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Biodiversity, biostratigraphy, disparity and macroecology of middle Eocene radiolarians (Rhizaria). Insights into their biotic response to the Middle Eocene Climatic Optimum (MECO).

Biodiversité, biostratigraphie, disparité et macroécologie des radiolaires (Rhizaria) de l'Éocène moyen. Aperçu de leur réponse biotique à l'Optimum Climatique de l'Éocène Moyen (MECO).

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Membres du jury :

Špela Goričan ZRC SAZU, Ljubljana, Slovénie	PR	Rapporteuse
Robert Speijer KU Leuven, Belgique	PR	Rapporteur
Catherine Crônier Université de Lille, France	PR	Examinatrice,
		Présidente du jury
Delphine Desmares Sorbonne Université, Paris, France	MCF	Examinatrice
Jakub Witkowski Université de Szczecin, Pologne	MCF	Examinateur
Taniel DanelianUniversité de Lille, France	PR	Directeur de thèse

Université de Lille UMR CNRS 8198 Evo-Eco-Paléo Bâtiment SN5 54 Avenue Paul Langevin Cité Scientifique 59650 Villeneuve-d'Ascq cedex France

Ah ! pauvre père ! auras-tu jamais deviné quel amour tu as mis en moi Et combien à travers toi j'aime toutes les choses de la terre ?

René Guy Cadou – Tout amour, 1951.

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Chapter I – Introduction

I.1. Rationale

Radiolarians are marine zooplankton, known to be major contributors to oceanic ecosystems and geochemical cycles. They left an abundant and detailed fossil record through the Cenozoic, which is conducive to biostratigraphic and paleoceanographic studies. These extensive geological archives also give a unique opportunity to understand the long-term evolution of plankton and to decipher the impact of past environmental changes on the biosphere. In a world threatened by global changes induced by human activities, it is indeed of paramount importance to characterize how biological systems respond to environmental perturbations in order to better anticipate future upheavals. In this respect, the middle Eocene (ca. 48–38 Ma) is of particular interest, as it represents a critical period in the evolution of the Cenozoic climate system. The general long-term cooling trend that characterized this geological interval was interrupted by several episodes of global warming, the most important of which being the Middle Eocene Climatic Optimum (MECO). This hyperthermal event occurred around 40 Ma and was related to perturbations of the carbon cycle similar to the present-day anthropogenic global warming, making it one of the best deep-time analogs for near-future climates (Burke et al., 2018).

Despite this promising research framework, Eocene radiolarian climate sensitivity is still poorly understood. Indeed, a substantial part of the middle Eocene radiolarian diversity preserved in the fossil record is still not formally described, hindering any accurate depiction of the biotic changes induced by the MECO warming. The first step of this study was therefore to improve the taxonomic resolution of middle Eocene radiolarians by reexamining and documenting at the species level two remarkable radiolarian assemblages preserved in oceanic sediments from ODP Site 1260 (western equatorial Atlantic) and ODP Site 1051 (western subtropical Atlantic). Based on this robust taxonomical framework, radiolarian paleodiversity dynamics and morphological disparity were then examined across the MECO interval, and compared with the established paleoclimatic proxies, to grasp the long-term macroecological impact of climate change on radiolarians.

I.2. Polycystine radiolarians: a biological proxy to deep time

Radiolarians are planktic single-celled eukaryotes, measuring from tens to hundreds of micrometers, although some species are known to form gelatinous colonies up to over 1 m in length (Boltovskoy et al., 2017). These protists are widely distributed in the world's oceans, from the subsurface down to the bathypelagic zone (Suzuki and Not, 2015; Boltovskoy and Correa, 2016). Radiolarian biogeography and abundance are controlled by ocean productivity and nutrient availability, as well as by the physical properties of the water masses, such as temperature and salinity (Boltovskoy, 2017a, 2017b; Boltovskoy et al., 2017). They feed on a large variety of prey, including phytoplankton, bacteria, and crustacean larvae (Anderson, 1978; Matsuoka, 2007), but numerous species are mixotrophs through symbiosis with intracellular eukaryotic microalgae or bacteria (Matsuoka and Anderson, 1992).

From a phylogenetic point of view, radiolarians are classified amongst the infrakingdom Rhizaria, a large group of amoeboid, mostly heterotrophic protists (Cavalier-Smith et al., 2018). With the foraminifera, they form a monophyletic taxon named Retaria, characterized by a peculiar feeding apparatus composed of reticulose (net-like) pseudopodia (Cavalier-Smith et al., 2018). With the exception of acantharians, whose internal skeleton is made of strontium sulfate mineral (Suzuki and Aita, 2011; Decelle and Not, 2015), most of the radiolarian species bear a morphologically complex skeleton of amorphous opaline silica (Anderson, 1983). They are thus deeply involved in the biogeochemical cycles of silica (De Wever et al., 2001; Llopis Monferrer et al., 2020), and their skeletons are commonly preserved in marine sediments. This vast fossil record, stretching back to the early Cambrian (Obut and Iwata, 2000; Pouille et al., 2011; Aitchison et al., 2017), offers advantages for paleoceanographic studies and for dating and correlating siliceous-bearing strata (De Wever et al., 2001).

After the description by Ehrenberg (1839) of the first fossil radiolarian species, Eocene radiolarians were amongst the first to receive sustained attention from micropaleontologists. A total of ~500 Eocene radiolarian species have been described during the nineteenth century from siliceous-rich chalk beds cropping on Barbados Island (Ehrenberg, 1846; 1847; 1874, 1876; Bury, 1862; Bütschli, 1882a, 1882b; Haeckel, 1887; Carter, 1893, 1895, 1896a, 1896b, 1896c, 1896d, 1896e; Sutton, 1896a, 1896b, 1896c, 1896d). However, many of these species have never been observed since their original description, and there are still uncertainties about their stratigraphic range and the precise extent of their intraspecific morphological disparity (Ogane et al., 2009). These taxa strongly deserve to be re-described and re-illustrated to be included in modern radiolarian studies.

In his classic monograph, Haeckel (1887) also introduced the first comprehensive supraspecific classification of Cenozoic radiolarians. However, this first attempt to classify radiolarians was mainly based on external characteristics and geometry rather than biological concepts. This artificial classification led to profound misconceptions about radiolarian evolution, the consequence of which was to consider radiolarians as displaying a high level of evolutionary conservatism, depriving them of any biostratigraphic value. (Danelian et al., 2017). This partly explains the relative paucity of taxonomic work published on Eocene radiolarians during the first half of the 20th century (e.g., Brandt, 1935; Clark and Campbell, 1942, 1945) and the general lack of interest in fossil radiolarian studies during this time interval (Danelian et al., 2017).

The subsequent development of scientific ocean drilling campaigns during the 1960s and 1970s has led to a renewal of interest in Cenozoic radiolarians. The increased recovery of sediments from deep marine environments allowed extensive studies of radiolarian assemblages from all oceanic basins and resulted in the establishment of the first tropical radiolarian biozonation for the Cenozoic (Riedel and Sanfilippo, 1970; Sanfilippo et al., 1985). The accumulation of fossil material has also favored the description of new species and the redescription, according to modern taxonomic standards, of numerous taxa published in early radiolarian studies (e.g., Riedel and Sanfilippo, 1970, 1971, 1978; Petrushevskaya and Kozlova, 1972; Foreman, 1973; Sanfilippo and Riedel, 1973). A few emblematic nassellarian families have also been the subject of detailed taxonomic investigations, leading to the establishment of several evolutionary lineages (e.g., Nigrini, 1977; Sanfilippo and Riedel, 1982, 1992; Sanfilippo and Caulet, 1998). However, the main goal of most of these studies was biostratigraphy, and little attention was paid to rare morphotypes of no biostratigraphic value, or those belonging to taxonomically challenging families. Finally, in spite of their undeniable importance in fossil plankton assemblages, a substantial part of the radiolarian diversity preserved in the fossil record is still not formally described and documented, hindering the expression of their full biostratigraphic and paleoceanographic potential.

I.3. Paleoclimatic context of the study

The Eocene (56–34 Ma) is a pivotal time for the understanding of global changes in Cenozoic climate system (Figure I.1). After the Early Eocene Climatic Optimum (ca. 56–47 Ma; Lourens et al., 2005; Stap et al., 2010; Sexton et al., 2011), during which global temperatures were more than 10°C higher than they are today, the Earth underwent a long-term gradual cooling that culminated in a shift to coolhouse conditions around the Eocene-Oligocene boundary (ca. 34 Ma; Zachos et al., 2008; Westerhold et al., 2020; Hutchinson et al., 2021). This transitional interval was characterized by significant polar glaciation by the early Oligocene, with the formation of nascent ice-sheet in eastern Antarctica (Miller et al., 1987; Zachos et al., 1996; Coxall et al., 2005; Scher et al., 2014).



Chapter I – Introduction

Figure I.1. Variation of geochemical proxies across the Paleogene (66–23 Ma). Stable isotope data and magnetostratigraphy are from Westerhold et al. (2020). Absolute ages for epochs and stages follow Gradstein et al. (2012). Abbreviations: Bar, Bartonian; Cha, Chattian; Dan, Danian; Lut, Lutetian; Oi-1, the first major glacial period in the Oligocene; Pri, Priabonian; Rup, Rupelian; Sel, Selandian; Tha, Thanetian; Ypr, Ypresian.

The middle–late Eocene cooling trend was interrupted by a global warming event and carbon cycle perturbation known as the Middle Eocene Climatic Optimum (MECO; Bohaty and Zachos, 2003; Bohaty et al., 2009; Westerhold and Röhl, 2013). The MECO occurred

during the early Bartonian, between 40.45 and 40.05 Ma, and lasted ~400 kyr (Westerhold and Röhl, 2013). It has been recognized in the isotopic record of many marine and continental sections (Figure I.2) as a steady decline of ~1.0–1.5‰ in the oxygen isotope (δ^{18} O) values of both benthic foraminifer and bulk sediments, interpreted as a rise of ~4–6°C in seawater temperature (Bohaty and Zachos, 2003; Bohaty et al., 2009; Bijl et al., 2010).



Figure I.2. Actual position of drill sites and sections on land where the Middle Eocene Climatic Optimum (MECO) has been described.

The warmest interval of the MECO is marked by a sharp decrease in δ^{18} O values at ca. 40 Ma (Westerhold and Röhl, 2013) and is accompanied at some sites by a weak negative excursion (~0.05‰) in carbon isotope (δ^{13} C) values (Giorgioni et al., 2019). The peak warming phase of the MECO lasted less than 100 kyr and was followed by a rapid return to pre-event baseline temperatures (Bohaty et al., 2009; Edgar et al., 2010; Westerhold and Röhl, 2013). The MECO differs from other Paleogene hyperthermal events, such as the Paleocene-Eocene Thermal Maximum (PETM; Kennett and Stott, 1991), by its relatively long duration, the abruptness of its return to pre-event conditions, and the spatial inconsistency of its carbon isotope signature (Giorgioni et al., 2019; Henehan et al., 2020). All these peculiar features make the MECO difficult to interpret, and thus, the actual triggering mechanism of this event still remains poorly understood. Modeling of the carbon cycle suggests an imbalance in long-term carbon fluxes, resulting in an increase of carbon dioxide emissions in the ocean-atmosphere system, which in turn induced ocean acidification through the entire water column and a shoaling of the carbonate saturation profile (Edgar et al., 2007; Bohaty et al., 2009; Sluijs et al., 2013; Cornaggia et al., 2020; Henehan et al., 2020). A favorable orbital configuration, due to a very long eccentricity cycle minimum, has also been put forward to explain the rise of the MECO (Henehan et al., 2020).

The impact of the MECO on oceanic plankton and benthic foraminifera has been extensively studied over the past decade. Significant assemblage changes across the MECO have been shown to occur in the fossil record of several microfossil groups, including planktic and benthic foraminifera (Boscolo Galazzo et al., 2013, 2015; D'Onofrio et al., 2021; Edgar et al., 2013; Luciani et al., 2010; Moebius et al., 2014, 2015), calcareous nannoplankton (Villa et al., 2008; Toffanin et al., 2011), dinocysts (Bijl et al., 2010; Cramwinckel et al., 2019), diatoms (Renaudie et al., 2010; Witkowski et al., 2014) and ebridians (Witkowski et al., 2012). These changes mainly affect the relative abundance and the geographical distribution of species (Lowery et al., 2020). No prominent faunal turnover was observed in any group, suggesting that the magnitude of perturbation of planktic communities reached during the MECO warming did not exceed the threshold to drive extinction. There is also evidence for symbiont 'bleaching' in planktic foraminifera induced by the MECO warming, associated with a reduction in average test size (Edgar et al., 2013). However, it is not yet possible to give a general picture of the impact of this warming event on planktic organisms because the available data have a sporadic geographical and bathymetric distribution, and because of irreconcilable discrepancies in

paleoproductivity reconstitutions depending on location and studied taxonomic groups (Cramwinckel et al., 2019; Moebius et al., 2015).

Although radiolarians are amongst the major groups of marine plankton, relatively few studies have been conducted on their climate sensitivity and diversity changes in response to the MECO. The MECO warming is known to be associated with an increase in accumulation rates of siliceous plankton (including radiolarians) in the Southern Ocean (Witkowski et al., 2012) and North Atlantic (Witkowski et al., 2014). However, in these two studies, radiolarians were not considered at the species level, hindering any precise interpretation of assemblage changes. Only two species-level radiolarian studies have been conducted previously in relation to the MECO. The first investigated early to middle Eocene radiolarian assemblages from the equatorial Pacific Ocean (IODP Site U1331) and showed a transient decrease in cool-water radiolarian species across the MECO interval (Kamikuri et al., 2013). The second study was carried out on radiolarian-rich sequences from the southwest Pacific Ocean (DSDP Site 277, Campbell Plateau) and highlighted the poleward migration of several tropical radiolarian species to the high latitudes during the MECO (Pascher et al., 2015). However, very few stratigraphic levels were investigated in these studies, and the biodiversity survey was limited to abundant or biostratigraphically important species, which represent only a minute fraction of the total radiolarian fauna.

I.4. Provenance of the studied material

This study is based on chalk samples obtained from archived ocean sediment cores from the low- to mid-latitude North Atlantic Ocean. Two sites were investigated: ODP Site 1260 (western equatorial Atlantic) and ODP Site 1051 (western North Atlantic; Figure I.3).



Figure I.3. Middle Eocene (ca. 40 Ma) paleogeographic map showing the location of ODP Site 1051 (Blake Nose, Leg 171B) and ODP Site 1260 (Demerara Rise, Leg 207). Paleogeographic reconstruction drawn after ODSN Plate Tectonic Reconstruction Service (http://www.odsn.de/odsn/services/paleomap/paleomap.html, last access: 31 July 2023).

I.4.1. ODP Site 1260 (western equatorial Atlantic)

ODP Site 1260 (9°16'N, 54°32'W) lies on the north-western margin of Demerara Rise, a submarine plateau stretching along the coast of Surinam and French Guiana (Figure I.3). This site is inferred to have been closer to the equator during the middle Eocene than today, with a paleolatitude of ~1°N (Suganuma and Ogg, 2006). Two holes (1260A and 1260B) were drilled at a modern water depth of 2,549 m below sea level, allowing the recovery of an expanded and nearly continuous Albian–Oligocene sequence (Shipboard Party, 2004). The middle Eocene interval of the site is characterized by nannofossil chalk enriched in biogenic silica, with abundant and diverse radiolarian assemblages (Danelian et al., 2005, 2007), and several other siliceous microfossil groups, including diatoms (Renaudie et al., 2010), ebridians, silicoflagellates and sponge spicules (Figure I.4.A).

Age control for ODP Site 1260 was formerly provided by biostratigraphy (Shipboard Party, 2004) and magnetostratigraphy (Suganuma and Ogg, 2006). However, a high-resolution astronomical framework based on iron (Fe) intensity data was subsequently developed for this site (Westerhold and Röhl, 2013). The orbitally tuned interval corresponds to a 97.26 m thick sequence accumulated between 39.81 and 44 Ma, during the late Lutetian/early Bartonian

(sedimentation rate evaluated at ~2.5 cm/kyr). Astrochronological calibration is available every 2 cm of sediment and allows each stratigraphic level to be dated with a high accuracy. For older parts of the radiolarian-rich interval (from 44 Ma to ~44.8 Ma), age-depth models based on magneto-biostratigraphy were used to estimate the age of the samples (Shipboard Party, 2004).

The geochemical framework of ODP Site 1260 is also well-established for the late middle Eocene interval. Notable shifts correlated with the MECO event were recorded in both stable oxygen (δ^{18} O) and carbon (δ^{13} C) isotope records (Bohaty et al., 2009; Edgar et al., 2007). At this site, the onset of the MECO is located around 52 rmcd, in the upper part of magnetochron C18r (Edgar et al., 2007), the benthic foraminiferal δ^{18} O values subsequently decreased (~1.0 ‰) to reach a minimum during the peak warming interval around 44 rmcd (Edgar et al., 2007; Westerhold and Röhl, 2013). It is noteworthy that the warmest interval of the MECO is also marked at this site by a negative excursion (~0.5‰) in foraminiferal benthic δ^{13} C values (Edgar et al., 2007). As is usual for this event, the peak warming was followed by a rapid return to preevent baseline conditions (Bohaty et al., 2009; Edgar et al., 2010; Westerhold and Röhl, 2013). Orbital calibration places the onset of the MECO at 40.50 ± 0.02 Ma, the peak-warming at 40.07 ± 0.02 Ma, and the end of the MECO at 40.05 ± 0.02 Ma (Westerhold and Röhl, 2013).

At ODP Site 1260 we focused on the richest radiolarian interval; a ~147 m-thick sequence ranging from the base of core 20R (~185 rmcd) to the top of core 6R (38.2 rmcd). The base of this sequence lies in the uppermost part of the *Dictyoprora mongolfieri* Zone (RP11; Shipboard Party, 2004), just before the first occurrence of the theoperid species *Eusyringium lagena* (Ehrenberg), which is dated 44.8 Ma in the equatorial Pacific (Kamikuri et al., 2012a). The top of the studied sequence corresponds to the lower part of the *Podocyrtis* (*L*.) *goetheana* Zone (RP16; Shipboard party, 2004), orbitally calibrated at 39.41 Ma (Westerhold and Röhl, 2013).

A. ODP Site 1260







Figure I.4. Summary of lithology, magnetostratigraphy, and biostratigraphy of the middle Eocene interval from **A.** ODP Site 1260 (Demerara Rise, Leg 207) and **B.** ODP Site 1051 (Blake Nose, Leg 171B). The lithologic column of ODP Site 1260 is based on data from the Shipboard Party (2004), magnetostratigraphy follows Suganuma and Ogg (2006), and biozonations are after the Shipboard Party (2004), except for radiolarian biozones, which were refined by Meunier and Danelian (2022). Lithologic column of ODP Site 1051 is based on data from Norris et al. (1998), magnetostratigraphy follows Ogg and Bardot (2001), radiolarian biostratigraphy is after Sanfilippo and Blome (2001), calcareous nannofossil biostratigraphy is from Mita (2001) and planktic foraminifera biostratigraphy follows Norris et al. (1998) and Edgar et al. (2010). Abbreviations: mcd, meters composite depth; Nanno., calcareous nannofossils; Foram., planktic foraminifera; Rad., radiolarians.

I.4.2. ODP Site 1051 (western North Atlantic)

ODP Leg 171B drilled five sites on a depth transect across the Blake Nose, a submerged promontory extending on the edge of the Blake Plateau, in the western North Atlantic Ocean (Norris et al., 1998; Figure I.3). ODP Site 1051 (30°03'N, 76°21'W) is located midway along the Blake Nose transect, at an intermediate point in the bathymetric slope profile. Two adjacent holes (1051A and 1051B) were drilled at this site at a modern water depth of ca. 1983 m below sea floor (mbsf; Norris et al., 1998). Hole 1051A was drilled to a depth of 644.6 mbsf, and Hole 1051B was drilled to 526.6 mbsf, providing an expanded and nearly continuous 630 m-thick Paleogene sequence.

The middle Eocene interval of ODP Site 1051 (~370 m-thick) contains mainly oozes and chalks rich in siliceous microfossils, including abundant radiolarians, diatoms and sponge spicules, and a few rare ebridians, silicoflagellates and endoskeletal dinoflagellates (Norris et al., 1998; Sanfilippo and Blome, 2001; Witkowski et al., 2014). The estimated sedimentation rate is ~4 cm/kyr for the middle Eocene sequence of the site (Norris et al., 1998; Edgar et al., 2010), at a paleo-water depth of 1000–2000 m below sea level (lower bathyal; Norris et al., 1998) and at a palaeolatitude of ~25°N (Ogg and Bardot, 2001). Age control for the middle Eocene interval of ODP Site 1051 is provided by biostratigraphy (Norris et al., 1998; Mita, 2001; Sanfilippo and Blome, 2001; Edgar et al., 2010) and magnetostratigraphy (Ogg and Bardot, 2001). The age-depth models of all Leg 171B sites have recently been updated by Witkowski et al. (2020).

At ODP Site 1051, the MECO is well-defined in stable δ^{13} C and δ^{18} O isotope records (Bohaty et al., 2009; Edgar et al., 2010). The onset of the MECO occurs in the upper part of magnetochron C18r, around 118 mcd (Edgar et al., 2010). Then, the benthic foraminiferal δ^{18} O record gradually decreased, reaching a transient minimum ca. 86 mcd, which also coincides with an abrupt decrease in δ^{13} C values (Bohaty et al., 2009; Edgar et al., 2010). This minimum is interpreted as the peak warming conditions of the MECO.

The studied sequence at ODP Site 1051 corresponds to the richest and most diverse radiolarian interval, which spans cores 2H to 18X (12.73–174.28 mcd) and was accumulated between 42.7 and 38.53 Ma (Witkowski et al., 2020). The base of the studied sequence lies in the lower part of the *Podocyrtis (L.) mitra* Zone (RP14), and the upper part of the sequence corresponds to the upper part of the *Podocyrtis (L.) goetheana* Zone (RP16) (Sanfilippo and Blome, 2001; Figure I.4.B)

I.5. Objectives and thesis structure

The main objectives of this thesis are to quantify the evolution of the taxonomic diversity and morphological disparity of middle Eocene radiolarians across the MECO interval. Diversity and biometric data will be compared with established paleoclimatic proxies to disentangle the long-term macroecological impact of climate change on radiolarian communities.

Chapter II presents the catalog of radiolarian species encountered in the middle Eocene interval from ODP Site 1260 (western equatorial Atlantic) and ODP Site 1051 (western North Atlantic). Unknown morphotypes are not illustrated, only the species already described by

previous workers are presented. This biodiversity survey is a necessary prerequisite for the subsequent studies that are presented in Chapters III and IV. Chapter II also contains a contribution to the description of Paleogene radiolarian diversity in the form of two taxonomic articles. This clarification of the middle Eocene radiolarian taxonomic framework also provided an opportunity to conduct a detailed biostratigraphic analysis at ODP Site 1260, which is presented in Chapter III. Our objective was to provide precise calibrations of radiolarian bioevents based on the exceptional cyclostratigraphic framework developed at this site and to assess the reliability of the late middle Eocene radiolarian biozonation by comparing our results with the equatorial Pacific record.

Chapter IV is at the heart of this research project. It is divided into two parts: the first part presents the whole fauna quantitative analysis carried out at ODP Site 1051, which answers these questions: 1 - What are the radiolarian diversity patterns during the MECO? Has global warming led to species turnover/extinction? 2 - Are radiolarian assemblages becoming unstable (e.g., dominance of one or a few species) during the MECO? How do the relative abundances of species vary? 3 - How did climatic and oceanographic changes affect the distribution of fossil radiolarian species? Are cool-water species disappearing during the warmest interval of the MECO? Are tropical species extending their range to higher latitudes? The second part of Chapter IV concerns the impact of the MECO on the morphological disparity of radiolarian shells. This time, the study was focused on a single nassellarian species (*Podocyrtis papalis* Ehrenberg). These questions drive this part of the thesis: 1 - How did the MECO affect the morphological disparity of *Podocyrtis papalis*? 2 - Are periods of increased morphological disparity correlated with periods of rapid environmental change?

Chapter II – Progress on middle Eocene tropical and subtropical radiolarian biodiversity

II.1. Introduction

This taxonomic chapter is divided into two subchapters. First, subchapter **II.2 Systematic paleontology** presents the complete list of all middle Eocene radiolarian species observed during our investigations at ODP Sites 1260 and 1051. A total of 245 taxa are documented from the early Lutetian to the middle Bartonian. This list concerns only the morphospecies that have already been described by previous workers, and for each of them, we provide an image and an exhaustive list of references.

The biodiversity survey conducted at these two sites resulted in the identification of numerous unknown morphotypes that may represent new radiolarian morphospecies. In an effort to improve the taxonomic resolution of the middle Eocene radiolarians, 36 of these unknown morphotypes have been formally described in two papers, which are reproduced as subchapter **II.3. New radiolarian species from ODP Site 1260 (western equatorial Atlantic)** and **ODP Site 1051 (western North Atlantic)**. We report the discovery of 15 new nassellarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and 17 nassellarian and four spumellarian species from ODP Site 1051 (Blake Nose, western subtropical Atlantic).

II.2. Systematic paleontology

The supra-generic classification used here is adapted from Riedel (1967a, 1967b), De Wever et

al. (2001), and Suzuki et al. (2021).

Infrakingdom Rhizaria Cavalier-Smith, 2002 emend. Cavalier-Smith, 2003 Phylum Retaria Cavalier-Smith, 1999 Class Polycystinea Ehrenberg, 1839 Order Spumellaria Ehrenberg, 1876 Superfamily Hexacromyoidea Haeckel, 1882 Family Hexacaryidae Haeckel, 1882 Genus *Hexancistra* Haeckel, 1879 *Type species.— Hexancistra quadricuspis* Haeckel, 1879, p. 705, pl. 16, fig. 2.

> ? *Hexancistra tricuspis* Haeckel, 1887 Plate II.1, Figure 1

1887 *Hexancistra (Hexancora) tricuspis* Haeckel, p. 188, pl. 22, fig. 9.
? 1973 *Astrosphaerin* sp. E Sanfilippo and Riedel, pl. 6, figs. 3, 4 (part).
Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Superfamily Lithocyclioidea Ehrenberg, 1846 Family Lithocycliidae Ehrenberg, 1846 Genus *Lithocyclia* Ehrenberg, 1846 *Type species.— Lithocyclia ocellus* Ehrenberg, 1854a, pl. 36, fig. 30.

Lithocyclia aristotelis (Ehrenberg, 1847) group

Plate II.1, Figures 4, 5

1847 Astromma Aristotelis [sic] Ehrenberg, p. 55, fig. 10.

1854a Hymeniastrum Pythagorae [sic] Ehrenberg, pl. 36, fig. 31.

1862 Hymeniastrum Pythagorae [sic] Ehrenberg – Haeckel, p. 490.

1862 Astromma Aristoteles [sic] Ehrenberg – Bury, pl. 4, fig. 2, pl. 14, figs. 2, 3 (part).

1862 Astromma ? Bury, pl. 15, figs. 5, 6 (part).

1873a Astromma Pythagorae [sic] Ehrenberg, p. 301.

1873b Astromma Pythagorae [sic] Ehrenberg - Ehrenberg, p. 284.

1874 Astromma Aristotelis [sic] Ehrenberg – Ehrenberg, p. 217.

1874 Astromma Pytagorae [sic] Ehrenberg – Ehrenberg, p. 217.

1876 Astromma Pythagorae [sic] Ehrenberg – Ehrenberg, p. 66, pl. 30, fig. 2.

1876 Astromma Aristotelis [sic] Ehrenberg – Ehrenberg, p. 66, pl. 30, figs. 3, 4.

1876 Hymeniastrum Pythagorae [sic] Ehrenberg – Ehrenberg, p. 76, pl. 30, fig. 5.

1882b Actinomma Aristotelis [sic] (Ehrenberg) - Bütschli, pl. 23, fig. 10.

1882b Hymeniastrum Pythagorae [sic] Ehrenberg - Bütschli, pl. 23, fig. 11.

- 1887 Trigonactura (Trigonacturium) pythagoræ [sic] (Ehrenberg) Haeckel, p. 471.
- 1887 Hymenactura (Hymenacturium) pythagoræ [sic] (Ehrenberg) Haeckel, p. 474.
- 1887 Hymeniastrum (Hymenastrella) pythagoræ [sic] Ehrenberg Haeckel, p. 531.
- 1957a Trigonactura sp. Riedel, p. 258, pl. 63, fig. 1.
- 1970 Lithocyclia aristotelis (Ehrenberg) group Riedel and Sanfilippo, p. 522.
- 1971 Lithocyclia aristotelis (Ehrenberg) group Riedel and Sanfilippo, p. 1588, pl. 3A, figs.
 4, 5.
- 1971 Lithocyclia aristotelis (Ehrenberg) group Moore, p. 737, pl. 4, figs. 4, 5.
- 1972 Astractinium aristotelis (Ehrenberg) group Petrushevskaya and Kozlova, p. 524, pl. 16, figs. 1–5.
- 1972 *Trigonactinium pythagorae* (Ehrenberg) Petrushevskaya and Kozlova, p. 524, pl. 17, fig. 1.
- 1974 Lithocyclia aristotelis (Ehrenberg) group Nigrini, p. 1065, pl. 2A, fig. 7.
- 1974 Lithocyclia aristotelis (Ehrenberg) group Johnson, p. 545, pl. 5, figs. 13, 14.
- 1975 Lithocyclia aristotelis (Ehrenberg) group Ling, p. 725, pl. 3, figs. 7, 8.
- 1977 Lithocyclia aristotelis (Ehrenberg) group Riedel and Sanfilippo, pl. 10, figs. 2, 3.
- 1978 Lithocyclia aristotelis (Ehrenberg) group Riedel and Sanfilippo, p. 70, pl. 6, fig. 6.
- 1986 Lithocyclia aristotelis (Ehrenberg) group Riedel and Sanfilippo, pl. 2, figs. 23, 24.
- 2006 Lithocyclia aristotelis (Ehrenberg) group Funakawa et al., p. 41, pl. P14, figs. 3a-4b.
- 2009 Hymeniastrum pythagorae Ehrenberg Ogane et al., pl. 34, figs. 1a–1d.
- 2009 Astromma aristotelis Ehrenberg Ogane et al., pl. 70, figs. 4a–4c, pl. 71, figs. 1a–2b, 4a–4c, pl. 72, figs. 1a–2c, pl. 73, figs. 1a–1d.
- 2012 Lithocyclia aristotelis (Ehrenberg) group Moore and Kamikuri, p. 8, pl. P5, figs. 6, 9.
- 2012a Lithocyclia aristotelis (Ehrenberg) group Kamikuri et al., p. 102, pl. 1, fig. 10.
- 2015 Lithocyclia aristotelis (Ehrenberg) group Kamikuri, pl. 16, figs. 8–11.
- 2020 Lithocyclia aristotelis (Ehrenberg) Hollis et al., pl. 2, fig. 9.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Lithocyclia ocellus Ehrenberg, 1854a group

Plate II.1, Figures 2, 3

- 1854a Lithocyclia Ocellus [sic] Ehrenberg, pl. 36, fig. 30.
- 1874 Lithocyclia Ocellus [sic] Ehrenberg Ehrenberg, p. 240.
- 1874 Stylocyclia dimidiata Ehrenberg, p. 257.
- 1876 Lithocyclia Ocellus [sic] Ehrenberg Ehrenberg, pl. 29, fig. 3.
- 1876 Stylocyclia dimidiata Ehrenberg Ehrenberg, p. 84, pl. 29, fig. 4.
- 1882b Lithocyclia Ocellus [sic] Ehrenberg Bütschli, pl. 23, fig. 6.
- 1887 Lithocyclia ocellus Ehrenberg Haeckel, p. 460.
- 1887 Stylocyclia dimidiata Ehrenberg Haeckel, p. 462.
- 1970 Lithocyclia ocellus Ehrenberg group Cita et al., p. 401, pl. 1, fig. C.
- 1970 Lithocyclia ocellus Ehrenberg group Riedel and Sanfilippo, p. 522, pl. 5, figs. 1, 2.
- 1971 Lithocyclia ocellus Ehrenberg group Riedel and Sanfilippo, p. 1588, pl. 3A, fig. 6.
- 1972 Lithocyclia ocellus Ehrenberg Petrushevskaya and Kozlova, p. 523, pl. 15, figs. 1–2.

- 1973 Lithocyclia ocellus Ehrenberg group Sanfilippo and Riedel, p. 523, pl. 10, figs. 1, 2.
- 1973 Lithocyclia ocellus Ehrenberg group Riedel and Sanfilippo, p. 739, pl. 2, figs. 7, 8.
- 1974 Lithocyclia ocellus Ehrenberg group Nigrini, p. 1065, pl. 1D, figs. 3–6.
- 1975 Lithocyclia ocellus Ehrenberg group Ling, p. 725, pl. 3, fig. 10.
- 1977 Lithocyclia ocellus Ehrenberg group Riedel and Sanfilippo, pl. 6, fig. 12.
- 1978 Lithocyclia ocellus Ehrenberg group Weaver and Dinkelman, p. 869, pl. 11, fig. 1.
- 1978 Lithocyclia ocellus Ehrenberg group Riedel and Sanfilippo, p. 70, pl. 6, fig. 8.
- 1986 Lithocyclia ocellus Ehrenberg group Riedel and Sanfilippo, pl. 3, figs. 4, 5.
- 2000 Lithocyclia ocellus Ehrenberg group Nigrini and Sanfilippo, p. 73, pl. 2, figs. 14–17.
- 2009 Lithocyclia ocellus Ehrenberg Ogane et al., pl. 15, figs. 3a–3c, pl. 32, figs. 2a–3.
- 2009 *Stylodictya dimidiata* Ehrenberg Ogane et al., pl. 16, figs. 1a–2c, pl. 17, figs. 1a–3b, pl. 32, figs. 1a–1c.
- 2012 Lithocyclia ocellus Ehrenberg group Moore and Kamikuri, p. 8, pl. P6, fig. 2.
- 2012b Lithocyclia ocellus Ehrenberg group Kamikuri et al., p. 4, pl. P2, fig. 6.
- 2013 Lithocyclia ocellus Ehrenberg Kamikuri et al., pl. 1, fig. 11.
- 2017 Lithocyclia ocellus Ehrenberg de Souza et al., pl. 1, fig. 3.
- 2020 Lithocyclia ocellus Ehrenberg Hollis et al., pl. 2, fig. 10.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Heliostylus Haeckel, 1882

Type species.— Sethostylus (Heliostylus) dentatus Haeckel, 1887, p. 429, pl. 34, fig. 1.

Heliostylus ? helianthus (Ehrenberg, 1874)

Plate II.1, Figure 6

1874 Haliomma Helianthus [sic] Ehrenberg, p. 235.

1876 Haliomma Helianthus [sic] Ehrenberg – Ehrenberg, p. 74, pl. 27, fig. 1.

1887 Heliodiscus (Heliodiscetta) helianthus (Ehrenberg) – Haeckel, p. 446.

2009 Haliomma helianthus Ehrenberg – Ogane et al., pl. 15, figs. 1a–2d.

Remarks. This species is tentatively assigned to the genus *Heliostylus* based on its large, lenticular, hollow cortical shell with two polar primary beams and a serrated equatorial girdle. Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

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.

Periphaena decora Ehrenberg, 1874

Plate II.1, Figure 7

1874 Periphaena decora Ehrenberg, p. 246.

- 1876 Periphaena decora Ehrenberg Ehrenberg, p. 80, pl. 28, fig. 6.
- 1882b Periphaena decora Ehrenberg Bütschli, pl. 22, figs. 6a, 6b.
- 1887 Periphæna decora [sic] Ehrenberg Haeckel, p. 426.

- 1887 Periphæna cincta [sic] Haeckel, p. 426, pl. 33, fig. 4.
- 1957a Periphaena decora Ehrenberg Riedel, p. 258, pl. 62, fig. 1.
- 1972 Periphaena decora Ehrenberg Petrushevskaya and Kozlova, p. 523, pl. 14, figs. 1, 2.
- 1973 *Periphaena decora* Ehrenberg Sanfilippo and Riedel, p. 523, pl. 8, figs. 8–10, pl. 27, figs. 2–4 (part).
- 1974 Periphaena decora Ehrenberg Nigrini, p. 1065, pl. 1C, figs. 1, 2, 4, 6 (part).
- 1975 Periphaena decora Ehrenberg Ling, p. 725, pl. 3, fig. 1 (part).
- 1977 Periphaena decora Ehrenberg Riedel and Sanfilippo, pl. 6, fig. 9 (part).
- 1978 Periphaena decora Ehrenberg Weaver and Dinkelman, p. 873, pl. 11, fig. 5.
- 1992 Periphaena decora Ehrenberg Takemura, p. 743, pl. 6, fig. 8.
- 1995 Periphaena decora Ehrenberg Strong et al., p. 209, fig. 10J.
- 1999 Periphaena heliasteriscus (Clark and Campbell) Kozlova, p. 87, pl. 34, fig. 2 (part).
- 1999 *Periphaena picta* (Kozlova) Kozlova, p. 174, pl. 16, fig. 4, pl. 19, fig. 12, pl. 40, figs. 10, 12.
- 2001 Periphaena cincta Haeckel De Wever et al., p. 122, fig. 67.7.
- 2003 Periphaena decora Ehrenberg Sanfilippo and Fourtanier, p. 12, pl. P2, fig. 26.
- 2005 Periphaena decora Ehrenberg Funakawa and Nishi, p. 233, pl. 2, fig. 13.
- not 2020 *Periphaena decora* Ehrenberg Hollis et al., pl. 2, fig. 3.

2021 Periphaena decora Ehrenberg – de Souza et al., p. 15, pl. 1, fig. 5.

Remarks. This name is used only for specimens with a marginal girdle that is not spinous.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Periphaena delta Sanfilippo and Riedel, 1973

Plate II.1, Figure 8

- 1973 Periphaena delta Sanfilippo and Riedel, p. 523, pl. 8, figs. 11, 12, pl. 27, figs. 6, 7.
- 1974 Periphaena delta Sanfilippo and Riedel Nigrini, p. 1065, pl. 1C, fig. 7.
- 1977 Periphaena delta Sanfilippo and Riedel Riedel and Sanfilippo, pl. 5, fig. 12.
- 1978 Periphaena delta Sanfilippo and Riedel Riedel and Sanfilippo, p. 71, pl. 7, fig. 9.
- 1986 Periphaena delta Sanfilippo and Riedel Riedel and Sanfilippo, pl. 3, fig. 3.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Periphaena heliasteriscus (Clark and Campbell, 1942)

Plate II.1, Figure 9

- 1942 Heliodiscus (Heliodiscetta) heliasteriscus Clark and Campbell, p. 39, pl. 3, figs. 10, 11.
- 1958 Heliosestrum craspedotum Haeckel Göke, pl. 2, fig. 1.
- 1973 *Periphaena heliasteriscus* (Clark and Campbell) Riedel and Sanfilippo, p. 523, pl. 9, figs. 1–6, pl. 27, figs. 8, 9.
- 1975 Periphaena decora Ehrenberg Ling, p. 725, pl. 3, fig. 2 (part).
- 1976 Heliodiscus heliasteriscus Clark and Campbell Dzinoridze et al., pl. 24, fig. 9.
- 1976 Heliodiscus perplexus Clark and Campbell Dzinoridze et al., pl. 24, fig. 8.
- not 1993 Heliodiscus heliasteriscus Clark and Campbell Vitukhin, pl. 7, fig. 1.
- 1995 Periphaena heliasteriscus (Clark and Campbell) Strong et al., p. 209, figs. 10H, 10I.

- 1999a Periphaena heliasteriscus (Clark and Campbell) O'Connor, p. 34, pl. 10, fig. 17.
- 1999 Periphaena heliasteriscus (Clark and Campbell) Kozlova, p. 87, pl. 34, figs. 11, 12, pl. 40, fig. 4 (part).
- 2008 Periphaena heliasteriscus (Clark and Campbell) Jackett et al., p. 57, pl. 4, fig. 14.
- 2009b Heliodiscus perplexus Clark and Campbell Suzuki et al., p. 247, pl. 3, fig. 11.
- 2015 Heliodiscus heliasteriscus Clark and Campbell Kamikuri, pl. 16, fig. 2.
- 2020 Periphaena heliasteriscus (Clark and Campbell) Hollis et al., pl. 2, fig. 4.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Periphaena humboldtii (Ehrenberg, 1847)

Plate II.1, Figure 10

- 1847 Haliomma Humboldtii [sic] Ehrenberg, p. 55, fig. 8.
- 1854a Haliomma Humboldtii [sic] Ehrenberg Ehrenberg, pl. 36, fig. 27.
- 1862 Heliodiscus humboldti [sic] (Ehrenberg) Haeckel, p. 438.
- 1876 Haliomma Humboldtii [sic] Ehrenberg Ehrenberg, p. 74, pl. 27, fig. 3.
- 1887 Heliodiscus (Heliodiscomma) cingillum Haeckel, p. 448, pl. 33, fig. 7.
- 1887 Heliodiscus (Heliodiscomma) humboldti [sic] (Ehrenberg) Haeckel, p. 449.
- 1957a Heliodiscus humboldtii (Ehrenberg) Riedel, p. 258, pl. 62, fig. 2.
- 1973 Periphaena decora Ehrenberg Sanfilippo and Riedel, p. 523, pl. 27, fig. 5 (part).
- 1974 Periphaena decora Ehrenberg Nigrini, p. 1065, pl. 1C, figs. 3, 5, pl. 2A, fig. 3 (part).
- 1977 Periphaena decora Ehrenberg Riedel and Sanfilippo, pl. 5, fig. 13 (part).
- 1986 Periphaena sp. Riedel and Sanfilippo, pl. 3, fig. 14.
- 1986 Heliodiscus humboldti [sic] (Ehrenberg) Göke, fig. 3.5.
- 2003 *Periphaena heliasteriscus* (Clark and Campbell) Sanfilippo and Fourtanier, p. 12, pl. P2, fig. 27.
- 2009 *Haliomma humboldtii* Ehrenberg Ogane et al., pl. 30, figs. 5a–5d, pl. 31, figs. 3a, 3b, 5a, 5b, pl. 68, figs. 2a–2f, pl. 69, figs. 3a–3d.
- 2021 Periphaena heliasteriscus (Clark and Campbell) de Souza et al., p. 15, pl. 1, fig. 6.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Periphaena pentasteriscus (Clark and Campbell, 1942) Plate II.1, Figure 11

- 1942 Heliodiscus (Heliodiscetta) pentasteriscus Clark and Campbell, p. 39, pl. 3, fig. 8.
- 1972 *Heliodiscus pentasteriscus* Clark and Campbell Petrushevskaya and Kozlova, p. 523, pl. 13, figs. 6, 7.
- Remarks. Cortical shell lenticular, smooth, with very small and dense pores.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Periphaena tripyramis triangula (Sutton, 1896a) Plate II.1, Figure 12

1896a Phacotriactis triangula Sutton, p. 61.



Plate II.1. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic). (1) ? *Hexancistra tricuspis* Haeckel, 1887: ODP 1260A-6R-2W, 55–57 cm. (2, 3) *Lithocyclia ocellus* Ehrenberg, 1854a group: (2) ODP 1260A-9R-5W, 55–57 cm; (3) ODP 1260A-10R-1W, 55–57 cm; (4, 5) *Lithocyclia aristotelis* (Ehrenberg, 1847) group: (4) ODP 1260A-6R-1W, 55–57 cm; (5) ODP 1260A-6H-1W, 55–57 cm. (6) *Heliostylus* ? *helianthus* (Ehrenberg, 1874): ODP 1260A-13H-1W, 54–56 cm. (7) *Periphaena decora* Ehrenberg, 1874: ODP 1260A-17R-CC, 63–177 cm. (8) *Periphaena delta* Sanfilippo and Riedel, 1973: ODP 1260A-6H-CC, 63–177 cm. (10) *Periphaena heliasteriscus* (Clark and Campbell, 1942): ODP 1260A-6H-2W, 55–57 cm. (12) *Periphaena tripyramis triangula* (Sutton, 1896a): ODP 1260A-20R-5W, 55–57 cm. All scale bars equal 50 μm.

