, Sanfilippo, and Moore, 2005, *T. tetracantha* (Ehrenberg, 1874), and *T. triacantha* (Ehrenberg, 1874) in having abdominal pores less than twice the size of thoracic pores and three short, perforated feet. The new species differs from *T. hirsuta* (Krasheninnikov, 1960), *T. rhizodon* (Ehrenberg, 1874), and *T. tarsipes* Foreman, 1973, in having an abdomen considerably wider than the thorax, and three short, usually divergent feet without distal enlargement. *Thyrsocyrtis kamikuri* n. sp. also differs from *T. norrisi* Sanfilippo and Blome, 2001, in not having a flared peristome and an unserrated apical horn. Finally, *Thyrsocyrtis kamikuri* n. sp. is distinguished from *Dictyopodium oxylophus* Ehrenberg, 1874, in having a campanulate thorax, a relatively larger cephalis that is not partially embedded in the thorax, and no tubular latticed feet.

Conclusion

Examination of the middle Eocene radiolarian fauna recovered from ODP Site 1051 resulted in the description of 21 new species, including three spumellarians and 18 nassellarians. We also took advantage of the richness of this material to re-describe and illustrate the morphological variability of the poorly known rhopalosyringiid species *Pterocyrtidium zitteli* Bütschli, 1882a.

Most of the new species described here are abundant throughout the studied interval and can thus be found in almost all the samples. Fourteen bioevents were recorded: these include the first occurrences of *Albatrossidium messiaeni* n. sp., *Botryocella* ? *alectrida* n. sp., *Ceratocyrtis oconnori* n. sp., *Cryptocarpium*? *judoka* n. sp., *Elaphospyris quadricornis* n. sp., *Eucyrtidium granatum* n. sp. and *Periphaena petrushevskayae* n. sp., and the last occurrences of *Apoplanius cryptodirus* n. sp., *A. hyalinus* n. sp., *Ceratocyrtis oconnori* n. sp., *Elaphospyris cordiformis* n. sp., *Lychnocanium croizoni* n. sp., *Spirocyrtis matsuokai* n. sp. and *Stylodictya oligodonta* n. sp. These species might prove to be useful in the future to improve the stratigraphic resolution of the subtropical Atlantic Ocean, where many biostratigraphically relevant species that define the tropical radiolarian biozonation are missing or have different ranges compared to the tropics (Sanfilippo and Blome, 2001).

With the exception of *Periphaena petrushevskayae* n. sp., which was observed at Demerara Rise (DSDP Site 144; Petrushevskaya and Kozlova, 1972), *Dictyoprora echidna* n. sp. and *Lychnocanium cingulatum* n. sp., which were recovered from the Yucatan Shelf (DSDP Site 94; Foreman, 1973; Sanfilippo and Riedel, 1973), *Thyrsocyrtis kamikuri* n. sp., which was found in the Caledonian Basin (DSDP Site 206C; Hollis et al., 2020), and *Lychnocanium cheni* n. sp., which is known from the Naturaliste Plateau (DSDP Site 264), the new species described here have never been reported elsewhere. For some species, such as *Botryocella*? *alectrida* n. sp. or *Pylobotrys*? *bineti* n. sp., the lack of previous mention may be due to their relative scarcity in the fossil record. On the other hand, the absence in the literature of abundant and easily identifiable species, such as *Albatrossidium messiaeni* n. sp. or *Apoplanius hyalinus* n. sp., suggests that the geographic range of these species is relatively limited. These results highlight the potential interest of these species for future paleoceanographic and paleoenvironmental studies.

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Declaration of competing interests

The authors declare they have no conflict of interest.

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