- 1970 Triactis tripyramis triangula (Sutton) Riedel and Sanfilippo, p. 521, pl. 4, figs. 9, 10.
- 1971 Triactis tripyramis triangula (Sutton) Moore, p. 737, pl. 1, fig. 9.
- 1973 *Periphaena tripyramis triangula* (Sutton) Riedel and Sanfilippo, p. 523, pl. 9, figs. 10, 11.
- 1974 Periphaena tripyramis triangula (Sutton) Nigrini, p. 1065, pl. 1D, figs. 1, 2.
- 1975 Periphaena tripyramis triangula (Sutton) Ling, p. 725, pl. 3, fig. 3.
- 1977 Periphaena tripyramis triangula (Sutton) Riedel and Sanfilippo, pl. 6, fig. 10.
- 1986 Phacotriactis triangula Sutton Göke, fig. 5.
- 2008 Periphaena tripyramis triangula (Sutton) Jackett et al., p. 57, pl. 4, fig. 15.
- 2012b Periphaena tripyramis triangula (Sutton) Kamikuri et al., p. 4, pl. P2, fig. 5.
- Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Genus Phacodiscus Haeckel, 1882

Type species.— Phacodiscus (Phacodiscinus) rotula Haeckel, 1887, p. 424, pl. 35, fig. 7.

Phacodiscus echinatus (Ehrenberg, 1874)

Plate II.2, Figures 1a, 1b

- 1874 Haliomma echinatum Ehrenberg, p. 234.
- 1876 Haliomma echinatum Ehrenberg Ehrenberg, p. 74, pl. 27, fig. 2.
- 1887 Sethodiscus (Sethodisculus) echinatus (Ehrenberg) Haeckel, p. 424.
- 2009 Haliomma echinatum Ehrenberg Ogane et al., pl. 30, figs. 1a–3b.
- 2019 Thecosphaerella tochilinae Vasilenko, p. 329, pl. 1, figs. 7a-8b.
- Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Superfamily Spongodiscoidea Haeckel, 1862 Family Spongodiscidae Haeckel, 1862

amily Spongodiscidae Haeckel, 1862

Genus Spongodiscus Ehrenberg, 1854b

Type species.— *Spongodiscus resurgens* Ehrenberg, 1854b, p. 246 (unfigured); Ehrenberg, 1854a, pl. 35B, fig. 16.

Spongodiscus communis Clark and Campbell, 1942

Plate II.2, Figure 2

1942 Spongodiscus (Spongocyclia) communis Clark and Campbell, p. 47, pl. 2, figs. 1, 11, 13, 14, pl. 3, figs. 1, 4.

? 1974 Spongaster aff. communis Clark and Campbell – Nigrini, p. 1066, pl. 6, fig. 5.

1988 Spongodiscus communis Clark and Campbell – Blueford, p. 252, pl. 7, figs. 4, 5.

- 1976 Stylospongia communis (Clark and Campbell) Dzinoridze et al., pl. 25, figs. 6, 8, 9.
- 1999 Spongotrochus ? pulcher (Clark and Campbell) Kozlova, p. 95, pl. 9, fig. 7.
- 1999 Spongotrochus paciferus (Lipman) Kozlova, pl. 13, fig. 10.
- not 2009b *Spongodiscus communis* Clark and Campbell Suzuki et al., p. 252, pl. 13, figs. 9a–12b.

2009b Flustrella sp. B Suzuki et al., p. 252, pl. 15, figs. 1a, 1b, 3a-6b (part).

not 2015 Spongodiscus communis Clark and Campbell – Kamikuri, pl. 16, fig. 14.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Spongodiscus rhabdostylus (Ehrenberg, 1874)

Plate II.2, Figure 3

1874 Spongosphaera rhabdostyla Ehrenberg, p. 256.

- 1876 Spongosphaera rhabdostyla Ehrenberg Ehrenberg, p. 82, pl. 26, figs. 1, 2.
- 1887 Stylotrochus (Stylotrochiscus) rhabdostylus (Ehrenberg) Haeckel, p. 584.
- 1973 *Spongodiscus rhabdostylus* (Ehrenberg) Sanfilippo and Riedel, p. 525, pl. 13, figs. 1–3, pl. 30, figs. 1, 2.
- 1974 Spongodiscus rhabdostylus (Ehrenberg) Nigrini, p. 1066, pl. 1E, figs. 1–3.
- 1977 Spongodiscus rhabdostylus (Ehrenberg) Riedel and Sanfilippo, pl. 6, fig. 11, pl. 9, fig.
 2.
- not 1978 Spongodiscus rhabdostylus (Ehrenberg) Weaver and Dinkelman, p. 873, pl. 11, fig. 3.
- 1999a Spongodiscus rhabdostylus (Ehrenberg) O'Connor, p. 38, pl. 8, fig. 14.
- 1999a Spongodiscus aff. rhabdostylus (Ehrenberg) O'Connor, p. 38, pl. 10, fig. 21.
- 2008 Spongodiscus rhabdostylus (Ehrenberg) group Jackett et al., p. 58, pl. 4, fig. 19 (part).
- 2009 Spongosphaera rhabdostyla Ehrenberg Ogane et al., pl. 33, figs. 1a–1c, pl. 68, figs. 1a–1c.
- 2009b Spongodiscus rhabdostyla (Ehrenberg) Suzuki et al., p. 251, pl. 13, figs. 1a-3c.
- 2015 Spongodiscus rhabdostylus (Ehrenberg) Kamikuri, pl. 17, figs. 11–13.
- 2020 Spongodiscus rhabdostylus (Ehrenberg) Hollis et al., pl. 2, fig. 17.
- 2021 Spongodiscus rhabdostylus (Ehrenberg) de Souza et al., p. 15, pl. 1, fig. 8.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Superfamily Trematodiscoidea Haeckel, 1862

Family Trematodiscidae Haeckel, 1862

Genus Flustrella Ehrenberg, 1839

Type species.—*Flustrella concentrica* Ehrenberg, 1839, p. 132 (unfigured); Ehrenberg, 1854a, pl. 20, fig. 42.

Flustrella concentrica Ehrenberg, 1839

Plate II.2, Figure 4

1839 Flustrella concentrica Ehrenberg, p. 132.

1854a Flustrella concentrica Ehrenberg – Ehrenberg, pl. 20, fig. 42.

1876 Flustrella concentrica Ehrenberg – Ehrenberg, p. 72, pl. 22, fig. 13.

1976 *Porodiscus* ? *parvus* Clark and Campbell group – Dzinoridze et al., pl. 36, figs. 8–14, pl. 39, figs. 4, 5 (part).

2009 Flustrella concentrica Ehrenberg – Ogane et al., pl. 66, figs. 3a–3c.

2009b Flustrella parva (Clark and Campbell) - Suzuki et al., p. 252, pl. 12, figs. 1-5.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Flustrella ? spirale (Ehrenberg, 1874)

Plate II.2, Figure 5

1874 Perichlamydium ? spirale Ehrenberg, p. 245.

1876 Perichlamydium ? spirale Ehrenberg – Ehrenberg, p. 80, pl. 22, fig. 12.

1887 Perichlamydium spirale Ehrenberg – Haeckel, p. 499.

? 1977 Litheliid ? gen. and sp. indet. Riedel and Sanfilippo, pl. 11, fig. 15.

2009 Perichlamydium ? spirale Ehrenberg – Ogane et al., pl. 14, figs. 1a–1d.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Stylodictya Ehrenberg, 1846

Type species.— *Stylodictya gracilis* Ehrenberg, 1854a, pl. 36, fig. 28; see Haeckel, 1862, p. 499 for the description.

Stylodictya inaequalispina Clark and Campbell, 1942

Plate II.2, Figure 6

- 1942 Stylodictya (Stylodictyon) inaequalispina Clark and Campbell, p. 45, pl. 3, fig. 5.
- 1972 *Stylodictya inaequalispina* Clark and Campbell Petrushevskaya and Kozlova, p. 526, pl. 18, fig. 8.

2015 Stylodictya inaequalispina Clark and Campbell – Kamikuri, pl. 17, fig. 15.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).



Plate II.2. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic). (**1a, 1b**) *Phacodiscus echinatus* (Ehrenberg, 1874): ODP 1051A-16H-5W, 55–57 cm. (**2**) *Spongodiscus communis* Clark and Campbell, 1942: ODP 1051A-9H-2W, 53–55 cm. (**3**) *Spongodiscus rhabdostylus* (Ehrenberg, 1874): ODP 1051A-2H-5W, 55–57 cm. (**4**) *Flustrella concentrica* Ehrenberg, 1839: ODP 1051A-9H-2W, 53–55 cm. (**5**) *Flustrella*? *spirale* (Ehrenberg, 1874): ODP 1051A-8H-5W, 53–55 cm. (**6**) *Stylodictya inaequalispina* Clark and Campbell, 1942: ODP 1260A-6R-2W, 55–57 cm. (**7**) *Stylodictya hastata* Ehrenberg, 1874: ODP 1051A-9H-2W, 53–55 cm. (**8**) *Actinomma*? *megaxyphos tetraxyphos* (Clark and Campbell, 1942): ODP 1260A-10R-5W, 55–57 cm. (**9**, **10**) *Cromyosphaera*? *fulgurans* Tetard et al., 2023: (**9**) ODP 1051A-9H-5W, 53–55 cm; (**10**) ODP 1051A-9H-5W, 53–55 cm. (**11**) *Haliomma eocenica* Clark and Campbell, 1945: ODP 1260A-9R-3W, 55–57 cm. All scale bars equal 50 μm.

Stylodictya hastata Ehrenberg, 1874

Plate II.2, Figure 7

- 1862 Stylodictya gracilis Ehrenberg Bury, pl. 2, fig. 1.
- 1874 Stylodictya hastata Ehrenberg, p. 257.
- 1876 Stylodictya hastata Ehrenberg Ehrenberg, p. 84, pl. 23, fig. 5.
- 1887 Stylodictya (Stylodictyon) hastata Ehrenberg Haeckel, p. 510.
- 1976 Stylodictya hastata Ehrenberg Dzinoridze et al., pl. 25, fig. 2.
- 2009 Stylodictya hastata Ehrenberg Ogane et al., pl. 5, figs. 1a–1c.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Superfamily Haliommoidea Ehrenberg, 1846

Family Actinommidae Haeckel, 1862

Genus Actinomma Haeckel, 1861

Type species.— *Actinomma trinacrium* Haeckel, 1861, p. 815 (unfigured); Haeckel, 1862, p. 441, pl. 24, fig. 6.

Actinomma ? megaxyphos tetraxyphos (Clark and Campbell, 1942)

Plate II.2, Figure 8

1942 *Stylosphaera (Stylosphaerantha) megaxyphos tetraxyphos* Clark and Campbell, p. 26, pl. 6, figs. 1, 8.

? 1977 Actinommid gen. et sp. indet. Riedel and Sanfilippo, pl. 1, fig. 6.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Family Haliommidae Ehrenberg, 1846 Genus *Cromyosphaera* Haeckel, 1882 *Type species.*— *Cromyosphaera quadruplex* Haeckel, 1887, p. 84, pl. 30, figs. 9, 9a. Cromyosphaera ? fulgurans Tetard et al., 2023 Plate II.2, Figures 9, 10

2023 Cromyosphaera fulgurans Tetard et al., p. 9, figs. 4r-4u, 6a-6f.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Haliomma Ehrenberg, 1839

Type species.— *Haliomma medusa* Ehrenberg, 1839, p. 130 (unfigured); Ehrenberg, 1854a, pl. 22, figs. A34, B34.

Haliomma eocenica Clark and Campbell, 1945

Plate II.2, Figure 11

- 1945 Cenosphaera (Circosphaera) eocenica Clark and Campbell, p. 7, pl. 1, figs. 4 (part).
- 1988 Cenosphaera eocenica Clark and Campbell Blueford, p. 247, pl. 3, figs. 4, 5.
- 1999 *Thecosphaerella eocenica* (Clark and Campbell) Kozlova, p. 78, pl. 6, fig. 4, pl. 7, fig. 5, pl. 19, fig. 8, pl. 32, fig. 6.
- 2015 Cenosphaera eocenica Clark and Campbell Kamikuri, pl. 15, figs. 7a, 7b.

Remarks. The genus *Cenosphaera* has been synonymized with the genus *Haliomma* by Suzuki et al. (2021, p. 438).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Haliomma rotunda (Borisenko, 1960)

Plate II.3, Figures 1a, 1b

- 1960 Thecosphaera rotunda Borisenko, p. 222, pl. 1, figs. 3a, 3b, v, pl. 3, figs. 2a-3b.
- 1973 *Thecosphaerella rotunda* (Borisenko) Sanfilippo and Riedel, p. 522, pl. 3, figs. 7–11, pl. 26, fig. 3.
- 1999 *Thecosphaerella rotunda* (Borisenko) Kozlova, p. 80, pl. 7, figs. 1, 2, pl. 11, figs. 1, 2, pl. 27, figs. 1, 4.
- 2015 Thecosphaerella rotunda (Borisenko) Kamikuri, pl. 14, figs. 9a–11b.

Remarks. The genus *Thecosphaera* has been synonymized with the genus *Haliomma* by Petrushevskaya (1975, p. 568).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Family Heliodiscidae Haeckel, 1882 sensu De Wever et al., 2001

Genus Excentrodiscus Hollande and Enjumet, 1960

Type species. — Excentrodiscus echinatus Hollande and Enjumet, 1960, p. 125, pl. 62, fig. 3.

Excentrodiscus ? entactinia (Ehrenberg, 1874)

Plate II.3, Figures 2a, 2b

1874 Haliomma Entactinia [sic] Ehrenberg, p. 235.

1876 Haliomma Entactinia [sic] Ehrenberg – Ehrenberg, p. 74, pl. 26, fig. 4.
1887 Carposphæra (Cerasosphæra) entactinia [sic] Ehrenberg – Haeckel, p. 74.

? 1993 Haliomma ? aff. extima Petrushevskaya – Vitukhin, pl. 13, figs. 3a, 3b.

2009 Haliomma entactinia Ehrenberg – Ogane et al., pl. 1, figs. 5a–5d (part).

Remarks. This species is tentatively assigned to the genus *Excentrodiscus* based on its double medullary shell with an eccentric microsphere (Plate II.3, Figure 2b).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Excentrodiscus kamikurii Dumitrică, 2019

Plate II.3, Figure 4

2019 *Excentrodiscus kamikurii* Dumitrică, p. 53, figs. 9f, 9g. Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Heliodiscus Haeckel, 1862

Type species.— *Haliomma phacodiscus* Haeckel, 1861, p. 815 (unfigured); Haeckel, 1862, p. 437, pl. 17, fig. 5.

Heliodiscus contiguus (Ehrenberg, 1874)

Plate II.1, Figure 3

1874 Haliomma contiguum Ehrenberg, p. 234.

1876 Haliomma contiguum Ehrenberg – Ehrenberg, p. 74, pl. 27, fig. 5.

1882b Heliodiscus contiguus (Ehrenberg) - Bütschli, pl. 22, figs. 5a, 5b.

1887 Heliosestrum (Heliosestantha) contiguum (Ehrenberg) – Haeckel, p. 439.

2003 Heliodiscus inca Clark and Campbell - Sanfilippo and Fourtanier, p. 12, pl. P1, fig. 6.

2009 Haliomma contiguum Ehrenberg – Ogane et al., pl. 31, figs. 1a–2b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Heliodiscus umbonatus (Ehrenberg, 1874)

Plate II.2, Figure 5

1874 Haliomma umbonatum Ehrenberg, p. 236.

1876 Haliomma umbonatum Ehrenberg – Ehrenberg, p. 74, pl. 27, fig. 4.

1887 Heliodiscus (Heliodiscomma) umbonatus (Ehrenberg) – Haeckel, p. 449.

2009 Haliomma umbonatum Ehrenberg – Ogane et al., pl. 14, figs. 5a–5d.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Superfamily Lithelioidea Haeckel, 1862 sensu Matsuzaki et al., 2015

Family Litheliidae Haeckel, 1862 emend. Suzuki et al., 2021

Genus Lithelius Haeckel, 1861

Type species.— *Lithelius haeckelspiralis* Haeckel, 1861, p. 843 (unfigured); Haeckel, 1862, p. 519, pl. 27, figs. 6, 7.



Plate II.3. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic). (**1a, 1b**) *Haliomma rotunda* (Borisenko, 1960): ODP 1051A-6H-5W, 53–55 cm. (**2a, 2b**) *Excentrodiscus*? *entactinia* (Ehrenberg, 1874): ODP 1051A-13H-5W, 58–60 cm. (**3**) *Heliodiscus contiguus* (Ehrenberg, 1874): ODP 1051A-12H-2W, 55–57 cm. (**4**) *Excentrodiscus kamikurii* Dumitrică, 2019: ODP 1051A-4H-5W, 56–X58 cm. (**5**) *Heliodiscus umbonatus* (Ehrenberg, 1874): ODP 1051A-6H-5W, 53–55 cm. (**7, 10**) *Larcopyle hayesi hayesi* (Chen, 1974): (**7**) ODP 1051A-10H-2W, 53–55 cm; (**10**) ODP 1051A-9H-2W, 53–55 cm (**8**) *Annulatospira odoghertyi* Dumitrică, 2020: ODP 1051A-10H-2W, 53–55 cm. All scale bars equal 50 μm.

Lithelius ? echinastrum Ehrenberg, 1874

Plate II.3, Figure 6

- 1874 Stylodictya Echinastrum [sic] Ehrenberg, p. 257.
- 1876 Stylodictya Echinastrum [sic] Ehrenberg Ehrenberg, p. 84, pl. 23, fig. 1.
- 1882b Lithelius Echinastrum [sic] (Ehrenberg) Bütschli, pl. 25, fig. 8a, 8b.
- 1887 Stylodictya (Stylospira) echinastrum Ehrenberg Haeckel, p. 513.
- 2009 Stylodictya echinastrum Ehrenberg Ogane et al., pl. 28, figs. 4a–4c, pl. 64, figs. 1a–3b.
- 2015 Stylodictya? echinastrum Ehrenberg Kamikuri, pl. 17, figs. 5, 8.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Family Pyloniidae Haeckel, 1881 emend. Dumitrică, 1989

Genus *Larcopyle* Dreyer, 1889

Type species.— Larcopyle buetschlii Dreyer, 1889, p. 48, pl. 5, fig. 70.

Larcopyle hayesi hayesi (Chen, 1974)

Plate II.3, Figures 7, 10

- 1974 Prunopyle hayesi Chen, p. 482, pl. 1, figs. 7, 8, pl. 2, figs. 1, 2.
- 1975 Prunopyle hayesi Chen Chen, p. 454, pl. 9, figs. 4, 5 (part).
- 1992 Prunopyle hayesi Chen Takemura, p. 742, pl. 1, figs. 13, 14.
- 1997 Prunopyle hayesi Chen Hollis et al., p. 48, pl. 2, figs. 12–14.
- 2003 Prunopyle hayesi Chen Sanfilippo and Fourtanier, p. 12, pl. P1, fig. 5.
- 2005 Larcopyle hayesi variety 'hayesi' (Chen) Lazarus et al., p. 119, pl. 11, figs. 1–8, 18–20.
- 2009b Larcopyle hayesi hayesi (Chen) Suzuki et al., p. 250, pl. 10, figs. 8-18b.
- 2015 Larcopyle hayesi hayesi (Chen) Kamikuri, pl. 17, fig. 4.
- 2020 Larcopyle hayesi (Chen) Hollis et al., pl. 4, fig. 4.
- 2021 Larcopyle hayesi (Chen) de Souza et al., p. 15, pl. 1, fig. 10.
- Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Superfamily Phorticioidea Haeckel, 1882 Family Circodiscidae Dumitrică, 1989

Fainity Cheodiscidae Dunninea, 1989

Genus Annulatospira Clark and Campbell, 1945

Type species.— *Spongodiscus (Annulatospira) pulcher* Clark and Campbell, 1945, p. 26, pl. 4, fig. 5.

Annulatospira odoghertyi Dumitrică, 2020

Plate II.3, Figure 8

2020 *Annulatospira odoghertyi* Dumitrică, p. 38, pl. 21, figs. 1–7, pl. 22, figs. 1–3 Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Annulatospira serratolabrum Dumitrică, 2020

- Plate II.3, Figure 9
- 1973 Spongodiscus pulcher Clark and Campbell Sanfilippo and Riedel, p. 525, pl. 29, fig. 3 (part).
- 2020 Annulatospira serratolabrum Dumitrică, p. 34, pl. 19, figs. 7, 8, pl. 20, figs. 1–3.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Genus *Circodiscus* Kozlova *in* Petrushevskaya and Kozlova, 1972 *Type species.— Trematodiscus microporus* Stöhr, 1880, p. 108, pl. 4, fig. 17.

> *Circodiscus circularis* (Clark and Campbell, 1942) Plate II.4, Figure 1

- 1942 Porodiscus (Trematodiscus) circularis Clark and Campbell, p. 42, pl. 2, figs. 2, 6, 10.
- 1942 Xiphodictya (Xiphodictyon) amphixiphos Clark and Campbell, p. 43, pl. 2, fig. 4.
- 1972 *Plectodiscus circularis* (Clark and Campbell) Petrushevskaya and Kozlova, p. 526, pl. 19, figs. 9–12.
- 1972 *Plectodiscus bergontianus* (Carnevale) Petrushevskaya and Kozlova, p. 526, pl. 19, fig. 13.
- 1973 *Xiphospira circularis* (Clark and Campbell) Sanfilippo and Riedel, p. 526, pl. 14, figs. 8–10, 12, pl. 31, fig. 7 (part).
- 1976 Plectodiscus circularis (Clark and Campbell) Dzinoridze et al., pl. 24, fig. 11.
- 1977 Xiphospira circularis (Clark and Campbell) Riedel and Sanfilippo, pl. 1, fig. 10.
- 1988 Plectodiscus circularis (Clark and Campbell) Blueford, p. 250, pl. 5, figs. 7, 8.
- 1992 *Xiphospira circularis* (Clark and Campbell) Nishimura, p. 329, pl. 2, fig. 13, pl. 12, fig. 9.
- not 1999 *Circodiscus circularis* (Clark and Campbell) Kozlova, p. 173, pl. 9, fig. 2.
- 2002 Plectodiscus circularis (Clark and Campbell) Hollis, p. 288, pl. 2, figs. 20–22.
- 2008 Circodiscus circularis (Clark and Campbell) Jackett et al., p. 50, pl. 4, fig. 12 (part).
- 2009b Circodiscus circularis (Clark and Campbell) Suzuki et al., p. 254, pl. 16, figs. 12–13b.
- ? 2009b *Circodiscus* sp. C Suzuki et al., p. 254, pl. 17, figs. 4a–9.
- 2015 Plectodiscus aff. runanganus O'Connor Kamikuri, pl. 17, figs. 6, 7, 9, 10.
- 2020 Circodiscus circularis (Clark and Campbell) Dumitrică, p. 23, pl. 12, figs. 1–10.
- ? 2020 Xiphospira circularis (Clark and Campbell) Hollis et al., pl. 2, fig. 12.

Family Cryptolarnaciidae Dumitrică, 1989

Genus Coccolarnacium Dumitrică, 1989

Type species.— Coccolarnacium periphaenoides Dumitrică, 1989, p. 242, pl. 10, fig. 1.

Coccolarnacium periphaenoides Dumitrică, 1989

Plate II.4, Figure 2

1973 Coccodiscid gen. et sp. indet. Riedel and Sanfilippo, pl. 3, fig. 2.

- 1989 Coccolarnacium periphaenoides Dumitrică, p. 242, pl. 10, figs. 1–4, pl. 14, figs. 2–4, 9.
- 2001 Coccolarnacium periphaenoides Dumitrică De Wever et al., p. 155, fig. 92.2.
- 2020 *Coccolarnacium periphaenoides* Dumitrică Dumitrică, p. 7, pl. 1, figs. 1, 2, 5, 6, 10, pl. 2, figs. 1–9, pl. 7, figs. 1, 2.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Family Histiastridae Dumitrică, 1989

Genus Amphicraspedula Haeckel, 1887

Type species.— *Amphicraspedum (Amphicraspedula) murrayanum* Haeckel, 1887, p. 523, pl. 44, fig. 10.

Amphicraspedula crucifera (Clark and Campbell, 1942) Plate II.4, Figure 3

- 1942 *Spongasteriscus (Spongasteriscinus) cruciferus* Clark and Campbell, p. 50, pl. 1, figs. 1–6, 8, 10, 11, 16–18.
- 1945 Spongasteriscus (Spongasteriscinus) cruciferus Clark and Campbell Clark and Campbell, p. 57, pl. 4, figs. 4, 6, 7.
- 1973 *Spongodiscus cruciferus* (Clark and Campbell) Sanfilippo and Riedel, p. 524, pl. 11, figs. 14–17, pl. 28, figs. 10, 11.
- 1977 Spongodiscus cruciferus (Clark and Campbell) Riedel and Sanfilippo, pl. 4, fig. 3.
- 1992 Spongodiscus cruciferus (Clark and Campbell) Nishimura, p. 329, pl. 2, fig. 14.
- Stylotrochus quadribrachiatus quadribrachiatus Sanfilippo and Riedel Hull, p. 12, pl.
 7, fig. 11, pl. 8, fig. 9.
- 1993 *Amphicraspedum murrayanum* Haeckel Blueford and Amon, p. 80, pl. 2, figs. 5, 7, pl. 3, figs. 1, 5, 6, pl. 6, figs. 4, 9 (part).
- 1993 *Spongasteriscus cruciferus* Clark and Campbell Blueford and Amon, p. 78, pl. 2, figs. 1, 4, pl. 3, figs. 2, 4 (part).
- 1993 *Spongasteriscus cruciferus* Clark and Campbell Vitukhin, pl. 1, fig. 5, pl. 9, fig. 1, pl. 22, fig. 2, pl. 31, fig. 4 (part).
- 1998a *Spongodiscus cruciferus* (Clark and Campbell) Sanfilippo and Nigrini, p. 273, pl. 13.2, fig. 8.
- 1999a Spongodiscus cruciferus (Clark and Campbell) O'Connor, p. 36, pl. 10, fig. 20.
- 1999a Spongodiscus cf. cruciferus (Clark and Campbell) O'Connor, p. 36, pl. 10, fig. 23.

- 1999 *Spongasteriscus cruciferus* Clark and Campbell Kozlova, p. 175, pl. 12, fig. 3, pl. 16, fig. 12, pl. 20, fig. 1, pl. 32, fig. 10, pl. 42, fig. 11.
- 1999 Spongasteriscus sp. cf. S. cruciferus Clark and Campbell Kozlova, pl. 6, fig. 9.
- 2005 Spongasteriscus cruciferus Clark and Campbell Funakawa and Nishi, p. 233, pl. 3, fig. 1.
- 2008 Spongodiscus cruciferus (Clark and Campbell) Jackett et al., p. 58, pl. 4, fig. 8.
- 2009b Spongodiscus cruciferus (Clark and Campbell) Suzuki et al., p. 252, pl. 14, figs. 1a– 5b.
- 2020 Spongodiscus cruciferus (Clark and Campbell) Hollis et al., pl. 2, pl. 15.
- Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Amphicraspedula murrayana (Haeckel, 1887) group

Plate II.4, Figures 4, 5

- 1887 Amphicraspedum (Amphicraspedula) murrayanum Haeckel, p. 523, pl. 44, fig. 10.
- 1973 Amphicraspedum murrayanum Haeckel Sanfilippo and Riedel, p. 524, pl. 10, figs. 3–
 6, pl. 28, fig. 1.
- 1974 Amphicraspedum murrayanum Haeckel Nigrini, p. 1065, pl. 3, fig. 2.
- 1977 Amphicraspedum murrayanum Haeckel Riedel and Sanfilippo, pl. 4, fig. 4.
- 1978 Amphicraspedum murrayanum Haeckel Johnson, p. 784, pl. 1, fig. 5.
- 1978 Amphicraspedum murrayanum Haeckel Weaver and Dinkelman, p. 867, pl. 11, fig. 2.
- 1978 Amphicraspedum murrayanum Haeckel Foreman, p. 784, pl. 1, fig. 5.
- 1987 Amphicraspedum murrayanum Haeckel Nishimura, p. 719, pl. 1, figs. 14, 18.
- 1993 *Amphicraspedum murrayanum* Haeckel Blueford and Amon, p. 80, pl. 1, figs. 9, 10, pl. 2, figs. 2, 3, 8 (part).
- 1998a Amphicraspedum murrayanum Haeckel Sanfilippo and Nigrini, p. 272, pl. 13.1, fig. 1.
- 1999a Amphicraspedum murrayanum Haeckel O'Connor, p. 31, pl. 10, fig. 7.
- 2000 *Amphicraspedum murrayanum* Haeckel Nigrini and Sanfilippo, p. 72, pl. 3, figs. 11– 13.
- 2001 Amphicraspedum murrayanum Haeckel var. A Sanfilippo and Blome, p. 208, fig. 8a.
- 2008 Amphicraspedum murrayanum Haeckel group Jackett et al., p. 47, pl. 4, figs. 1, 2.
- 2020 Amphicraspedum murrayanum Haeckel Hollis et al., pl. 3, fig. 1.
- Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Amphymenium Haeckel, 1882

Type species.— *Amphymenium (Ommatogramma) zygartus* Haeckel, 1887, p. 515, pl. 44, fig. 7.

Amphymenium connicinum Kim, 1992 Plate II.4, Figures 6, 9

1992 Amphymenium connicinum Kim, p. 38, pl. 1, figs. 5, 6.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Amphymenium splendiarmatum Clark and Campbell, 1942

Plate II.4, Figures 7, 8

- 1942 *Amphymenium (Ommathymenium) splendiarmatum* Clark and Campbell, p. 46, pl. 1, fig. 12, 14
- 1973 Amphymenium splendiarmatum Clark and Campbell Sanfilippo and Riedel, p. 524, pl.
 11, fig. 6–8; pl. 28, fig. 6–8.
- 1975 *Amphymenium ? splendiarmatum* Clark and Campbell Petrushevskaya, p. 577, pl. 7, fig. 1, pl. 37, fig. 1–3.
- 1984 *Amphymenium splendiarmatum* Clark and Campbell Westberg-Smith and Riedel, p. 488, pl. 6, fig. 17.
- 1987 Amphymenium splendiarmatum Clark and Campbell Nishimura, p. 719, pl. 1, fig. 20.
- 1992 Amphymenium splendiarmatum Clark and Campbell Blome, p. 643, pl. 2, fig. 10.
- 1996 Spongocore sp. Hull, p. 136, pl. 3, fig. 14.
- 1997 Amphymenium cf. splendiarmatum Clark and Campbell Hollis et al., p. 49, pl. 3, fig.
 9.
- 2003 *Amphymenium splendiarmatum* Clark and Campbell Sanfilippo and Fourtanier, p. 11, pl. P2, fig. 18.
- 2009b *Amphymenium splendiarmatum* Clark and Campbell Suzuki et al., p. 253, pl. 6, fig. 9–12.
- 2015 Amphymenium amphistylium Haeckel Kamikuri, pl. 16, fig. 3.
- 2020 Amphymenium splendiarmatum Clark and Campbell Hollis et al., pl. 3, figs. 8, 9.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Histiastrum Ehrenberg, 1846

Type species.— *Histiastrum quaternarium* Ehrenberg, 1874, p. 237 (unfigured); Ehrenberg, 1876, p. 74, pl. 24, fig. 3.

Histiastrum coronatum Haeckel, 1887

Plate II.4, Figure 10

- 1862 Stephanastrum ? Bury, pl. 4, fig. 1.
- 1887 Histiastrum (Histiastromma) coronatum Haeckel, p. 546.
- 2020 *Histiastrum quadribrachiatus quadribrachiatus* (Sanfilippo and Riedel) Hollis et al., pl. 3, figs. 10, 11.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).



Plate II.4. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic). (1) *Circodiscus circularis* (Clark and Campbell, 1942): ODP 1051A-13H-5W, 58–60 cm. (2) *Coccolarnacium periphaenoides* Dumitrică, 1989: ODP 1260A-13R-5W, 54–56 cm. (3) *Amphicraspedula crucifera* (Clark and Campbell, 1942): ODP 1260A-10R-1W, 55–57 cm. (4, 5) *Amphicraspedula murrayana* (Haeckel, 1887) group: (4) ODP 1260A-13R-5W, 55–56 cm; (5) ODP 1260A-9R-3W, 55–57 cm. (6, 9) *Amphymenium connicinum* Kim, 1992: (6) ODP 1260A-8R-3W, 54–56 cm; (9) ODP 1260A-8R-3W, 54–56 cm. (7, 8) *Amphymenium splendiarmatum* Clark and Campbell, 1942: (7) ODP 1260A-11R-1W, 55–57 cm; (8) ODP 1260A-6R-2W, 55–57 cm. (10) *Histiastrum quaternarium* Ehrenberg, 1874: ODP 1260A-13R-5W, 54–56 cm. (11) *Histiastrum coronatum* Haeckel, 1887: ODP 1260A-6R-1W, 55–57 cm. (12) *Homunculodiscus tainemplekta* (Caulet, 1991): ODP 1051A-10H-5W, 52–54 cm. All scale bars equal 50 μm.

Histiastrum quaternarium Ehrenberg, 1874 Plate II.4, Figure 11

1862 Astromma ? Bury, pl. 5, fig. 1.

1874 Histiastrum quaternarium Ehrenberg, p. 237.

1876 Histiastrum quaternarium Ehrenberg – Ehrenberg, p. 74, pl. 24, fig. 3.

not 1882b *Histiastrum quaternarium* Ehrenberg – Bütschli, pl. 25, fig. 5.

1887 Histiastrum (Histiastromma) quaternarium Ehrenberg – Haeckel, p. 545.

1887 Histiastrum (Histiastromma) gladiatum Haeckel, p. 545.

not 1987 *Histiastrum quaternarium* Ehrenberg – Nishimura, p. 726, pl. 1, fig. 16. Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Superfamily Pseudoaulophacoidea Riedel, 1967a sensu De Wever et al., 2001

Family Suttoniidae Schaaf, 1976 sensu Dumitrică, 2019

Genus Homunculodiscus Dumitrică, 2019

Type species.— Stylodictya tainemplekta Caulet, 1991, p. 533, pl. 1, fig. 8.

Homunculodiscus tainemplekta (Caulet, 1991) Plate II.4, Figure 12

1991 Stylodictya tainemplekta Caulet, p. 533, pl. 1, figs. 8, 9.

2015 Stylodictya tainemplekta Caulet - Kamikuri, p. 148, pl. 18, fig. 6.

2019 Homunculodiscus tainemplecta [sic] (Caulet) - Dumitrică, p. 42, figs. 3e, 3g, 4a-4d.

2021 Stylodictya tainemplekta Caulet – de Souza et al., p. 15, pl. 1, fig. 9.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Suttonium Schaaf, 1976

Type species.— Suttonium praedicator Schaaf, 1976, p. 790, pl. 1, fig. 1.

Suttonium anomalum (Sutton, 1896b)

- Plate II.5, Figure 1
- 1896b Rhopalastrum ? anomalum Sutton, p. 59, fig. 1.
- 1983 Suttonium anomalum (Sutton) Dumitrică, p. 42, pl. 2, figs. 1–4, pl. 3, figs. 3, 4, 6–8, 11.
- 1986 Suttonium anomalum (Sutton) Göke, fig. 5.
- 2015 Suttonium anomalum (Sutton) Kamikuri, pl. 18, fig. 9.
- 2019 Suttonium anomalum (Sutton) Dumitrică, p. 46, fig. 6c.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Superfamily Stylosphaeroidea Haeckel, 1887

Family Entapiidae Dumitrică in De Wever et al., 2001

Genus Entapium Sanfilippo and Riedel, 1973

Type species.— Entapium regulare Sanfilippo and Riedel, 1973, p. 492, pl. 24, figs. 1, 2.

Entapium regulare Sanfilippo and Riedel, 1973

Plate II.5, Figure 2

1973 Entapium regulare Sanfilippo and Riedel, p. 492, pl. 1, figs. 10–19, pl. 24, figs. 1–3.

- 1992 Entapium regulare Sanfilippo and Riedel Blome, p. 644, pl. 3, fig. 20.
- 1999 Entapium regulare Sanfilippo and Riedel Kozlova, p. 73, pl. 8, figs. 8, 9.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Genus Zealithapium O'Connor, 1999a

Type species.— Zealithapium oamaru O'Connor, 1999a, p. 5, pl. 5, figs 29a, 29b.

Zealithapium anoectum (Riedel and Sanfilippo, 1970)

Plate II.5, Figures 4, 5

- 1970 Lithapium ? anoectum Riedel and Sanfilippo, p. 520, pl. 4, figs. 4, 5.
- 1973 Lithapium anoectum Riedel and Sanfilippo Sanfilippo and Riedel, p. 516, pl. 24, figs.
 6, 7.
- 1974 Lithapium anoectum Riedel and Sanfilippo Nigrini, p. 1064, pl. 1A, figs. 1, 2.
- 1977 Lithapium anoectum Riedel and Sanfilippo Riedel and Sanfilippo, pl. 8, fig. 10.
- 1978 Lithapium anoectum Riedel and Sanfilippo Riedel and Sanfilippo, p. 69, pl. 5, fig. 17.
- 1992 Lithapium anoectum Riedel and Sanfilippo Takemura, p. 742, pl. 7, fig. 1.
- ? 1999 Lithapium anoectum Riedel and Sanfilippo Kozlova, p. 125, pl. 32, fig. 19.
- 1999a Zealithapium anoectum (Riedel and Sanfilippo) O'Connor, p. 5.
- 2001 Zealithapium anoectum (Riedel and Sanfilippo) De Wever et al., p. 119, fig. 65.3.
- 2012 Zealithapium cf. Z. anoectum (Riedel and Sanfilippo) Moore and Kamikuri, p. 13, pl. P10, figs. 6, 7.
- 2012b Zealithapium anoectum (Riedel and Sanfilippo) Kamikuri et al., p. 5, pl. P1, figs. 6a, 6b.
- 2020 Zealithapium anoectum (Riedel and Sanfilippo) Hollis et al., pl. 1, fig. 9.
- Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Zealithapium mitra (Ehrenberg, 1874) Plate II.5, Figure 6

- 1862 *Podocyrtis* ? Bury, pl. 9, fig. 4 (part).
- 1874 Cornutella Mitra [sic] Ehrenberg, p. 221.
- 1876 Cornutella Mitra [sic] Ehrenberg Ehrenberg, p. 68, pl. 2, figs. 8.
- 1882a Ceratocyrtis mitra (Ehrenberg) Bütschli, p. 536.
- 1887 Cornutella (Cornutissa) mitra Ehrenberg Haeckel, p. 1181.
- 1887 Sethoconus (Conarachnium) mitra (Ehrenberg) Haeckel, p. 1291.
- 1970 Lithapium ? mitra (Ehrenberg) Riedel and Sanfilippo, p. 520, pl. 4, figs. 6, 7.
- 1971 Lithapium? mitra (Ehrenberg) Moore, p. 736, pl. 3, fig. 1.
- 1977 Lithapium mitra (Ehrenberg) Riedel and Sanfilippo, pl. 8, fig. 15.
- 1978 Lithapium mitra (Ehrenberg) Riedel and Sanfilippo, p. 69, pl. 6, fig. 1 (part).
- 1992 Lithapium cf. mitra (Ehrenberg) Takemura, p. 742, pl. 7, fig. 2.
- 1997 Lithapium mitra (Ehrenberg) Hollis et al., p. 45, pl. 1, fig. 20.
- 1999a Zealithapium mitra (Ehrenberg) O'Connor, p. 5, pl. 9, fig. 47.
- 2012 Zealithapium mitra (Ehrenberg) Moore and Kamikuri, p. 13, pl. P10, fig. 5.
- 2020 Zealithapium mitra (Ehrenberg) Hollis et al., pl. 1, fig. 10.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Zealithapium plegmacantha Riedel and Sanfilippo, 1970 Plate II.5, Figure 3

- 1970 Lithapium ? plegmacantha Riedel and Sanfilippo, p. 520, pl. 4, figs. 2, 3.
- 1971 Lithapium ? plegmacantha Riedel and Sanfilippo Moore, p. 736, pl. 1, fig. 1.
- 1973 *Lithapium plegmacantha* Riedel and Sanfilippo Sanfilippo and Riedel, p. 516, pl. 3, figs. 1, 2, pl. 24, figs. 8, 9.
- 1974 Lithapium plegmacantha Riedel and Sanfilippo Nigrini, p. 1064, pl. 1A, figs. 3–5.
- 1977 Lithapium plegmacantha Riedel and Sanfilippo Riedel and Sanfilippo, pl. 6, fig. 8.
- 1986 Lithapium plegmacantha Riedel and Sanfilippo Riedel and Sanfilippo, pl. 2, figs. 4,
 5.
- 1999a Zealithapium plegmacantha (Riedel and Sanfilippo) O'Connor, p. 5.
- 2012b Zealithapium plegmacantha (Riedel and Sanfilippo) Kamikuri et al., p. 5, pl. P1, figs. 7a, 7b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Family Stylosphaeridae Haeckel, 1887 sensu Dumitrică, 1985 Genus *Lithomespilus* Haeckel, 1882

Type species.— Lithomespilus phloginus Haeckel, 1887, p. 302, pl. 14, fig. 16.

Lithomespilus coronatus Squinabol, 1904

Plate II.5, Figures 7, 8

1904 Lithomespilus coronatus Squinabol, p. 198, pl. 4, fig. 7.

- 1973 Druppatractus cf. coronatus (Squinabol) Dumitrică, p. 787, pl. 6, figs. 4, 6, pl. 12, fig. 1.
- 2002 Lithomespilus coronatus Squinabol Hollis, pl. 1, fig. 12.
- 1960 Ellipsidium ? mendosum Krasheninnikov, p. 281, pl. 1, fig. 14a, 14b.
- 1973 Lithomespilus mendosa (Krasheninnikov) Sanfilippo and Riedel, p. 517, pl. 4, figs. 6,
 7, pl. 24, figs. 10, 11.
- 1977 Lithomespilus mendosa (Krasheninnikov) Riedel and Sanfilippo, pl. 1, fig. 4.
- 1992 Lithomespilus mendosa (Krasheninnikov) Blome, pl. 2, figs. 16.

Genus Stauroxiphos Haeckel, 1887

Type species.— Stauroxiphos gladius Haeckel, 1887, p. 163, pl. 15, fig. 7.

Stauroxiphos ? gladius Haeckel, 1887

Plate II.5, Figure 10

1887 Stauroxiphos gladius Haeckel, p. 163, pl. 15, fig. 7.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Genus Stylosphaera Ehrenberg, 1846

Type species.— *Stylosphaera hispida* Ehrenberg, 1854c, p. 246 (unfigured); Ehrenberg, 1854a, pl. 36, fig. 26.

Stylosphaera ? agdaraensis (Mamedov, 1969a)

Plate II.5, Figure 9

? 1969a Sphaerostylus agdaraensis Mamedov, p. 96, pl. 2, figs. 1, 2.

1973 *Thecosphaerella* sp. cf. *T. agdaraensis* (Mamedov) – Sanfilippo and Riedel, p. 521, pl. 2, figs. 7–9, pl. 25, fig. 15.

Remarks. This species is tentatively assigned to the genus *Stylosphaera* based on its overall morphology.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Stylosphaera carduus Ehrenberg, 1874

Plate II.5, Figures 11, 12

1874 Stylosphaera Carduus [sic] Ehrenberg, p. 258.

1876 Stylosphaera Carduus [sic] Ehrenberg – Ehrenberg, p. 84, pl. 25, fig. 7.

- 1887 Stylatractus (Stylatractylis) carduus (Ehrenberg) Haeckel, p. 330.
- not 1972 Axoprunum carduum (Ehrenberg) Petrushevskaya and Kozlova, p. 521, pl. 10, fig. 1.

1977 Stylatractus sp. Riedel and Sanfilippo, pl. 13, fig. 1.

1995 Stylatractus ostracion (Haeckel) – Shilov, p. 124, pl. 3, figs. 3a, 3b.

2009 Stylosphaera carduus Ehrenberg – Ogane et al., pl. 12, figs. 5a–5d, pl. 29, figs. 1a–1d.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Stylosphaera coronata Ehrenberg, 1874 Plate II.6, Figure 1

- 1874 Stylosphaera coronata Ehrenberg, p. 258.
- 1876 Stylosphaera (Xiphostylantha) coronata Ehrenberg Ehrenberg, p. 84, pl. 25, fig. 4.
- 1887 Xiphostylus phasianus Haeckel, p. 127, pl. 13, fig. 9.
- 1887 Druppatractus (Druppatractylis) coronatus (Ehrenberg) Haeckel, p. 326.
- 1942 Lithatractus (Lithatractaria) hederae Clark and Campbell, p. 33, pl. 5, fig. 3.
- 1942 Druppatractus (Druppatractaria) trichopterus Clark and Campbell, p. 34, pl. 5, fig. 4.
- 1942 Ellipsostylus (Ellipsostyletta) anisoxyphos Clark and Campbell, p. 32, pl. 5, figs. 7, 11.
- 1972 Stylatractus coronatus (Ehrenberg) Petrushevskaya and Kozlova, p. 520, pl. 11, fig. 9.
- 1973 Stylosphaera coronata coronata Ehrenberg Sanfilippo and Riedel, p. 520, pl. 1, figs. 13–17, pl. 25, fig. 4.
- 1973 Druppatractus sp. Dumitrică, p. 787, pl. 12, fig. 3.
- 1974 Stylosphaera coronata coronata Ehrenberg Nigrini, p. 1064, pl. 1B, figs. 1–3.
- 1986 Stylosphaera coronata coronata Ehrenberg Riedel and Sanfilippo, pl. 5, fig. 7.
- 1987 Stylosphaera coronata coronata Ehrenberg Nishimura, p. 729, pl. 1, figs. 1, 2.
- 1992 Stylosphaera coronata coronata Ehrenberg Nishimura, p. 325, pl. 1, fig. 2, pl. 11, fig. 9.
- 1994 Stylosphaera coronata sabaca Sanfilippo and Riedel Weinheimer et al., p. 312, pl. 1, fig. 6.
- 1995 Stylosphaera coronata Ehrenberg Shilov, p. 124, pl. 2, figs. 2a–2c.
- 1999 Amphisphaera sp. ef gr. A. coronata (Ehrenberg) Kozlova, pl. 22, figs. 7, 9, pl. 33, fig. 11 (part).
- 2008 Stylosphaera coronata coronata Ehrenberg Jackett et al., p. 58, pl. 3, fig. 10.
- 2009 Stylosphaera coronata Ehrenberg Ogane et al., pl. 12, figs. 1a–1d.
- 2009b Stylosphaera ex. gr. radiosa Ehrenberg Suzuki et al., p. 244, pl. 1, figs. 8a, 8b.
- 2009b Stylosphaera gigantea (Haeckel) Suzuki et al., p. 244, pl. 1, figs. 9a, 9b.
- 2013 Stylosphaera coronata coronata Ehrenberg Kamikuri et al., pl. 1, figs. 6a, 6b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Stylosphaera laevis Ehrenberg, 1874

Plate II.6, Figures 2, 3

- 1874 Stylosphaera laevis Ehrenberg, p. 259.
- 1876 Stylosphaera laevis Ehrenberg Ehrenberg, p. 84, pl. 25, fig. 6.
- 1887 Ellipsostylus (Ellipsostyletta) psittacus Haeckel, p. 300, pl. 13, fig. 6.
- 1887 Druppatractus (Druppatractona) lævis [sic] (Ehrenberg) Haeckel, p. 327.
- ? 1942 Ellipsostylus (Ellipsostyletta) parvus Clark and Campbell, p. 32, pl. 5, fig. 16.
- 1958 Druppatractus sp. Göke, pl. 3, fig. 3.
- 1972 Stylosphaera ? laevis Ehrenberg Petrushevskaya and Kozlova, p. 520, pl. 11, fig. 8.
- 1973 Stylosphaera coronata laevis Ehrenberg Sanfilippo and Riedel, p. 520, pl. 1, fig. 19, pl. 25, figs. 5, 6.



Plate II.5. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic). (1) *Suttonium anomalum* (Sutton, 1896b): ODP 1051A-14H-5W, 52–54 cm. (2) *Entapium regulare* Sanfilippo and Riedel, 1973: ODP 1260A-8R-5W, 54–56 cm. (3) *Zealithapium plegmacantha* Riedel and Sanfilippo, 1970: ODP 1260A-17R-3W, 55–57 cm. (4, 5) *Zealithapium anoectum* (Riedel and Sanfilippo, 1970): (4) closed specimen, ODP 1260A-11R-4W, 55–57 cm; (5) specimen with a pylome, ODP 1260A-11R-4W, 55–57 cm. (6) *Zealithapium mitra* (Ehrenberg, 1874): ODP 1260A-8R-6W, 54–56 cm. (7, 8) *Lithomespilus coronatus* Squinabol, 1904: (7) ODP 1260A-9R-3W, 55–57 cm; (8) ODP 1260A-11R-1W, 55–57 cm. (10) *Stauroxiphos* ? *gladius* Haeckel, 1887: ODP 1260A-17R-CC, 63–177 cm. (11, 12) *Stylosphaera carduus* Ehrenberg, 1874: (11) ODP 1260A-11R-7W, 55–57 cm; (12) ODP 1260A-6R-4W, 55–57 cm. All scale bars equal 50 μm.

- not 2005 Stylosphaera coronata laevis Ehrenberg Funakawa and Nishi, p. 238, pl. 1, figs. 10a, 10b.
- 2009 *Stylosphaera laevis* Ehrenberg Ogane et al., pl. 29, figs. 3a–4b, 6a, 6b, pl. 61, figs. 2a–2c, pl. 63, figs. 2a, 2b.
- 2012 Stylosphaera laevis Ehrenberg form A Kamikuri and Wade, pl. 1, figs. 10a, 10b.
- 2012 Stylosphaera laevis Ehrenberg form B Kamikuri and Wade, pl. 1, figs. 9a, 9b.
- 2015 Stylosphaera laevis Ehrenberg form A Kamikuri, pl. 14, figs. 5a, 5b, pl. 19, figs. 3a, 3b.
- 2015 Stylosphaera laevis Ehrenberg form B Kamikuri, pl. 14, figs. 1a-3b, pl. 19, figs. 5a, 5b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Stylosphaera radiosa Ehrenberg, 1874

Plate II.6, Figure 4

- 1874 *Stylosphaera radiosa* Ehrenberg, p. 259.
- 1876 Stylosphaera radiosa Ehrenberg Ehrenberg, p. 84, pl. 24, fig. 5.
- 1887 Xiphatractus (Xiphatractium) radiosus (Ehrenberg) Haeckel, p. 334.
- 1975 Amphisphaera radiosa (Ehrenberg) group Petrushevskaya, p. 570, pl. 2, figs. 18–20.
- 1990 Stylosphaera radiosa Ehrenberg Abelmann, p. 692, pl. 2, fig. 4A-4C.
- 1997 Amphisphaera radiosa (Ehrenberg) Hollis et al., p. 43, pl. 1, figs. 5, 6.
- 1997 Ellipsoxiphus ? sp. Hollis et al., pl. 1, figs. 3, 4.
- ? 1999 Amphisphaera radiosa (Ehrenberg) Kozlova, p. 173, pl. 17, fig. 2.
- 2008 Stylosphaera goruna Sanfilippo and Riedel Jackett et al., p. 58, pl. 10, fig. 12.
- 2009 Stylosphaera radiosa Ehrenberg Ogane et al., pl. 12, figs. 2a–3d, pl. 61, figs. 1a–1d.
- 2015 Stylosphaera goruna Sanfilippo and Riedel Kamikuri, pl. 19, fig. 4.
- 2020 Amphisphaera radiosa (Ehrenberg) Hollis et al., pl. 1, figs. 5a, 5b.
- 2020 Amphisphaera aff. radiosa (Ehrenberg) Hollis et al., pl. 1, figs. 6a, 6b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Stylosphaera spinulosa Ehrenberg, 1874

Plate II.6, Figure 5

- 1874 Stylosphaera spinulosa Ehrenberg 1874, p. 259.
- 1876 Stylosphaera spinulosa Ehrenberg Ehrenberg, pl. 25, fig. 8.
- 1887 Xiphatractus (Xiphatractylis) spinulosus Ehrenberg Haeckel, p. 332.
- 1972 *Stylatractus spinulosus* (Ehrenberg) group Petrushevskaya and Kozlova, p. 519, pl. 11, figs. 2–4.
- 1973 Stylosphaera goruna Sanfilippo and Riedel, p. 521, pl. 1, fig. 20–22, pl. 25, fig. 9–10.
- 1973 Druppatractus cf. coronatus (Squinabol) Dumitrică, p. 787, pl. 6, figs. 4, 6, pl. 12, fig. 1.
- 1977 Stylosphaera goruna Sanfilippo and Riedel Riedel and Sanfilippo, pl. 1, fig. 5.
- 1980 Stylosphaera goruna Sanfilippo and Riedel Westberg et al., p. 432, pl. 1, fig. 1.
- 1984 *Stylosphaera goruna* Sanfilippo and Riedel Westberg-Smith and Riedel, p. 487, pl. 6, fig. 11.
- 1987 Stylosphaera goruna Sanfilippo and Riedel Nishimura, p. 729, pl. 1, fig. 3.
- 1992 Stylosphaera goruna Sanfilippo and Riedel Nishimura, p. 326, pl. 1, fig. 1, pl. 11, fig. 8.
- 1992 Stylosphaera goruna Sanfilippo and Riedel Blome, p. 646, pl. 1, figs. 17–20.
- 1992 Stylosphaera goruna Sanfilippo and Riedel Kim, p. 38, pl. 1, figs. 3, 4.
- 1995 Amphisphaera spinulosa (Ehrenberg) Strong et al., p. 208, figs. 9A, 10A, 10B.
- 2002 Amphisphaera goruna (Sanfilippo and Riedel) Hollis, pl. 1, fig. 5.
- 2006 Stylosphaera goruna Sanfilippo and Riedel Funakawa et al., p. 40, pl. P3, figs. 3-4.
- 2009 Stylosphaera liostylus Ehrenberg Ogane et al., pl. 12, figs. 6a–6f (part).
- 2020 Amphisphaera spinulosa (Ehrenberg) Hollis et al., pl. 1, fig. 2.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Genus Spongatractus Haeckel, 1887

Type species.— *Spongosphaera pachystyla* Ehrenberg, 1874, p. 256 (unfigured); Ehrenberg, 1876, p. 82, pl. 26, fig. 3.

Spongatractus balbis Sanfilippo and Riedel, 1973

Plate II.6, Figure 6

- 1973 Spongatractus balbis Sanfilippo and Riedel, p. 518, pl. 2, figs. 1–3, pl. 25, figs. 1, 2.
- 1974 Spongatractus balbis Sanfilippo and Riedel Nigrini, p. 1064, pl. 1A, figs. 6, 7.
- 1977 Spongatractus balbis Sanfilippo and Riedel Riedel and Sanfilippo, pl. 5, fig. 6.
- 1986 Spongatractus balbis Sanfilippo and Riedel Riedel and Sanfilippo, pl. 3, fig. 6.
- 2017 Spongatractus balbis Sanfilippo and Riedel de Souza et al., pl. 1, figs. 1a, 1b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Spongatractus pachystylus (Ehrenberg, 1874)

Plate II.6, Figure 7

1862 Spongosphæra var. Bury, pl. 4, fig. 6.

1874 Spongosphaera pachystyla Ehrenberg, p. 256.

- 1876 Spongosphaera pachystyla Ehrenberg Ehrenberg, p. 82, pl. 26, fig. 3.
- 1882b Spongosphaera pachystyla Ehrenberg Bütschli, pl. 24, fig. 1.
- 1887 Spongatractus pachystylus (Ehrenberg) Haeckel, p. 350.
- 1887 Spongoxiphus prunococcus Haeckel, p. 354, pl. 17, figs. 12, 13.
- 1958 Spongatractus pachystylus (Ehrenberg) Göke, pl. 2, fig. 3.
- 1970 Spongatractus pachystylus (Ehrenberg) Cita et al., p. 401, pl. 1, fig. B.
- 1970 Spongatractus pachystylus (Ehrenberg) Riedel and Sanfilippo, pl. 4, fig. 1.
- 1972 Spongosphaera pachystyla Ehrenberg Petrushevskaya and Kozlova, p. 521, pl. 10, fig.
 5.
- 1973 Spongatractus pachystylus (Ehrenberg) Sanfilippo and Riedel, p. 519, pl. 2, figs. 4–6, pl. 25, fig. 3.
- 1974 Spongatractus pachystylus (Ehrenberg) Nigrini, p. 1064, pl. 1A, figs. 8–11.
- 1977 Spongatractus pachystylus (Ehrenberg) Riedel and Sanfilippo, pl. 6, fig. 7.
- 1986 Spongatractus pachystylus (Ehrenberg) Riedel and Sanfilippo, pl. 3, figs. 7, 8.
- 2008 Spongatractus pachystylus (Ehrenberg) Jackett et al., p. 58, pl. 3, fig. 9.
- 2009 Spongosphaera pachystyla Ehrenberg Ogane et al., pl. 13, figs. 1a–1d, 3a, 3b, pl. 27, figs. 2a–2d.
- 2012 Spongatractus pachystylus (Ehrenberg) Moore and Kamikuri, p. 10, pl. P7, fig. 10.
- 2017 Spongatractus pachystylus (Ehrenberg) de Souza et al., pl. 1, figs. 2a, 2b.
- 2020 Spongatractus pachystylus (Ehrenberg) Hollis et al., pl. 1, fig. 18.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Spongatractus ? klausi Sanfilippo and Blome, 2001

Plate II.6, Figure 8

2001 Spongatractus klausi Sanfilippo and Blome, p. 202, figs. 6a-6c.

2020 Lithocyclia sp. Hollis et al., pl. 2, fig. 8.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Order Entactinaria Kozur and Mostler, 1982

Superfamily Heliosaturnaloidea Kozur and Mostler, 1972

Family Axoprunidae Dumitrică, 1985

Genus Axoprunum Haeckel, 1887

Type species.— Axoprunum stauraxonium Haeckel, 1887, p. 239, pl. 48, fig. 4.

Axoprunum pierinae (Clark and Campbell, 1942) group Plate II.6, Figures 10, 11

1942 Lithatractus (Lithatractona) pierinae Clark and Campbell, p. 34, pl. 5, fig. 25.

- 1969a Stylatractus pictus Mamedov, p. 99, pl. 2, fig. 4-4a.
- 1972 *Axoprunum liostylum* (Ehrenberg) group Petrushevskaya and Kozlova, p. 521, pl. 10, fig. 3.

- 1973 Axoprunum pierinae (Clark and Campbell) group Sanfilippo and Riedel, p. 488, pl. 1, figs. 6–12, pl. 23, fig. 3.
- 1975 Axoprunum liostylum (Ehrenberg) group Petrushevskaya, p. 571, pl. 2, fig. 22.
- 1976 Axoprunum pierinae (Clark and Campbell) Dzinoridze et al., pl. 22, fig. 19.
- 1977 Axoprunum pierinae (Clark and Campbell) group Riedel and Sanfilippo, pl. 4, fig. 16.
- 1987 Axoprunum pierinae (Clark and Campbell) Nishimura, p. 720, pl. 1, fig. 6.
- 1989 Sphaerostylus nicholasi Blueford Lazarus and Pallant, p. 364, pl. 6, figs. 19, 20, 23.
- 1992 Axoprunum pierinae (Clark and Campbell) Takemura, p. 742, pl. 6, figs. 3–6.
- 1992 Axoprunum magnum Kim, p. 37, pl. 1, figs. 1, 2.
- 1993 Stylosphaera minor brevichastata Clark and Campbell Vitukhin, pl. 6, fig. 7.
- 1993 Axoprunum liostylum (Ehrenberg) group Vitukhin, pl. 15, figs. 1–4.
- 1995 Axoprunum losbanosensis (Clark and Campbell) Shilov, p. 124, pl. 3, figs. 1a, 1b.
- 1995 Axoprunum pierinae (Clark and Campbell) Strong et al., p. 208, fig. 10C.
- 1997 Axoprunum pierinae (Clark and Campbell) Hollis et al., p. 44, pl. 1, figs. 7–13.
- 1997 Axoprunum pierinae (Clark and Campbell) Takemura and Ling, p. 111, pl. 1, fig. 1.
- 1999a Axoprunum pierinae (Clark and Campbell) O'Connor, p. 31, pl. 10, fig. 12.
- 1999 Axoprunum chabakovi (Lipman) Kozlova, p. 68, pl. 27, fig. 7, pl. 28, fig. 3, pl. 29, fig. 3, pl. 38, fig. 1.
- 2003 *Axoprunum pierinae* (Clark and Campbell) group Sanfilippo and Fourtanier, p. 11, pl. P2, fig. 7.
- 2005 Axoprunum pierinae (Clark and Campbell) Funakawa and Nishi, p. 231, pl. 1, figs. 5a, 5b.
- 2006 Axoprunum pierinae (Clark and Campbell) Funakawa et al., p. 39, pl. P13, figs. 15a, 15b.
- 2008 Axoprunum pierinae (Clark and Campbell) Jackett et al., p. 47, pl. 3, fig. 14.
- 2009b Axoprunum venustum (Borisenko) Suzuki et al., p. 241, pl. 1, figs. 1a, 1b.
- 2009b Axoprunum aff. venustum (Borisenko) Suzuki et al., p. 241, pl. 1, figs. 2a, 2b.
- 2009b Axoprunum bispiculum (Popofsky) Suzuki et al., p. 241, pl. 1, figs. 3a, 3b (part).
- ? 2009 Stylosphaera liostylus Ehrenberg Ogane et al., pl. 26, figs. 2a–2c, pl. 63, figs. 1a–1e (part).
- 2019 Amphistylus gladiusiacus Vasilenko, p. 327, pl. 1, figs. 1-6.
- 2020 Axoprunum pierinei [sic] (Clark and Campbell) group Holli et al., pl. 1, figs. 14, 15.
- 2021 Axoprunum pierinae (Clark and Campbell) de Souza et al., p. 15, pl. 1, figs. 4a, 4b.

Axoprunum minor (Clark and Campbell, 1942)

Plate II.6, Figure 9

- 1942 *Stylosphaera (Stylosphaerantha) minor* Clark and Campbell, p. 27, pl. 5, figs. 1, 2, 2a, 12.
- 1945 *Stylosphaera (Stylosphaerantha) minor* Clark and Campbell Clark and Campbell, p. 11, pl. 1, figs. 13–19.

- 1972 *Stylosphaera minor* Clark and Campbell Petrushevskaya and Kozlova, p. 520, pl. 10, fig. 9.
- 1973 *Amphisphaera minor* (Clark and Campbell) Sanfilippo and Riedel, p. 486, pl. 1, figs. 1–5, pl. 22, fig. 4.
- 1975 Amphisphaera minor (Clark and Campbell) Chen, p. 452, pl. 3, fig. 1.
- not 1976 Stylosphaera minor Clark and Campbell Dzinoridze et al., pl. 22, figs. 12, 13.
- 1987 Amphisphaera minor (Clark and Campbell) Nishimura, p. 719, pl. 1, fig. 5.
- 1988 Stylosphaera minor Clark and Campbell Blueford, p. 247, pl. 4, figs. 4, 5 (part).
- 1992 Amphisphaera minor (Clark and Campbell) Blome, p. 643, pl. 3, fig. 23.
- 1992 Amphistylus ? sp. Takemura, p. 741, pl. 5, figs. 9, 10.
- 1993 Stylosphaera minor leptoxyphos Clark and Campbell Vitukhin, pl. 6, fig. 6.
- 1993 Stylosphaera minor minor Clark and Campbell Vitukhin, pl. 22, fig. 5.
- 1993 Stylosphaera minor Clark and Campbell Vitukhin, pl. 32, fig. 2.
- 1995 Stylosphaera minor Clark and Campbell Shilov, p. 124, pl. 3, fig. 2.
- ? 1999a Stylosphaera minor Clark and Campbell O'Connor, p. 38, pl. 8, fig. 23, pl. 10, fig. 28.
- 1999 Stylosphaera minor Clark and Campbell Kozlova, p. 175, pl. 8, fig. 7, pl. 38, fig. 3.
- 2002 Stylosphaera minor Clark and Campbell Hollis, pl. 1, fig. 13.
- 2003 *Amphisphaera minor* (Clark and Campbell) Sanfilippo and Fourtanier, p. 11, pl. P2, fig. 6.
- 2008 Amphisphaera minor (Clark and Campbell) Jackett et al., p. 47, pl. 3, fig. 13.
- 2009b Axoprunum minor (Clark and Campbell) Suzuki et al., p. 241, pl. 1, figs. 5a-6c.
- 2009b Xiphosphaerantha pallas Haeckel Suzuki et al., p. 241, pl. 1, figs. 7a-7b.
- 2020 Axoprunum minor (Clark and Campbell) Hollis et al., pl. 1, fig. 12.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Family Saturnulidae Suzuki in Suzuki et al., 2021

Genus Saturnalis Haeckel, 1882

Type species.— Saturnalis (Saturnalina) circularis Haeckel, 1887, p. 131 (unfigured).

Saturnalis kennetti Dumitrică, 1985

Plate II.6, Figure 12

- 1973 ? Saturnulus sp. cf. planetes Haeckel Dumitrică, p. 787, pl. 1, figs. 7, 8, pl. 5, fig. 7.
- 1976 Saturnulus planetes Haeckel Johnson, p. 784, pl. 1, fig. 8.
- 1978 Saturnulus planetes Haeckel Foreman, p. 784, pl. 1, fig. 8.
- 1985 Saturnalis kennetti Dumitrică, p. 189, pl. 2, figs. 1, 2, pl. 3, fig. 15.
- 1992 Saturnalis sp. A Blome, p. 645, pl. 4, fig. 9.
- 2002 Saturnalis kennetti Dumitrică Hollis, pl. 1, fig. 17.
- 2008 Saturnalis circularis Haeckel Jackett et al., p. 57, pl. 3, fig. 15.
- 2017 Saturnalis kennetti Dumitrică Dumitrică and Hungerbühler, p. 122, pl. 6, figs. 1–2a.
- 2020 Saturnalis circularis Haeckel Hollis et al., pl. 1, fig. 17.
- Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).



Plate II.6. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic). (1) *Stylosphaera coronata* Ehrenberg, 1874: ODP 1260A-6R-CC, 66–177 cm. (2, 3) *Stylosphaera laevis* Ehrenberg, 1874: (2) ODP 1260A-13R-5W, 55–57 cm; (3) ODP 1051A-18X-5W, 54–56 cm. (4) *Stylosphaera radiosa* Ehrenberg, 1874: ODP 1260A-8R-3W, 54–56 cm. (5) *Stylosphaera spinulosa* Ehrenberg, 1874: ODP 1260A-8R-3W, 54–56 cm. (6) *Spongatractus balbis* Sanfilippo and Riedel, 1973: ODP 1260A-17R-3W, 55–57 cm. (7) *Spongatractus pachystylus* (Ehrenberg, 1874): ODP 1260A-10R-6W, 55–57 cm. (8) *Spongatractus*? *klausi* Sanfilippo and Blome, 2001: ODP 1051A-9R-5W, 53–55 cm. (9) *Axoprunum minor* (Clark and Campbell, 1942): ODP 1260A-6R-4W, 55–57 cm. (10, 11) *Axoprunum pierinae* (Clark and Campbell, 1942) group: (10) ODP 1260A-13R-5W, 55–57 cm; (11) ODP 1260A-15R-1W, 55–57 cm.(12) *Saturnalis kennetti* Dumitrică, 1985: ODP 1260A-9R-3W, 55–57 cm. All scale bars equal 50 μm.

Order Nassellaria Ehrenberg, 1876 Superfamily Amphipyndacoidea Riedel, 1967a Family Amphipyndacidae Riedel, 1967a Genus *Amphipternis* Foreman, 1973

Type species.— *Lithocampe ? clava* Ehrenberg, 1874, p. 238 (unfigured); Ehrenberg, 1876, p. 76, pl. 4, fig. 2.

? Amphipternis articulatum (Ehrenberg, 1874)

Plate II.7, Figure 2

1874 Eucyrtidium articulatum Ehrenberg, p. 226.

1876 Eucyrtidium articulatum Ehrenberg – Ehrenberg, p. 70, pl. 11, figs. 2, 3.

1882a Lithostrobus articulatus (Ehrenberg) - Bütschli, p. 529.

1887 Dictyomitra (Dictyomitrella) articulata (Ehrenberg) – Haeckel, p. 1476.

? 1887 Stichocapsa compacta Haeckel, p. 1517, pl. 76, fig. 3.

1973 Amphipternis clava (Ehrenberg) – Foreman, p. 430, pl. 7, figs. 16, 17, pl. 9, figs. 2.

1976 Amphipternis clava (Ehrenberg) – Dzinoridze et al., pl. 29, fig. 11.

1977 Amphipternis clava (Ehrenberg) – Riedel and Sanfilippo, pl. 6, fig. 6.

1978 Amphipternis clava (Ehrenberg) – Johnson, p. 784, pl. 1, fig. 12.

1978 Amphipternis clava (Ehrenberg) – Foreman, p. 784, pl. 1, fig. 12.

1999 Amphipternis clava (Ehrenberg) – Kozlova, pl. 3, fig. 11.

2008 Amphipternis clava (Ehrenberg) – Jackett et al., p. 47, pl. 3, figs. 20, 21.

2009 Eucyrtidium articulatum Ehrenberg – Ogane et al., pl. 22, figs. 1a–1f.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Amphipternis clava (Ehrenberg, 1874)

Plate II.7, Figure 1

1874 *Lithocampe ? Clava* [sic] Ehrenberg, p. 238.

1876 Lithocampe ? Clava [sic] Ehrenberg – Ehrenberg, p. 76, pl. 4, fig. 2.

1882a Eucyrtidium Clava [sic] (Ehrenberg) – Bütschli, p. 529.

1882b Eucyrtidium clava (Ehrenberg) – Bütschli, pl. 30, fig. 22.

1887 Lithocampe (Lithocampium) clava Ehrenberg – Haeckel, p. 1507.

2009 Lithocampe clava Ehrenberg – Ogane et al., pl. 25, figs. 2a–2c.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Superfamily Archaeodictyomitroidea Pessagno, 1976

Family Archaeodictyomitridae Pessagno, 1976

Genus Dictyomitra Zittel, 1876

Type species.— Dictyomitra multicostata Zittel, 1876, p. 81, pl. 2, fig. 2.

Dictyomitra parva (Kim, 1992)

Plate II.7, Figure 3

- 1974 Theoperid gen. et sp. indet. Johnson, 1974, pl. 3, fig. 12 (part).
- 1974 sp. cf. *Lithomitra elizabethae* Clark and Campbell Nigrini, p. 1070, pl. 1M, figs. 14– 17, pl. 4, figs. 6, 7.
- 1977 Siphocampe elizabethae (Clark and Campbell) Nigrini, p. 256, pl. 3, fig. 6.
- 1992 Archaeodictyomitra ? sp. Takemura, p. 744, pl. 3, figs. 1, 2.
- 1992 Eucyrtidium parva Kim, p. 43, pl. 2, figs. 7, 8.
- 1995 Dictyomitra amygdala Shilov, p. 126, pl. 1, fig. 4-6b.
- 1997 *Siphocampe*? "*elizabethae*" (Clark and Campbell) Hollis et al., p. 55, pl. 4, figs. 21–26.
- 1999 Siphocampe minuta (Clark and Campbell) Kozlova, p. 141, pl. 18, fig. 9, pl. 24, fig. 9.
- 1999 Siphocampe ? pusilla Kozlova, p. 141, pl. 18, fig. 10 (part).
- 2002 Siphocampe ? elizabethae (Clark and Campbell) Apel et al., p. 21, pl. P9, fig. 18.
- 2009b Dictyoprora ? amygdala (Shilov) Suzuki et al., p. 263, pl. 18, fig. 3.
- 2020 Siphocampe ? amygdala (Shilov) Hollis et al., pl. 8, figs. 11, 12.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

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, 1854a, pl. 22, fig. 27.

Eucyrtidium montiparum Ehrenberg, 1874

Plate II.7, Figure 4

1874 *Eucyrtidium montiparum* Ehrenberg, p. 230.

- 1876 Eucyrtidium montiparum Ehrenberg Ehrenberg, p. 72, pl. 9, fig. 11.
- 1882a Eucyrtidium montiparum Ehrenberg Bütschli, p. 529.
- 1887 Eucyrtidium (Artocyrtis) montiparum Ehrenberg Haeckel, p. 1493.
- 1974 Theoperid gen. et sp. indet. Johnson, pl. 4, figs. 13, 14 (part).
- 1997 Eucyrtidium montiparum Ehrenberg Hollis et al., p. 61, pl. 5, figs. 25–27.
- 1999a Eucyrtidium ventriosum O'Connor, p. 21, pl. 3, fig. 17–21b, pl. 6, fig. 28a–31.
- not 2006 *Eucyrtidium montiparum* Ehrenberg Funakawa et al., p. 23, pl. P5, figs. 10a– 10b.
- 2006 Eucyrtidium sp. F Funakawa et al., p. 23, pl. P6, figs. 1a-2b (part).
- 2009 Eucyrtidium montiparum Ehrenberg Ogane et al., pl. 1, figs. 6a-6e (part).
- 2020 Eucyrtidium montiparum Ehrenberg Hollis et al., pl. 10, fig. 4.
- 2021 Eucyrtidium montiparum Ehrenberg de Souza et al., p. 15, pl. 3, figs. 1a, 1b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Eucyrtidium ? microporum Ehrenberg, 1874

Plate II.7, Figure 5

- 1874 Eucyrtidium microporum Ehrenberg, p. 230.
- 1876 Eucyrtidium microporum Ehrenberg Ehrenberg, p. 72, pl. 11, fig. 20.
- 1882a Lithostrobus microporus (Ehrenberg) Bütschli, p. 529.
- 1887 Lithostrobus (Cyrtostrobus) microporus (Ehrenberg) Haeckel, p. 1474.
- 1972 *Stichopodium ? microporum* (Ehrenberg) Petrushevskaya and Kozlova, p. 548, pl. 25, figs. 4–6.
- 2006 Stichopodium ? microporum (Ehrenberg) Funakawa et al., p. 37, pl. P13, figs. 3a-4b.
- 2009 Eucyrtidium microporum Ehrenberg Ogane et al., pl. 6, figs. 5a-5c, pl. 85, figs. 5a-5f.
- 2020 Eucyrtidium microporum Ehrenberg Hollis et al., pl. 10, fig. 3.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Family Lithostrobidae Petrushevskaya, 1975

Genus Lithostrobus Bütschli, 1882a

Type species.— *Eucyrtidium argus* Ehrenberg, 1874, p. 225 (unfigured); Ehrenberg, 1876, p. 70, pl. 9, fig. 1.

Lithostrobus argus (Ehrenberg, 1874)

Plate II.7, Figure 6

- 1874 Eucyrtidium Argus [sic] Ehrenberg, p. 225.
- 1876 Eucyrtidium Argus [sic] Ehrenberg Ehrenberg, p. 70, pl. 9, fig. 1.
- 1882a Lithostrobus Argus [sic] (Ehrenberg) Bütschli, p. 529.
- 2009 Eucyrtidium argus Ehrenberg Ogane et al., pl. 48, figs. 8a-8f.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Lithostrobus picus Ehrenberg, 1874 Plate II.7, Figures 7, 8

1874 *Eucyrtidium Picus* [sic] Ehrenberg, p. 232.

1876 Eucyrtidium Picus [sic] Ehrenberg – Ehrenberg, p. 72, pl. 11, fig. 1.

1882a Lithostrobus Picus [sic] (Ehrenberg) - Bütschli, p. 529.

not 1976 *Eucyrtidium ? picus* Ehrenberg – Dzinoridze et al., pl. 29, fig. 9.

1977 Artostrobiid gen. et sp. indet. Riedel and Sanfilippo, pl. 9, fig. 16.

2009 Eucyrtidium picus Ehrenberg – Ogane et al., pl. 86, figs. 6a–6g

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Superfamily Plectopyramidoidea Haecker, 1908

Family Plectopyramididae Haecker, 1908

Genus Bathropyramis Haeckel, 1882

Type species.— Bathropyramis (Acropyramis) acephala Haeckel, 1887, p. 1159 (unfigured).

Bathropyramis scalaris (Ehrenberg, 1874)

Plate II.7, Figure 9

1874 Cornutella scalaris Ehrenberg, p. 221.

1876 Cornutella scalaris Ehrenberg – Ehrenberg, p. 68, pl. 2, fig. 1.

1887 Sethopyramis (Sestropyramis) scalaris (Ehrenberg) – Haeckel, p. 1253.

? 1887 Sethopyramis (Cephalopyramis) enneactis Haeckel, p. 1254, pl. 56, fig. 7.

1887 Plectopyramis (Hexapleuris) magnifica Haeckel, p. 1257.

- 1945 Sethopyramis (Sestropyramis) pulcherrima Clark and Campbell, p. 39, pl. 10, fig. 3.
- 1972 Bathropyramis scalaris (Ehrenberg) Petrushevskaya and Kozlova, p. 551, pl. 31, fig.
 6.

2009 Cornutella scalaris Ehrenberg – Ogane et al., pl. 21, 6a-6d.

2020 Cinclopyramis scalaris (Ehrenberg) – Hollis et al., pl. 8, figs. 28, 29.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Cornutella Ehrenberg, 1839

Type species.— *Cornutella clathrata* Ehrenberg, 1839, p. 129; Ehrenberg, 1854a, pl. 22, fig. 39a.

Cornutella californica Campbell and Clark, 1944

Plate II.7, Figure 10

- 1944 Cornutella (Cornutissa) californica Campbell and Clark, p. 22, pl. 7, fig. 42.
- 1944 *Cornutella (Cornutissa) californica* var. brevis Campbell and Clark, p. 23, pl. 7, figs. 33, 34, 43.
- 1973 Cornutella californica Clark and Campbell Dumitrică, p. 788, pl. 10, fig. 1.
- 1976 *Cornutella* sp. aff. *C. californica* Clark and Campbell Bjørklund, p. 1124, pl. 23, figs. 23, 24.
- 1976 Cornutella sp. aff. C. californica Clark and Campbell Dzinoridze et al., pl. 32, fig. 30.

- 1992 Cornutella californica Clark and Campbell Blome, p. 644, pl. 3, figs. 13, 24.
- 1996 Cornutella sp. aff. C. californica Clark and Campbell Hull, p. 138, pl. 5, fig. 6.
- 1996 Cornutella profunda Ehrenberg group Hull, p. 138, pl. 5, fig. 17.
- 1996 Cornutella sp. Hull, p. 138, pl. 5, fig. 7.
- 1999a Cornutella californica Clark and Campbell O'Connor, p. 31, pl. 9, fig. 12.
- 1999 Cornutella californica Clark and Campbell Kozlova, p. 173, pl. 3, fig. 9.
- 2002 Cornutella californica Clark and Campbell Hollis, pl. 6, fig. 5 (part).
- 2002 Cornutella profunda Ehrenberg group Apel et al., p. 17, pl. P6, fig. 15 (part).
- 2013 Cornutella profunda Ehrenberg Kochhann et al., p. 541, pl. 3, fig. A.
- 2021 Cornutella profunda Ehrenberg de Souza et al., p. 15, pl. 2, fig. 15.

Cornutella circularis Ehrenberg, 1874

Plate II.7, Figure 12

- 1874 Cornutella circularis Ehrenberg, p. 221.
- 1876 Cornutella circularis Ehrenberg Ehrenberg, p.68, pl. 2, fig. 4.
- 1882a Ceratocyrtis circularis (Ehrenberg) Bütschli, p. 536.
- 1887 Cornutella (Cornutissa) circularis Ehrenberg Haeckel, p. 1181.
- 1978 Lithapium mitra (Ehrenberg) Riedel and Sanfilippo, p. 69, pl. 6, fig. 2 (part).
- 2015 Cornutella sp. A Kamikuri, pl. 13, figs. 28a, 28b.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Cornutella clava Petrushevskaya in Petrushevskaya and Kozlova, 1972

Plate II.7, Figure 11

- 1972 *Cornutella clava* Petrushevskaya *in* Petrushevskaya and Kozlova, p. 551, pl. 30, figs. 11, 16.
- 1977 Cornutella sp. Riedel and Sanfilippo, pl. 15, fig. 4 (part).
- Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Cornutella stiligera Ehrenberg, 1854a

Plate II.7, Figure 13

- 1854a Cornutella stiligera Ehrenberg, pl. 36, fig. 4.
- 1876 Cornutella stiligera Ehrenberg Ehrenberg, p. 68, pl. 2, fig. 3.
- 1882a Cornutella stiligera Ehrenberg Bütschli, p. 537.
- 1887 Cornutella (Cornutellium) stiligera Ehrenberg Haeckel, p. 1181.
- 1972 Cornutella stiligera Ehrenberg group Petrushevskaya and Kozlova, p. 551, pl. 30, figs.
 14, 15.
- 1975 Cornutella profunda Ehrenberg Ling, p. 728, pl. 9, figs. 5-8.
- 1976 Cornutella longisetta [sic] Ehrenberg Dzinoridze et al., pl. 32, fig. 31.
- 1977 Cornutella sp. Riedel and Sanfilippo, pl. 7, fig. 14, pl. 15, fig. 3 (part).
- 2002 Cornutella profunda Ehrenberg group Apel et al., p. 17, pl. P6, figs. 13, 14 (part).
- 2009 Cornutella stiligera Ehrenberg Ogane et al., pl. 7, figs. 6a, 6b, pl. 21, figs. 8a–9c.



Plate II.7. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic). (1) *Amphipternis clava* (Ehrenberg, 1874): ODP 1260A-20R-1W, 55–57 cm. (2) ? *Amphipternis articulatum* (Ehrenberg, 1874): ODP 1260A-9R-2W, 55–57 cm. (3) *Dictyomitra parva* (Kim, 1992): ODP 1260A-18R-2W, 55–57 cm. (4) *Eucyrtidium montiparum* Ehrenberg, 1874: ODP 1260A-6R-1W, 55–57 cm. (5) *Eucyrtidium* ? *microporum* Ehrenberg, 1874: ODP 1260A-18R-2W, 55–57 cm. (6) *Lithostrobus argus* (Ehrenberg, 1874): ODP 1260A-11R-7W, 55–57 cm. (7, 8) *Lithostrobus picus* Ehrenberg, 1874: (7) ODP 1260A-17R-2W, 55–57 cm; (8) ODP 1260A-13R-4W, 55–57 cm. (10) *Cornutella californica* Campbell and Clark, 1944: ODP 1260A-13R-6W, 54–56 cm. (11) *Cornutella clava* Petrushevskaya *in* Petrushevskaya and Kozlova, 1972: ODP 1051A-11H-5W, 59–61 cm. (12) *Cornutella circularis* Ehrenberg, 1874: ODP 1260A-12R-1W, 55–57 cm. All scale bars equal 50 μm.

2009b *Cornutella profunda* Ehrenberg – Suzuki et al., p. 263, pl. 22, figs. 12a, 12b. Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Superfamily Carpocanioidea Haeckel, 1882

Family Carpocaniidae Haeckel, 1882 sensu Sugiyama, 1998

Genus Carpocanium Ehrenberg, 1846

Type species.— *Lithocampe solitaria* Ehrenberg, 1839, p. 130 (unfigured); Ehrenberg, 1854a, pl. 22, fig. 28.

Carpocanium azyx (Sanfilippo and Riedel, 1973)

Plate II.8, Figure 1

1973 Carpocanistrum ? azyx Sanfilippo and Riedel, p. 530, pl. 35, fig. 9.

1984 Carpocanistrum ? azyx Sanfilippo and Riedel – Saunders et al., p. 412, pl. 5, figs. 2, 3.

- 1984 Cryptoprora ornata Ehrenberg Saunders et al., p. 412, pl. 5, fig. 4.
- 1992 Carpocanistrum azyx Sanfilippo and Riedel Riedel and Sanfilippo, pl. 11, fig. 5.
- 1978 Carpocanistrum azyx Sanfilippo and Riedel Riedel and Sanfilippo, p. 67, pl. 4, fig. 5.
- 1992 Cryptocarpium azyx (Sanfilippo and Riedel) Sanfilippo and Riedel, p. 6, pl. 2, fig. 21
- 2000 *Cryptocarpium azyx* (Sanfilippo and Riedel) Nigrini and Sanfilippo, p. 72, pl. 2, figs. 4–6.
- 2006 Cryptocarpium azyx (Sanfilippo and Riedel) Funakawa et al., p. 28, pl. P9, figs. 5a, 5b.
- 2012 Cryptocarpium azyx (Sanfilippo and Riedel) Moore and Kamikuri, p. 5, pl. P2, fig. 1.
- 2012 Cryptocarpium azyx (Sanfilippo and Riedel) Kamikuri and Wade, pl. 1, fig. 14.

2012a Cryptocarpium azyx (Sanfilippo and Riedel) – Kamikuri et al., p. 96, pl. 3, figs. 9a, 9b.

- 2015 Cryptocarpium azyx (Sanfilippo and Riedel) Kamikuri, pl. 12, figs. 17a–18.
- not 2020 *Cryptocarpium azyx* (Sanfilippo and Riedel) Hollis et al., pl. 17, figs. 6a, 6b.

Remarks. The combination used here is derived from O'Dogherty et al. (2021). Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Genus *Carpocanopsis* Riedel and Sanfilippo, 1971 *Type species.— Carpocanopsis cingulatum* Riedel and Sanfilippo, 1971, p. 1597, pl. 8, fig. 8.

Carpocanopsis ballisticum O'Connor, 1999a

Plate II.8, Figure 2

1999a *Carpocanopsis ballisticum* O'Connor, p. 11, pl. 2, figs. 1–5, pl. 5, figs. 25a–28. Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Carpocanopsis ornata (Ehrenberg, 1874)

Plate II.8, Figure 3

1874 *Cryptoprora ornata* Ehrenberg, p. 222.

1876 Cryptoprora ornata Ehrenberg – Ehrenberg, p. 68, pl. 5, fig. 8.

1882a Cryptoprora ornata Ehrenberg – Bütschli, p. 535.

1882b Cryptoprora ornata Ehrenberg - Bütschli, pl. 31, fig. 8.

1887 Alacorys ornata Ehrenberg – Haeckel, p. 1375.

1974 Cryptoprora ornata Ehrenberg – Johnson, p. 550, pl. 5, fig. 9.

1992 Cryptocarpium ornata (Ehrenberg) – Sanfilippo and Riedel, p. 6, 36, pl. 2, figs. 18–20.

1997 Cryptocarpium ornatum (Ehrenberg) – Hollis et al., p. 66, pl. 6, figs. 24, 25 (part).

? 2006 Cryptocarpium ornatum (Ehrenberg) – Funakawa et al., p. 28, pl. P9, figs. 8a, 8b (part).

2009 Cryptoprora ornata Ehrenberg – Ogane et al., pl. 6, figs. 2a–2c, pl. 83, figs. 5a–6d.

not 2012 *Cryptocarpium ornatum* (Ehrenberg) – Moore and Kamikuri, p. 6, pl. P2, figs. 2–4.

? 2012 Cryptocarpium ornatum (Ehrenberg) - Kamikuri and Wade, pl. 1, figs. 4a, 4b.

? 2015 Cryptocarpium ornatum (Ehrenberg) - Kamikuri, pl. 12, figs. 21a, 21b.

2017 Cryptocarpium ornatum (Ehrenberg) – de Souza et al., pl. 1, fig. 5.

2020 Cryptocarpium ornatum (Ehrenberg) – Hollis et al., pl. 17, figs. 9a, 9b.

2021 Cryptocarpium ornatum (Ehrenberg) – de Souza et al., p. 15, pl. 3, fig. 17a, 17b.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Superfamily Artostrobioidea Riedel, 1967a

Family Artostrobiidae Riedel, 1967a sensu Sugiyama, 1998

Genus Botryostrobus Haeckel, 1887 emend. Nigrini, 1977

Type species.— *Lithostrobus (Botryostrobus) botryocyrtis* Haeckel, 1887, p. 1475, pl. 79, figs. 18, 19.

Botryostrobus joides Petrushevskaya, 1975

Plate II.8, Figure 4

1972 Botryostrobus sp. P Petrushevskaya and Kozlova, p. 539, pl. 24, figs. 8–11

- 1975 Botryostrobus joides Petrushevskaya, p. 585, pl. 10, fig. 37.
- 1976 Botryostrobus joides Petrushevskaya Bjørklund, pl. 23, figs. 7–14.
- not 1976 Botryostrobus joides Petrushevskaya Dzinoridze et al., pl. 29, fig. 8.
- 1979 Botryostrobus joides narratus Petrushevskaya and Kozlova, p. 148, fig. 361.
- 1989 *Botryostrobus joides* Petrushevskaya group Lazarus and Pallant, p. 361, pl. 4, fig. 13 (part).
- 1989 Nassellarian gen. et sp. indet. Lazarus and Pallant, pl. 4, figs. 17, 18.
- 1996 Botryostrobus joides Petrushevskaya Hull, p. 137, pl. 4, figs. 5, 6, 20.
- 1997 Spirocyrtis sp. A Hollis et al., p. 56, pl. 4, figs. 33–35.
- 2002 Spirocyrtis greeni O'Connor Apel et al., p. 21, pl. P9, fig. 1.
- 2003 Botryostrobus joides Petrushevskaya Sanfilippo and Fourtanier, p. 11, pl. P1, figs.3, 12.
- 2009b Lithostrobus cyrtoceras Haeckel Suzuki et al., p. 259, pl. 21, fig. 16.
- 2020 Spirocyrtis greeni O'Connor Hollis et al., pl. 8, figs. 13a, 13b.

not 2020 Spirocyrtis joides (Petrushevskaya) – Hollis et al., pl. 8, figs. 14a, 14b.

2021 Botryostrobus joides Petrushevskaya – de Souza et al., p. 15, pl. 2, fig. 12.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Botryostrobus kerguelensis Caulet, 1991

Plate II.8, Figure 5

1985 Botryostrobus sp. Caulet, pl. 6, fig. 2.

- 1991 Botryostrobus kerguelensis Caulet, p. 535, pl. 3, figs. 6-8.
- 2002 Botryostrobus kerguelensis Caulet Apel et al., p. 17, pl. P9, fig. 2.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Buryella Foreman, 1973

Type species.— Buryella tetradica Foreman, 1973, p. 433, pl. 9, fig. 14.

Buryella ? apiculata Tetard et al., 2023

Plate II.8, Figure 8

2023 *Buryella apiculata* Tetard et al., p. 8, figs. 4k, 4l, 5k–5o. Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic)

Buryella clinata Foreman, 1973

Plate II.8, Figure 6

1970 Lithocampe sp. Cita et al., p. 404, pl. 2, fig. M.

1970 Lithocampium sp. Riedel and Sanfilippo, p. 533, pl. 10, fig. 8.

1973 Buryella clinata Foreman, p. 433, pl. 8, figs. 1–3, pl. 9, fig. 19.

- 1974 Buryella clinata Foreman Nigrini, p. 1067, pl. 4, fig. 1.
- 1975 Buryella clinata Foreman Foreman, p. 620, pl. 9, figs. 35, 36.
- 1977 Buryella clinata Foreman Riedel and Sanfilippo, pl. 7, fig. 16.

1978 Buryella clinata Foreman – Weaver and Dinkelman, p. 867, pl. 8, figs. 6, 7.

1978 Buryella clinata Foreman - Riedel and Sanfilippo, p. 65, pl. 3, fig. 4.

1985 Buryella clinata Foreman – Sanfilippo et al., p. 668, figs. 14.1a–14.1f.

1987 Buryella clinata Foreman – Nishimura, p. 720, pl. 2, figs. 5, 6.

1998a Buryella clinata Foreman - Sanfilippo and Nigrini, p. 272, pl. 13.1, figs. 5, 6.

1999 Buryella clinata Foreman – Kozlova, p. 135, pl. 24, fig. 11, pl. 44, fig. 20.

2008 Buryella clinata Foreman – Jackett et al., p. 48, pl. 2, fig. 17.

2015 Buryella clinata Foreman – Kamikuri, pl. 12, fig. 9.

2017 Buryella clinata Foreman – de Souza et al., pl. 2, figs. 3a, 3b.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Buryella tetradica Foreman, 1973

Plate II.8, Figure 7

1971 Lithocampium sp. A Riedel and Sanfilippo, p. 1594, pl. 7, fig. 12.

1972 Lithocampium sp. A Benson, p. 1093, pl. 2, figs. 8, 9.

1973 Buryella tetradica Foreman, p. 433, pl. 8, figs. 4, 5, pl. 9, figs. 13, 14.

1975 Buryella tetradica Foreman – Petrushevskaya, pl. 8, fig. 23.

1978 Buryella tetradica Foreman – Johnson, p. 784, pl. 1, fig. 11.

1978 Buryella tetradica Foreman – Riedel and Sanfilippo, p. 65, pl. 3, fig. 5.

1978 Buryella tetradica Foreman – Foreman, p. 784, pl. 1, fig. 11.

1980 Buryella tetradica Foreman – Westberg et al., p. 431, pl. 1, fig. 9.

1985 Buryella tetradica Foreman – Sanfilippo et al., p. 668, figs. 14.3a, 14.3b.

1985 Buryella tetradica Foreman – Riedel and Sanfilippo, pl. 5, fig. 14.

1987 Buryella tetradica Foreman – Nishimura, p. 721, pl. 2, fig. 8.

1992 Buryella tetradica Foreman – Nishimura, p. 329, pl. 10, fig. 12.

1992 Buryella tetradica Foreman – Kim, p. 42, pl. 1, figs. 12, 13.

1993 Buryella tetradica Foreman – Hull, p. 12, pl. 7, fig. 2.

not 1993 Buryella tetradica Foreman – Vitukhin, p. 84, pl. 1, fig. 4.

1995 Buryella tetradica Foreman – Strong et al., p. 208, figs. 8N, 9Q, 9R.

1997 Buryella tetradica Foreman – Hollis et al., p. 81, pl. 21, figs. 16–19.

1998a Buryella tetradica Foreman – Sanfilippo and Nigrini, p. 272, pl. 13.1, figs. 8, 9.

1999 *Buryella tetradica* Foreman – Kozlova, p. 136, pl. 7, fig. 8, pl. 8, fig. 16, pl. 14, fig. 11, pl. 44, fig. 25.

2000 ? Buryella tetradica Foreman – Nigrini and Sanfilippo, p. 72, pl. 3, fig. 3.

2001 Buryella tetradica Foreman – Sanfilippo and Blome, p. 210.

2001 Buryella tetradica Foreman var. A - Sanfilippo and Blome, p. 210, figs. 8d, 8e.

2002 Buryella tetradica tetradica Foreman – Hollis, p. 300, pl. 4, figs. 13, 14.

2008 Buryella tetradica Foreman s.s. – Jackett et al., p. 48, pl. 2, fig. 20.

2008 Buryella tetradica Foreman var. A – Jackett et al., p. 48, pl. 2, fig. 21.

2015 Buryella tetradica Foreman – Kamikuri, pl. 12, fig. 12.

2017 Buryella tetradica Foreman – de Souza et al., pl. 2, figs. 4a, 4b.

2020 Buryella tetradica Foreman – Hollis et al., pl. 8, fig. 3.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Dictyoprora Haeckel, 1887

Type species.— Dictyocephalus (Dictyoprora) amphora Haeckel, 1887, p. 1305, pl. 62, fig. 4.

Dictyoprora armadillo (Ehrenberg, 1874) group

Plate II.8, Figure 9

- 1874 *Eucyrtidium Armadillo* [sic] Ehrenberg, p. 225.
- 1876 Eucyrtidium Armadillo [sic] Ehrenberg Ehrenberg, p. 70, pl. 9, fig. 10.
- 1882a Eucyrtidium Armadillo [sic] Ehrenberg Bütschli, p. 528.
- 1887 Sethocorys armadillo (Ehrenberg) Haeckel, p. 1302.
- 1971 *Theocampe armadillo* (Ehrenberg) group Riedel and Sanfilippo, p. 1601, pl. 3E, figs. 3, 5 (part).
- 1974 Theocampe armadillo (Ehrenberg) group Nigrini, p. 1070, pl. 1M, fig. 6 (part).
- 1977 Theocampe armadillo (Ehrenberg) group Riedel and Sanfilippo, pl. 11, fig. 8 (part).
- 1977 Dictyoprora armadillo (Ehrenberg) Nigrini, p. 250, pl. 4, fig. 4.
- 1981 Dictyoprora armadillo (Ehrenberg) De Wever, p. 511, pl. 4, fig. 5.
- 2005 Dictyoprora armadillo (Ehrenberg) group Nigrini et al., p. 31, pl. 6, fig. 9
- 2006 Dictyoprora armadillo (Ehrenberg) Funakawa et al., p. 17, pl. P2, figs. 3a-4b.
- 2009 Eucyrtidium armadillo Ehrenberg Ogane et al., pl. 83, figs. 1a–2b.
- 2012 Dictyoprora armadillo (Ehrenberg) group Moore and Kamikuri, p. 6, pl. P2, fig. 5.
- 2015 Dictyoprora armadillo (Ehrenberg) Kamikuri, pl. 12, figs. 7 (part).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Dictyoprora crassiceps (Ehrenberg, 1874) group

Plate II.8, Figure 14

- 1874 Eucyrtidium crassiceps Ehrenberg, p. 227.
- 1876 Eucyrtidium crassiceps Ehrenberg Ehrenberg, p. 70, pl. 11, fig. 4.
- 1887 Dictyocephalus (Dictyoprora) urceolus Haeckel, p. 1305, pl. 62, fig. 4.
- 1887 Dictyocephalus (Dictyoprora) crassiceps (Ehrenberg) Haeckel, p. 1306.
- 1971 Lithomitra sp. aff. L. lineata (Ehrenberg) group Riedel and Sanfilippo, pl. 3E, figs. 17, 18 (part).
- 1973 Theocampe urceolus (Haeckel) Foreman, p. 432, pl. 8, figs. 14–17, pl. 9, figs. 6, 7.
- 1977 Dictyoprora urceolus (Haeckel) Nigrini, p. 251, pl. 4, figs. 9, 10.
- 1981 Dictyoprora urceolus (Haeckel) De Wever, p. 511, pl. 4, fig. 14.
- 1987 Dictyoprora urceolus (Haeckel) Nishimura, p. 725, pl. 2, fig. 2 (part).
- 1992 Dictyoprora pirum (Ehrenberg) Takemura, p. 743, pl. 5, fig. 11.
- 1995 Theocampe urceolus (Haeckel) Strong et al., p. 209, fig. 10Q.
- 1997 Theocampe urceolus (Haeckel) Hollis et al., p. 56, pl. 4, figs. 36, 37.
- 2003 Dictyoprora urceolus (Haeckel) Sanfilippo and Fourtanier, p. 12, pl. P2, fig. 10 (part).
- 2008 Dictyoprora urceolus (Haeckel) Jackett et al., p. 52, pl. 3, fig. 17.
- 2020 Theocampe urceolus (Haeckel) Hollis et al., pl. 8, fig. 22.
- 2021 Dictyoprora urceolus (Haeckel) de Souza et al., p. 15, pl. 2, fig. 13.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Dictyoprora excellens (Ehrenberg, 1874) group

Plate II.8, Figures 11, 12

1874 Eucyrtidium excellens Ehrenberg, p. 228.

1876 Eucyrtidium excellens Ehrenberg – Ehrenberg, p. 70, pl. 10, fig. 2.

1882a Eucyrtidium excellens Ehrenberg – Bütschli, pl. 33, figs. 31a, 31b.

1882b Eucyrtidium excellens Ehrenberg – Bütschli, pl. 30, fig. 18.

1887 Dictyocephalus (Dictyoprora) amphora Haeckel, p. 1305, pl. 62, fig. 4.

1887 Dictyocephalus (Dictyoprora) excellens (Ehrenberg) – Haeckel, p. 1306.

1973 *Theocampe amphora* (Haeckel) group – Foreman, p. 431, pl. 8, figs. 7, 9–13.

1974 Theocampe amphora (Haeckel) group - Nigrini, p. 1070, pl. 1M, figs. 2-5 (part).

1977 Theocampe amphora (Haeckel) group – Riedel and Sanfilippo, pl. 9, fig. 13 (part).

1977 Dictyoprora amphora (Haeckel) group – Nigrini, p. 250, pl. 4, figs. 1, 2

1986 Dictyoprora amphora (Haeckel) group – Riedel and Sanfilippo, pl. 4, fig. 8.

? 1987 Dictyoprora amphora (Haeckel) – Nishimura, p. 725, pl. 2, fig. 3.

not 1989 ? *Dictyoprora amphora* (Haeckel) – Lazarus and Pallant, p. 363, pl. 6, figs. 8, 9.

? 1999 Buryella longa Kozlova – Kozlova, p. 136, pl. 23, fig. 13.

not 2006 *Dictyoprora amphora* (Haeckel) group – Funakawa et al., p. 16, pl. P2, figs. 1a– 2b.

2008 Dictyoprora amphora (Haeckel) – Jackett et al., p. 52, pl. 3, fig. 18.

2009 Eucyrtidium gemmatum Ehrenberg – Ogane et al., pl. 48, figs. 1a–1c (part).

2009 Eucyrtidium excellens Ehrenberg – Ogane et al., pl. 48, figs. 2a–4d (part).

2020 Theocampe amphora (Haeckel) – Hollis et al., pl. 8, figs. 20a, 20b.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Dictyoprora gibsoni O'Connor, 1994

Plate II.8, Figure 16

1971 *Lithomitra* sp. aff. *L. lineata* (Ehrenberg) group – Riedel and Sanfilippo, pl. 3E, fig. 15 (part).

1981 Dictyoprora pirum (Ehrenberg) – De Wever, p. 511, pl. 4, fig. 7.

1994 Dictyoprora gibsoni O'Connor, p. 338, pl. 1, figs. 5, 6, 8, pl. 3, figs. 4–7.

1997 Theocampe urceolus (Haeckel) – Hollis et al., p. 56, pl. 4, fig. 36 (part).

? 2003 *Dictyoprora urceolus* (Haeckel) – Sanfilippo and Fourtanier, p. 12, pl. P2, figs. 11, 12 (part).

2015 Dictyoprora gibsoni O'Connor - Kamikuri, pl. 12, fig. 13.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Dictyoprora mongolfieri (Ehrenberg, 1854a)

Plate II.8, Figure 13

1854a Eucyrtidium Mongolfieri [sic] Ehrenberg, pl. 36, fig. 18.

1862 Eucyrtidium Mongolfieri [sic] Ehrenberg – Bury, p. 5, fig. 2. ? 1874 Eucyrtidium gemmatum Ehrenberg, p. 229. 1874 Eucyrtidium Mongolfieri [sic] Ehrenberg – Ehrenberg, p. 230. ? 1876 Eucyrtidium gemmatum Ehrenberg – Ehrenberg, p. 70, pl. 10, fig. 6. 1876 Eucyrtidium Mongolfieri [sic] Ehrenberg – Ehrenberg, p. 72, pl. 10, fig. 3. ? 1882a Eucyrtidium gemmatum Ehrenberg - Bütschli, p. 528. 1882a Eucyrtidium Mongolfieri [sic] Ehrenberg - Bütschli, p. 528. 1887 Sethamphora (Dictyoprona) mongolfieri (Ehrenberg) – Haeckel, p. 1251. Sethamphora (Dictyoprona) costata Haeckel, p. 1251, pl. 62, fig. 3. 1887 ? 1887 Theocampe (Theocamptra) gemmata (Ehrenberg) – Haeckel, p. 1425. 1887 Theocampe (Theocamptra) costata Haeckel, p. 1426, pl. 66, fig. 24. 1944 Dictyocephalus (Dictyoprora) sp. Campbell and Clark, p. 28, pl. 7, fig. 20. 1957a Sethamphora mongolfieri (Ehrenberg) - Riedel, p. 260, pl. 63, fig. 6. 1957b Sethamphora mongolfieri (Ehrenberg) - Riedel, p. 81, pl. 1, fig. 7. 1970 Sethamphora mongolfieri (Ehrenberg) - Cita et al., p. 401, pl. 1, fig. F. 1970 Theocampe mongolfieri (Ehrenberg) - Riedel and Sanfilippo, p. 536, pl. 12, fig. 9. 1971 Theocampe mongolfieri (Ehrenberg) – Riedel and Sanfilippo, p. 1601, pl. 3E, fig. 13. 1971 Theocampe mongolfieri (Ehrenberg) – Moore, p. 744, pl. 2, fig. 3. 1973 Theocampe mongolfieri (Ehrenberg) - Foreman, p. 432, pl. 8, fig. 6, pl. 9, fig. 17. 1974 Theocampe mongolfieri (Ehrenberg) - Nigrini, p. 1070, pl. 1M, figs. 7-10, pl. 2E, fig. 9. 1974 Theocampe mongolfieri (Ehrenberg) – Johnson, p. 552, pl. 2, figs. 3, 5, pl. 5, fig. 1. 1975 Theocampe amphora (Haeckel) group - Ling, p. 732, pl. 13, figs. 14. 1975 Theocampe mongolfieri (Ehrenberg) - Ling, p. 732, pl. 13, figs. 16, 17. 1977 Theocampe mongolfieri (Ehrenberg) – Riedel and Sanfilippo, pl. 8, fig. 7. 1977 Theocampe amphora (Haeckel) group - Riedel and Sanfilippo, pl. 9, fig. 14 (part). 1977 Dictyoprora mongolfieri (Ehrenberg) - Nigrini, p. 250, pl. 4, fig. 7 Theocampe mongolfieri (Ehrenberg) - Riedel and Sanfilippo, p. 76, pl. 9, fig. 13. 1978 1981 Dictyoprora mongolfieri (Ehrenberg) – De Wever, p. 511, pl. 4, figs. 8–10. 1986 Dictyoprora mongolfieri (Ehrenberg) – Riedel and Sanfilippo, pl. 4, fig. 9. Dictyoprora mongolfieri (Ehrenberg) - Takemura, p. 743, pl. 7, fig. 12. 1992 1995 Dictyoprora mongolfieri (Ehrenberg) – Shilov, p. 126, pl. 2, fig. 6. 1995 Theocampe mongolfieri (Ehrenberg) – Strong et al., p. 209, fig. 10P. 2000 Dictyoprora mongolfieri (Ehrenberg) - Nigrini and Sanfilippo, p. 72, pl. 1, fig. 10, pl. 2, fig. 9. 2006 Dictyoprora mongolfieri (Ehrenberg) – Funakawa et al., p. 17, pl. P2, figs. 5a-6b. 2009b Dictyoprora mongolfieri (Ehrenberg) - Suzuki et al., p. 263, pl. 18, figs. 2a, 2b. ? 2009 Eucyrtidium gemmatum Ehrenberg – Ogane et al., pl. 18, figs. 9a–9e (part). 2012 Dictyoprora mongolfieri (Ehrenberg) – Moore and Kamikuri, p. 6, pl. P2, fig. 6. 2012 Dictyoprora mongolfieri (Ehrenberg) – Kamikuri and Wade, pl. 1, fig. 15. 2012a Dictyoprora mongolfieri (Ehrenberg) – Kamikuri et al., p. 98, pl. 3, figs. 6a, 6b. 2012b Dictyoprora mongolfieri (Ehrenberg) - Kamikuri et al., p. 3, pl. P1, fig. 9. 2015 Dictyoprora mongolfieri (Ehrenberg) - Kamikuri, pl. 12, figs. 15, 16. 2017 Dictyoprora mongolfieri (Ehrenberg) – de Souza et al., pl. 1, figs. 4a, 4b.



Plate II.8. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic). (1) Carpocanium azyx (Sanfilippo and Riedel, 1973): ODP 1051A-4H-5W, 56-58 cm. (2) Carpocanopsis ballisticum O'Connor, 1999a: ODP 1051A-18X-5W, 54–56 cm. (3) Carpocanopsis ornata (Ehrenberg, 1874): ODP 1260A-17R-2W, 55-57 cm. (4) Botryostrobus joides Petrushevskaya, 1975: ODP 1260A-9R-2W, 55-57 cm. (5) Botryostrobus kerguelensis Caulet, 1991: ODP 1051A-4H-5W, 56-58 cm. (6) Burvella clinata Foreman, 1973: ODP 1051A-38X-5W, 55-57 cm. (7) Buryella tetradica Foreman, 1973: ODP 1051A-6H-5W, 53-55 cm. (8) Buryella? apiculata Tetard et al., 2023: ODP 1260A-8R-5W, 54-56 cm. (9) Dictyoprora armadillo (Ehrenberg, 1874) group: ODP 1260A-6R-3W, 55-57 cm. (10) Dictyoprora ovata (Haeckel, 1887) group: ODP 1260A-9R-3W, 55-57 cm. (11, 12) Dictyoprora excellens (Ehrenberg, 1874) group: (11) ODP 1260A-12R-4W, 55–57 cm; (12) ODP 1260A-11R-7W, 55-57 cm. (13) Dictvoprora mongolfieri (Ehrenberg, 1854a): ODP 1260A-13R-5W, 55-57 cm. (14) Dictyoprora crassiceps (Ehrenberg, 1874) group: ODP 1260A-6R-3W, 55-57 cm. (15) Dictvoprora pirum (Ehrenberg, 1874): ODP 1051A-9H-5W, 53-55 cm. (16) Dictyoprora gibsoni O'Connor, 1994: ODP 1260A-11R-7W, 55-57 cm. All scale bars equal 50 µm.

2020 Theocampe mongolfieri (Ehrenberg) – Hollis et al., pl. 8, figs. 18a, 18b.

2020 Theocampe cf. mongolfieri (Ehrenberg) – Hollis et al., pl. 8, figs. 19a, 19b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Dictyoprora ovata (Haeckel, 1887) group

Plate II.8, Figure 10

- 1887 Theocorys (Theocoronium) ovata Haeckel, p. 1416, pl. 69, fig. 16.
- 1958 Theocorys sp. Göke, pl. 4, fig. 2.
- 1971 *Theocampe armadillo* (Ehrenberg) group Riedel and Sanfilippo, p. 1601, pl. 3E, figs.
 4, 6 (part).
- 1974 Theocampe amphora (Haeckel) group Nigrini, p. 1070, pl. 2E, fig. 7 (part).
- 1974 Theocampe armadillo (Ehrenberg) group Nigrini, p. 1070, pl. 2E, fig. 8 (part).
- 1974 Theocampe amphora (Haeckel) group Johnson, p. 552, pl. 4, fig. 2 (part).
- 1975 Theocampe armadillo (Ehrenberg) Ling, p. 732, pl. 13, fig. 15.
- 1977 Theocampe armadillo (Ehrenberg) group Riedel and Sanfilippo, pl. 11, fig. 9 (part).
- 2005 Dictyoprora cf. D. ovata (Haeckel) Nigrini et al., pl. P6, fig. 8.
- 2006 Dictyoprora ovata (Haeckel) Funakawa et al., p. 17, pl. P2, figs. 7a, 7b
- 2015 Dictyoprora armadillo (Ehrenberg) Kamikuri, pl. 12, figs. 4a, 4b (part).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Dictyoprora pirum (Ehrenberg, 1874)

Plate II.8, Figure 15

1874 *Eucyrtidium Pirum* [sic] Ehrenberg, p. 232.

1876 Eucyrtidium Pirum [sic] Ehrenberg – Ehrenberg, p. 72, pl. 10, fig. 14. 1882a Eucyrtidium Pirum [sic] Ehrenberg – Bütschli, p. 528. 1887 Theocampe (Theocampana) pirum (Ehrenberg) – Haeckel, p. 1423. 1971 Theocampe pirum (Ehrenberg) – Riedel and Sanfilippo, p. 1601, pl. 3E, figs. 10, 11. 1974 Theocampe pirum (Ehrenberg) – Nigrini, p. 1070, pl. 2E, fig. 10. 1974 Theocampe pirum (Ehrenberg) – Johnson, p. 552, pl. 6, fig. 14. 1974 Theocampe vanderhoofi Campbell and Clark – Johnson, pl. 1, fig. 9. 1975 Theocampe pirum (Ehrenberg) – Ling, p. 732, pl. 13, fig. 18. Theocampe pirum (Ehrenberg) - Riedel and Sanfilippo, pl. 11, fig. 7. 1977 1977 Dictyoprora pirum (Ehrenberg) – Nigrini, p. 251, pl. 4, fig. 8. 1978 Theocampe pirum (Ehrenberg) - Riedel and Sanfilippo, p. 76, pl. 9, fig. 14. 1989 Siphocampe spp. group B Lazarus and Pallant, p. 363, pl. 6, fig. 4 (part). 1998a Dictvoprora urceolus (Haeckel) - Sanfilippo and Nigrini, p. 272, pl. 13.1, fig. 11. 1999a Dictyoprora urceolus (Haeckel) - O'Connor, p. 32, pl. 9, fig. 44. 1999 Dictyoprora urceolus (Haeckel) - Kozlova, p. 137, pl. 18, fig. 8, pl. 44, figs. 22, 23. Dictyoprora pirum (Ehrenberg) s.s. - Sanfilippo and Blome, p. 211, fig. 8b. 2001 2005 Dictyoprora pirum (Ehrenberg) – Nigrini et al., p. 31, pl. P6, figs. 10, 11. 2006 Dictyoprora pirum (Ehrenberg) – Funakawa et al., p. 18, pl. P2, figs. 8–9b

- 2015 Dictyoprora pirum (Ehrenberg) Kamikuri, pl. 12, fig. 14.
- 2020 Theocampe pirum (Ehrenberg) Hollis et al., pl. 8, figs. 21a, 21b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Plannapus O'Connor, 1997a

Type species.— Dicolocapsa microcephala Haeckel, 1887, p. 1312, pl. 57, fig. 1.

Plannapus hornibrooki O'Connor, 1999a

Plate II.9, Figure 1

1999a *Plannapus hornibrooki* O'Connor, p. 7, pl. 1, figs. 7a–10, pl. 5, figs. 8a–11. Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Plannapus microcephalus (Haeckel, 1887)

Plate II.9, Figure 2

1887 Dicolocapsa microcephala Haeckel, p. 1312, pl. 57, fig. 1.

1970 Dicolocapsa microcephala Haeckel - Sanfilippo and Riedel, pl. 1, fig. 7.

1975 Dicolocapsa microcephala Haeckel – Ling, p. 731, pl. 13, fig. 9.

1977 Dicolocapsa microcephala Haeckel – Riedel and Sanfilippo, pl. 15, fig. 18.

1983 Dicolocapsa microcephala Haeckel – Johnson, p. 788, pl. 1, fig. 10.

- 1989 ? Dicolocapsa microcephala Haeckel Lazarus and Pallant, p. 362, pl. 5, figs. 2, 3.
- 1992 Dicolocapsa microcephala Haeckel Takemura, p. 746, pl. 4, figs. 14, 15.
- 1992 Plannapus microcephalus (Haeckel) Sanfilippo and Fourtanier, p. 12, pl. P2, fig. 5.
- 1997a *Plannapus microcephalus* (Haeckel) O'Connor, p. 70, pl. 1, figs. 10–14, pl. 5, figs. 10–12, pl. 6, figs. 1–5.
- 2005 Dicolocapsa microcephala Haeckel Funakawa and Nishi, p. 231, pl. 3, figs. 10a, 10b.
- 2021 Dicolocapsa microcephala Haeckel de Souza et al., p. 15, pl. 2, figs. 9a, 9b.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Siphocampe Haeckel, 1882

Type species.— Siphocampe (Siphocampula) annulosa Haeckel, 1887, p. 1500, pl. 79, fig. 10.

Siphocampe acephala (Ehrenberg, 1874)

Plate II.9, Figure 3

- 1874 Eucyrtidium acephalum Ehrenberg, p. 224.
- 1874 Eucyrtidium ? obstipum Ehrenberg, p. 231.
- 1876 Eucyrtidium acephalum Ehrenberg Ehrenberg, p. 70, pl. 11, fig. 5.
- 1876 Eucyrtidium ? obstipum Ehrenberg Ehrenberg, p. 72, pl. 11, fig. 17.
- 1882a Lithomitra acephala (Ehrenberg) Bütschli, p. 529.
- 1882a Lithomitra obstipa (Ehrenberg) Bütschli, p. 529.
- ? 1887 Tricolocampe (Tricolocampium) amphizona Haeckel, p. 1413, pl. 66, fig. 17.
- 1887 Lithomitra (Lithomitrella) acephala (Ehrenberg) Haeckel, p. 1484.
- 1942 Lithocampe (Lithocampula) urnula Clark and Campbell, p. 91, pl. 9, fig. 19.
- 1942 Lithocampe (Lithocampula) elizabethae Clark and Campbell, p. 92, pl. 9, fig. 18.
- 1942 Lithocampe (Lithocampula) minuta Clark and Campbell, p. 93, pl. 9, fig. 17.
- 1975 Lithomitra sp. cf. L. elizabethae Clark and Campbell Ling, p. 731, pl. 13, fig. 12.
- 1975 *Theocampe minuta* (Clark and Campbell) Petrushevskaya, p. 578, pl. 10, fig. 7, pl. 26, figs. 5, 6.
- 1976 Lithomitra sp. Bjørklund, p. 1124, pl. 23, figs. 1–3.
- 1976 Lithomitra ? elegans Ehrenberg group Dzinoridze et al., pl. 32, fig. 20 (part).
- 1976 Lithomitra ? minuta (Clark and Campbell) Dzinoridze et al., pl. 32, fig. 22–24.
- 1976 Lithomitra ? sp. aff. Eucyrtidium elegans Ehrenberg Dzinoridze et al., pl. 32, fig. 21.
- 1976 *Lithomitra* ? sp. P. Dzinoridze et al., pl. 29, fig. 4, pl. 32, figs. 2–7, pl. 33, figs. 2–4 (part).
- 1976 Lithomitra ? sp. T. Dzinoridze et al., pl. 33, fig. 5 (part).
- 1977 Siphocampe acephala (Ehrenberg) Nigrini, p. 254, pl. 3, fig. 5.
- 1979 Lithomitrella acephala (Ehrenberg) Petrushevskaya and Kozlova, p. 150, figs. 380, 409.
- 1981 Siphocampe acephala (Ehrenberg) De Wever, p. 511, pl. 4, fig. 11.
- 1981 Siphocampe elizabethae (Clark and Campbell) De Wever, p. 511, pl. 4, fig. 12.
- 1989 Siphocampe acephala (Ehrenberg) Lazarus and Pallant, p. 363, pl. 6, figs. 10, 11.
- 1992 Siphocampe acephala (Ehrenberg) Takemura, p. 743, pl. 6, fig. 9.
- ? 1995 Lithomitra micropore Shilov, p. 126, pl. 1, figs. 9, 10.
- 1993 Lithomitrella sp. Vitukhin, pl. 1, fig. 3 (part).
- ? 1993 Lithomitrella elegans (Ehrenberg) Vitukhin, pl. 5, fig. 8.
- 1995 Lithomitrella minuta Clark and Campbell Shilov, p. 127, pl. 2, fig. 5.
- 1996 Siphocampe minuta (Clark and Campbell) Hull, p. 141, pl. 8, figs. 7–9.

- 1997 *Siphocampe acephala* (Ehrenberg) group Hollis et al., p. 54, pl. 4, figs. 9, 10, 12, 14, 19, 20 (part).
- 1999a Siphocampe cf. acephala (Ehrenberg) O'Connor, p. 36, pl. 9, fig. 41.
- 2009 Eucyrtidium ? obstipum Ehrenberg Ogane et al., pl. 6, figs. 4a-4e.
- 2009 Eucyrtidium acephalum Ehrenberg Ogane et al., pl. 83, figs. 7a–7e.
- 2009b Siphocampe minuta (Clark and Campbell) Suzuki et al., p. 264, pl. 18, figs. 6a, 6b (part).
- 2020 Siphocampe ? acephala (Ehrenberg) group Hollis et al., pl. 8, fig. 9 (part).

2021 *Siphocampe ? acephala* (Ehrenberg) group – de Souza et al., p. 15, pl. 2, figs. 10a, 10b. Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Siphocampe ? elegans (Ehrenberg, 1854a)

Plate II.9, Figure 4

- 1854a Eucyrtidium elegans Ehrenberg, pl. 36, fig. 17.
- 1876 Eucyrtidium elegans Ehrenberg Ehrenberg, p. 70, pl. 11, fig. 12.
- 1882a Eucyrtidium elegans Ehrenberg Bütschli, p. 528.
- 1887 Theocorys (Theocorypha) elegans (Ehrenberg) Haeckel, p. 1406.
- 1976 Lithomitra ? elegans Ehrenberg group Dzinoridze et al., pl. 32, figs. 18, 19 (part).
- 1993 Lithomitrella sp. Vitukhin, pl. 19, fig. 14 (part).
- 1997 Siphocampe acephala (Ehrenberg) group Hollis et al., p. 54, pl. 4, figs. 11, 13, 15–18 (part).
- 1999 Lithomitrella insensis Kozlova Kozlova, p. 139, pl. 3, fig. 19.
- 2009 Eucyrtidium elegans Ehrenberg Ogane et al., pl. 6, figs. 11a, 11b.
- 2009b Dictyoprora sp. A Suzuki et al., p. 263, pl. 18, figs. 4a, 4b.
- 2020 Siphocampe ? acephala (Ehrenberg) group Hollis et al., pl. 8, fig. 10 (part).
- Remarks. This species is assigned to the genus Siphocampe based on its overall morphology.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Siphocampe ewingensis Kochhann in Kochhann et al., 2013

Plate II.9, Figure 5

- ? 1996 Siphocampe acephala (Ehrenberg) Hull, p. 140, pl. 7, figs. 1–3.
- ? 1996 Siphocampe septata Petrushevskaya Hull, p. 141, pl. 7, figs. 5, 6.
- 1997 Siphocampe acephala (Ehrenberg) group Hollis et al., p. 54, pl. 4, figs. 15–18 (part).
- 2002 Siphocampe acephala (Ehrenberg) group Apel et al., p. 20, pl. P9, figs. 14–17.
- 2013 Siphocampe ewingensis Kochhann in Kochhann et al., p. 541, pl. 3, figs. F-P.
- 2020 Siphocampe ? acephala (Ehrenberg) group Hollis et al., pl. 8, fig. 8 (part).

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Siphocampe imbricata (Ehrenberg, 1874)

Plate II.9, Figure 6

- 1874 Eucyrtidium imbricatum Ehrenberg, p. 229
- 1876 Eucyrtidium imbricatum Ehrenberg Ehrenberg, p. 72, pl. 11, fig. 22.

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- 1882a Lithomitra imbricata (Ehrenberg) Bütschli, p. 529.
- 1887 Lithomitra (Lithomitrella) nodosaria Haeckel, p. 1484, pl. 79, fig. 1.
- 1967 Lithomitra nodosaria Haeckel Petrushevskaya, pl. 83, figs. 8, 9.
- ? 1969 Lithomitra nodosaria Haeckel group Kruglikova, pl. 4, fig. 3.
- 1972 Lithomitra nodosaria Haeckel group Petrushevskaya and Kozlova, p. 539, pl. 24, figs.
 29, 30.
- ? 1972 Lithomitra eruca Haeckel Petrushevskaya and Kozlova, p. 539, pl. 24, figs. 32, 33.
- 1973 cf. Lithomitra lineata (Ehrenberg) group Foreman, pl. 8, fig. 18.
- 1973 Lithomitra lineata (Ehrenberg) group Foreman, p. 431, pl. 8, fig. 19.
- 1975 Lithomitra nodosaria Haeckel group Petrushevskaya, p. 586, pl. 10, fig. 18.
- 1977 Siphocampe nodosaria (Haeckel) Nigrini, p. 256, pl. 3, fig. 11.
- 1989 Siphocampe spp. group A Lazarus and Pallant, p. 363, pl. 6, figs. 1, 2.
- 1991 Siphocampe imbricata (Ehrenberg) Caulet, p. 539, pl. 3, fig. 13.
- 1992 Siphocampe sp. aff. S. arachnea (Ehrenberg) group Blome, p. 645, pl. 1, figs. 5, 6.
- 1992 Siphocampe nodosaria (Haeckel) Takemura, p. 743, pl. 3, fig. 15.
- 1993 Siphocampe eruca (Haeckel) Vitukhin, pl. 5, fig. 7, pl. 11, fig. 4.
- 1996 Siphocampe imbricata (Ehrenberg) Hull, p. 141, pl. 8, fig. 13.
- 1997 Siphocampe nodosaria (Haeckel) Hollis et al., p. 55, pl. 4, figs. 28–32.
- 1999a Siphocampe nodosaria (Haeckel) O'Connor, p. 36, pl. 9, fig. 42.
- 1999 Siphocampe sp. aff. S. nodosaria (Haeckel) Kozlova, p. 142, pl. 3, fig. 17.
- 2002 Siphocampe nodosaria (Haeckel) Hollis, p. 300, pl. 5, figs. 4a, 4b.
- 2002 Siphocampe nodosaria (Haeckel) Apel et al., p. 21, pl. P9, fig. 11.
- 2003 Siphocampe nodosaria (Haeckel) Sanfilippo and Fourtanier, p. 12, pl. P2, figs. 14, 15.
- 2008 Siphocampe altamontensis (Campbell and Clark) Jackett et al., p. 58, pl. 3, fig. 19.
- 2009 Eucyrtidium imbricatum Ehrenberg Ogane et al., pl. 6, figs. 7a–7c.
- 2009b Siphocampe elegans (Ehrenberg) Suzuki et al., p. 263, pl. 18, fig. 10.
- 2009b Siphocampe imbricata (Ehrenberg) Suzuki et al., p. 264, pl. 18, figs. 12a, 12b.
- 2013 Siphocampe nodosaria (Haeckel) Kochhann et al., p. 542, pl. 3, fig. Q.
- 2020 Siphocampe nodosaria (Haeckel) Hollis et al., pl. 8, fig. 7.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Siphocampe missilis O'Connor, 1994

Plate II.9, Figure 7

1994 *Siphocampe missilis* O'Connor, p. 340, pl. 1, figs. 7, 9–12, pl. 3, figs. 8–12. Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Siphocampe ? paupera (Ehrenberg, 1874)

Plate II.9, Figure 8

1874 Eucyrtidium pauperum Ehrenberg, p. 231.

- 1876 Eucyrtidium pauperum Ehrenberg Ehrenberg, p. 72, pl. 11, fig. 13
- 1882a Lithomitra paupera (Ehrenberg) Bütschli, p. 529.
- 1882b Lithomitra paupera (Ehrenberg) Bütschli, pl. 30, fig. 25.

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1887 Theocyrtis (Theocorypha) paupera (Ehrenberg) – Haeckel, p. 1407.

2009 Eucyrtidium pauperum Ehrenberg – Ogane et al., pl. 82, figs. 7a-7c.

Remarks. This species is assigned to the genus *Siphocampe* based on its overall morphology. Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Siphocampe pupa (Ehrenberg, 1861a)

Plate II.9, Figure 9

1861a Eucyrtidium Pupa [sic] Ehrenberg, p. 768.

1861b Eucyrtidium Pupa [sic] Ehrenberg – Ehrenberg, p. 823.

1873a Eucyrtidium Pupa [sic] Ehrenberg – Ehrenberg, p. 292, pl. 7, fig. 16.

1873b Eucyrtidium Pupa [sic] Ehrenberg – Ehrenberg, p. 311.

1882a Eucyrtidium Pupa [sic] Ehrenberg – Bütschli, p. 528.

1887 Tricolocampe (Tricolocampium) pupa (Ehrenberg) – Haeckel, p. 1412.

? 1972 Lithamphora ? sp. Petrushevskaya and Kozlova, pl. 24, fig. 7 (part).

1993 Siphocampe kylindrica Vitukhin, p. 84, pl. 5, figs. 5, 6.

2009a Eucyrtidium pupa Ehrenberg - Suzuki et al., pl. 55, figs. 8a-8c.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Siphocampe ? quadrata (Petrushevskaya in Petrushevskaya and Kozlova, 1972) Plate II.9, Figures 10, 11

- 1972 *Lithamphora sacculifera quadrata* Petrushevskaya *in* Petrushevskaya and Kozlova, p. 539, pl. 30, figs. 4–6.
- 1972 *Lithamphora* sp. Petrushevskaya and Kozlova, p. 539, pl. 30, fig. 2.
- 1972 Lithamphora ? sp. Petrushevskaya and Kozlova, pl. 30, fig. 1 (part).
- 1973 Lithomitra docilis Foreman, p. 431, pl. 8, figs. 20–22, pl. 9, figs. 3–5.
- 1974 Lithomitra docilis Foreman Johnson, p. 552, pl. 3, fig. 16.
- 1975 *Lithamphora quadrata* Petrushevskaya and Kozlova Petrushevskaya, p. 585, pl. 10, figs. 19, 20.
- 1976 Lithamphora sp. aff. L. quadrata Petrushevskaya and Kozlova Dzinoridze et al., pl. 29, fig. 1.
- 1977 Siphocampe ? quadrata (Petrushevskaya and Kozlova) Nigrini, p. 257, pl. 3, fig. 12.
- 1974 Lithomitra docilis Foreman Riedel and Sanfilippo, pl. 3, fig. 13.
- 1992 Lithomitra docilis Foreman Blome, p. 645, pl. 1, fig. 4.
- 1992 Lithomitra docilis Foreman Nishimura, p. 329, pl. 10, fig. 11, pl. 13, fig. 19.
- 1992 Siphocampe ? quadrata (Petrushevskaya and Kozlova) Takemura, p. 743, pl. 7, fig. 7.
- 1995 Siphocampe quadrata (Petrushevskaya and Kozlova) Strong et al., p. 209, fig. 10R.
- 1997 Siphocampe quadrata (Petrushevskaya and Kozlova) Hollis et al., p. 55, pl. 4, fig. 27.
- 2002 Siphocampe quadrata (Petrushevskaya and Kozlova) Hollis, p. 301, pl. 5, figs. 5, 6.
- 2003 Siphocampe ? quadrata (Petrushevskaya and Kozlova) Sanfilippo and Fourtanier, p. 12, pl. P2, fig. 24.
- 2006 Siphocampe quadrata (Petrushevskaya and Kozlova) Funakawa et al., p. 19, pl. 2, figs. 14a–15b.

- 2009b Siphocampe quadrata (Petrushevskaya and Kozlova) Suzuki et al., p. 264, pl. 18, fig.
 9.
- 2009b Siphocampe sacculifera (Clark and Campbell) Suzuki et al., p. 264, pl. 18, figs. 11a, 11b.
- 2015 Lithomitra docilis Foreman Kamikuri, pl. 12, fig. 5.
- 2020 Siphocampe quadrata (Petrushevskaya and Kozlova) Hollis et al., pl. 8, fig. 6.
- 2021 *Siphocampe quadrata* (Petrushevskaya and Kozlova) de Souza et al., p. 15, pl. 2, fig. 11.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Spirocyrtis Haeckel, 1882 emend. Nigrini, 1977 Type species.— Spirocyrtis (Spirocyrtidium) scalaris Haeckel, 1887, p. 1509, pl. 76, fig. 14.

Spirocyrtis proboscis O'Connor, 1994

Plate II.9, Figure 12

1994 *Spirocyrtis proboscis* O'Connor, p. 341, pl. 2, fig. 1–4, pl. 3, fig. 13–16. Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Family Rhopalosyringiidae Empson-Morin, 1981

? Genus Artostrobus Haeckel, 1887

Type species.— Cornutella ? annulata Bailey, 1856, p. 3, pl. 1, fig. 5b.

Artostrobus quadriporus Bjørklund, 1976 Plate II.9, Figure 13

- 1976 Artostrobus quadriporus Bjørklund, p. 1125, pl. 23, figs. 15–21.
- 1976 *Lithamphora* sp. aff. *Corocalyptra kruegeri* Popofsky Dzinoridze et al., pl. 32, figs. 13–15 (part), pl. 33, fig. 1.
- 1979 *Lithamphora quadripora* Bjørklund Petrushevskaya and Kozlova, p. 149, figs. 358, 479–481, 536.
- 1989 *Botryostrobus joides* Petrushevskaya group Lazarus and Pallant, p. 361, pl. 4, figs. 15, 16 (part).
- 1996 Artostrobus quadriporus Bjørklund Hull, p. 137, pl. 4, fig. 12.
- 2013 Artostrobus quadriporus Bjørklund Kochhann, p. 540, pl. 2, fig. AA.
- Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Genus Pterocyrtidium Bütschli, 1882a

Type species.— *Pterocanium barbadense* Ehrenberg, 1874, p. 254 (unfigured); Ehrenberg, 1876, p. 82, pl. 17, fig. 6.

Pterocyrtidium ? austellum (Sanfilippo and Blome, 2001) Plate II.9, Figure 14

2001 Sethochytris austellus Sanfilippo and Blome, p. 206, figs. 6h, 6i.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Pterocyrtidium barbadense (Ehrenberg, 1874)

Plate II.9, Figures 15, 16

- 1874 Pterocanium barbadense Ehrenberg, p. 254.
- 1876 Pterocanium barbadense Ehrenberg Ehrenberg, p. 82, pl. 17, fig. 6.
- 1882a Pterocyrtidium barbadense (Ehrenberg) Bütschli, p. 531.
- 1887 Pterocorys (Pterocyrtidium) barbadensis (Ehrenberg) Haeckel, p. 1318.
- 1972 *Pterocyrtidium barbadense* (Ehrenberg) group Petrushevskaya and Kozlova, p. 552, pl. 27, fig. 19 (part).
- not 1975 *Pterocyrtidium barbadense* (Ehrenberg) Ling, p. 729, pl. 10, fig. 17.
- 1975 Pterocyrtidium sp. Ling, p. 729, pl. 10, figs. 18, 19.
- 1977 Lipmanella ? sp. Riedel and Sanfilippo, pl. 7, fig. 11.
- 1998 Lophocyrtis (Lophocyrtis ?) barbadense (Ehrenberg) Sanfilippo and Caulet, p. 8, pl. 4, figs. 9, 10a, 10b.
- 2006 Lophocyrtis (Lophocyrtis ?) barbadense (Ehrenberg) Funakawa et al., p. 26, pl. P8, figs. 4a–5b.
- Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Genus Rhopalosyringium Campbell and Clark, 1944

Type species.— Rhopalosyringium magnificum Campbell and Clark, 1944, p. 30, pl. 7, fig. 16.

Rhopalosyringium ? auriculaleporis (Clark and Campbell, 1942)

Plate II.10, Figure 2

- 1942 *Lophophaena (Lophophaenula) auriculaleporis* Clark and Campbell, p. 76, pl. 8, figs. 20, 27–29.
- 1970 Lophocyrtis biaurita (Ehrenberg) Cita et al., p. 404, pl. 2, fig. K (part).
- 1973 Lophocyrtis biaurita (Ehrenberg) Foreman, p. 442, pl. 8, fig. 23 (part).
- 1974 Lophocyrtis biaurita (Ehrenberg) Johnson, p. 552, pl. 2, fig. 2 (part).
- 1976 Eucyrtidium ? biauritum Ehrenberg Dzinoridze et al., pl. 32, fig. 8.
- 1976 Lophocyrtis sp. Dzinoridze et al., pl. 28, fig. 13 (part).
- 1976 Lophocyrtis ? sp. aff. Lophocorys auriculaleporis (Clark and Campbell) Dzinoridze et al., pl. 28, fig. 16.
- 1977 Lophocyrtis biaurita (Ehrenberg) Riedel and Sanfilippo, pl. 8, fig. 9.
- 1979 *Artobotrys auriculaleporis* (Clark and Campbell) Petrushevskaya and Kozlova, p. 137, fig. 515.
- 1988 Lophophaena auriculaleporis Clark and Campbell Blueford, p. 246, pl. 3, figs. 1–3.
- 1991 Artobotrys auriculaleporis (Clark and Campbell) Caulet, p. 537.
- 1995 Artobotrys auriculaleporis (Clark and Campbell) Shilov, p. 127, pl. 4, figs. 4a, 4b.
- 1995 Lophocyrtis ? auriculaleporis (Clark and Campbell) Strong et al., p. 208, figs. 10S, 10T.
- 1997 Cycladophora ? auriculaleporis (Clark and Campbell) Hollis et al., p. 59, pl. 3, fig. 31.

- 1999 *Artobotrys auriculaleporis* (Clark and Campbell) Kozlova, p. 133, pl. 27, fig. 14, pl. 31, figs. 2, 3, pl. 46, fig. 1 (part).
- 2003 Lophocyrtis biaurita (Ehrenberg) Sanfilippo and Fourtanier, p. 12, pl. P2, fig. 23 (part).
- 2009b Artobotrys auriculaleporis (Clark and Campbell) Suzuki et al., p. 258, pl. 21, figs. 1a, 1b.
- 2009b Artobotrys biauritus (Ehrenberg) Suzuki et al., p. 258, pl. 21, figs. 2a, 2b.
- 2009b Artobotrys norvegiensis (Bjørklund and Kellogg) Suzuki et al., p. 258, pl. 21, fig. 3.
- 2020 Artobotrys auriculaleporis (Clark and Campbell) Hollis et al., pl. 7, figs. 1a–3b.
- Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Rhopalosyringium ? biauritum (Ehrenberg, 1874)

Plate II.10, Figure 1

- 1874 Eucyrtidium biauritum Ehrenberg, p. 226.
- 1874 Eucyrtidium bicorne Ehrenberg, p. 226.
- 1876 Eucyrtidium biauritum Ehrenberg Ehrenberg, p. 70, pl. 10, figs. 7, 8.
- 1876 Eucyrtidium bicorne Ehrenberg Ehrenberg, p. 70, pl. 11, fig. 7.
- 1882a Eucyrtidium biauritum Ehrenberg Bütschli, pl. 33, figs. 38a-38f.
- 1882b Eucyrtidium biauritum Ehrenberg Bütschli, pl. 31, fig. 1.
- 1887 Lophocyrtis biaurita (Ehrenberg) Haeckel, p. 1411.
- 1970 Lophocyrtis biaurita (Ehrenberg) Cita et al., p. 404, pl. 2, figs. I, J (part).
- 1973 Lophocyrtis biaurita (Ehrenberg) Foreman, p. 442, pl. 8, figs. 24–26 (part).
- 1974 Lophocyrtis biaurita (Ehrenberg) Nigrini, p. 1070, pl. 1M, fig. 11–13.
- 1974 Lophocyrtis biaurita (Ehrenberg) Johnson, p. 552, pl. 2, fig. 1 (part).
- 1975 Lophocyrtis biaurita (Ehrenberg) Chen, p. 461, pl. 3, fig. 2.
- 1976 Lophocyrtis biaurita (Ehrenberg) Bjørklund, p. 1124, pl. 21, figs. 16, 17.
- 1976 Lophocyrtis ? bicorne (Ehrenberg) Dzinoridze et al., pl. 28, fig. 12, pl. 34, fig. 4.
- 1978 Lophocyrtis biaurita (Ehrenberg) Riedel and Sanfilippo, p. 70, pl. 6, fig. 13.
- 1984 Lophocyrtis biaurita (Ehrenberg) Westberg-Smith and Riedel, p. 493, pl. 6, fig. 13.
- 1992 Lophocyrtis biaurita (Ehrenberg) Takemura, p. 747, pl. 7, fig. 8.
- 1999 Artobotrys auriculaleporis (Clark and Campbell) Kozlova, p. 133, pl. 31, fig. 1 (part).
- 2003 Lophocyrtis biaurita (Ehrenberg) Sanfilippo and Fourtanier, p. 12, pl. P2, fig. 22 (part).
- 2009 *Eucyrtidium biauritum* Ehrenberg Ogane et al., pl. 18, figs. 8a–8d, pl. 20, figs. 1a–2b,
 6.
- 2009 Eucyrtidium bicorne Ehrenberg Ogane et al., pl. 20, figs. 3a, 3b, 4a–4c, 5a–5c.
- 2020 Artobotrys biaurita (Ehrenberg) Hollis et al., pl. 7, figs. 4, 5.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).



Plate II.9. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic). (1) Plannapus hornibrooki O'Connor, 1999a: ODP 1051A-2H-5W, 55-57 cm. (2) Plannapus microcephalus (Haeckel, 1887): ODP 1051A-14H-5W, 55–57 cm. (3) Siphocampe acephala (Ehrenberg, 1874): ODP 1260A-8R-5W, 54-56 cm. (4) Siphocampe? elegans (Ehrenberg, 1854a): ODP 1260A-6R-2W, 55–57 cm. (5) Siphocampe ewingensis Kochhann in Kochhann et al., 2013: ODP 1051A-12H-2W, 55-57 cm. (6) Siphocampe imbricata (Ehrenberg, 1874): ODP 1260A-9R-3W, 55–57 cm. (7) Siphocampe missilis O'Connor, 1994: ODP 1051A-2H-5W, 55-57 cm. (8) Siphocampe ? paupera (Ehrenberg, 1874): ODP 1051A-2H-5W, 55-57 cm. (9) Siphocampe pupa (Ehrenberg, 1861a): ODP 1260A-10R-4W, 55-57 cm. (10, 11) Siphocampe ? quadrata (Petrushevskaya in Petrushevskaya and Kozlova, 1972): (10) ODP 1260A-11R-7W, 55–57 cm; (11) ODP 1260A-8R-2W, 55–57 cm. (12) Spirocyrtis proboscis O'Connor, 1994: ODP 1051A-6H-5W, 53-55 cm. (13) Artostrobus quadriporus Bjørklund, 1976: ODP 1260A-8R-3W, 54–56 cm. (14) Pterocyrtidium ? austellum (Sanfilippo and Blome, 2001): ODP 1051A-12H-2W, 55-57 cm. (15, 16) Pterocyrtidium barbadense (Ehrenberg, 1874): (15) ODP 1260A-13R-5W, 54-56 cm; (16) ODP 1260A-11R-6W, 55-57 cm. All scale bars equal 50 µm.

Superfamily Acanthodesmioidea Haeckel, 1862 sensu Dumitrică *in* De Wever et al., 2001 Family Acanthodesmiidae Haeckel, 1862

Genus Dictyospyris Ehrenberg, 1846

Type species.— *Dictyospyris triloba* Ehrenberg, 1854a, pl. 36, figs. 24a, 24b; description in Haeckel, 1862, p. 292.

Dictyospyris gigas Ehrenberg, 1874

Plate II.10, Figure 3

- 1874 Dictyospyris Gigas [sic] Ehrenberg, p. 224.
- 1876 Dictyospyris Gigas [sic] Ehrenberg Ehrenberg, p. 68, pl. 19, fig. 6.
- 1882a Dictyospyris Gigas [sic] Ehrenberg Bütschli, pl. 32, figs. 14a, 14b.
- 1882b Dictyospyris Gigas [sic] Ehrenberg Bütschli, pl. 28, fig. 14, pl. 29, fig. 1.
- 1887 *Circospyris gigas* (Ehrenberg) Haeckel, p. 1072.
- 1973 *Dictyospyris gigas* Ehrenberg Sanfilippo and Riedel, p. 527, pl. 16, figs. 9, 10, pl. 32, figs. 10, 11.
- 1987 Dictyospyris gigas Ehrenberg Nishimura, p. 725, pl. 3, fig. 20.

2002 Dendrospyris stabilis Goll – Apel et al., p. 18, pl. P8, figs. 8a, 8b (part).

not 2009 *Dictyospyris gigas* Ehrenberg – Ogane et al., pl. 18, figs. 1a, 1b.

2015 Dictyospyris gigas Ehrenberg – Kamikuri, pl. 19, fig. 11.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Dictyospyris melissium Sanfilippo and Riedel, 1973 Plate II.10, Figure 9

1973 Dictyospyris melissium Sanfilippo and Riedel, p. 527, pl. 17, figs. 1, 2, pl. 32, fig. 13.

2001 Dictyospyris melissium Sanfilippo and Riedel – De Wever et al., p. 231, fig. 146.7.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Dictyospyris tetrastoma Ehrenberg, 1874

Plate II.10, Figure 4

- 1874 Dictyospyris tetrastoma Ehrenberg, p. 224.
- 1876 Dictyospyris tetrastoma Ehrenberg Ehrenberg, p. 70, pl. 19, fig. 12.
- 1887 Dictyospyris (Dictyospyrissa) tetrastoma Ehrenberg Haeckel, p. 1075.
- 1999 *Dicryospyrella asymmetrica* [sic] Kozlova, p. 163, pl. 15, figs. 16, 17, 21, pl. 18, fig. 15, pl. 20, fig. 11 (part).
- 2002 Dendrospyris sp. A Apel et al., pl. P8, figs. 6a, 6b.

2009 Dictyospyris tetrastoma Ehrenberg – Ogane et al., pl. 38, figs. 2a, 2b (part).

2009 Dictyospyris tetrasoma [sic] Ehrenberg – Ogane et al., pl. 18, figs. 2a-2c.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Dictyospyris tristoma Ehrenberg, 1874

Plate II.10, Figure 5

1874 Dictyospyris tristoma Ehrenberg, p. 224.

- 1876 Dictyospyris tristoma Ehrenberg Ehrenberg, p. 70, pl. 19, fig. 9.
- 1887 Dictyospyris (Dictyospyrella) tristoma Ehrenberg Haeckel, p. 1074.
- 1999 Dictyospyrella tristoma (Ehrenberg) Kozlova, p. 164, pl. 36, figs. 22, 23.
- 2009 Dictyospyris tristoma Ehrenberg Ogane et al., pl. 75, figs. 3a–3c.
- 2015 Dictyospyris tristoma Ehrenberg Kamikuri, pl. 11, fig. 22.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Genus Eucoronis Haeckel, 1882

Type species.— Eucoronis (Acrocoronis) perspicillum Haeckel, 1887, p. 977, pl. 82, fig. 6.

Eucoronis hertwigii Bütschli, 1882a

Plate II.10, Figures 7, 8

- 1862 Acanthodesmia Bury, pl. 23, fig. 7.
- 1882a Acanthodesmia Hertwigii [sic] Bütschli, p. 499, pl. 32, fig. 9a-9c.
- 1882b Acanthodesmia Hertwigii [sic] Bütschli Bütschli, pl. 28, fig. 12.
- 1887 Tristephanium (Triostephus) hertwigii (Bütschli) Haeckel, p. 983.
- 1972 *Eucoronis hertwigii* (Bütschli) group Petrushevskaya and Kozlova, p. 533, pl. 41, figs. 15–17.
- 1975 Eucoronis hertwigii (Bütschli) group Ling, p. 727, pl. 8, fig. 14.
- 2015 Eucoronis hertwigii (Bütschli) group Kamikuri, pl. 13, fig. 18.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Tympaniscus Haeckel, 1887

Type species.— Tympaniscus corona Haeckel, 1887, p. 1001 (unfigured).

Tympaniscus fibula Ehrenberg, 1874

Plate II.10, Figures 6, 10

1874 Ceratospyris Fibula [sic] Ehrenberg, p. 219.

1876 Ceratospyris Fibula [sic] Ehrenberg – Ehrenberg, p. 66, pl. 20, fig. 3.

1882b Ceratospyris Fibula [sic] Ehrenberg – Bütschli, pl. 29, fig. 3.

1887 Tympaniscus fibula (Ehrenberg) – Haeckel, p. 1002.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Family Cephalospyrididae Haeckel, 1882

Genus Ceratospyris Ehrenberg, 1846

Type species.— *Haliomma ? radicatum* Ehrenberg, 1844, p. 83 (unfigured); Ehrenberg, 1854a, pl. 22, fig. 37.

Ceratospyris articulata Ehrenberg, 1874

Plate II.10, Figure 11

1874 Ceratospyris articulata Ehrenberg, p. 218.

- 1876 Ceratospyris articulata Ehrenberg Ehrenberg, p. 66, pl. 20, fig. 4.
- 1887 Hexaspyris (Hexacorethra) articulata (Ehrenberg) Haeckel, p. 1048.
- 1973 *Ceratospyris articulata* Ehrenberg Sanfilippo and Riedel, p. 526, pl. 15, figs. 1–3, pl. 31, figs. 8, 9
- 1978 Ceratospyris articulata Ehrenberg Riedel and Sanfilippo, p. 67, pl. 4, figs. 9, 10.
- 1987 Ceratospyris articulata Ehrenberg Nishimura, p. 721, pl. 3, fig. 16.
- 2009 Ceratospyris articulata Ehrenberg Ogane et al., pl. 18, figs. 3a–3c.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Ceratospyris clavata Bütschli, 1882a Plate II.10, Figure 12

1882a Ceratospyris clavata Bütschli, p. 539, pl. 32, figs. 13a-13c.

not 1975 *Ceratospyris clavata* Bütschli – Ling, p. 726, pl. 4, fig. 11.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Ceratospyris echinus Ehrenberg, 1874

Plate II.10, Figure 13

1874 *Ceratospyris Echinus* [sic] Ehrenberg, p. 219.

- 1876 Ceratospyris Echinus [sic] Ehrenberg Ehrenberg, p. 66, pl. 20, fig. 12.
- 1887 Ceratospyris (Lophospyris) echinus Ehrenberg Haeckel, p. 1068.



Plate II.10. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic). (1) Rhopalosyringium ? biauritum (Ehrenberg, 1874): ODP 1260A-10R-4W, 55-57 cm. (2) Rhopalosyringium ? auriculaleporis (Clark and Campbell, 1942): ODP 1260A-9R-3W, 55-57 cm. (3) Dictyospyris gigas Ehrenberg, 1874: ODP 1051A-38X-5W, 55-57 cm. (4) Dictyospyris tetrastoma Ehrenberg, 1874: ODP 1260A-20R-4W, 63–177 cm. (5) Dictyospyris tristoma Ehrenberg, 1874: ODP 1260A-20R-4W, 63-177 cm. (6, 10) Tympaniscus fibula (Ehrenberg, 1874): (6) ODP 1260A-7R-4W, 54–56 cm; (10) ODP 1260A-7R-4W, 54–56 cm. (7, 8) Eucoronis hertwigii Bütschli, 1882a: (7) ODP 1260A-8R-6W, 54-56 cm; (8) ODP 1260A-9R-4W, 55-57 cm. (9) Dictyospyris melissium Sanfilippo and Riedel, 197: ODP 1051A-12R-2W, 55-57 cm. (11) Ceratospyris articulata Ehrenberg, 1874: ODP 1260A-14R-CC, 63–177 cm. (12) Ceratospyris clavata Bütschli, 1882a: ODP 1260A-8R-3W, 54–56 cm. (13) Ceratospyris echinus Ehrenberg, 1874: ODP 1051A-4H-5W, 56-58 cm. (14) Ceratospyris? metroid Tetard et al., 2023: ODP 1260A-6R-1W, 55–57 cm. (15) Ceratospyris? okazakii Tetard et al., 2023: ODP 1260A-9R-6W, 55-57 cm. (16, 17) Dendrospyris fragoides Sanfilippo and Riedel, 1973: (16) ODP 1260A-9R-3W, 55–57 cm; (17) ODP 1051A-38X-5W, 55–57 cm. All scale bars equal 50 µm.

1957a Ceratospyris aff. C. echinus Ehrenberg - Riedel, p. 259, pl. 63, fig. 4.

1975 Ceratospyris sp. cf. C. echinus Ehrenberg – Ling, p. 726, pl. 4, figs. 12, 13.

? 1999a Dendrospyris inferispina Goll – O'Connor, p. 31, pl. 10, fig. 37.

2009 Ceratospyris echinus Ehrenberg – Ogane et al., pl. 9, figs. 5a–5d.

2015 Dendrospyris echinus (Ehrenberg) - Kamikuri, pl. 19, fig. 16.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Ceratospyris ? metroid Tetard et al., 2023

Plate II.10, Figure 14

2023 *Ceratospyris metroid* Tetard et al., p. 5, figs. 4a–4d, 5a–5d. Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Ceratospyris? okazakii Tetard et al., 2023

Plate II.10, Figure 15

2023 *Ceratospyris okazakii* Tetard et al., p. 5, figs. 4e–4g, 5e, 5f. Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Dendrospyris Haeckel, 1882

Type species.— *Ceratospyris stylophora* Ehrenberg, 1874, 220 (unfigured); Ehrenberg, 1876, p. 66, pl. 20, fig. 10.

Dendrospyris fragoides Sanfilippo and Riedel, 1973 Plate II.10, Figures 16, 17

1973 *Dendrospyris fragoides* Sanfilippo and Riedel, p. 526, pl. 15, figs. 8–13, pl. 31, figs. 13, 14.

2015 Dendrospyris fragoides Sanfilippo and Riedel – Kamikuri, pl. 11, fig. 23.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Dendrospyris golli Nishimura, 1992

Plate II.11, Figure 1

1992 *Dendrospyris golli* Nishimura, p. 330, pl. 3, figs. 1, 2, pl. 12, fig. 11. Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Dendrospyris stylophora (Ehrenberg, 1874)

Plate II.11, Figure 2

1874 Ceratospyris stylophora Ehrenberg, p. 220.

1876 Ceratospyris stylophora Ehrenberg – Ehrenberg, p. 66, pl. 20, fig. 10.

1887 Dendrospyris stylophora (Ehrenberg) – Haeckel, p. 1038.

1968 Dendrospyris stylophora (Ehrenberg) – Goll, p. 1423, pl. 173, figs. 21–24, text-fig. 8.

2009 Ceratospyris stylophora Ehrenberg – Ogane et al., pl. 38, fig. 6a–6c, pl. 39, figs. 6a, 6b.

2009b *Triceraspyris palmipodiscus* Petrushevskaya in Petrushevskaya and Kozlova – Suzuki et al., p. 258, pl. 19, figs. 14a, 14b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Desmospyris Haeckel, 1882

Type species.— Desmospyris mammillata Haeckel, 1887, p. 1089, pl. 83, fig. 14.

Desmospyris biloba Tetard et al., 2023

Plate II.11, Figure 7

? 1999 Desmospyris ? sp. Kozlova, pl. 31, fig. 18.

2023 Desmospyris biloba Tetard et al., p. 8, figs. 4h-4j, 5g-5j.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Desmospyris cyrillium (Sanfilippo and Riedel, 1973)

Plate II.11, Figure 3

- 1973 Giraffospyris cyrillium Sanfilippo and Riedel, p. 528, pl. 18, figs. 1–3, pl. 33, fig. 3.
- 1978 *Giraffospyris cyrillium* Sanfilippo and Riedel Weaver and Dinkelman, p. 869, pl. 5, fig. 8.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Desmospyris lata (Goll, 1969)

Plate II.11, Figure 4

- 1969 Giraffospyris lata Goll, p. 334, pl. 58, figs. 22, 24–26, text-fig. 2.
- 1972 Desmospyris sp. aff. Giraffospyris lata (Goll) Petrushevskaya and Kozlova, p. 532, pl. 38, fig. 1.
- 1975 Desmospyris ? lata (Goll) Petrushevskaya, pl. 10, fig. 30.
- 1973 Giraffospyris lata Goll Sanfilippo and Riedel, p. 529, pl. 18, figs. 3–7, pl. 33, fig. 4.
- 1978 Giraffospyris lata Goll Weaver and Dinkelman, p. 869, pl. 5, fig. 7.
- 1981 Giraffospyris lata Goll De Wever, p. 511, pl. 2, fig. 5.
- 1993 Giraffospyris lata Goll Hull, p. 12, pl. 7, fig. 4, pl. 8, fig. 4.
- 1998a Giraffospyris lata Goll Sanfilippo and Nigrini, p. 272, pl. 13.1, figs. 12, 13.
- 2008 Girafospyris lata [sic] Goll Jackett et al., p. 52, pl. 4, fig. 16.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Desmospyris obtusus Bütschli, 1882a

Plate II.11, Figure 8

- 1882a Dictyocephalus obtusus Bütschli, p. 535, pl. 36, figs. 20a-20c.
- 1882b Dictyocephalus obtusus Bütschli Bütschli, pl. 31, figs. 10a, 10b.
- 1887 Desmospyris mammillata Haeckel, p. 1089, pl. 83, fig. 14.
- 1975 Dendrospyris stabilis Goll Chen, p. 455, pl. 7, fig. 3.
- 1975 Desmospyris sp. cf. D. anthocyrtoides (Bütschli) Ling, p. 726, pl. 7, fig. 1.
- 1992 Dendrospyris stabilis Goll Takemura, p. 743, pl. 4, fig. 7.
- 2002 Dendrospyris stabilis Goll Apel et al., p. 18, pl. P8, fig. 7 (part).

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Dorcadospyris Haeckel, 1882

Type species.— Dorcadospyris dentata Haeckel, 1887, p. 1040, pl. 85, fig. 6.

Dorcadospyris anastasis Sanfilippo in Nigrini et al., 2005 Plate II.11, Figure 5

- 2005 Dorcadospyris anastasis Sanfilippo in Nigrini et al., p. 33, pl. P1, figs. 11, 12.
- 2012 *Dorcadospyris anastasis* Sanfilippo *in* Nigrini et al. Moore and Kamikuri, p. 6, pl. P2, figs. 7, 8.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Dorcadospyris ombros Sanfilippo in Nigrini, 2005

Plate II.11, Figure 6

- 2005 Dorcadospyris ombros Sanfilippo in Nigrini et al., p. 36, pl. P2, figs. 5, 6.
- 2012 Dorcadospyris ombros Sanfilippo in Nigrini et al. Moore and Kamikuri, p. 7, pl. P3, figs. 3, 4.
- Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Dorcadospyris? flexuosa (Ehrenberg, 1874)

Plate II.11, Figure 9

1862 Rhabdolithes pipa [sic] Ehrenberg – Bury, pl. 3, fig. 4 (part).

1874 Stylosphaera flexuosa Ehrenberg, p. 258.

1876 Stylosphaera flexuosa Ehrenberg – Ehrenberg, p. 84, pl. 25, fig. 5.

1887 Sphærostylus (Sphærostylantha) flexuosus [sic] (Ehrenberg) – Haeckel, p. 138.

1986 Stylosphaera flexuosa Ehrenberg – Göke, fig. 3.2.

2009 Stylosphaera flexuosa Ehrenberg – Ogane et al., pl. 11, fig. 4d (part).

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Elaphospyris Haeckel, 1882

Type species.— *Ceratospyris heptaceros* Ehrenberg, 1874, p. 219 (unfigured); Ehrenberg, 1876, p. 66, pl. 20, fig. 2.

Elaphospyris didiceros (Ehrenberg, 1874) group

Plate II.11, Figures 10, 11

- 1862 Petalospiris diaboliscus [sic] Ehrenberg Bury, pl. 17, fig. 6.
- 1874 Ceratospyris didiceros Ehrenberg, p. 218.
- 1876 Ceratospyris didiceros Ehrenberg Ehrenberg, p. 66, pl. 21, fig. 6.
- 1887 Triceraspyris (Triospyris) didiceros (Ehrenberg) Haeckel, p. 1030.
- 1887 Triceraspyris (Triospyrium) giraffa Haeckel, p. 1031, pl. 84, fig. 11.
- 1958 Aegospyris longibarba (Ehrenberg) Göke, pl. 3, fig. 1.
- 1969 Giraffospyris didiceros (Ehrenberg) Goll, p. 332, pl. 60, figs. 5–7, 9, text-fig. 2.
- 1970 Giraffospyris didiceros (Ehrenberg) group Riedel and Sanfilippo, pl. 5, figs. 3–5.
- 1970 Dendrospyris didiceros (Ehrenberg) group Petrushevskaya and Kozlova, p. 532, pl. 40, fig. 12.
- 1974 Giraffospyris didiceros (Ehrenberg) Johnson, p. 547, pl. 3, fig. 7.
- 1975 Giraffospyris didiceros (Ehrenberg) Chen, p. 456, pl. 3, fig. 4.
- 1975 Dendrospyris didiceros (Ehrenberg) group Ling, p. 726, pl. 4, fig. 16.
- 1977 Spyrid gen. and sp. indet. Riedel and Sanfilippo, pl. 6, fig. 15 (part).
- 1981 Giraffospyris didiceros (Ehrenberg) De Wever, p. 511, pl. 2, fig. 13.
- 1992 Giraffospyris didiceros (Ehrenberg) Kim, p. 40, pl. 1, figs. 8, 9.
- 1995 Spyrida gen. et spp. undet. Strong et al., fig. 10N (part).
- 2009 *Ceratospyris heptaceros* Ehrenberg Ogane et al., pl. 18, figs. 4a–4e, pl. 38, figs. 7a– 7c, pl. 39, figs. 7a, 7b (part).
- 2009 Ceratospyris didiceros Ehrenberg Ogane et al., pl. 39, figs. 1a–1c.
- 2009b *Giraffospyris incertecoronata* (Clark and Campbell) Suzuki et al., p. 258, pl. 19, figs. 12a, 12b.
- 2013 Dendrospyris didiceros (Ehrenberg) Kamikuri et al., pl. 1, fig. 7.
- 2015 Dorcadospyris aff. furcata (Ehrenberg) Kamikuri, pl. 13, fig. 15, pl. 19, fig. 15.
- 2020 Giraffospyris didiceros (Ehrenberg) Hollis et al., pl. 5, fig. 2.

Remarks. The combination used here is derived from O'Dogherty et al. (2021). Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Liriospyris Haeckel, 1882

Type species.— Liriospyris hexapoda Haeckel, 1887, p. 1049, pl. 86, fig. 7.

Liriospyris clathrata (Ehrenberg, 1854a)

Plate II.11, Figures 12, 13

1854a Dictyospyris clathrus Ehrenberg, pl. 36, fig. 25.

1862 Petalospyris clathrus (Ehrenberg) – Haeckel, p. 295.

1874 Dictyospyris clathrata Ehrenberg – Ehrenberg, p. 224.

1876 Dictyospyris clathrata Ehrenberg – Ehrenberg, p. 68, pl. 19, fig. 7.

1882a Dictyospyris clathrata Ehrenberg - Bütschli, p. 506, pl. 32, figs. 10a, 10b.

1887 Liriospyris clathrata (Ehrenberg) – Haeckel, p. 1049.

1968 Liriospyris clathrata (Ehrenberg) – Goll, p. 175, figs. 12, 13, 16, 17.

- 1972 Dictyospyris? clathrata Ehrenberg Petrushevskaya and Kozlova, pl. 39, fig. 14.
- 1972 Liriospyris sp. aff. D. clathrata Ehrenberg Petrushevskaya and Kozlova, p. 531, pl. 39, fig. 15.

1975 Liriospyris clathrata (Ehrenberg) – Ling, p. 726, pl. 7, figs. 6–9.

not 1999a Liriospyris clathrata (Ehrenberg) – O'Connor, p. 32, pl. 10, fig. 39.

2009 Ceratospyris heptaceros Ehrenberg – Ogane et al., pl. 1, figs. 2a–2c (part).

2015 Liriospyris spinulosa (Ehrenberg) – Kamikuri, pl. 13, figs. 26–27b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Liriospyris ramosa (Ehrenberg, 1847)

Plate II.12, Figures 1, 2

1847 Cladospyris ramosa Ehrenberg, p. 54.

1874 Ceratospyris ramosa (Ehrenberg) – Ehrenberg, p. 219.

1876 Ceratospyris ramosa (Ehrenberg) – Ehrenberg, p. 66, pl. 20, fig. 7.

1887 Ceratospyris (Cladospyris) ramosa (Ehrenberg) – Haeckel, p. 1069.

2009 Ceratospyris ramosa (Ehrenberg) - Ogane et al., pl. 76, figs. 4a-4d.

2015 Liriospyris spinulosa (Ehrenberg) – Kamikuri, pl. 13, figs. 26–27b.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Liriospyris turrita (Ehrenberg, 1874)

Plate II.12, Figure 3

1874 Ceratospyris turrita Ehrenberg, p. 220.

1876 Ceratospyris turrita Ehrenberg – Ehrenberg, p. 66, pl. 20, fig. 1.

1887 Liriospyris turrita (Ehrenberg) – Haeckel, p. 1050.

2009 Ceratospyris turrita Ehrenberg – Ogane et al., pl. 76, figs. 1a–2c.



Plate II.11. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic). (1) *Dendrospyris golli* Nishimura, 1992: ODP 1260A-13R-1W, 54–55 cm. (2) *Dendrospyris stylophora* (Ehrenberg, 1874): ODP 1260A-10R-1W, 55–57 cm. (3) *Desmospyris cyrillium* (Sanfilippo and Riedel, 1973): ODP 1510A-38X-5W, 55–57 cm. (4) *Desmospyris lata* (Goll, 1969): ODP 1051A-38X-5W, 55–57 cm. (5) *Dorcadospyris anastasis* Sanfilippo in Nigrini et al., 2005: ODP 1260A-6R-2W, 55–57 cm. (6) *Dorcadospyris ombros* Sanfilippo in Nigrini, 2005: ODP 1260A-6R-3W, 55–57 cm. (7) *Desmospyris ? biloba* Tetard et al., 2023: ODP 1260A-6R-2W, 55–57 cm. (8) *Desmospyris obtusus* Bütschli, 1882a: ODP 1260A-6R-3W, 55–57 cm. (10, 11) *Elaphospyris didiceros* (Ehrenberg, 1874) group: (10) ODP 1260A-6R-2W, 55–57 cm. (11) ODP 1260A-11R-4W, 55–57 cm. (12, 13) *Liriospyris clathrata* (Ehrenberg, 1854a): ODP 1051A-9H-2W, 53–55 cm; (13) ODP 1260A-9R-4W, 55–57 cm. All scale bars equal 50 μm.

2015 *Dorcadospyris costatescens* Goll – Kamikuri, pl. 13, figs. 5–7. Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Genus *Petalospyris* Ehrenberg, 1846 *Type species.— Petalospyris diaboliscus* Ehrenberg, 1847, p. 55, fig. 6.

> Petalospyris argiscus Ehrenberg, 1874 Plate II.12, Figure 4

1874 Petalospyris Argiscus [sic] Ehrenberg, p. 246.

? 1874 Petalospyris carinata Ehrenberg, p. 246.

1874 Petalospyris eupetala Ehrenberg, p. 247.

1876 Petalospyris Argiscus [sic] Ehrenberg – Ehrenberg, p. 80, pl. 22, figs. 1, 2.

? 1876 Petalospyris carinata Ehrenberg – Ehrenberg, p. 80, pl. 22, fig. 6.

1876 Petalospyris eupetala Ehrenberg – Ehrenberg, p. 80, pl. 22, fig. 4.

1882a Petalospyris Argiscus [sic] Ehrenberg - Bütschli, p. 539, pl. 32, figs. 17a, 17b.

1882b Petalospyris Argiscus [sic] Ehrenberg - Bütschli, pl. 29, figs. 6a, 6b.

1887 Petalospyris (Petalospyrissa) eupetala Ehrenberg – Haeckel, p. 1061.

1887 Petalospyris (Petalospyromma) argiscus Ehrenberg – Haeckel, p. 1062.

1957a Petalospyris platyacantha Ehrenberg - Riedel, p. 259, pl. 63, fig. 3.

1969 Dorcadospyris argisca (Ehrenberg) – Goll, p. 336, pl. 56, figs. 9–11.

1975 Dorcadospyris argisca (Ehrenberg) – Chen, p. 456, pl. 3, fig. 9.

1975 Petalospyris foveolata Ehrenberg – Ling, p. 727, pl. 7, fig. 23.

? 1975 Petalospyris sp. cf. P. foveolata Ehrenberg – Ling, p. 727, pl. 7, fig. 24.

1981 Dorcadospyris argisca (Ehrenberg) – De Wever, p. 511, pl. 2, fig. 12.

? 2008 Petalospyris platyacantha Ehrenberg group – Jackett et al., p. 52, pl. 4, fig. 17.

2009 *Petalospyris argiscus* Ehrenberg – Ogane et al., pl. 2, fig. 11, pl. 18, figs. 7a–7e, pl. 39, figs. 8a–8c (part).

? 2009 Petalospyris carinata Ehrenberg - Ogane et al., pl. 40, figs. 5a-5d.

2009 Petalospyris eupetala Ehrenberg – Ogane et al., pl. 39, figs. 9a–9c.

2009 Petalospyris flabellum Ehrenberg – Ogane et al., pl. 2, figs. 14a, 14b (part).

2009b Petalospyris cf. eupetala Ehrenberg - Suzuki et al., p. 258, pl. 19, figs. 13a, 13b.

2015 Dorcadospyris argisca (Ehrenberg) – Kamikuri, pl. 13, figs. 1a, 1b, 22.

2020 Dorcadospyris argisca (Ehrenberg) – Hollis et al., pl. 5, fig. 1.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Petalospyris confluens Ehrenberg, 1874

Plate II.12, Figures 5, 6

1874 Petalospyris confluens Ehrenberg, p. 246.

1876 Petalospyris confluens Ehrenberg – Ehrenberg, p. 80, pl. 22, fig. 5.

1887 Patagospyris confluens (Ehrenberg) – Haeckel, p. 1088.

1969 Dorcadospyris confluens (Ehrenberg) – Goll, p. 337, pl. 58, figs. 9–12, text-fig. 2.

not 1973 Dorcadospyris confluens (Ehrenberg) – Sanfilippo and Riedel, p. 528, pl. 17, figs. 6–10, pl. 33, fig. 1.

not 1987 Dorcadospyris confluens (Ehrenberg) – Nishimura, p. 725, pl. 3, figs. 18, 19.

not 1999 Patagospyris confluens (Ehrenberg) – Kozlova, p. 166, pl. 8, fig. 14.

2009 Petalospyris confluens Ehrenberg – Ogane et al., pl. 75, fig. 5a, 5b, pl. 77, fig. 2a–2c (part).

2015 Dorcadospyris confluens (Ehrenberg) – Kamikuri, pl. 13, figs. 16, 17.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Petalospyris diaboliscus Ehrenberg, 1847

Plate II.12, Figure 7

1847 Petalospyris Diaboliscus [sic] Ehrenberg, p. 55, fig. 6.

1874 Petalospyris Diaboliscus [sic] Ehrenberg – Ehrenberg, p. 246.

1887 Anthospyris diaboliscus (Ehrenberg) – Haeckel, p. 1065.

1975 Petalospyris diaboliscus Ehrenberg – Ling, p. 727, pl. 7, fig. 22.

1981 Spyrid De Wever, pl. 2, fig. 11.

2009 Petalospyris diaboliscus Ehrenberg – Ogane et al., pl. 5, figs. 6a–6c, pl. 76, 3a–3c.

2015 Dorcadospyris diaboliscus Ehrenberg – Kamikuri, pl. 13, fig. 23.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Petalospyris flabellum Ehrenberg, 1874

Plate II.12, Figure 8

1874 Petalospyris Flabellum [sic] Ehrenberg, p. 247.

1876 Petalospyris Flabellum [sic] Ehrenberg – Ehrenberg, p. 80, pl. 22, fig. 7.

1887 Phænocalpis flabellum [sic] (Ehrenberg) – Haeckel, p. 1174.

2009 *Petalospyris flabellum* Ehrenberg – Ogane et al., pl. 2, figs. 13a, 13b, pl. 5, figs. 4a, 4b, pl. 18, figs. 5a, 5b (part).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Petalospyris pentas Ehrenberg, 1874

Plate II.12, Figures 9, 10

- 1874 Petalospyris Pentas [sic] Ehrenberg, p. 247.
- 1876 Petalospyris Pentas [sic] Ehrenberg Ehrenberg, p. 80, pl. 22, fig. 11.
- 1887 Gorgospyris (Gorgospyrium) ehrenbergii Haeckel, p. 1070.
- 1972 Patagospyris pentas (Ehrenberg) Petrushevskaya and Kozlova, p. 532, pl. 39, figs. 32, 33.
- 1987 Dorcadospyris pentas (Ehrenberg) Nishimura, p. 725, pl. 3, fig. 17.
- 1995 Gorgospyris hemisphaerica Clark and Campbell Shilov, p. 127, pl. 1, figs. 7, 8.
- 1999 Petalospyrella pentas (Ehrenberg) Kozlova, p. 167, pl. 14, fig. 19.
- 2005 ? Pentaspyris paradoxa Clark and Campbell Funakawa and Nishi, p. 233, pl. 3, fig. 8.
- 2009 Petalospyris pentas Ehrenberg Ogane et al., pl. 9, figs. 1a-1e.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Petalospyris platyacantha Ehrenberg, 1874 group

Plate II.12, Figure 11

- 1874 Petalospyris platyacantha Ehrenberg, p. 247.
- 1876 Petalospyris platyacantha Ehrenberg Ehrenberg, p. 80, pl. 22, fig. 8.
- 1887 Petalospyris (Petalospyrella) platyacantha Ehrenberg Haeckel, p. 1060.
- 1973 Dorcadospyris platyacantha (Ehrenberg) Sanfilippo and Riedel, p. 528, pl. 17, figs. 11–15, pl. 33, fig. 2.
- 1975 Patagospyris confluens (Ehrenberg) Ling, p. 727, pl. 7, fig. 21.
- ? 1977 Spyrid gen. and sp. indet. Riedel and Sanfilippo, pl. 6, fig. 15 (part).
- 1992 Dorcadospyris platyacantha (Ehrenberg) Nishimura, p. 329, pl. 3, figs. 3–4b.
- 1994 Dorcadospyris platyacantha (Ehrenberg) Weinheimer et al., p. 311, pl. 1, fig. 7.
- 2009 Petalospyris platyacantha Ehrenberg Ogane et al., pl. 77, figs. 3a–3c.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Semantidium Haeckel, 1887

Type species.— Semantidium hexastoma Haeckel, 1887, p. 960, pl. 92, fig. 6.

Semantidium haeckelii (Bütschli, 1882a)

Plate II.12, Figure 12

1882a Stephanolithis Haeckelii [sic] Bütschli, p. 538, pl. 32, figs. 6a, 6b.

- 1882b Stephanolithis Haeckelii [sic] Bütschli, pl. 28, fig. 11.
- 1969 Giraffospyris haeckelii (Bütschli) Goll, p. 334, pl. 57, figs. 5–7, text-fig. 2.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Chapter II – Progress on middle Eocene radiolarian biodiversity



Plate II.12. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic). (**1**, **2**) *Liriospyris ramosa* (Ehrenberg, 1847): ODP 1260A-6R-1W, 55–57 cm; (**2**) ODP 1051A-10H-2W, 53–55 cm. (**3**) *Liriospyris turrita* (Ehrenberg, 1874): ODP 1051A-2H-5W, 55–57 cm. (**4**) *Petalospyris argiscus* Ehrenberg, 1874: ODP 1260A-11R-4W, 55–57 cm. (**5**, **6**) *Petalospyris confluens* Ehrenberg, 1874: (**5**) ODP 1260A-6R-2W, 55–57 cm; (**6**) ODP 1260A-12R-2W, 55–57 cm. (**7**) *Petalospyris diaboliscus* Ehrenberg, 1847: ODP 1051A-8H-5W, 53–55 cm. (**9**, **10**) *Petalospyris flabellum* Ehrenberg, 1874: ODP 1051A-8H-5W, 53–55 cm. (**9**, **10**) *Petalospyris pentas* Ehrenberg, 1874: (**9**) ODP 1260A-19R-6W, 55–57 cm; (**10**) ODP 1260A-20R-4W, 63–177 cm. (**11**) *Petalospyris platyacantha* Ehrenberg, 1874 group: ODP 1260A-7R-4W, 54–56 cm. (**12**) *Semantidium haeckelii* (Bütschli, 1882a): ODP 1260A-11R-7W, 55–57 cm. (**13**) *Zygocircus butschlii* Haeckel, 1887: ODP 1260A-9R-4W, 55–57 cm. (**14**) *Zygocircus ? spinescens* (Ehrenberg, 1854a): ODP 1260A-6R-2W, 55–57 cm. (**15**) *Zygocircus cimelium* Petrushevskaya *in* Petrushevskaya and Kozlova, 1972: ODP 1260A-13R-1W, 54–56 cm. All scale bars equal 50 µm.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Family Stephaniidae Haeckel, 1882

Genus Zygocircus Bütschli, 1882a

Type species.— Lithocircus productus Hertwig, 1879, p. 197, pl. 7, fig. 4.

Zygocircus butschlii Haeckel, 1887

Plate II.12, Figure 13

- 1887 Zygocircus bütschlii [sic] Haeckel, p. 948.
- 1972 Zygocircus bütschlii [sic] Haeckel Petrushevskaya and Kozlova, p. 534, pl. 41, figs. 8–11.
- 1986 Dendrocircus barbadensis Haeckel Göke, fig. 3.6.
- 1992 Zygocircus bütschli [sic] Haeckel Takemura, 1992, p. 743, pl. 5, fig. 4.
- 1997 Zygocircus bütschli [sic] Haeckel Hollis et al., p. 51, pl. 3, fig. 11.
- 1997 Zygocircus bütschli [sic] Haeckel Takemura and Ling, p. 114, pl. 1, fig. 4.
- 1999a Zygocircus buetschlii [sic] Haeckel O'Connor, p. 40, pl. 10, fig. 43.
- 2005 Zygocircus bütschlii [sic] Haeckel Funakawa and Nishi, p. 238, pl. 3, fig. 9.
- 2009b Zygocircus triangularis (Clark and Campbell) Suzuki et al., p. 257, pl. 22, fig. 15.
- 2020 Zygocircus bütschli [sic] Haeckel Hollis et al., pl. 5, fig. 4.

2021 Zygocircus bütschli [sic] Haeckel – de Souza et al., p. 15, pl. 2, fig. 2.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Zygocircus cimelium Petrushevskaya in Petrushevskaya and Kozlova, 1972 Plate II.12, Figure 15

- 1972 Zygocircus cimelium Petrushevskaya in Petrushevskaya and Kozlova, p. 534, pl. 41, figs. 5, 6.
- 2005 *Zygocircus cimelium* Petrushevskaya *in* Petrushevskaya and Kozlova Nigrini et al., p. 56, pl. P3, figs. 9–12.
- 2012 Zygocircus cimelium Petrushevskaya in Petrushevskaya and Kozlova Moore and Kamikuri, p. 13, pl. P10, figs. 8, 9.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Zygocircus ? *spinescens* (Ehrenberg, 1854a) Plate II.12, Figure 14

1854a Stephanolithis spinescens Ehrenberg, p. 160, pl. 1, fig. 29.

1876 Stephanolithis spinescens Ehrenberg – Ehrenberg, pl. 36, figs. B57, C57.

1882a Stephanolithis spinescens Ehrenberg - Bütschli, p. 497, pl. 32, figs. 7a, 7b.

1882b Stephanolithis spinescens Ehrenberg – Bütschli, pl. 28, fig. 10.

1887 Semantis spinescens (Ehrenberg) – Haeckel, p. 958.

1957a Semantis spinescens (Ehrenberg) - Riedel, p. 259, pl. 63, fig. 2.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Superfamily Archipilioidea Haeckel, 1882 sensu Sandin et al., 2019

Family Theophormididae Haeckel, 1882 emend. Suzuki et al., 2021

Genus Velicucullus Riedel and Campbell, 1952

Type species.— *Soreuma (Soreumium ?) magnificum* Clark and Campbell, 1942, p. 51, pl. 4, fig. 15.

? Velicucullus discoides (Ehrenberg, 1874)

Plate II.13, Figures 1, 2

1874 *Cycladophora discoides* Ehrenberg, p. 222.

1876 Cycladophora ? discoides Ehrenberg – Ehrenberg, p. 68, pl. 18, fig. 4.

1887 Theocalyptra discoides (Ehrenberg) – Haeckel, p. 1397.

2009 Cycladophora discoides Ehrenberg – Ogane et al., pl. 6, figs. 6a–6c, pl. 80, figs. 1a–1d.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Superfamily Theopilioidea Haeckel, 1882 emend. Suzuki et al., 2021 Family Anthocyrtididae Haeckel, 1882 emend. Suzuki et al., 2021 Genus *Anthocyrtis* Ehrenberg, 1846

Type species.— Anthocyrtis mespilus Ehrenberg, 1847, p. 55, fig. 9.

Anthocyrtis collaris Ehrenberg, 1874

Plate II.13, Figure 3

1874 Anthocyrtis collaris Ehrenberg, p. 215.

1876 Anthocyrtis collaris Ehrenberg – Ehrenberg, p. 64, pl. 6, fig. 8.

1887 Anthocyrtium (Anthocyrtarium) collare (Ehrenberg) – Haeckel, p. 1273.

1887 Clathrocyclas (Clathrocyclia) collaris Haeckel, p. 1387, pl. 74, fig. 8.

1975 Anthocyrtella sp. Ling, p. 728, pl. 8, fig. 19.

2009 Anthocyrtis collaris Ehrenberg – Ogane et al., pl. 50, figs. 3a–3h.

2015 Anthocyrtis collaris Ehrenberg – Kamikuri, pl. 10, fig. 2a, 2b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Anthocyrtis mespilus Ehrenberg, 1847

Plate II.13, Figure 4

1847 Anthocyrtis Mespilus [sic] Ehrenberg, p. 55, fig. 9.

1854a Anthocyrtis mespilus [sic] Ehrenberg - Ehrenberg, pl. 36, fig. 13.

1874 Anthocyrtis furcata Ehrenberg, 1847, p. 216.

1876 Anthocyrtis furcata Ehrenberg – Ehrenberg, p. 64, pl. 6, fig. 2.

1876 Anthocyrtis mespilus Ehrenberg – Ehrenberg, p. 66, pl. 6, figs. 4, 5.

1887 Anthocyrtis (Anthocyrtella) mespilus Ehrenberg – Haeckel, p. 1269.

1887 Anthocyrtis (Anthocyrtella) furcata Ehrenberg – Haeckel, p. 1269.

2006 Anthocyrtis furcata Ehrenberg – Funakawa et al., p. 38, pl. P13, figs. 5a, 5b.

2009 Anthocyrtis mespilus Ehrenberg – Ogane et al., pl. 50, figs. 2a, 2b, pl. 80, figs. 5a–5e, pl. 81, figs. 1a–2d.

2009 Anthocyrtis furcata Ehrenberg – Ogane et al., pl. 80, figs. 4a–4f.

2015 Anthocyrtis mespilus Ehrenberg - Kamikuri, pl. 10, figs. 4a-6.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Anthocyrtis ? spatiosa (Ehrenberg, 1874)

Plate II.13, Figures 5, 6

1874 Cycladophora spatiosa Ehrenberg, p. 222.

1876 Cycladophora spatiosa Ehrenberg – Ehrenberg, p. 68, pl. 18, figs. 5, 6.

1882a Cycladophora spatiosa Ehrenberg – Bütschli, p. 527.

1882b Cycladophora spatiosa Ehrenberg - Bütschli, pl. 30, fig. 15.

1887 Cycladophora (Cyclampterium) spatiosa Ehrenberg – Haeckel, p. 1379.

- 1972 *Anthocyrtella spatiosa* (Ehrenberg) group Petrushevskaya and Kozlova, p. 541, pl. 33, figs. 1–3.
- 1977 Anthocyrtella sp. Riedel and Sanfilippo, pl. 10, fig. 7.
- 2006 Anthocyrtella spatiosa (Ehrenberg) group Funakawa et al., p. 38, pl. P13, figs. 7a-8b.

2009 Cycladophora spatiosa Ehrenberg – Ogane et al., pl. 87, figs. 4a, 4b, pl. 9, figs. 6a, 6b.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus *Eurystomoskevos* Caulet, 1991 emend. O'Connor, 1999a *Type species.— Eurystomoskevos petrushevskayae* Caulet, 1991, p. 536, pl. 3, fig. 14.

Eurystomoskevos petrushevskayae Caulet, 1991

Plate II.13, Figure 7

- 1972 Diplocyclas sp. A group Petrushevskaya and Kozlova, p. 541, pl. 33, fig. 14–16.
- 1975 Diplocyclas sp. A group Petrushevskaya, p. 587, pl. 24, fig. 4.
- 1975 Diplocyclas sp. A group Chen, p. 460, pl. 7, fig. 4, 5.
- 1991 Eurystomoskevos petrushevskayae Caulet, p. 536, pl. 3, fig. 14, 15.
- 1992 Diplocyclas sp. Takemura, p. 746, pl. 3, fig. 16.
- 1997 Eurystomoskevos petrushevskayaae [sic] Caulet Hollis et al., p. 62, pl. 5, figs. 22, 23.
- 2002 Eurystomoskevos petrushevskaae [sic] Caulet Hollis, p. 310, pl. 7, figs. 7-10.
- 2002 Eurystomoskevos petrushevskaae [sic] Caulet Apel et al., p. 18, pl. P7, fig. 13.
- 2005 *Eurystomoskevos petrushevskaae* [sic] Caulet Funakawa and Nishi, p. 233, pl. 4, figs. 13a, 13b.
- 2005 ? *Cycladophora conica* Lombari and Lazarus Funakawa and Nishi, p. 231, pl. 4, figs. 11a, 11b.
- 2006 Eurystomoskevos petrushevskaae [sic] Caulet Funakawa et al., p. 38, pl. P13, figs. 9a, 9b.
- 2009b Eurystomoskevos petrushevskaae [sic] Caulet Suzuki et al., p. 265, pl. 22, figs. 5a-6.
- 2020 Eurystomoskevos petrushevskaae [sic] Caulet Hollis et al., pl. 10, fig. 8.
- 2021 Eurystomoskevos petrushevskaae [sic] Caulet de Souza et al., p. 15, pl. 3, fig. 4.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Superfamily Stichopilioidea Haeckel, 1882 Family Stichopiliidae Haeckel, 1882

Genus Lophoconus Haeckel, 1887

Type species.—*Eucyrtidium antilope* Ehrenberg, 1873a, p. 308 (unfigured); Ehrenberg, 1873b, p. 290, pl. 9, fig. 18.

Lophoconus antilope (Ehrenberg, 1874)

Plate II.13, Figure 8

- 1873a Eucyrtidium antilope Ehrenberg, p. 308.
- 1873b Eucyrtidium antilope Ehrenberg Ehrenberg, p. 290, pl. 9, fig. 18.
- 1887 Lophoconus antilope (Ehrenberg) Haeckel, p. 1404.
- 1977 Theoperid gen. et sp. indet. Riedel and Sanfilippo, pl. 7, fig. 7.
- 2009a Eucyrtidium antilope Ehrenberg Suzuki et al., pl. 77, figs. 1a-1d.
- Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Superfamily Plagiacanthoidea Hertwig, 1879 emend. Sandin et al., 2019

Family Lophophaenidae Haeckel, 1882 sensu Petrushevskaya, 1971

Genus Ceratospyris Haeckel, 1882

Type species.— *Cornutella* ? *cucullaris* Ehrenberg, 1874, p. 221 (unfigured); Ehrenberg, 1876, p. 68, pl. 2, fig. 7.

Ceratospyris ampliata (Ehrenberg, 1874)

Plate II.13, Figure 9

1874 Cornutella ampliata Ehrenberg, p. 221.

1876 Cornutella ampliata Ehrenberg – Ehrenberg, p. 68, pl. 2, fig. 5.

1882a Ceratocyrtis ampliata (Ehrenberg) - Bütschli, p. 536.

1887 Sethoconus (Conarachnium) ampliatus (Ehrenberg) – Haeckel, p. 1291.

1999 Ceratocyrtis ampliata (Clark and Campbell) – Kozlova, p. 173, pl. 35, fig. 9.

1999 Ceratocyrtis rhabdophora (Clark and Campbell) – Kozlova, p. 115, pl. 47, fig. 14.

2009 Cornutella ampliata Ehrenberg – Ogane et al., pl. 35, figs. 1a–1g (part).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Ceratocyrtis rhabdophora (Clark and Campbell, 1945)

Plate II.13, Figure 10

1882a Ceratocyrtis cucullaris (Ehrenberg) - Bütschli, pl. 33, figs. 36a, 36b.

1945 Bathrocalpis rhabdophora Clark and Campbell, p. 34, pl. 7, figs. 36–41.

1976 Ceratocyrtis cucullaris (Ehrenberg) – Dzinoridze et al., pl. 26, fig. 12, pl. 37, figs. 4-6.

? 1977 Lamprotripus ? sp. Riedel and Sanfilippo, pl. 7, fig. 5.

2009b *Ceratocyrtis rhabdophora* (Clark and Campbell) – Suzuki et al., p. 255, pl. 20, figs. 12a, 12b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Lophophaena Ehrenberg, 1847 emend. Petrushevskaya, 1971

Type species.— *Lophophaena galeaorci* Ehrenberg, 1854c, p. 245 (unfigured); Stöhr, 1880, p. 99, pl. 3, fig. 17.

Lophophaena capito Ehrenberg, 1874

Plate II.13, Figures 14, 15

- 1874 Lophophaena Capito [sic] Ehrenberg, p. 242.
- 1876 Lophophaena Capito [sic] Ehrenberg Ehrenberg, p. 78, pl. 8, fig. 6.
- 1972 *Lophophaena* ? *capito* Ehrenberg group Petrushevskaya and Kozlova, p. 535, pl. 33, figs. 20–23.

not 1975 *Lophophaena ? capito* Ehrenberg group – Petrushevskaya, pl. 9, fig. 21.

- 1975 Lophophaena sp. G Petrushevskaya, pl. 9, fig. 22
- 1975 Lamptonium sanfilippoae Foreman Ling, p. 729, pl. 9, fig. 23 (part).
- 1977 Plagoniid gen. et sp. indet. Riedel and Sanfilippo, pl. 7, fig. 3, pl. 8, fig. 11 (part).

Chapter II – Progress on middle Eocene radiolarian biodiversity



Plate II.13. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic). (**1**, **2**) ? *Velicucullus discoides* (Ehrenberg, 1874): (**1**) ODP 1051A-11H-2W, 62–64 cm; (**2**) ODP 1260A-9H-2W, 53–55 cm. (**3**) *Anthocyrtis collaris* Ehrenberg, 1874: ODP 1051A-11H-2W, 62–64 cm. (**4**) *Anthocyrtis mespilus* Ehrenberg, 1847: ODP 1260A-13R-3W, 54–56 cm. (**5**, **6**) *Anthocyrtis* ? *spatiosa* (Ehrenberg, 1874) group: (**5**) ODP 1260A-13R-3W, 54–56 cm; (**6**) ODP 1260A-11R-4W, 55–57 cm. (**7**) *Eurystomoskevos petrushevskayae* Caulet, 1991: ODP 1260A-9R-3W, 55–57 cm. (**8**) *Lophoconus antilope* (Ehrenberg, 1874): ODP 1260A-13R-4W, 55–57 cm. (**10**) *Ceratospyris ampliata* (Ehrenberg, 1874): ODP 1260A-13R-4W, 55–57 cm. (**11**) *Lophophaena radians* Ehrenberg, 1874: ODP 1260A-9R-6W, 55–57 cm. (**12**) ODP 1260A-11R-7W, 55–57 cm. (**13**) ODP 1051A-9H-5W, 53–55 cm. (**14**, **15**) *Lophophaena capito* Ehrenberg, 1874: (**14**) ODP 1260A-11R-7W, 55–57 cm. (**15**) ODP 1260A-9R-5W, 55–57 cm. All scale bars equal 50 µm.

- not 2002 *Lophophaena capito* Ehrenberg Apel et al., p. 18, pl. P6, fig. 6.
- 2006 Lophophaena capito Ehrenberg group Funakawa et al., p. 20, Pl. P3, figs. 3, 4.
- 2009 Lophophaena capito Ehrenberg Ogane et al., pl. 19, figs. 8a–8c, pl. 34, figs. 3a–3c, pl. 79, figs. 2a–2c.
- 2015 Lithomelissa lautouri O'Connor Kamikuri, pl. 11, figs. 10-12.
- 2020 Lophophaena capito Ehrenberg Hollis et al., pl. 6, fig. 15.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Lophophaena galeaorci Ehrenberg, 1854c

Plate II.13, Figures 12, 13

- 1854c Lophophaena Galea Orci [sic] Ehrenberg, p. 245.
- 1862 Lophophaena Galea Orci [sic] Ehrenberg Haeckel, p. 298.
- 1874 Lophophaena apiculata Ehrenberg, p. 242.
- 1876 Lophophaena apiculata Ehrenberg Ehrenberg, p. 78, pl. 8, figs. 11.
- 1880 Lophophaena Galea Orci [sic] Ehrenberg Stöhr, p. 99, pl. 3, fig. 17.
- 1882a Dictyocephalus Galea Orci [sic] (Ehrenberg) Bütschli, p. 535.
- 1882a Dictyocephalus apiculata (Ehrenberg) Bütschli, p. 535.
- 1887 Lophophæna (Lophophænula) galea [sic] Ehrenberg Haeckel, p. 1303.
- 1977 Plagoniid gen. et sp. indet. Riedel and Sanfilippo, pl. 7, fig. 1 (part).
- 1983 Artostrobid, gen. et sp. indet. Johnson, pl. 2, fig. 8.
- 1999 Plagiacanthidae gen. et sp. indet. Kozlova, pl. 3, fig. 8.
- 2006 Sethoperid sp. A Funakawa et al., pl. P3, figs. 10a, 10b, 11a-12b.
- 2006 Sethoperid sp. B Funakawa et al., pl. P3, figs. 13a, 13b, 14a-15b.
- 2009 Lophophaena apiculata Ehrenberg Ogane et al., pl. 25, figs. 3a–3d.
- 2015 Dictyocephalus obtusa (Ehrenberg) Kamikuri, pl. 11, figs. 4-6.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Lophophaena radians Ehrenberg, 1874

Plate II.13, Figure 11

1874 Lophophaena radians Ehrenberg, p. 243.

1876 Lophophaena radians Ehrenberg – Ehrenberg, p. 78, pl. 8, figs. 7–9.

1887 Lophophæna (Lophophænula) radians [sic] Ehrenberg – Haeckel, p. 1303.

- 2006 Lophophaena radians Ehrenberg Funakawa et al., p. 20, pl. P3, figs. 5a-6b.
- 2009 Lophophaena radians Ehrenberg Ogane et al., pl. 3, figs. 3a–3e, 5a-5d, pl. 79, figs. 4a–4c.

2015 Lophophaena radians Ehrenberg – Kamikuri, pl. 13, figs. 30a, 30b.

not 2020 *Lophophaena radians* Ehrenberg – Hollis et al., pl. 6, fig. 16.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Lithomelissa Ehrenberg, 1847

Type species.— *Lithomelissa microptera* Ehrenberg, 1854a, pl. 36, fig. 2; description in Haeckel, 1862, p. 303.

Lithomelissa ? acutispina Clark and Campbell, 1942 Plate II.14, Figure 1

1942 *Lithomelissa (Acromelissa) acutispina* Clark and Campbell, p. 69, pl. 9, fig. 21. Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Lithomelissa dupliphysa Caulet, 1991

Plate II.14, Figure 2

1991 Lithomelissa dupliphysa Caulet, p. 534, pl. 2, fig. 4.

2021 Lithomelissa challengerae Chen – de Souza et al., p. 15, pl. 2, figs. 3a, 3b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Lithomelissa macroptera Ehrenberg, 1874

Plate II.14, Figure 3

1874 Lithomelissa macroptera Ehrenberg, p. 241.

- 1876 Lithomelissa macroptera Ehrenberg Ehrenberg, p. 78, pl 3, figs. 9, 10 (part).
- 1887 Lithomelissa (Acromelissa) macroptera Ehrenberg Haeckel, p. 1204.
- 1976 *Lithomelissa macroptera* Ehrenberg Dzinoridze et al., pl. 29, figs. 14, 15, pl. 37, fig. 9 (part).
- 2009 *Lithomelissa macroptera* Ehrenberg Ogane et al., pl. 19, figs. 6a–6d, pl. 79, figs. 6a–6c (part).
- 1978 Lithomelissa sp. cf. L. macroptera Ehrenberg Weaver and Dinkelman, p. 869, pl. 1, fig. 11.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Lithomelissa tricornis Chen, 1975

Plate II.14, Figure 4

1975 Lithomelissa tricornis Chen, p. 458, pl. 8, figs. 6, 7.

1990 Lithomelissa tricornis Chen – Abelmann, p. 695, pl. 5, fig. 3.

1992 Lithomelissa tricornis Chen – Takemura, p. 744, pl. 2, figs. 5, 6.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Genus Pelagomanes Trubovitz et al., 2022

Type species.— *Lithomelissa* ? *kozoi* Renaudie and Lazarus, 2013a, p. 73, pl. 5, figs. 10a–11, 13a, 13b, 15, pl. 8, fig. 5.

Pelagomanes thaumasia (Caulet, 1991)

Plate II.14, Figure 5

1991 Lophophaena? thaumasia Caulet, p. 534, pl. 2, figs. 5, 6.

2022 Pelagomanes thaumasia (Caulet) – Trubovitz et al., p. 83, pl. 39, figs. 10a–11.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Family Plagiacanthidae Hertwig, 1879 sensu Dumitrică, 2004 Genus *Neosemantis* Popofsky, 1913

Type species.— Neosemantis distephanus Popofsky, 1913, p. 229, pl. 29, fig. 2.

Neosemantis mimicus Goll, 1979

Plate II.14, Figure 6

1979 *Neosemantis bjoerklundi mimicus* Goll, p. 383, pl. 3, figs. 1–12. Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

> Family Ximolzidae Dumitrică *in* Suzuki et al., 2021 Genus *Rhabdolithis* Ehrenberg, 1847

Type species.— *Rhabdolithis pipa* Ehrenberg, 1854a, pl. 36, fig. 59; description in Ehrenberg, 1876, p. 159.

Rhabdolithis ellida Sanfilippo and Riedel, 1973

Plate II.14, Figure 7

1973 Rhabdolithis ellida Sanfilippo and Riedel, p. 529, pl. 18, figs. 8–11, pl. 33, figs. 5–8.

1977 Rhabdolithis ellida Sanfilippo and Riedel – Riedel and Sanfilippo, pl. 4, fig. 5.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Rhabdolithis pipa Ehrenberg, 1854a Plate II.14, Figures 8, 9

1854a Rhabdolithis Pipa [sic] Ehrenberg, pl. 36, fig. 59.



Plate II.14. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic).(1) *Lithomelissa ? acutispina* Clark and Campbell, 1942: ODP 1051A-14H-5W, 52–54 cm. (2) *Lithomelissa dupliphysa* Caulet, 1991: ODP 1260A-11R-7W, 55–57 cm. (3) *Lithomelissa macroptera* Ehrenberg, 1874: ODP 1260A-6R-2W, 55–57 cm. (4) *Lithomelissa tricornis* Chen, 1975: ODP 1260A-9R-6W, 55–57 cm. (5) *Pelagomanes thaumasia* (Caulet, 1991): ODP 1051A-6H-5W, 53–55 cm. (6) *Neosemantis mimicus* Goll, 1979: ODP 1260A-9R-3W, 55–57 cm. (7, 8) *Rhabdolithis pipa* Ehrenberg, 1854a: (7) ODP 1260A-11R-6W, 55–57 cm; (8) ODP 1260A-10R-4W, 55–57 cm. (9) *Rhabdolithis ellida* Sanfilippo and Riedel, 1973: ODP 1260A-13R-5W, 54–56 cm. (10) *Botryocella nucula* (Ehrenberg, 1874): ODP 1051A-13H-2W, 52–54 cm. (11) *Botryocella adspersa* (Ehrenberg, 1874: (12) ODP 1260A-13R-5W, 55–57 cm; (13) ODP 1260A-12R-1W, 55–57 cm. All scale bars equal 50 μm.

- 1862 *Rhabdolithes pipa* [sic] Ehrenberg Bury, pl. 2, fig. 4 (part).
- 1876 Rhabdolithis Pipa [sic] Ehrenberg Ehrenberg, p. 159, pl. 1, fig. 27.
- 1882b Rhabdolithis Pipa [sic] Ehrenberg Bütschli, pl. 21, fig. 8.
- 1887 Xiphostylus (Xiphostylissa) falco Haeckel, p. 130, pl. 13, fig. 14.
- 1887 Xiphostylus (Xiphostylomma) emberiza Haeckel, p. 131, pl. 13, fig. 11.
- 1973 *Rhabdolithis pipa* Ehrenberg Sanfilippo and Riedel, p. 529, pl. 18, figs. 12–16, pl. 33, figs. 9, 10.
- 1973 Rhabdolithis pipa Ehrenberg Riedel and Sanfilippo, 739, pl. 3, figs. 7, 8.
- 1977 Rhabdolithis pipa Ehrenberg Riedel and Sanfilippo, pl. 9, fig. 3.
- 1978 Rhabdolithis pipa Ehrenberg Riedel and Sanfilippo, p. 72, pl. 9, figs. 3, 4.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

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.

Botryocella adspersa (Ehrenberg, 1854a)

Plate II.14, Figure 11

1854a Lithobotrys adspersa Ehrenberg, pl. 36, fig. 5.

1874 *Lithobotrys adspersa* Ehrenberg – Ehrenberg, p. 237.

1876 Lithobotrys adspersa Ehrenberg – Ehrenberg, p. 76, pl. 3, fig. 15.

2009 Lithobotrys adspersa Ehrenberg – Ogane et al., 2009, pl. 61, figs. 4a–5d.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

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Botryocella nucula (Ehrenberg, 1874)

Plate II.14, Figure 10

1874 Lithobotrys Nucula [sic] Ehrenberg, p. 238.

1876 Lithobotrys Nucula [sic] Ehrenberg – Ehrenberg, p. 76, pl. 3, fig. 16.

1887 Botryocella nucula (Ehrenberg) – Haeckel, p. 1116.

2009 Lithobotrys nucula Ehrenberg – Ogane et al., 2009, pl. 6, figs. 8a–8d.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Lithocorythium Ehrenberg, 1847

Type species.— *Lithobotrys galea* Ehrenberg, 1844, p. 83 (unfigured); Ehrenberg, 1854a, pl. 22, figs. 29a, 29b.

Lithocorythium ? amblyostauros Ehrenberg, 1874

Plate II.14, Figures 12, 13

1874 *Lithopera amblyostauros* Ehrenberg, p. 241.

1876 Lithopera amblyostauros Ehrenberg – Ehrenberg, p. 78, pl. 3, fig. 5.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Lithocorythium ? niduspendulus Ehrenberg, 1874

Plate II.15, Figures 1, 2

1874 *Lithopera Nidus pendulus* [sic] Ehrenberg, p. 241.

1876 Lithopera Nidus pendulus [sic] Ehrenberg – Ehrenberg, p. 78, pl. 3, fig. 7.

1882a Lithomelissa microptera Ehrenberg – Bütschli, pl. 30, fig. 2.

1882a Anthocyrtis Nidus pendulus [sic] Ehrenberg - Bütschli, p. 533.

1887 Sethocapsa nidus [sic] (Ehrenberg) – Haeckel, p. 1311.

- 1970 Gen. et sp. indet. Riedel and Sanfilippo, pl. 12, fig. 10.
- 1973 Cannobotrythids gen(n). et sp(p). indet. Sanfilippo and Riedel, pl. 21, fig. 6–10, 12, pl. 36, figs. 6–8 (part).

1977 Cannobotrythid gen. et sp. indet. Riedel and Sanfilippo, pl. 8, fig. 8.

1979 Lithobotrys geminata (Ehrenberg) – Petrushevskaya and Kozlova, fig. 275 (part).

2009 Lithopera nidus-pendulus [sic] Ehrenberg – Ogane et al., pl. 21, figs. 4a–4c.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Superfamily Sethoperoidea Haeckel, 1882

Family Sethoperidae Haeckel, 1882 emend. Suzuki et al., 2021

Genus Clathrocorys Haeckel, 1882

Type species.— *Clathrocorys murrayi* Haeckel, 1887, p. 1219, pl. 64, fig. 8.

Clathrocorys atavia (Goll, 1979)

Plate II.15, Figure 3

1979 *Callimitra atavia* Goll, p. 388, pl. 5, figs. 1, 5–9, 11.

? 1999a Callimitra atavia Goll – O'Connor, p. 31, pl. 9, fig. 4.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Clathrocorys tribrachiata (Ehrenberg, 1874)

Plate II.15, Figure 4

- 1874 Cladospyris tribrachiata Ehrenberg, p. 220.
- 1876 Cladospyris tribrachiata Ehrenberg Ehrenberg, p. 68, pl. 21, fig. 8.
- 1882b Ceratospyris tribrachiata Ehrenberg Bütschli, pl. 29, fig. 5.
- 1887 Tripospyris (Tripospyromma) tribrachiata (Ehrenberg) Haeckel, p. 1029.
- 1942 Tripilidium (Tristylocorys) clavipes Clark and Campbell, p. 64, pl. 9, fig. 29.
- 1979 *Tripodiscinus clavipes* (Clark and Campbell) Petrushevskaya and Kozlova, p. 115, fig. 302.
- 1988 *Tripilidium (Tristylocorys) clavipes* Clark and Campbell Blueford, p. 244, pl. 1, figs. 7–9.
- 1997 Tripodiscinus clavipes (Clark and Campbell) Hollis et al., p. 53, pl. 3, figs. 28, 29.
- 2002 Tripodiscinus clavipes (Clark and Campbell) Apel et al., p. 21, pl. P6, fig. 9.
- not 2005 *Tripilidium clavipes* Clark and Campbell Funakawa and Nishi, p. 238, pl. 4, figs. 8a, 8b.
- 2005 *Tripilidium* cf. *clavipes* Clark and Campbell Funakawa and Nishi, p. 238, pl. 4, figs. 7a, 7b.
- 2009 *Cladospyris tribrachiata* Ehrenberg Ogane et al., pl. 35, figs. 2a– 2c, pl. 15, figs. 1a– 2d.
- 2020 Tripodiscinus clavipes (Clark and Campbell) Hollis et al., pl. 6, fig. 27.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Superfamily Lithochytridoidea Ehrenberg, 1846

Family Lithochytrididae Ehrenberg, 1846 sensu Suzuki in Matsuzaki et al., 2015

? Genus Dictyophimus Ehrenberg, 1847 sensu Nigrini, 1967

Type species.— *Dictyophimus crisae* Ehrenberg, 1854c, p. 241 (unfigured); Suzuki et al., 2009a, pl. 35, figs. 1a–1d.

Dictyophimus craticula Ehrenberg, 1874

Plate II.15, Figure 5

- 1862 Actiniscus ? Bury, pl. 7, fig. 5.
- 1874 Dictyophimus Craticula [sic] Ehrenberg, p. 223.
- 1876 Dictyophimus Craticula [sic] Ehrenberg Ehrenberg, p. 68, pl. 5, figs. 4, 5.

1882a Dictyophimus Craticula [sic] Ehrenberg - Bütschli, pl. 33, fig. 35.

1882b Dictyophimus Craticula [sic] Ehrenberg - Bütschli, pl. 29, fig. 10.

1887 Dictyophimus (Dictyophimium) craticula Ehrenberg – Haeckel, p. 1196.

1970 Dictyophimus craticula Ehrenberg – Riedel and Sanfilippo, pl. 10, fig. 6.

1973 Dictyophimus craticula Ehrenberg – Sanfilippo and Riedel, p. 529, pl. 19, fig. 1 (part).

1977 Dictyophimus craticula Ehrenberg – Riedel and Sanfilippo, pl. 7, fig. 6.

1978 Dictyophimus craticula Ehrenberg – Riedel and Sanfilippo, p. 68, pl. 4, fig. 19.

1986 Dictyophimus craticula Ehrenberg – Riedel and Sanfilippo, pl. 4, figs. 13, 14.

2009 *Dictyophimus craticula* Ehrenberg – Ogane et al., pl. 21, fig. 5, pl. 36, figs. 1a–1f, pl. 37, figs. 2a–4.

2012b Dictyophimus craticula Ehrenberg - Kamikuri et al., p. 3, pl. P2, fig. 7.

2020 Dictyophimus craticula Ehrenberg – Hollis et al., pl. 12, figs. 4a, 4b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Lithochytris Ehrenberg, 1846

Type species.— *Lithochytris vespertilio* Ehrenberg, 1874, p. 239 (unfigured); Ehrenberg, 1876, p. 76, pl. 4, fig. 10.

Lithochytris pyramidalis Ehrenberg, 1874

Plate II.15, Figures 9, 10

1874 Lithochytris pyramidalis Ehrenberg, p. 239.

1874 Lithochytris Vespertilio [sic] Ehrenberg, p. 239.

1876 Lithochytris pyramidalis Ehrenberg – Ehrenberg, p. 76, pl. 5, fig. 1.

1876 Lithochytris Vespertilio [sic] Ehrenberg – Ehrenberg, p. 76, pl. 4, fig. 10.

1882a Lithochytris pyramidalis Ehrenberg – Bütschli, p. 532.

1882a Lithochytris Vespertilio [sic] Ehrenberg – Bütschli, p. 532.

1882b Lithochytris Vespertilio [sic] Ehrenberg – Bütschli, pl. 31, fig. 4.

1887 Lithochytris (Lithochytridium) lucerna Haeckel, p. 1364, pl. 67, fig. 14.

1887 Lithochytris (Lithochytridium) pyramidalis Ehrenberg – Haeckel, p. 1364.

1887 Lithochytris (Lithochytridium) pteropus Haeckel, p. 1364, pl. 67, fig. 15.

1887 Lithochytris (Lithochytridium) vespertilio Ehrenberg – Haeckel, p. 1365.

1942 Lithochytris (Lithochytridium) cheopsis Clark and Campbell, p. 81, pl. 9, fig. 37.

1957a Lithochytris aff. L. cheopsis Clark and Campbell – Riedel, p. 261, pl. 62, fig. 5.

? 1970 Lithochytris sp(p) Cita et al., p. 403, pl. 2, figs. D, E.

1970 Lithochytris vespertilio Ehrenberg – Riedel and Sanfilippo, p. 518, pl. 9, figs. 8, 9.

1971 Lithochytris vespertilio Ehrenberg – Moore, p. 741, pl. 1, fig.4.

1973 Lithochytris vespertilio Ehrenberg – Foreman, p. 436, pl. 2, figs. 2, 3, pl. 11, fig. 3.

1974 Lithochytris vespertilio Ehrenberg – Nigrini, p. 1067, pl. 1G, figs. 4–6.

1975 Lithochytris vespertilio Ehrenberg – Chen, p. 461, pl. 1, fig. 1.

1975 Lithochytris vespertilio Ehrenberg – Ling, p. 729, pl. 10, figs. 1–3.

1977 Lithochytris vespertilio Ehrenberg – Riedel and Sanfilippo, pl. 7, fig. 15.

1978 Lithochytris vespertilio Ehrenberg – Riedel and Sanfilippo, p. 69, pl. 6, fig. 4.

1986 Lithochytris pyramidalis Ehrenberg – Göke, fig. 3.1.
2000 *Lithochytris vespertilio* Ehrenberg – Nigrini and Sanfilippo, p. 73, pl. 1, fig. 15, pl. 2, fig. 10.

2008 Lithochytris vespertilio Ehrenberg – Jackett et al., p. 56, pl. 2, fig. 19.

2009 Lithochytris vespertilio Ehrenberg – Ogane et al., pl. 45, figs. 1a–3e.

2009 Lithochytris pyramidalis Ehrenberg – Ogane et al., pl. 61, figs. 6a-6c.

2012 Lithochytris vespertilio Ehrenberg – Moore and Kamikuri, p. 8, pl. P5, fig. 4.

2020 Lithochytris vespertilio Ehrenberg – Hollis et al., pl. 12, fig. 18.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Genus Lychnocanium Ehrenberg, 1846

Type species.— Lychnocanium lucerna Ehrenberg, 1847, p. 55, Figure 5.

Lychnocanium alma O'Connor, 1999a

Plate II.15, Figure 13

1999a Lychnocanium alma O'Connor, p. 24, pl. 4, figs. 1-5, pl. 7, figs. 8a-11.

2020 Lychnocanium alma O'Connor – Hollis et al., pl. 12, figs. 24a, 24b.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Lychnocanium bellum Clark and Campbell, 1942

Plate II.16, Figure 5

- 1942 Lychnocanium (Lychnocanissa) bellum Clark and Campbell, p. 72, pl. 9, figs. 35, 39.
- 1957a Lychnocanium sp. Riedel, p. 259, pl. 63, fig. 5.
- 1970 Lychnocanium bellum Clark and Campbell Cita et al., p. 401, pl. 1, fig. E.
- 1970 Lychnocanium bellum Clark and Campbell Riedel and Sanfilippo, p. 529, pl. 10, fig.
 5.
- 1973 Lychnocanoma bellum (Clark and Campbell) Foreman, p. 437, pl. 11, fig. 9 (part).
- 1974 Lychnocanoma bellum (Clark and Campbell) Nigrini, p. 1068, pl. 1H, figs. 1–3, pl. 2D, fig. 1.
- 1977 Lychnocanoma bellum (Clark and Campbell) Riedel and Sanfilippo, pl. 10, fig. 10.
- 1978 Lychnocanoma bellum (Clark and Campbell) Weaver and Dinkelman, p. 873, pl. 5, figs. 9, 10.
- 1986 Lychnocanoma bellum (Clark and Campbell) Riedel and Sanfilippo, pl. 1, fig. 12.
- 1986 Lychnocanium sp. Göke, fig. 3.4.
- 1987 Lychnocanoma bellum (Clark and Campbell) Nishimura, p. 727, pl. 3, fig. 8.
- 1995 Lychnocanoma bellum (Clark and Campbell) Strong et al., 209, figs. 11I, 11J.
- 1997 Lychnocanium bellum Clark and Campbell Hollis et al., p. 63, pl. 6, figs. 5, 6.
- 1999 *Lychnocanium bellum* Clark and Campbell Kozlova, p. 128, pl. 23, figs. 16, 17, pl. 31, figs. 6, 7, pl. 45, fig. 2.
- 2001 Lychnocanoma bellum (Clark and Campbell) Sanfilippo and Blome, p. 214, fig. 9n.
- 2008 Lychnocanoma bellum (Clark and Campbell) Jackett et al., p. 56, pl. 2, fig. 18.
- 2009b Lychnocanoma bellum (Clark and Campbell) Suzuki et al., p. 261, pl. 19, figs. 1a, 1b.
- 2015 Lychnocanoma aff. bellum (Clark and Campbell) Kamikuri, pl. 1, figs. 7a, 7b.
- 2017 Lychnocanoma bellum (Clark and Campbell) de Souza et al., pl. 3, figs. 14a, 14b.

2020 *Lychnocanium bellum* Clark and Campbell – Hollis et al., pl. 13, fig. 6. Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Lychnocanium carinatum Ehrenberg, 1874

Plate II.15, Figure 15

1874 *Lychnocanium carinatum* Ehrenberg, p. 243.

1876 Lychnocanium carinatum Ehrenberg – Ehrenberg, p. 78, pl. 8, fig. 5.

1887 Lychnocanium (Lychnocanella) carinatum Ehrenberg – Haeckel, p. 1226.

not 1987 *Lychnocanium* ? *carinatum* Ehrenberg – Nishimura, p. 727, pl. 3, figs. 6, 11.

not 2008 *Lychnocanium carinatum* Ehrenberg – Jackett et al., p. 56, pl. 1, fig. 25.

2009 Lychnocanium carinatum Ehrenberg – Ogane et al., pl. 44, figs. 3a–3f.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Lychnocanium continuum Ehrenberg, 1874

Plate II.15, Figure 16

1874 Lychnocanium continuum Ehrenberg, p. 243.

1876 Lychnocanium continuum Ehrenberg – Ehrenberg, p.78, pl. 7, fig. 11.

1887 Lychnocanium (Lychnocanella) continuum Ehrenberg – Haeckel, p. 1225.

2006 Lychnocanium continuum Ehrenberg – Funakawa et al., p. 37, pl. P12, figs. 7a, 7b.

2009 Lychnocanium continuum Ehrenberg – Ogane et al., pl. 98, figs. 5a–5d.

2015 Lychnocanium continuum Ehrenberg – Kamikuri, pl. 2, figs. 3a, 3b.

2020 Lychnocanium continuum Ehrenberg – Hollis et al., pl. 13, figs. 12a, 12b.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Lychnocanium falciferum Ehrenberg, 1854a

Plate II.16, Figure 2

1854a Lychnocanium falciferum Ehrenberg, pl. 36, fig. 7.

1862 Lithomelissa falcifera (Ehrenberg) – Haeckel, p. 303.

1876 Lychnocanium falciferum Ehrenberg – Ehrenberg, p.78, pl. 8, fig. 4.

1887 Lychnocanium (Lychnocanissa) falciferum Ehrenberg – Haeckel, p. 1227.

not 1999 Lychnocanium falciferum Ehrenberg – Kozlova, p. 174, pl. 45, fig. 8.

2009 Lychnocanium falciferum Ehrenberg – Ogane et al., p. 43, figs. 1a–1c.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Lychnocanium lucerna Ehrenberg, 1847

Plate II.15, Figure 8

1847 Lychnocanium Lucerna [sic] Ehrenberg, p. 55, fig. 5.

1854a Lychnocanium Lucerna [sic] Ehrenberg – Ehrenberg, pl. 36, fig. 6.

1862 Lychnocanium lucerna Ehrenberg – Haeckel, p. 311.

1874 Lychnocanium Lucerna [sic] Ehrenberg – Ehrenberg, p. 244.

1876 Lychnocanium Lucerna [sic] Ehrenberg – Ehrenberg, p. 80, pl. 8, fig. 3.

1887 Dictyophimus (Dictyophimium) lucerna (Ehrenberg) – Haeckel, p. 1199.

- 2009 *Lychnocanium lucerna* Ehrenberg Ogane et al., pl. 42, figs. 4a, 4b, pl. 43, figs. 6a, 6b, pl. 44, figs. 1a–1d.
- 2001 Lychnocanoma lucerna (Ehrenberg) Sanfilippo and Blome, p. 214, figs. 9k–9m.
- 2015 Lychnocanoma lucerna (Ehrenberg) Kamikuri, pl. 3, figs. 6a, 6b.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Lychnocanium pileatum (Ehrenberg, 1874)

Plate II.15, Figure 11

- 1874 Lithochytris pileata Ehrenberg, p. 239.
- 1874 Lithochytris Tripodium [sic] Ehrenberg, p. 239.
- 1876 Lithochytris pileata Ehrenberg Ehrenberg, p. 76, pl. 5, fig. 3.
- 1876 Lithochytris Tripodium [sic] Ehrenberg Ehrenberg, p. 76, pl. 4, fig. 11.
- 1882a Lithochytris pileata Ehrenberg Bütschli, p. 532.
- 1887 Lychnocanium (Lychnocanoma) tripodium Ehrenberg Haeckel, p. 1229.
- 1887 Lithochytris (Lithochytridium) pileata Ehrenberg Haeckel, p. 1363.
- 1970 Gen. et sp. indet. Riedel and Sanfilippo, p. 528, pl. 9, fig. 4.
- 2009 Lithochytris pileata Ehrenberg Ogane et al., pl. 22, figs. 9a–9c.
- 2009 Lithochytris tripodium Ehrenberg Ogane et al., pl. 22, figs. 9a–9c.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Lychnocanium tribulus (Ehrenberg, 1874) group Plate II.15, Figure 12

- 1874 Lychnocanium Tribulus [sic] Ehrenberg, p. 245.
- 1876 Lychnocanium Tribulus [sic] Ehrenberg Ehrenberg, p. 80, pl. 7, fig. 5.
- 1887 Lychnocanium (Lychnocanella) tribulus Ehrenberg Haeckel, p. 1226.
- 1942 Dictyophimus (Dictyophimium) babylonis Clark and Campbell, p. 67, pl. 9, figs. 32, 36.
- 1944 Dictyophimus (Dictyophimium) hindsi Campbell and Clark, p. 24, pl. 7, fig. 29.
- 1957b Dictyophimus babylonis Clark and Campbell Riedel, p. 81, pl. 1, fig. 6.
- 1958 Lychnocanium ventricosum Ehrenberg Göke, pl. 3, fig. 2.
- 1970 Dictyophimus babylonis Clark and Campbell Cita et al., p. 401, pl. 1, fig. D.
- 1970 Sethochytris babylonis (Clark and Campbell) group Riedel and Sanfilippo, p. 528, pl. 9, figs. 1–3.
- 1970 Sethochytris babylonis (Clark and Campbell) group Riedel and Sanfilippo, p. 1595, pl. 3B, fig. 13.
- 1971 Sethochytris babylonis (Clark and Campbell) group Moore, p. 741, pl. 3, figs. 9, 10.
- 1973 Lychnocanoma babylonis (Clark and Campbell) group Foreman, p. 437, pl. 2, fig. 1.
- 1974 Lychnocanoma babylonis (Clark and Campbell) group Nigrini, p. 1068, pl. 1G, figs. 9–14, pl. 2D, fig. 4.
- 1974 Lychnocanoma babylonis (Clark and Campbell) group Johnson, p. 548, pl. 2, fig. 13.
- 1975 Lychnocanoma babylonis (Clark and Campbell) Chen, p. 462, pl. 2, fig. 8.
- 1975 Lychnocanoma babylonis-turgidulum [sic] group Ling, p. 729, pl. 10, figs. 8, 9.
- 1977 Lychnocanoma babylonis (Clark and Campbell) group Riedel and Sanfilippo, pl. 7, fig. 17.



Plate II.15. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic). (1, 2) Lithocorvthium? niduspendulus Ehrenberg, 1874: (1) ODP 1260A-11R-1W, 55-57 cm; (2) ODP 1260A-11R-7W, 55-57 cm. (3) Clathrocorys atavia (Goll, 1979): ODP 1260A-6R-4W, 55-57 cm. (4) Clathrocorys tribrachiata (Ehrenberg, 1874): ODP 1260A-10R-4W, 55–57 cm. (5) Dictyophimus craticula Ehrenberg, 1874: ODP 1260A-11R-4W, 55–57 cm. (6, 7) Sethochytris triconiscus Haeckel, 1887: (6) 1051A-11H-5W, 59-61 cm; (7) ODP 1051A-14H-5W, 52-54 cm. (8) Lychnocanium lucerna Ehrenberg, 1847: ODP 1051A-4H-5W, 56-58 cm. (9, 10) Lithochytris pyramidalis Ehrenberg, 1874: (9) ODP 1260A-13R-5W, 54-56 cm; (10) ODP 1260A-17R-CC, 63–177 cm. (11) Lychnocanium pileatum (Ehrenberg, 1874): ODP 1260A-11R-7W, 55-57 cm. (12) Lychnocanium tribulus (Ehrenberg, 1874) group: ODP 1260A-10R-6W, 55-57 cm. (13) Lychnocanium alma O'Connor, 1999a: ODP 1051A-9H-2W, 53-55 cm. (14) Lychnocanium waiareka O'Connor, 1999a: ODP 1051A-2H-5W, 55-57 cm. (15) Lychnocanium carinatum Ehrenberg, 1874: ODP 1260A-9R-5W, 55-57 cm. (16) Lychnocanium continuum Ehrenberg, 1874: ODP 1051A-11H-2W, 62-64 cm. All scale bars equal 50 µm.

- 1986 Lychnocanoma babylonis (Clark and Campbell) Riedel and Sanfilippo, pl. 2, fig. 17.
 not 1992 Lychnocanoma cf. babylonis (Clark and Campbell) Takemura, p. 747, pl. 7, fig. 13.
- ? 1995 Lychnocanoma babylonis (Clark and Campbell) Strong et al., p. 208, figs. 11A, 11B.
- 1997 Sethochytris babylonis (Clark and Campbell) Hollis et al., p. 65, pl. 5, fig. 32.

1999a Sethochytris babylonis (Clark and Campbell) group - O'Connor, p. 36, pl. 9, fig. 40.

not 1999 Lychnocanoma babylonis (Clark and Campbell) – Kozlova, pl. 12, fig. 10.

- 2006 *Lychnocanoma babylonis* (Clark and Campbell) group Funakawa et al., p. 35, pl. P13, figs. 1a, 1b.
- 2009 Lychnocanium tribulus Ehrenberg Ogane et al., pl. 43, figs. 3a–4c, pl. 44, figs. 4a–4c, pl. 61, figs. 3a–3c.
- 2012 *Lychnocanoma babylonis* (Clark and Campbell) group Moore and Kamikuri, p. 9, pl. P7, fig. 3.
- 2012 Lychnocanoma babylonis (Clark and Campbell) Kamikuri and Wade, pl. 1, fig. 11.
- 2015 Lychnocanoma babylonis (Clark and Campbell) group Kamikuri, pl. 2, figs. 4, 10a, 10b.
- 2020 Lychnocanium babylonis (Clark and Campbell) Hollis et al., pl. 13, figs. 4a–5.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Lychnocanium trichopus Ehrenberg, 1874

Plate II.16, Figure 1

1874 Lychnocanium Trichopus [sic] Ehrenberg, p. 244.

1876 Lychnocanium Trichopus [sic] Ehrenberg – Ehrenberg, p. 80, pl. 7, fig. 5.

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1887 Lychnocanium (Lychnocanissa) trichopus Ehrenberg – Haeckel, p. 1228.

2009 Lychnocanium trichopus Ehrenberg – Ogane et al., pl. 42, figs. 2a–2d (part).

2020 Lychnocanium trichopus Ehrenberg – Hollis et al., pl. 14, figs. 1–3b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Lychnocanium turgidum Ehrenberg, 1874

Plate II.16, Figure 3

1874 Lychnocanium turgidum Ehrenberg, p. 245.

1876 Lychnocanium turgidum Ehrenberg – Ehrenberg, p. 80, pl. 7, fig. 6.

1887 Pterocorys (Pterocyrtidium) turgida (Ehrenberg) – Haeckel, p. 1319.

- 1970 Gen. et sp. indet. Riedel and Sanfilippo, pl. 8, fig. 10.
- 1972 *Lithochytris (Lithochytrodes) turgidum* (Ehrenberg) Petrushevskaya and Kozlova, p. 552, pl. 27, figs. 8, 9.

1975 Lychnocanoma babylonis-turgidulum [sic] group – Ling, p. 729, pl. 10, fig. 10.

2005 Lychnocanium turgidum Ehrenberg – Nigrini et al., p. 44, pl. P4, fig. 6.

2015 Lychnocanoma turgidum Ehrenberg – Kamikuri, pl. 8, figs. 4a, 4b.

2020 Lychnocanium turgidum Ehrenberg – Hollis et al., pl. 14, figs. 5a, 5b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Lychnocanium waiareka O'Connor, 1999a Plate II.15, Figure 14

? 1974 Lychnocanoma sp. Johnson, pl. 2, fig. 10.

1999a Lychnocanium waiareka O'Connor, p. 25, pl. 4, figs. 6-11, pl. 7, figs. 12a-15.

2015 Lychnocanium waiareka O'Connor – Kamikuri, pl. 1, figs. 1a, 1b.

? 2020 Lychnocanium waiareka O'Connor – Hollis et al., pl. 14, figs. 6a, 6b.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Lychnocanoma Haeckel, 1887

Type species.—*Lychnocanium (Lychnocanoma) clavigerum* Haeckel, 1887, p. 1230, pl. 61, fig. 4.

Lychnocanoma amphitrite Foreman, 1973

Plate II.16, Figure 6

1971 Lychnocanium sp. aff. L. bellum Clark and Campbell Riedel and Sanfilippo, pl. 3C, figs. 1, 2.

1973 Lychnocanoma amphitrite Foreman, p. 437, pl. 11, fig. 10.

? 1973 Lychnocanoma bellum (Clark and Campbell) – Foreman, p. 437, pl. 1, fig. 17 (part).

1974 Lychnocanoma amphitrite Foreman – Nigrini, p. 1067, pl. 2D, figs. 2, 3.

- 1975 Lychnocanoma amphitrite Foreman Chen, p. 462, pl. 2, fig. 7.
- 1975 Lychnocanoma sp. A Ling, p. 729, pl. 10, fig. 13.
- 1977 Lychnocanoma amphitrite Foreman Riedel and Sanfilippo, pl. 10, fig. 9.
- 1978 Lychnocanoma amphitrite Foreman Riedel and Sanfilippo, p. 70, pl. 7, figs. 2, 3.
- 1978 Lychnocanoma amphitrite Foreman Sanfilippo and Riedel, p. 504, pl 1, figs. 5, 6.

1984 Lychnocanoma amphitrite Foreman – Westberg-Smith and Riedel, p. 493, pl. 6, fig. 14.

1986 Lychnocanoma amphitrite Foreman – Riedel and Sanfilippo, pl. 1, fig. 13.

1992 Lychnocanoma amphitrite Foreman – Kim, p. 46, pl. 2, figs. 12, 13.

1992 Lychnocanoma amphitrite Foreman – Takemura, p. 747, pl. 7, figs. 9, 10.

1995 Lychnocanoma amphitrite Foreman – Strong et al., p. 208, figs. 11K, 11L.

1997 Lychnocanoma amphitrite Foreman – Takemura and Ling, p. 114, pl. 1, fig. 21.

1997 Lychnocanium amphitrite (Foreman) – Hollis et al., p. 63, pl. 6, figs. 1–4.

1999a Lychnocanium amphitrite (Foreman) – O'Connor, p. 34, pl. 9, fig. 33.

2001 Lychnocanoma amphitrite Foreman – Sanfilippo and Blome, p. 214, figs. 9g–9j.

2005 Lychnocanoma amphitrite Foreman – Funakawa and Nishi, p. 233, pl. 4, figs. 14a, 14b.

2006 Lychnocanoma amphitrite Foreman – Funakawa et al., p. 35, pl. P12, figs, 8a, 8b.

2009b Lychnocanoma amphitrite Foreman - Suzuki et al., p. 261, pl. 19, figs. 5a-6b.

2012 Lychnocanoma amphitrite Foreman – Moore and Kamikuri, p. 9, pl. P7, figs. 1, 2.

2015 Lychnocanoma amphitrite Foreman – Kamikuri, pl. 8, figs. 3a, 3b, 7.

2020 Lychnocanium amphitrite (Foreman) – Hollis et al., pl. 12, figs. 25–28.

2021 Lychnocanoma amphitrite Foreman – de Souza et al., p. 15, pl. 3, fig. 6.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Lychnocanoma bajunensis Renz, 1984

Plate II.16, Figure 4

1975 Lychnocanoma sp. B Ling, p. 729, pl. 10, fig. 14.

1977 *Lychnocanoma* sp. Riedel and Sanfilippo, pl. 7, fig. 12.

1984 Lychnocanoma bajunensis Renz, p. 459, pl. 1, figs. 4-6.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Sethochytris Haeckel, 1882

Type species.— Sethochytris triconiscus Haeckel, 1887, p. 1239, pl. 57, fig. 13.

Sethochytris triconiscus Haeckel, 1887

Plate II.15, Figures 6, 7

1862 *Rhopalocanium* Bury, pl. 5, fig. 4.

1887 Sethochytris triconiscus Haeckel, p. 1239, pl. 57, fig. 13.

? 1970 Gen. et sp. indet. Riedel and Sanfilippo, pl. 9, fig. 5.

1970 ? Sethochytris triconiscus Haeckel – Riedel and Sanfilippo, p. 528, pl. 9, fig. 6.

1971 ? Sethochytris triconiscus Haeckel – Moore, p. 741, pl. 3, fig. 11.

1975 Sethochytris triconiscus Haeckel – Ling, p. 727, pl. 11, figs. 4–6.

1977 Sethochytris triconiscus Haeckel – Riedel and Sanfilippo, pl. 9, fig. 7.

1978 Sethochytris triconiscus Haeckel – Riedel and Sanfilippo, p. 73, pl. 9, fig. 6.

1991 Sethochytris triconiscus Haeckel – Scherer, p. 352, pl. 4, fig. 5 (part).

2000 Sethochytris triconiscus Haeckel – Nigrini and Sanfilippo, p. 74, pl. 1, fig. 8.

2001 Sethochytris triconiscus Haeckel – Sanfilippo and Blome, p. 217, fig. 11a.

2012 Sethochytris triconiscus Haeckel – Moore and Kamikuri, p. 10, pl. P7, fig. 14.

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2017 Sethochytris triconiscus Haeckel – de Souza et al., pl. 3, fig. 13.

2020 Sethochytris triconiscus Haeckel – Hollis et al., pl. 14, figs. 27a, 27b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Verutotholus O'Connor, 1999a Type species.— Verutotholus doigi O'Connor, 1999a, p. 14, pl. 6, figs. 1a, 1b.

Verutotholus doigi O'Connor, 1999a

Plate II.16, Figure 7

1999a Verutotholus doigi O'Connor, p. 14, pl. 2, figs. 12a-16, pl. 6, figs. 1a-4.

2015 Cycladophora spatiosa Ehrenberg – Kamikuri, pl. 10, figs. 7a, 7b.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Superfamily Pterocorythoidea Haeckel, 1882 emend. Suzuki et al., 2021 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, Figure 5a.

Apoplanius asperus (Ehrenberg, 1874) Plate II.16, Figure 8

1874 *Eucyrtidium asperum* Ehrenberg, p. 226.

- 1876 Eucyrtidium asperum Ehrenberg Ehrenberg, p. 70, pl. 8, fig. 15.
- 1882a Thyrsocyrtis aspera (Ehrenberg) Bütschli, p. 527.
- 1887 Theocyrtis (Theocorusca) aspera (Ehrenberg) Haeckel, p. 1408.
- 1972 Calocyclas asperum (Ehrenberg) Petrushevskaya and Kozlova, p. 548, pl. 28, figs. 16–18.
- 1992 *Calocyclas* sp. B Takemura, p. 745, pl. 5, fig. 13.
- ? 1995 Calocyclas asperum (Ehrenberg) Strong et al., p. 208, fig. 9E.
- 1997 Calocyclas sp. B Hollis et al., p. 58, pl. 5, figs. 7–10.
- 1997 Calocyclas sp. B Takemura and Ling, p. 111, pl. 1, fig. 15.
- 1998 Theocorys minuta Takemura and Ling, p. 162, figs. 3.16–3.21, 5.5, 5.6.
- 1998 Lophocyrtis (Apoplanius) aspera (Ehrenberg) Sanfilippo and Caulet, p. 14, pl. 3A, figs. 5–10, pl. 3B, figs. 1, 2, 5–9, pl. 6, figs. 6–8.
- 1999a Lophocyrtis (Apoplanius) aspera (Ehrenberg) O'Connor, p. 32, pl. 9, fig. 5.
- 1999 Calocyclas asperum (Ehrenberg) Kozlova, p. 153, pl. 35, fig. 6, pl. 46, fig. 10.
- 2006 Lophocyrtis (Apoplanius) aspera (Ehrenberg) Funakawa et al., p. 25, pl. P7, figs. 4a–7b.
- 2009 Eucyrtidium asperum Ehrenberg Ogane et al., pl. 89, figs. 3a-3g.
- 2013 Lophocyrtis (Apoplanius) aspera (Ehrenberg) Kamikuri et al., pl. 1, figs. 3a, 3b.
- 2015 Lophocyrtis (Apoplanius) aspera (Ehrenberg) Kamikuri, pl. 6, figs. 3a, 3b.

2020 Lophocyrtis (Apoplanius) aspera (Ehrenberg) form B – Hollis et al., pl. 15, figs. 17a– 19b.

2021 Lophocyrtis (Apoplanius) aspera (Ehrenberg) – de Souza et al., p. 15, pl. 3, fig. 12.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Apoplanius kerasperus (Sanfilippo and Caulet, 1998) Plate II.16, Figure 10

- 1998 Lophocyrtis (Apoplanius) keraspera Sanfilippo and Caulet, p.14, pl. 3A, figs. 13–15, pl. 3B, figs. 12–14, pl. 6, figs. 9–12.
- 2020 Lophocyrtis (Apoplanius) keraspera Sanfilippo and Caulet Hollis et al., pl. 15, figs. 20–24.
- 2021 Lophocyrtis (Apoplanius) keraspera Sanfilippo and Caulet de Souza et al., p. 15, pl. 3, figs. 13a, 13b.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Apoplanius klydus (Sanfilippo and Caulet, 1998)

Plate II.16, Figure 11

1998 Lophocyrtis (Apoplanius) klydus Sanfilippo and Caulet, p. 12, pl. 3A, figs. 11, 12, pl. 3B, figs. 10, 11, pl. 5, figs. 4a–5b, 8, 10, 11.

Remarks. The combination used here is derived from O'Dogherty et al. (2021). Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Genus Lophocyrtis Haeckel, 1887

Type species.— Eucyrtidium stephanophorum Ehrenberg, 1874, p. 233 (unfigured); Ehrenberg, 1876, p. 72, pl. 8, fig. 14.

Lophocyrtis alauda (Ehrenberg, 1874)

Plate II.16, Figures 12–15

1874 Eucyrtidium Alauda [sic] Ehrenberg, p. 225.

1874 Eucyrtidium versipellis Ehrenberg, p. 233.

1876 Eucyrtidium Alauda [sic] Ehrenberg – Ehrenberg, p. 70, pl. 9, fig. 4.

1876 Eucyrtidium versipellis Ehrenberg – Ehrenberg, p. 72, pl. 11, fig. 14.

1882a Eucyrtidium Alauda [sic] Ehrenberg – Bütschli, p. 528.

1882a Eucyrtidium versipellis Ehrenberg – Bütschli, p. 528.

1882b Eucyrtidium Alauda [sic] Ehrenberg – Bütschli, pl. 30, fig. 17.

1887 Theocorys (Theocorythium) alauda (Ehrenberg) – Haeckel, p. 1418.

1887 Theocampe (Theocamptra) versipellis (Ehrenberg) – Haeckel, p. 1425.

1942 *Calocyclas* (*Calocycletta*) *semipolita semipolita* Clark and Campbell, p. 83, pl. 8, figs. 12, 14, 17–19, 22, 23.



Plate II.16. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic). (1) *Lychnocanium trichopus* Ehrenberg, 1874: ODP 1260A-13R-5W, 54–56 cm. (2) *Lychnocanium falciferum* Ehrenberg, 1854a: ODP 1051A-9H-2W, 53–55 cm. (3) *Lychnocanium turgidum* Ehrenberg, 1874: ODP 1260A-10R-5W, 55–57 cm. (4) *Lychnocanoma bajunensis* Renz, 1984: ODP 1260A-10R-1W, 55–57 cm. (5) *Lychnocanium bellum* Clark and Campbell, 1942: ODP 1051A-18X-5W, 54–56 cm. (6) *Lychnocanoma amphitrite* Foreman, 1973: ODP 1051A-4H-5W, 56–58 cm. (7) *Verutotholus doigi* O'Connor, 1999a: ODP 1051A-13H-2W, 52–54 cm. (8) *Apoplanius aspera* (Ehrenberg, 1874): ODP 1260A-11R-1W, 55–57 cm. (10) *Apoplanius keraspera* (Sanfilippo and Caulet, 1998): ODP 1051A-9H-2W, 53–5 cm. (11–14) *Lophocyrtis alauda* (Ehrenberg, 1874): (11) ODP 1260A-13R-4W, 55–57 cm; (12) ODP 1260A-13R-1W, 54–56 cm; (13) ODP 1260A-17R-3W, 55–57 cm; (14) ODP 1260A-11R-7W, 55–57 cm. All scale bars equal 50 μm.

- 1945 *Calocyclas (Calocycletta) semipolita semipolita* Clark and Campbell, p.44, pl. 6, fig. 12 (part).
- 1975 ? Calocyclas semipolita Clark and Campbell Chen, p. 459, pl. 6, figs. 3, 6 (part).
- not 1988 *Calocyclas semipolita* Clark and Campbell Blueford, p. 246, pl. 2, figs. 4, 5.
- 1998 Lophocyrtis (Lophocyrtis?) cf. semipolita (Clark and Campbell) Sanfilippo and Caulet, p. 10, pl. 4, fig. 7.
- 2009 Eucyrtidium alauda Ehrenberg Ogane et al., pl. 49, figs. 1a–1e.
- 2009 *Eucyrtidium versipellis* Ehrenberg Ogane et al., pl. 2, figs. 1a–1d, pl. 22, fig. 5, pl. 49, fig. 3, pl. 89, fig. 4a–4c.
- Remarks. The combination used here is derived from O'Dogherty et al. (2021). Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Lophocyrtis attenuata (Ehrenberg, 1874)

Plate II.17, Figures 1, 2

- 1874 Eucyrtidium attenuatum Ehrenberg, p. 226.
- ? 1874 Eucyrtidium Hillaby [sic] Ehrenberg, p. 229.
- 1876 Eucyrtidium attenuatum Ehrenberg Ehrenberg, p. 70, pl. 11, fig. 16.
- ? 1876 Eucyrtidium Hillaby [sic] Ehrenberg Ehrenberg, p. 72, pl. 11, fig. 8.
- 1882a Eucyrtidium attenuatum Ehrenberg Bütschli, p. 528.
- 1887 Theocorys (Theocorythium) attenuata (Ehrenberg) Haeckel, p. 1417.
- ? 1975 Theocyrtis (Theocorypha) diabloensis Clark and Campbell Chen, p. 459, pl. 5, figs. 4, 5, 6 (part).
- 2009 Eucyrtidium attenuatum Ehrenberg Ogane et al., pl. 23, figs. 3a–4c, pl. 48, figs. 5a, 5b.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

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Lophocyrtis ? coronata (Ehrenberg, 1874) Plate II.17, Figure 7

1874 Eucyrtidium coronatum Ehrenberg, p. 227.

1876 Eucyrtidium coronatum Ehrenberg – Ehrenberg, p. 70, pl. 10, fig. 9.

1887 Lophocyrtis coronata (Ehrenberg) – Haeckel, p. 1411.

2009 Eucyrtidium coronatum Ehrenberg - Ogane et al., pl. 19, figs. 4a-4e.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Lophocyrtis cortesei Tetard et al., 2023

Plate II.17, Figure 6

2023 *Lophocyrtis cortesei* Tetard et al., p. 8, figs. 40–4q, 5r, 5s. Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Lophocyrtis microtheca (Ehrenberg, 1874)

Plate II.17, Figures 3, 4

1874 Eucyrtidium microtheca Ehrenberg, p. 230.

1876 Eucyrtidium microtheca Ehrenberg – Ehrenberg, p. 72, pl. 11, fig. 10.

1882a Thyrsocyrtis microtheca (Ehrenberg) - Bütschli, p. 528.

1887 Theocyrtis (Theocorypha) microtheca (Ehrenberg) – Haeckel, p. 1407.

1974 Theoperid gen. et sp. indet. Johnson, pl. 2, figs. 14, 15, 17 (part).

2006 Eucyrtidium ? hillaby Ehrenberg – Funakawa et al., p. 22, pl. P5, figs. 6a-8b.

2009 Eucyrtidium microtheca Ehrenberg – Ogane et al., pl. 84, fig. 2a–2c.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Lophocyrtis panthera (Ehrenberg, 1874)

Plate II.17, Figure 5

1874 Eucyrtidium Panthera [sic] Ehrenberg, p. 231.

1876 Eucyrtidium Panthera [sic] Ehrenberg – Ehrenberg, p. 72, pl. 11, fig. 18.

- 1882a Thyrsocyrtis Panthera [sic] (Ehrenberg) Bütschli, p. 528.
- 1887 Tricolocampe (Tricolocampium) panthera (Ehrenberg) Haeckel, p. 1413.
- 1975 *Theocyrtis (Theocorypha) diabloensis* Clark and Campbell Chen, p. 459, pl. 5, fig. 7 (part).
- 1975 Eucyrtidium sp. cf. E. panthera Ehrenberg Ling, p. 731, pl. 12, fig. 18.

2006 Eucyrtidium ? panthera Ehrenberg – Funakawa et al., p. 23, pl. P5, figs. 9a, 9b.

2009 Eucyrtidium panthera Ehrenberg – Ogane et al., pl. 6, figs. 10a, 10b, pl. 84, figs. 1a–1d.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Paralampterium Sanfilippo, 1990

Type species.— *Lophocyrtis (Paralampterium) dumitricai* Sanfilippo, 1990, p. 308, pl. 3, fig. 8.

Paralampterium ? eurylophus (Ehrenberg, 1874) Plate II.17, Figure 8

1887 Dictyopodium eurylophus Ehrenberg – Haeckel, p. 1352.

1978 Theoperid gen. et sp. indet. Weaver and Dinkelman, pl. 8, fig. 10 (part).

2006 Dictyopodium eurylophus Ehrenberg – Funakawa et al., pl. P6, figs. 8a-10.

2015 Dictyopodium eurylophus Ehrenberg - Kamikuri, pl. 19, figs. 7a, 7b.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Family Pterocorythidae Haeckel, 1882 emend. Riedel, 1967b emend. Moore, 1972 Genus *Lamprocyclas* Haeckel, 1882

Type species.— Lamprocyclas (Lamprocyclia) nuptialis Haeckel, 1887, p. 1390, pl. 74, fig. 15.

? Lamprocyclas inexpectata Caulet, 1991

Plate II.17, Figures 9, 10

1991 *Lamprocyclas inexpectata* Caulet, p. 534, pl. 3, figs. 2, 3. Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Genus *Phormocyrtis* Haeckel, 1887 *Type species.— Phormocyrtis longicornis* Haeckel, 1887, p. 1370, pl. 69, fig. 15.

Phormocyrtis embolum (Ehrenberg, 1874)

Plate II.17, Figure 11

- 1874 Eucyrtidium Embolum [sic] Ehrenberg, p. 228.
- 1876 Eucyrtidium Embolum [sic] Ehrenberg Ehrenberg, p. 70, pl. 10, fig. 5.
- 1882a Eucyrtidium Embolum [sic] Ehrenberg Bütschli, p. 528.
- 1887 *Phormocyrtis embolum* (Ehrenberg) Haeckel, p. 1369.
- 1957b Phormocyrtis embolum (Ehrenberg) Riedel, p. 88, pl. 3, fig. 6 (part).
- 1942 Phormocyrtis ligulata Clark and Campbell, p. 81, pl. 7, figs. 22, 23, 27, 28.
- 1945 *Phormocyrtis ligulata* Clark and Campbell Clark and Campbell, p. 43, pl. 6, figs. 10, 11.
- 1957b Phormocyrtis embolum (Ehrenberg) Riedel, p. 88, pl. 3, fig. 6 (part).
- 1970 Phormocyrtis embolum (Ehrenberg) Cita et al., p. 403, pl. 2, fig. E.
- 1974 Phormocyrtis embolum (Ehrenberg) Nigrini, p. 1068, pl. 1H, figs. 4, 5.
- 1974 Phormocyrtis embolum (Ehrenberg) Johnson, p. 548, pl. 2, fig. 11, pl. 4, fig. 5 (part).
- 1975 Phormocyrtis embolum (Ehrenberg) group Ling, p. 729, pl. 10, fig. 15.
- 1986 Phormocyrtis embolum (Ehrenberg) Riedel and Sanfilippo, pl. 7, fig. 2.
- 1988 Phormocyrtis ligulata Clark and Campbell Blueford, p. 246, pl. 2, figs. 7–9.



Plate II.17. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic). (**1**, **2**) *Lophocyrtis attenuata* (Ehrenberg, 1874): (**1**) ODP 1260A-11R-3W, 55–57 cm; (**2**) ODP 1260A-17R-3W, 55–57 cm. (**3**, **4**) *Lophocyrtis microtheca* (Ehrenberg, 1874): (**3**) ODP 1051A-9H-2W, 53–55 cm; (**4**) ODP 1051A-14H-5W, 52–54 cm. (**5**) *Lophocyrtis panthera* (Ehrenberg, 1874): ODP 1051A-2H-5W, 55–57 cm. (**6**) *Lophocyrtis cortesei* Tetard et al., 2023: ODP 1260A-6R-4W, 55–57 cm. (**7**) *Lophocyrtis*? *coronata* (Ehrenberg, 1874): ODP 1051A-12H-2W, 55–57 cm. (**8**) *Paralampterium*? *eurylophus* (Ehrenberg, 1874): ODP 1051A-12H-2W, 53–55 cm; (**10**) ODP 1051A-9H-2W, 53–55 cm. (**11**) *Phormocyrtis embolum* (Ehrenberg, 1874): ODP 1260A-14R-1W, 55–57 cm. (**12**) *Phormocyrtis striata striata* Brandt *in* Wetzel, 1935: ODP 1051A-38X-5W, 55–57 cm. (**13–15**) *Podocyrtis (Podocyrtis) papalis* Ehrenberg, 1847: (**13**) ODP 1260A-10R-6W, 55–57 cm; (**14**) ODP 1260A-8R-6W, 54–56 cm; (**15**) ODP 1260A-9R-3W, 55–57 cm. (**16**)? *Podocyrtis (Lampterium) acalles* Sanfilippo and Riedel, 1992: ODP 1260A-20R-4W, 55–57 cm. All scale bars equal 50 µm.

1993 Cryptocarpium sp. Hull, p. 13, pl. 7, fig. 3.

1995 Phormocyrtis ligulata Clark and Campbell – Strong et al., p. 209, figs. 11U, 11V.

1999 Phormocyrtis embolum (Ehrenberg) – Kozlova, p. 148, pl. 31, fig. 14.

2009 Eucyrtidium embolum Ehrenberg – Ogane et al., pl. 22, figs. 6a–6c.

2013 Phormocyrtis embolum (Ehrenberg) - Kamikuri et al., pl. 1, fig. 1a, 1b.

? 2015 Phormocyrtis embolum (Ehrenberg) – Kamikuri, pl. 19, fig. 12

2020 Phormocyrtis ligulata Clark and Campbell – Hollis et al., pl. 10, figs. 17a, 17b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Phormocyrtis striata striata Brandt in Wetzel, 1935

Plate II.17, Figure 12

1935 Phormocyrtis striata Brandt in Wetzel, p. 55, pl. 9, fig. 12.

- 1969b Theocorys costata Mamedov, p. 37, pl. 1, fig. 5.
- 1970 Phormocyrtis striata Brandt Cita et al., p. 404, pl. 2, fig. F.
- 1970 Phormocyrtis striata Brandt Riedel and Sanfilippo, p. 532, pl. 10, fig. 7.
- 1971 Phormocyrtis striata Brandt Moore, p. 742, pl. 1, fig. 2.

1972 Phormocyrtis striata Brandt – Benson, p. 1093, pl. 2, fig. 5.

1972 Eusyringium striata (Brandt) – Petrushevskaya and Kozlova, p. 549, pl. 32, figs. 1, 2.

1973 Phormocyrtis striata striata Brandt – Foreman, p. 438, pl. 7, figs. 5, 6, 9.

1973 Phormocyrtis striata striata Brandt - Nigrini, p. 1068, pl. 1F, figs. 15-18.

1974 Phormocyrtis striata striata Brandt – Johnson, p. 548, pl. 2, figs. 6, 7.

1975 Phormocyrtis striata striata Brandt – Chen, p. 456, pl. 3, fig. 8.

1977 Phormocyrtis striata striata Brandt – Riedel and Sanfilippo, pl. 3, fig. 11.

1978 Phormocyrtis striata striata Brandt – Weaver and Dinkelman, p. 873, pl. 8, fig. 5.

1978 Phormocyrtis striata striata Brandt – Riedel and Sanfilippo, p. 71, pl. 7, fig. 11.

1984 Phormocyrtis striata striata Brandt – Westberg-Smith and Riedel, p. 493, pl. 6, fig. 12.

1985 Phormocyrtis striata striata Brandt – Sanfilippo et al., p. 679, figs. 20.1a, 20.1b.

1987 Phormocyrtis striata striata Brandt – Nishimura, p. 727, pl. 2, figs. 10, 11.

1993 Phormocyrtis striata striata Brandt – Hull, p. 12, pl. 7, fig. 5.

1994 Phormocyrtis striata striata Brandt – Weinheimer et al., p. 311, pl. 1, figs. 10a, 10b.

1995 Eusyringium striata (Brandt) – Shilov, p. 126, pl. 2, figs. 3a, 3b.

1995 Phormocyrtis striata striata Brandt – Strong et al., p. 209, figs. 9O, 9P.

1998a Phormocyrtis striata striata Brandt - Sanfilippo and Nigrini, p. 273, pl. 13.2, fig. 2.

1999 Phormocyrtis striata striata Brandt - Kozlova, p. 156, pl. 15, fig. 10, pl. 18, fig. 6.

2008 Phormocyrtis striata striata Brandt – Jackett et al., p. 57, pl. 1, fig. 19.

2015 Phormocyrtis striata striata Brandt – Hollis, pl. 12, fig. 8.

2017 Phormocyrtis striata striata Brandt – de Souza et al., pl. 2, figs. 8a, 8b.

2020 Phormocyrtis striata striata Brandt – Hollis et al., pl. 10, figs. 19a, 19b.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Podocyrtis Ehrenberg, 1846

Type species.— Podocyrtis papalis Ehrenberg, 1847, p. 55, fig. 2.

? Podocyrtis (Lampterium) acalles Sanfilippo and Riedel, 1992 Plate II.17, Figure 16

1970 Podocyrtis (Lampterium) acalles Sanfilippo and Riedel, p. 12, pl. 3, figs. 2-5.

1993 Podocyrtis (Lampterium) acalles Sanfilippo and Riedel – Hull, p. 13, pl. 8, fig. 1.

- 1994 *Podocyrtis (Lampterium) acalles* Sanfilippo and Riedel Weinheimer et al., p. 312, pl. 1, fig. 14.
- 1998a *Podocyrtis (Lampterium) acalles* Sanfilippo and Riedel Sanfilippo and Nigrini, p. 273, pl. 13.2, fig. 4.
- ? 2017 Podocyrtis (Lampterium) acalles Sanfilippo and Riedel de Souza et al., pl. 1, figs. 6a, 6b.
- 2020 Podocyrtis (Lampterium) acalles Sanfilippo and Riedel Hollis et al., pl. 17, figs. 19a, 19b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Podocyrtis (Lampterium) chalara Riedel and Sanfilippo, 1970

Plate II.18, Figure 7

- 1862 Podocyrtis ? Bury, pl. 12, fig. 2 (part).
- 1958 Podocyrtis eulophos Ehrenberg Göke, pl. 1, fig. 5.
- 1970 Podocyrtis (Lampterium) chalara Riedel and Sanfilippo, p. 535, pl. 12, figs. 2, 3.
- 1971 *Podocyrtis (Lampterium) chalara* Riedel and Sanfilippo Moore, p. 743, pl. 3, figs. 5, 6.
- 1972 Lampterium chalara Riedel and Sanfilippo Petrushevskaya and Kozlova, p. 543, pl. 32, fig. 12.
- 1972 Lampterium sp. G Petrushevskaya and Kozlova, pl. 32, fig. 10.
- 1977 Podocyrtis chalara Riedel and Sanfilippo Riedel and Sanfilippo, pl. 10, fig. 1.

- 1978 Podocyrtis chalara Riedel and Sanfilippo Riedel and Sanfilippo, p. 71, pl. 8, fig. 3.
- 1985 Podocyrtis (Lampterium) chalara Riedel and Sanfilippo Sanfilippo et al., p. 697, fig. 30.11.
- 1986 *Podocyrtis (Lampterium) chalara* Riedel and Sanfilippo Riedel and Sanfilippo, pl. 2, fig. 14, pl. 4, figs. 10, 11.
- 1991 Podocyrtis chalara Riedel and Sanfilippo Scherer, p. 352, pl. 4, fig. 3.
- 2012 *Podocyrtis (Lampterium) chalara* Riedel and Sanfilippo Moore and Kamikuri, p. 9, pl. P7, fig. 8.
- 2012a *Podocyrtis (Lampterium) chalara* Riedel and Sanfilippo Kamikuri et al., p. 103, pl. 3, figs. 2a, 2b.
- 2012b Podocyrtis (Lampterium) chalara Riedel and Sanfilippo Kamikuri et al., p. 4, pl. P1, figs. 2a, 2b.
- 2023 *Podocyrtis (Lampterium) chalara* Riedel and Sanfilippo Pínto et al., p. 3, pl. 1, figs. A, B.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Podocyrtis (Lampterium) goetheana (Haeckel, 1887) Plate II.18, Figure 8

- ? 1887 Alacorys (Tetralacorys) lutheri Haeckel, p. 1370, pl. 65, fig. 4.
- 1887 Cycladophora (Lampterium) gætheana [sic] Haeckel, p. 1376, pl. 65, fig. 5.
- 1970 Podocyrtis (Lampterium) goetheana (Haeckel) Riedel and Sanfilippo, p. 535.
- 1971 *Podocyrtis (Lampterium) goetheana* (Haeckel) Riedel and Sanfilippo, p. 1598, pl. 8, fig. 13.
- 1971 Podocyrtis (Lampterium) goetheana (Haeckel) Moore, p. 743, pl. 3, figs. 7, 8.
- 1972 *Lampterium* sp. aff. *L. goetheana* (Haeckel) Petrushevskaya and Kozlova, pl. 32, fig. 14 (part).
- 1977 Podocyrtis goetheana (Haeckel) Riedel and Sanfilippo, pl. 11, fig. 6.
- 1978 Podocyrtis goetheana (Haeckel) Riedel and Sanfilippo, p. 72, pl. 8, fig. 6.
- 1978 Podocyrtis goetheana (Haeckel) Riedel and Sanfilippo, pl. 4, fig. 12.
- 2005 Podocyrtis (Lampterium) goetheana (Haeckel) Nigrini et al., p. 45, pl. P5, figs. 11, 12.
- 2006 Podocyrtis (Lampterium) goetheana (Haeckel) Funakawa et al., p. 29, pl. P9, figs. 12a, 12b.
- 2006 *Podocyrtis (Lampterium) chalara* Riedel and Sanfilippo Funakawa et al., p. 29, pl. P9, figs. 11a, 11b (diminutive form).
- 2012 *Podocyrtis (Lampterium) goetheana* (Haeckel) Moore and Kamikuri, p. 9, pl. P7, fig.
 9.
- 2012a Podocyrtis (Lampterium) goetheana (Haeckel) Kamikuri et al., p. 103, pl. 3, fig. 1.
- 2012b Podocyrtis (Lampterium) goetheana (Haeckel) Kamikuri et al., p. 4, pl. P1, figs. 3a, 3b.
- 2015 Podocyrtis (Lampterium) goetheana (Haeckel) Kamikuri, pl. 6, fig. 6.
- 2023 Podocyrtis (Lampterium) goetheana (Haeckel) Pínto et al., p. 3, pl. 1, figs. M–O.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Podocyrtis (Lampterium) fasciolata Nigrini, 1974 Plate II.18, Figure 9

- 1973 Podocyrtis sp. A Riedel and Sanfilippo, p. 739, pl. 4, figs.1, 2 (part).
- 1974 Podocyrtis (Podocyrtis) ampla fasciolata Nigrini, p. 1069, pl. 1K, figs. 1, 2, pl. 4, figs. 2, 3.
- 1978 Podocyrtis ampla fasciolata Nigrini Riedel and Sanfilippo, p. 71, pl. 8, fig. 2.

1985 Podocyrtis (Lampterium) fasciolata Nigrini – Sanfilippo et al., p. 697, fig. 30.7.

2017 Podocyrtis (Lampterium) fasciolata Nigrini – de Souza et al., pl. 1, fig. 9.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Podocyrtis (Lampterium) helenae Nigrini, 1974

Plate II.18, Figure 6

1973 Podocyrtis sp. B Riedel and Sanfilippo, p. 739, pl. 4, figs. 4-6.

1974 Podocyrtis (Lampterium) helenae Nigrini, p. 1070, pl. 1L, figs. 9-11, pl. 4, figs. 4, 5.

2017 Podocyrtis (Lampterium) helenae Nigrini - de Souza et al., pl. 1, figs. 10a, 10b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Podocyrtis (Lampterium) mitra Ehrenberg, 1854a

Plate II.18, Figures 3, 4

1854a Podocyrtis Mitra [sic] Ehrenberg, pl. 36, fig. 20.

- not 1862 *Podocyrtis mitra* Ehrenberg Bury, pl. 5, fig. 3.
- 1874 Podocyrtis eulophos Ehrenberg, p. 251.
- 1874 Podocyrtis Mitra [sic] Ehrenberg Ehrenberg, p. 251.
- 1876 Podocyrtis Eulophos [sic] Ehrenberg Ehrenberg, p. 82, pl. 14, fig. 6.
- 1876 Podocyrtis Mitra [sic] Ehrenberg Ehrenberg, p. 82, pl. 15, fig. 4.
- 1882b Podocyrtis Eulophus [sic] Ehrenberg Bütschli, pl. 30, fig. 12.
- 1887 Podocyrtis (Podocyrtidium) mitra Ehrenberg Haeckel, p. 1345.
- 1887 Podocyrtis (Podocyrtidium) eulophos Ehrenberg Haeckel, p. 1346.
- 1887 Podocyrtis (Podocyrtonium) pedicellaria Haeckel, p. 1347, pl. 72, fig. 8.
- 1887 Podocyrtis (Podocyrtonium) lithoconus Haeckel, p. 1348, pl. 72, fig. 3.
- 1970 Podocyrtis (Lampterium) mitra Ehrenberg Riedel and Sanfilippo, p. 534, pl. 11, figs. 5, 6.
- 1971 *Podocyrtis (Lampterium) mitra* Ehrenberg Riedel and Sanfilippo, p. 1598, pl. 3D, fig. 19.
- 1973 Podocyrtis mitra Ehrenberg Riedel and Sanfilippo, p. 739, pl. 3, fig. 1.
- 1974 Podocyrtis (Lampterium) mitra Ehrenberg Nigrini, p. 1070, pl. 1L, figs. 5, 6.
- 1974 Podocyrtis (Lampterium) mitra Ehrenberg Johnson, p. 551, pl. 4, fig. 15.
- 1974 Podocyrtis sp. Johnson, pl. 4, fig. 16 (part).
- 1975 Podocyrtis (Lampterium) mitra Ehrenberg Ling, p. 731, pl. 13, figs. 3, 4.
- 1975 Podocyrtis mitra Ehrenberg Riedel and Sanfilippo, pl. 9, fig. 11.
- 1978 Podocyrtis mitra Ehrenberg Riedel and Sanfilippo, p. 72, pl. 8, fig. 7.

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- 1986 Podocyrtis (Lampterium) mitra Ehrenberg Riedel and Sanfilippo, pl. 2, fig. 13.
- 1991 Podocyrtis (Lampterium) mitra Ehrenberg Scherer, p. 352, pl. 4, fig. 4.
- 2000 Podocyrtis (Lampterium) mitra Ehrenberg Nigrini and Sanfilippo, p. 74, pl. 1, fig. 12.
- 2001 *Podocyrtis (Lampterium) mitra* Ehrenberg Sanfilippo and Blome, p. 215, figs. 10a, 10b.
- 2001 Podocyrtis pedicellaria Haeckel De Wever et al., p. 259, fig. 169.4.
- 2001 Podocyrtis goetheana (Haeckel) De Wever et al., p. 259, fig. 169.5.
- 2012a Podocyrtis (Lampterium) mitra Ehrenberg Kamikuri et al., p. 103, pl. 3, figs. 3a, 3b.
- 2012b Podocyrtis (Lampterium) mitra Ehrenberg Kamikuri et al., p. 4, pl. P1, fig. 1.
- 2017 Podocyrtis (Lampterium) mitra Ehrenberg de Souza et al., pl. 1, figs. 11a, 11b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Podocyrtis (Lampterium) sinuosa Ehrenberg, 1874

Plate II.18, Figures 1, 2

- 1874 Podocyrtis sinuosa Ehrenberg, p. 253.
- 1876 Podocyrtis sinuosa Ehrenberg Ehrenberg, p. 82, pl. 15, fig. 5.
- 1882a Podocyrtis sinuosa Ehrenberg Bütschli, p. 540, pl. 33, fig. 33.
- 1887 Podocyrtis (Podocyrtonium) sinuosa Ehrenberg Haeckel, p. 1347.
- 1969 Podocyrtis sinuosa Ehrenberg Riedel and Hays, pl. 1, fig. E.
- 1970 Podocyrtis sp. A Cita et al., p. 403, pl. 1, fig. I.
- 1970 ? *Podocyrtis (Lampterium) sinuosa* Ehrenberg Riedel and Sanfilippo, p. 534, pl. 11, figs. 3, 4.
- 1973 ? *Podocyrtis (Lampterium) sinuosa* Ehrenberg Riedel and Sanfilippo, p. 532, pl. 21, figs. 4, 5.
- 1974 ? Podocyrtis (Lampterium) sinuosa Ehrenberg Nigrini, p. 1070, pl. 1L, figs. 1–4.
- 1974 Podocyrtis (Lampterium) sinuosa Ehrenberg Johnson, p. 551, pl. 4, fig. 18.
- 1977 Podocyrtis sinuosa Ehrenberg Riedel and Sanfilippo, pl. 8, fig. 4.
- 1978 ? Podocyrtis sinuosa Ehrenberg Weaver and Dinkelman, p. 873, pl. 5, fig. 4.
- 1978 Podocyrtis sinuosa Ehrenberg Riedel and Sanfilippo, p. 72, pl. 8, fig. 9.
- 1987 Podocyrtis sinuosa Ehrenberg Nishimura, p. 728, pl. 2, fig. 18.
- 1992 Podocyrtis (Lampterium) sinuosa Ehrenberg Sanfilippo and Riedel, pl. 3, fig. 6.
- 1993 Podocyrtis (Lampterium) sinuosa Ehrenberg Hull, p. 13, pl. 7, fig. 9.
- 2012a Podocyrtis (Lampterium) sinuosa Ehrenberg Kamikuri et al., p. 103, pl. 1, figs. 11a, 11b.
- 2017 Podocyrtis (Lampterium) sinuosa Ehrenberg de Souza et al., pl. 1, figs. 13a, 13b.
- Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Podocyrtis (Lampterium) trachodes Riedel and Sanfilippo, 1970 Plate II.18, Figure 5

1970 *Podocyrtis (Lampterium) trachodes* Riedel and Sanfilippo, p. 535, pl. 11, fig. 7; pl. 12, fig. 1.

- 1974 *Podocyrtis* (Lampterium) *trachodes* Riedel and Sanfilippo Nigrini, p. 1070, pl. 1L, figs. 7, 8.
- 1974 *Podocyrtis* (Lampterium) *trachodes* Riedel and Sanfilippo Johnson, p. 551, pl. 5, figs. 11, 12.
- 1978 Podocyrtis trachodes Riedel and Sanfilippo Riedel and Sanfilippo, p. 72, pl. 8, fig. 10.
- 1985 *Podocyrtis (Lampterium) trachodes* Riedel and Sanfilippo Sanfilippo et al., p. 699, fig. 30.14.
- 2000 *Podocyrtis (Lampterium) trachodes* Riedel and Sanfilippo Nigrini and Sanfilippo, p. 74, pl. 2, fig. 13.
- 2001 *Podocyrtis (Lampterium) trachodes* Riedel and Sanfilippo Sanfilippo and Blome, p. 215, fig. 10c.
- 2012 *Podocyrtis (Lampterium) trachodes* Riedel and Sanfilippo Moore and Kamikuri, p. 9, pl. P7, fig. 5.
- 2017 *Podocyrtis (Lampterium) trachodes* Riedel and Sanfilippo de Souza et al., pl. 2, figs. 1a, 1b.
- Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Podocyrtis (Podocyrtoges) ampla Ehrenberg, 1874 Plate II.18, Figure 12

- 1874 Podocyrtis ? ampla Ehrenberg, p. 248.
- 1876 Podocyrtis ? ampla Ehrenberg Ehrenberg, p. 80, pl. 16, fig. 7.
- 1882a Cycladophora ampla (Ehrenberg) Bütschli, p. 527, pl. 32, fig. 16.
- 1887 Podocyrtis (Podocyrtonium) ampla Ehrenberg Haeckel, p. 1348.
- 1970 Podocyrtis (Podocyrtis) ampla Ehrenberg Riedel and Sanfilippo, p. 533, pl. 12, figs. 7, 8.
- 1971 Podocyrtis (Podocyrtis) ampla Ehrenberg Moore, p. 743, pl. 2, fig. 6.
- 1977 Podocyrtis ampla Ehrenberg Riedel and Sanfilippo, pl. 8, fig. 14.
- 1978 Podocyrtis ampla ampla Ehrenberg Riedel and Sanfilippo, p. 71, pl. 8, fig. 1.
- 1986 Podocyrtis (Podocyrtis) ampla Ehrenberg Riedel and Sanfilippo, pl. 2, fig. 16.
- 1992 Podocyrtis (Podocyrtoges) ampla Ehrenberg Sanfilippo and Riedel, p. 14, pl. 5, fig.
 4.
- 2012a Podocyrtis (Podocyrtoges) ampla Ehrenberg Kamikuri et al., p. 103, pl. 3, figs. 8a, 8b.
- 2017 Podocyrtis (Podocyrtoges) ampla Ehrenberg de Souza et al., pl. 1, figs. 7a, 7b.
- Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Podocyrtis (Podocyrtoges) diamesa Riedel and Sanfilippo, 1970 Plate II.18, Figure 10

- 1970 Podocyrtis (Podocyrtis) diamesa Riedel and Sanfilippo, p. 533, pl. 12, fig. 4 (part).
- 1971 Podocyrtis (Podocyrtis) diamesa Riedel and Sanfilippo Moore, p. 743, pl. 2, fig. 5.
- 1973 *Podocyrtis (Podocyrtis) diamesa* Riedel and Sanfilippo Sanfilippo and Riedel, p. 531, pl. 20, figs. 9, 10, pl. 35, figs. 10, 11.

- 1974 Podocyrtis (Podocyrtis) diamesa Riedel and Sanfilippo Nigrini, p. 1069, pl. 1K, figs. 3–5.
- 1977 Podocyrtis diamesa Riedel and Sanfilippo Riedel and Sanfilippo, pl. 8, fig. 5.
- 1978 Podocyrtis diamesa Riedel and Sanfilippo Riedel and Sanfilippo, p. 72, pl. 8, fig. 4.
- 1992 Podocyrtis (Podocyrtoges) diamesa Sanfilippo and Riedel Sanfilippo and Riedel, p. 14.
- 2005 *Podocyrtis (Podocyrtoges) diamesa* Sanfilippo and Riedel Nigrini et al., p. 46, pl. P5, fig. 10.
- 2021a Podocyrtis (Podocyrtoges) diamesa Sanfilippo and Riedel Kamikuri et al., p. 4, pl. P2, figs. 4a, 4b.
- 2015 Podocyrtis (Podocyrtoges) diamesa Sanfilippo and Riedel Kamikuri, pl. 9, figs. 3a, 3b, 5a, 5b.
- 2017 Podocyrtis (Podocyrtis) diamesa Sanfilippo and Riedel de Souza et al., pl. 1, figs. 8a,
 8b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Podocyrtis (Podocyrtoges) phyxis Sanfilippo and Riedel, 1973

Plate II.18, Figure 11

- 1970 Podocyrtis (Podocyrtis) diamesa Riedel and Sanfilippo, p. 533, pl. 12, fig. 6 (part).
- 1973 Podocyrtis (Podocyrtis) phyxis Sanfilippo and Riedel, p. 531.
- 1977 Podocyrtis phyxis Sanfilippo and Riedel Riedel and Sanfilippo, pl. 8, fig. 6.
- 1978 Podocyrtis phyxis Sanfilippo and Riedel Riedel and Sanfilippo, p. 72, pl. 8, fig. 8.
- 1986 Podocyrtis (Podocyrtis) phyxis Sanfilippo and Riedel Riedel and Sanfilippo, pl. 2, fig.
 15.
- 1992 Podocyrtis (Podocyrtoges) physis Sanfilippo and Riedel Sanfilippo and Riedel, p. 14.
- 2012a *Podocyrtis (Podocyrtoges) phyxis* Sanfilippo and Riedel Kamikuri et al., p. 103, pl. 1, fig. 13.

2017 Podocyrtis (Podocyrtoges) phyxis Sanfilippo and Riedel – de Souza et al., pl. 1, fig. 12.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Podocyrtis (Podocyrtis) papalis Ehrenberg, 1847 Plate II.17, Figures 13–15

- 1847 Podocyrtis papalis Ehrenberg, p. 55, fig. 2.
- 1854a Podocyrtis papalis Ehrenberg Ehrenberg, pl. 36, fig. 23.
- 1862 Podocyrtis papalis Ehrenberg Bury, pl. 10, fig. 5.
- 1874 Podocyrtis Mitrella [sic] Ehrenberg, p. 251.
- 1874 Podocyrtis papalis Ehrenberg Ehrenberg, p. 251.
- 1876 Podocyrtis Mitrella [sic] Ehrenberg Ehrenberg, p. 82, pl. 15, fig. 3.
- 1887 Podocyrtis (Podocyrtidium) papalis Ehrenberg Haeckel, p. 1344.
- 1887 Podocyrtis (Podocyrtidium) mitrella Ehrenberg Haeckel, p. 1345.
- 1942 Podocyrtis (Podocyrtidium) fasciata Clark and Campbell, p. 80, pl. 7, figs. 29, 33.
- 1958 Podocyrtis papalis Ehrenberg Göke, pl. 1, fig. 3.
- 1969 Podocyrtis papalis Ehrenberg Riedel and Hays, pl. 1, fig. C.

- 1970 Podocyrtis (Podocyrtis) papalis Ehrenberg Cita et al., p. 403, pl. 1, fig. H.
- 1970 Podocyrtis (Podocyrtis) papalis Ehrenberg Riedel and Sanfilippo, p. 533, pl. 11, fig.
 1.
- 1971 Podocyrtis (Podocyrtis) papalis Ehrenberg Moore, p. 743, pl. 2, fig. 4.
- 1971 *Podocyrtis (Podocyrtis) papalis* Ehrenberg Riedel and Sanfilippo, p. 1598, pl. 3E, fig. 1.
- 1972 Podocyrtis papalis Ehrenberg Petrushevskaya and Kozlova, p. 543, pl. 35, fig. 1.
- 1972 Podocyrtis sp. Petrushevskaya and Kozlova, pl. 35, fig. 2.
- 1973 *Podocyrtis (Podocyrtis) papalis* Ehrenberg Sanfilippo and Riedel, p. 531, pl. 20, figs. 11–14, pl. 36, figs. 2, 3.
- 1974 Podocyrtis (Podocyrtis) papalis Ehrenberg Nigrini, p. 1069, pl. 1K, figs. 7–10.
- 1974 Podocyrtis (Podocyrtis) papalis Ehrenberg Johnson, p. 551, pl. 4, fig. 12.
- 1975 Podocyrtis (Podocyrtis) papalis Ehrenberg Ling, p. 731, pl. 13, fig. 5.
- 1977 Podocyrtis papalis Ehrenberg Riedel and Sanfilippo, pl. 9, fig. 12.
- 1985 Podocyrtis papalis Ehrenberg Sanfilippo et al., fig. 30.1.
- 1986 Podocyrtis papalis Ehrenberg Riedel and Sanfilippo, pl. 7, fig. 1.
- 1987 Podocyrtis papalis Ehrenberg Nishimura, p. 727, pl. 2, fig. 7.
- 1988 *Podocyrtis fasciata* Clark and Campbell Blueford, p. 246, pl. 1, figs. 10–12.
- 1992 Podocyrtis (?) sp. aff. P. papalis Nishimura, p. 329, pl. 10, figs. 1-3, pl. 13, fig. 18.
- 1993 Podocyrtis (Podocyrtis) papalis Ehrenberg Hull, p. 13, pl. 7, figs. 7, 8, pl. 8, fig. 10.
- 1995 Podocyrtis mitrella Ehrenberg Shilov, p. 127, pl. 1, fig. 3.
- 1995 Podocyrtis papilis [sic] Ehrenberg Strong et al., p. 209, fig. 9S.
- 1998a Podocyrtis papalis Ehrenberg Sanfilippo and Nigrini, p. 273, pl. 13.2, fig. 5.
- 1999 Podocyrtis papalis Ehrenberg Kozlova, p. 151, pl. 15, fig. 6, pl. 24, figs. 16, 17.
- 2000 *Podocyrtis (Podocyrtis) papalis* Ehrenberg Nigrini and Sanfilippo, p. 74, pl. 2, fig. 11, pl. 3, figs. 6, 7.
- 2001 Podocyrtis (Podocyrtis) papalis Ehrenberg Sanfilippo and Blome, p. 215, fig. 1f.
- 2005 Podocyrtis (Podocyrtis) papalis Ehrenberg Nigrini et al., p. 46, pl. P5, fig. 13.
- 2008 Podocyrtis (Podocyrtis) papalis Ehrenberg Jackett et al., p. 57, pl. 2, fig. 22.
- 2009 Podocyrtis mitrella Ehrenberg Ogane et al., pl. 24, figs. 4a-4c, pl. 57, figs. 3a-3d.
- 2009 Podocyrtis papalis Ehrenberg Ogane et al., pl. 58, figs. 1a-1f.
- 2012 Podocyrtis (Podocyrtis) papalis Ehrenberg Kamikuri and Wade, pl. 1, figs. 6a, 6b.
- 2012 Podocyrtis (Podocyrtis) papalis Ehrenberg Moore and Kamikuri, p. 9, pl. P7, fig. 6.
- 2015 Podocyrtis (Podocyrtis) papalis Ehrenberg Kamikuri, pl. 9, figs. 2a, 2b (part).
- 2020 Podocyrtis (Podocyrtis) papalis Ehrenberg Hollis et al., pl. 17, figs. 20a, 20b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Podocyrtis (Podocyrtopsis) apeza Sanfilippo and Riedel, 1992 Plate II.18, Figure 13

- 1992 Podocyrtis (Podocyrtopsis) apeza Sanfilippo and Riedel, p. 14, pl. 3, figs. 13-15.
- 2012 *Podocyrtis (Podocyrtopsis) apeza* Sanfilippo and Riedel Moore and Kamikuri, p. 10, pl. P7, fig. 7.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Anthocyrtoma Haeckel, 1887

Type species.—*Anthocyrtoma serrulata* Ehrenberg, 1874, p. 217 (unfigured); Ehrenberg, 1876, p. 64, pl. 6, fig. 7.

Anthocyrtoma leptostyla (Ehrenberg, 1874)

Plate II.19, Figures 1, 2

1874 Anthocyrtis leptostyla Ehrenberg, p. 216.

1876 Anthocyrtis leptostyla Ehrenberg – Ehrenberg, p. 64, pl. 6, fig. 1.

1887 Anthocyrtidium (Anthocyrtonium) leptostylum (Ehrenberg) – Haeckel, p. 1275.

2009 Anthocyrtis leptostyla Ehrenberg – Ogane et al., pl. 52, figs. 3a–3f.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Anthocyrtoma serrulata (Ehrenberg, 1874)

Plate II.18, Figure 14

1874 Anthocyrtis serrulata Ehrenberg, p. 217.

1874 Anthocyrtis ventricosa Ehrenberg, p. 217.

1874 Cycladophora Erinaceus [sic] Ehrenberg, p. 222.

1876 Anthocyrtis serrulata Ehrenberg – Ehrenberg, p. 66, pl. 6, fig. 7.

1876 Anthocyrtis ventricosa Ehrenberg – Ehrenberg, p. 66, pl. 8, fig. 1.

1876 Cycladophora Erinaceus [sic] Ehrenberg – Ehrenberg, p. 68, pl. 18, fig. 2.

1882a Thyrsocyrtis Erinaceus [sic] (Ehrenberg) - Bütschli, p. 527.

1882a Anthocyrtis serrulata Ehrenberg – Bütschli, p. 533.

1882a Anthocyrtis ventricosa Ehrenberg – Bütschli, p. 533.

1887 Anthocyrtoma serrulata (Ehrenberg) – Haeckel, p. 1268.

1887 Anthocyrtis (Anthocyrtella) ventricosa Ehrenberg – Haeckel, p. 1270.

1887 Calocyclas (Calocyclissa) erinaceus (Ehrenberg) – Haeckel, p. 1383.

1969b Anthocyrtidium apscheronense Mamedov, p. 33, pl. 1, fig. 1.

1969b Anthocyrtium mirandum Mamedov, p. 34, pl. 1, figs. 2, 3.

1970 Anthocyrtoma sp. Riedel and Sanfilippo, p. 524, pl. 6, figs. 2–4

1972 Anthocyrtoma sp. Petrushevskaya and Kozlova, pl. 34, figs. 1, 2

1973 Anthocyrtoma sp. Riedel and Sanfilippo, p. 737, pl. 3, fig. 5.

1974 Anthocyrtoma sp. Nigrini, p. 1066, pl. 1E, figs. 5–9.

1977 Calocycloma ampulla (Ehrenberg) – Riedel and Sanfilippo, pl. 8, fig. 1.

1978 Anthocyrtoma sp. Weaver and Dinkelman, p. 867, pl. 8, fig. 9.

2005 Anthocyrtoma spp. Nigrini et al., 2005, p. 25, pl. P3, figs. 15, 16.

2009 Anthocyrtis serrulata Ehrenberg – Ogane et al., pl. 51, figs. 1a–2d.

2009 Anthocyrtis ventricosa Ehrenberg – Ogane et al., pl. 51, figs. 3a–3d.

2009 Cycladophora erinaceus Ehrenberg – Ogane et al., pl. 52, figs. 1a-1g.

2012 Anthocyrtoma spp. Moore and Kamikuri, p. 5, pl. P1, fig. 1.



Plate II.18. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic). (1, 2) Podocvrtis (Lampterium) sinuosa Ehrenberg, 1874: (1) ODP 1260A-20R-1W, 55-57 cm; (2) ODP 1260A-17R-CC, 63-177 cm. (3, 4) Podocyrtis (Lampterium) mitra Ehrenberg, 1854a: (3) ODP 1260A-9R-5W, 55-57 cm; (4) ODP 1051A-16H-5W, 55-57 cm. (5) Podocyrtis (Lampterium) trachodes Riedel and Sanfilippo, 1970: ODP 1260A-10R-6W, 55-57 cm. (6) Podocyrtis (Lampterium) helenae Nigrini, 1974: ODP 1260A-12R-CC, 63-177 cm. (7) Podocyrtis (Lampterium) chalara Riedel and Sanfilippo, 1970: ODP 1260A-6R-4W, 55-57 cm. (8) Podocyrtis (Lampterium) goetheana (Haeckel, 1887): ODP 1260A-6R-2W, 55-57 cm. (9) Podocyrtis (Lampterium) fasciolata Nigrini, 1974: ODP 1260A-11R-7W, 55-57 cm. (10) Podocyrtis (Podocyrtoges) diamesa Riedel and Sanfilippo, 1970: ODP 1260A-17R-CC, 63-177 cm. (11) Podocyrtis (Podocyrtoges) phyxis Sanfilippo and Riedel, 1973: ODP 1260A-16R-1W, 55-57 cm. (12) Podocyrtis (Podocyrtoges) ampla Ehrenberg, 1874: ODP 1260A-17R-3W, 55-57 cm. (13) Podocyrtis (Podocyrtopsis) apeza Sanfilippo and Riedel, 1992: ODP 1260A-10R-6W, 55-57 cm. (14) Anthocyrtoma serrulata (Ehrenberg, 1874): ODP 1260A-13R-5W, 54–56 cm. All scale bars equal 50 µm.

2015 Anthocyrtoma serrulata (Ehrenberg) – Kamikuri, pl. 1, fig. 5.

2015 Anthocyrtoma ventricosa (Ehrenberg) – Kamikuri, pl. 10, figs. 8–9b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Family Theocotylidae Petrushevskaya, 1981

Genus Lamptonium Haeckel, 1887

Type species.— Cycladophora (Lamptonium) enneapleura Haeckel, 1887, p. 1378 (unfigured).

Lamptonium fabaeforme fabaeforme (Krasheninnikov, 1960)

Plate II.19, Figure 3

- 1960 Cyrtocalpis fabaeformis Krasheninnikov, p. 296, pl. 3, fig. 11.
- 1969b Eucyrtidium cybaeum Mamedov, p. 38, pl. 1, fig. 6.
- 1970 Lamptonium ? fabaeforme fabaeforme (Krasheninnikov) Riedel and Sanfilippo, p. 523, pl. 5, fig. 6.
- 1971 Lamptonium ? fabaeforme ? fabaeforme (Krasheninnikov) Moore, p. 740, pl. 1, fig. 6.
- 1973 Lamptonium fabaeforme ? fabaeforme (Krasheninnikov) Foreman, p. 436, pl. 6, figs. 6–9.
- 1974 Lamptonium fabaeforme ? fabaeforme (Krasheninnikov) Nigrini, p. 1067, pl. 1G, fig.3.
- 1978 Lamptonium fabaeforme fabaeforme (Krasheninnikov) Johnson, p. 784, pl. 2, fig. 5.
- 1978 Lamptonium fabaeforme fabaeforme (Krasheninnikov) Weaver and Dinkelman, p. 869, pl. 6, figs. 7–10.
- 1978 *Lamptonium fabaeforme fabaeforme* (Krasheninnikov) Riedel and Sanfilippo, p. 69, pl. 5, fig. 13.

- 1978 Lamptonium fabaeforme fabaeforme (Krasheninnikov) Foreman, p. 784, pl. 2, fig. 5.
- 1985 Lamptonium ? fabaeforme fabaeforme (Krasheninnikov) Sanfilippo et al., p. 674, fig.
 18.2.
- 1987 Lamptonium ? fabaeforme fabaeforme (Krasheninnikov) Nishimura, p. 726, pl. 2, fig. 20.
- 1998a Lamptonium fabaeforme fabaeforme (Krasheninnikov) Sanfilippo and Nigrini, p. 272, pl. 13.1, fig. 17.
- 1999 Lamptonium sp. cf. L. fabaeforme fabaeforme (Krasheninnikov) Kozlova, p. 158, pl. 22, fig. 12, pl. 23, fig. 14, pl. 46, fig. 20.
- 2008 *Lamptonium fabaeforme fabaeforme* (Krasheninnikov) Jackett et al., p. 54, pl. 2, fig. 12.
- ? 2017 *Lamptonium fabaeforme fabaeforme* (Krasheninnikov) de Souza et al., pl. 3, figs. 1a, 1b.
- Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Lamptonium fabaeforme chaunothorax Riedel and Sanfilippo, 1970 Plate II.19, Figure 4

- 1970 Lamptonium fabaeforme chaunothorax Riedel and Sanfilippo, p. 524, pl. 5, figs. 8, 9.
- 1971 *Lamptonium ? fabaeforme ? chaunothorax* Riedel and Sanfilippo Moore, p. 740, pl. 1, fig. 6.
- 1973 Lamptonium ? fabaeforme ? chaunothorax Riedel and Sanfilippo Dinkelman, p. 777, pl. 2, fig. 3.
- 1973 Lamptonium fabaeforme ? chaunothorax Riedel and Sanfilippo Foreman, p. 436, pl. 6, figs. 10–12.
- 1974 Lamptonium fabaeforme ? chaunothorax Riedel and Sanfilippo Nigrini, p. 1067, pl. 1G, fig. 1.
- 1978 *Lamptonium fabaeforme chaunothorax* Riedel and Sanfilippo Riedel and Sanfilippo, p. 69, pl. 5, fig. 11.
- 1978 *Lamptonium fabaeforme chaunothorax* Riedel and Sanfilippo Foreman, p. 784, pl. 2, fig. 3.
- 1998a *Lamptonium fabaeforme chaunothorax* Riedel and Sanfilippo Sanfilippo and Nigrini, p. 272, pl. 13.1, fig. 14.
- 2008 *Lamptonium fabaeforme chaunothorax* Riedel and Sanfilippo Jackett et al., p. 54, pl. 2, fig. 13.
- Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Genus Theocotyle Sanfilippo and Riedel, 1970

Type species.— Theocotyle venezuelensis Riedel and Sanfilippo, p. 525, pl. 6, fig. 10.

Theocotyle conica Foreman, 1973

Plate II.19, Figure 7

? 1969c *Theocampe piriformis* Mamedov, p. 28, pl. 2, figs. 2, 3.

- 1973 *Theocotyle (Theocotyle) cryptocephala (?) conica* Foreman, p. 440, pl. 4, fig. 11, pl. 12, figs. 19, 20.
- 1974 Theocotyle (Theocotyle) cryptocephala (?) conica Foreman Nigrini, p. 1068, pl. 1I, fig. 4.
- 1977 Theocotyle cryptocephala conica Foreman Riedel and Sanfilippo, pl. 6, fig. 4.
- 1982 Theocotyle conica Foreman Sanfilippo and Riedel, p. 177, pl. 2, fig. 13.
- 1987 Theocotyle cryptocephala (?) conica Foreman Nishimura, p. 729, pl. 2, fig. 22.
- 2017 Theocotyle (Theocotyle) conica Foreman de Souza et al., pl. 2, figs. 9a, 9b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Theocotyle cryptocephala (Ehrenberg, 1874)

Plate II.19, Figure 6

- 1874 *Eucyrtidium cryptocephalum* Ehrenberg, p. 277.
- 1876 Eucyrtidium cryptocephalum Ehrenberg Ehrenberg, p. 70, pl. 11, fig. 11.
- 1882a Eucyrtidium cryptocephalum Ehrenberg Bütschli, p. 528.
- 1887 Theocampe (Theocamptra) cryptocephala (Ehrenberg) Haeckel, p. 1426.
- 1970 ? *Theocotyle cryptocephala cryptocephala* (Ehrenberg) Riedel and Sanfilippo, p. 525, pl. 6, figs. 7, 8.
- 1973 ? *Theocotyle (Theocotyle) cryptocephala cryptocephala* (Ehrenberg) Foreman, p. 440, pl. 4, figs. 6, 7, pl. 12, fig. 18.
- 1974 ? *Theocotyle* (*Theocotyle*) *cryptocephala cryptocephala* (Ehrenberg) Nigrini, p. 1068, pl. 1I, figs. 2, 3.
- 1974 *Theocotyle (Theocotyle) cryptocephala cryptocephala* (Ehrenberg) Johnson, p. 549, pl. 2, fig. 8.
- 1975 *Theocotyle (Theocotyle) cryptocephala cryptocephala* (Ehrenberg) Ling, p. 730, pl. 10, fig. 14.
- 1978 *Theocotyle cryptocephala cryptocephala* (Ehrenberg) Riedel and Sanfilippo, p. 78, pl. 9, fig. 19.
- 1982 Theocotyle cryptocephala (Ehrenberg) Sanfilippo and Riedel, p. 178, pl. 2, figs. 4–7.
- 1994 Theocotyle cryptocephala (Ehrenberg) Weinheimer et al., p. 312, pl. 1, figs. 9a, 9b.
- 2009 Eucyrtidium cryptocephalum Ehrenberg Ogane et al., pl. 95, figs. 2a–2d.
- 2012a Theocotyle cryptocephala (Ehrenberg) Kamikuri et al., p. 104, pl. 3, figs. 14a, 14b.
- 2017 Theocotyle cryptocephala (Ehrenberg) de Souza et al., pl. 2, figs. 10a, 10b.
- Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Theocotyle nigriniae Riedel and Sanfilippo, 1970

Plate II.19, Figure 5

- 1970 Theocorys sp. Cita et al., p. 404, pl. 2, fig. L.
- 1970 Theocotyle cryptocephala (?) nigriniae Riedel and Sanfilippo, p. 525, pl. 6, fig. 5 (part).
- 1971 *Theocotyle cryptocephala* (?) *nigriniae* Riedel and Sanfilippo Moore, p. 740, pl. 1, fig. 10.

- 1973 *Theocotyle (Theocotyle) cryptocephala (?) nigriniae* Riedel and Sanfilippo Foreman, p. 440, pl. 4, figs. 3–5 (part).
- 1974 *Theocotyle (Theocotyle) cryptocephala (?) nigriniae* Riedel and Sanfilippo Nigrini, p. 1068, pl. 1I, fig. 1.
- 1976 *Theocotyle (Theocotyle) cryptocephala (?) nigriniae* Riedel and Sanfilippo Johnson, p. 784, pl. 2, fig. 15.
- 1977 *Theocotyle cryptocephala nigriniae* Riedel and Sanfilippo Riedel and Sanfilippo, pl. 5, fig. 3.
- 1978 *Theocotyle cryptocephala nigriniae* Riedel and Sanfilippo Weaver and Dinkelman, p. 873, pl. 9, figs. 9–11.
- 1978 *Theocotyle cryptocephala nigriniae* Riedel and Sanfilippo Riedel and Sanfilippo, p. 78, pl. 10, figs. 1, 2.
- 1978 *Theocotyle (Theocotyle) cryptocephala nigriniae* Riedel and Sanfilippo Foreman, p. 784, pl. 2, fig. 15.
- 1982 *Theocotyle nigriniae* Riedel and Sanfilippo Riedel and Sanfilippo, p. 178, pl. 2, figs. 1–3.
- 1986 Theocotyle nigriniae Riedel and Sanfilippo Riedel and Sanfilippo, pl. 1, figs. 17, 18.
- 1994 *Theocotyle nigriniae* Riedel and Sanfilippo Weinheimer et al., p. 312, pl. 1, figs. 8a, 8b.
- 1998a Theocotyle nigriniae Riedel and Sanfilippo Sanfilippo and Nigrini, p. 273, pl. 13.2, figs. 17, 18.
- 2001 *Theocotyle nigriniae* Riedel and Sanfilippo Sanfilippo and Blome, p. 219, figs. 11e, 11f.
- 2008 Theocotyle nigriniae Riedel and Sanfilippo Jackett et al., p. 59, pl. 2, fig. 7.
- 2012a Theocotyle nigriniae Riedel and Sanfilippo Kamikuri et al., p. 104, pl. 1, fig. 12.
- ? 2017 Theocotyle nigriniae Riedel and Sanfilippo de Souza et al., pl. 2, fig. 11.
- 2020 Theocotyle nigriniae Riedel and Sanfilippo Hollis et al., pl. 11, fig. 10.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Theocotyle venezuelensis Riedel and Sanfilippo, 1970 Plate II.19, Figure 8

- 1970 *Theocotyle venezuelensis* Riedel and Sanfilippo, p. 525, pl. 6, figs. 9, 10, pl. 7, figs. 1, 2.
- 1971 Theocotyle venezuelensis Riedel and Sanfilippo Moore, p. 740, pl. 1, fig. 11.
- 1973 *Theocotyle (Theocotyle) venezuelensis* Riedel and Sanfilippo Foreman, p. 440, pl. 4, fig. 12.
- 1977 Theocotyle venezuelensis Riedel and Sanfilippo Riedel and Sanfilippo, pl. 7, fig. 18.
- 1982 *Theocotyle venezuelensis* Riedel and Sanfilippo Sanfilippo and Riedel, p. 179, pl. 2, figs. 8–12.
- 2017 Theocotyle venezuelensis Riedel and Sanfilippo de Souza et al., pl. 2, figs. 12a, 12b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Genus Theocotylissa Foreman, 1973

Type species.—*Eucyrtidium ficus* Ehrenberg, 1874, p. 228 (unfigured); Ehrenberg, 1876, p. 70, pl. 11, fig. 19.

Theocotylissa ficus (Ehrenberg, 1874)

Plate II.19, Figure 9

1874 Eucyrtidium Ficus [sic] Ehrenberg, p. 228.

1876 Eucyrtidium Ficus [sic] Ehrenberg – Ehrenberg, p. 70, pl. 11, fig. 19.

1882a Anthocyrtis Ficus [sic] (Ehrenberg) - Bütschli, p. 533.

1882b Anthocyrtis ? Ficus [sic] (Ehrenberg) - Bütschli, pl. 31, fig. 7.

1887 Theoconus (Theocorbis) ficus (Ehrenberg) – Haeckel, p. 1403.

1969c Cyrtocalpis originaris Mamedov, p. 26, pl. 2, figs. 4, 5.

1970 Theocotyle ? ficus (Ehrenberg) - Riedel and Sanfilippo, p. 525, pl. 7, figs. 3-5.

1971 Theocotyle ? ficus (Ehrenberg) – Moore, p. 740, pl. 1, fig. 12.

1973 Theocotyle (Theocotylissa) ficus (Ehrenberg) – Foreman, p. 441, pl. 4, figs. 16–20.

1974 Theocotyle (Theocotylissa) ficus (Ehrenberg) – Nigrini, p. 1068, pl. 1I, figs. 5-8.

1974 Theocotyle (Theocotylissa) ficus (Ehrenberg) – Johnson, p. 549, pl. 4, figs. 10, 11.

1977 Theocotyle ficus (Ehrenberg) – Riedel and Sanfilippo, pl. 9, fig. 8.

- 1982 Theocotylissa ficus (Ehrenberg) Sanfilippo and Riedel, p. 180, pl. 2, figs. 19, 20.
- 1987 Theocotyle ? ficus (Ehrenberg) Nishimura, p. 729, pl. 2, fig. 23.
- 1994 Theocotylissa ficus (Ehrenberg) Weinheimer et al., p. 312, pl. 1, fig. 11.

1998a Theocotylissa ficus (Ehrenberg) - Sanfilippo and Nigrini, p. 273, pl. 13.2, fig. 21.

2001 Theocotylissa ficus (Ehrenberg) – De Wever et al., p. 280, fig. 185.1.

2005 Theocotylissa ficus (Ehrenberg) – Nigrini et al., p. 49, pl. P5, fig. 1.

2008 Theocotylissa ficus (Ehrenberg) – Jackett et al., p. 59, pl. 2, fig. 8.

2009 Eucyrtidium ficus Ehrenberg – Ogane et al., pl. 59, figs. 2a-2c

2012 Theocotylissa ficus (Ehrenberg) – Moore and Kamikuri, p. 10, pl. P7, fig. 16.

2015 Theocotylissa ficus (Ehrenberg) - Kamikuri, pl. 8, figs. 1a, 1b.

2017 Theocotylissa ficus (Ehrenberg) – de Souza et al., pl. 3, figs. 10a, 10b.

2020 Theocotylissa ficus (Ehrenberg) – Hollis et al., pl. 11, fig. 11.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Thyrsocyrtis Ehrenberg, 1847

Type species.— *Thyrsocyrtis rhizodon* Ehrenberg, 1874, p. 262 (unfigured); Ehrenberg, 1876, p. 84, pl. 12, fig.1.

Thyrsocyrtis (Thyrsocyrtis) argulus (Ehrenberg, 1874)

Plate II.19, Figure 11

- 1862 Podocyrtis ? mitra Ehrenberg Bury, pl. 10, fig. 4.
- 1874 Podocyrtis Argulus [sic] Ehrenberg, p. 248.
- 1874 Podocyrtis Argus [sic] Ehrenberg, p. 248.
- 1874 Podocyrtis attenuata Ehrenberg, p. 249.
- 1874 Thyrsocyrtis Rhizodon [sic] Ehrenberg, p. 262.
- 1876 Podocyrtis Argulus [sic] Ehrenberg Ehrenberg, p. 80, pl. 16, fig. 2.

1876 Podocyrtis Argus [sic] Ehrenberg – Ehrenberg, p. 80, pl. 16, fig. 9.

- 1876 Podocyrtis attenuata Ehrenberg Ehrenberg, p. 80, pl. 16, fig. 5.
- 1876 Thyrsocyrtis Rhizodon [sic] Ehrenberg Ehrenberg, p. 84, pl. 12, fig. 1.
- 1882b Podocyrtis Rhizodon [sic] (Ehrenberg) Bütschli, pl. 30, fig. 11.
- 1887 Podocyrtis (Podocyrtarium) tripodiscus Haeckel, p. 1338, pl. 72, fig. 4.
- ? 1887 Podocyrtis (Podocyrtarium) corythæola Haeckel, p. 1339, pl. 72, fig. 2.
- 1887 Podocyrtis (Podocyrtarium) surena Haeckel, p. 1340, pl. 72, fig. 10.
- 1887 Podocyrtis (Podocyrtecium) divergens Haeckel, p. 1340, pl. 72, fig. 6.
- 1887 Podocyrtis (Podocyrtecium) argulus Ehrenberg Haeckel, p. 1344.
- 1887 Podocyrtis (Podocyrtidium) argus Ehrenberg Haeckel, p. 1346.
- 1887 Thyrsocyrtis rhizodon Ehrenberg Haeckel, p. 1350.
- 1957a Podocyrtis aff. P. argus Ehrenberg Riedel, p. 260, pl. 62, fig. 4, pl. 63, fig. 8.
- 1958 Podocyrtis rhizodon (Ehrenberg) Göke, pl. 1, fig. 1.
- 1969c Podocyrtis trifidus Mamedov, p. 29, pl. 2, fig. 1.
- 1970 Thyrsocyrtis rhizodon Ehrenberg Riedel and Sanfilippo, p. 525, pl. 7, figs. 6, 7.
- 1971 Thyrsocyrtis rhizodon Ehrenberg Riedel and Sanfilippo, p. 1596, pl. 3C, fig. 6.
- 1971 Thyrsocyrtis rhizodon Ehrenberg Moore, p. 740, pl. 2, figs. 8, 9.
- 1973 Thyrsocyrtis rhizodon Ehrenberg Foreman, p. 442, pl. 3, fig. 1, 2.
- 1974 Thyrsocyrtis rhizodon Ehrenberg Johnson, p. 549, pl. 4, figs. 6–9.
- 1975 Thyrsocyrtis rhizodon Ehrenberg Holdsworth, p. 531, pl. 1, figs. 15, 22, 23.
- 1975 Thyrsocyrtis ? rhizodon Ehrenberg Holdsworth, pl. 1, fig. 24.
- 1975 *Thyrsocyrtis rhizodon* Ehrenberg Ling, p. 730, pl. 11, fig. 18.
- 1977 Thyrsocyrtis rhizodon Ehrenberg Riedel and Sanfilippo, pl. 9, fig. 9.
- 1982 *Thyrsocyrtis (Thyrsocyrtis) rhizodon* Ehrenberg Sanfilippo and Riedel, p. 173, pl. 1, figs. 14–16, pl. 3, figs. 12–17.
- 1994 *Thyrsocyrtis (Thyrsocyrtis) rhizodon* Ehrenberg Weinheimer et al., p. 312, pl. 1, fig. 12.
- 2000 *Thyrsocyrtis (Thyrsocyrtis) rhizodon* Ehrenberg Nigrini and Sanfilippo, p. 75, pl. 1, fig. 14.
- 2001 Thyrsocyrtis rhizodon Ehrenberg Sanfilippo and Blome, p. 220, figs. 7k, 7o.
- 2001 Thyrsocyrtis (Thyrsocyrtis) rhizodon Ehrenberg De Wever et al., p. 280, fig. 185.5.
- 2008 Thyrsocyrtis (Thyrsocyrtis) rhizodon Ehrenberg Jackett et al., p. 59, pl. 2, fig. 11.
- 2009 Podocyrtis argulus Ehrenberg Ogane et al., pl. 24, figs. 5a-5d.
- 2009 Podocyrtis argus Ehrenberg Ogane et al., pl. 10, figs. 6a–6c, pl. 95, figs. 3a–3d.
- 2009 Podocyrtis attenuata Ehrenberg Ogane et al., pl. 56, figs. 2a–2d.
- 2009 Thyrsocyrtis rhizodon Ehrenberg Ogane et al., pl. 56, figs. 1a-1e.
- 2012 *Thyrsocyrtis (Thyrsocyrtis) rhizodon* Ehrenberg Moore and Kamikuri, p. 12, pl. P10, fig. 1.
- 2012 Thyrsocyrtis (Thyrsocyrtis) rhizodon Ehrenberg Kamikuri and Wade, pl. 1, figs. 3a, 3b.
- 2015 *Thyrsocyrtis (Thyrsocyrtis) rhizodon* Ehrenberg Kamikuri, pl. 11, figs. 1a–2b, 7a, 7b, pl. 19, fig. 6a, 6b.
- 2017 Thyrsocyrtis (Thyrsocyrtis) rhizodon Ehrenberg de Souza et al., pl. 3, figs. 4a, 4b.

2020 *Thyrsocyrtis (Thyrsocyrtis) rhizodon* Ehrenberg – Hollis et al., pl. 11, figs. 16a–18b. Remarks. The combination used here is derived from O'Dogherty et al. (2021). Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Thyrsocyrtis (Thyrsocyrtis) bromia Ehrenberg, 1874 group

Plate II.19, Figure 13

- 1874 Thyrsocyrtis Bromia [sic] Ehrenberg, p. 260.
- 1876 Thyrsocyrtis Bromia [sic] Ehrenberg Ehrenberg, p. 84, pl. 12, fig. 12.
- 1887 Podocyrtis (Podocyrtonium) bromia (Ehrenberg) Haeckel, p. 1349.
- 1971 Thyrsocyrtis bromia Ehrenberg Riedel and Sanfilippo, p. 1596, pl. 8, fig. 6.
- 1971 Thyrsocyrtis bromia Ehrenberg Moore, p. 740, pl. 5, figs. 1–3.
- 1973 Thyrsocyrtis bromia Ehrenberg Dinkelman, p. 787, pl. 3, figs. 1–4, 6.
- 1973 Thyrsocyrtis sp. aff. T. bromia Ehrenberg Dinkelman, pl. 3, figs. 5.
- 1974 Thyrsocyrtis bromia Ehrenberg Nigrini, p. 1068, pl. 2D, fig. 6.
- 1974 Thyrsocyrtis bromia Ehrenberg Johnson, p. 549, pl. 5, fig. 7.
- 1975 Thyrsocyrtis bromia Ehrenberg Holdsworth, p. 531, pl. 1, figs. 12–14, 19–21.
- 1975 Thyrsocyrtis bromia Ehrenberg Ling, p. 730, pl. 11, figs. 15, 16.
- 1977 *Thyrsocyrtis bromia* Ehrenberg Riedel and Sanfilippo, pl. 11, fig. 2.
- 1978 Thyrsocyrtis bromia Ehrenberg Riedel and Sanfilippo, p. 78, pl. 10, figs. 4, 5.
- 1982 *Thyrsocyrtis (Thyrsocyrtis) bromia* Ehrenberg Sanfilippo and Riedel, p. 172, pl. 1, fig. 20 (part).
- 1986 Thyrsocyrtis bromia Ehrenberg Riedel and Sanfilippo, pl. 6, fig. 1.
- 2006 *Thyrsocyrtis (Thyrsocyrtis) bromia* Ehrenberg Funakawa et al., p. 33, pl. P11, figs. 3a, 3b.
- 2006 *Thyrsocyrtis (Thyrsocyrtis) bromia* Ehrenberg form A– Funakawa et al., p. 33, pl. P11, figs. 4a–6b.
- 2012 *Thyrsocyrtis (Thyrsocyrtis) bromia* Ehrenberg Moore and Kamikuri, p. 11, pl. P9, figs. 3–10.
- 2012 Thyrsocyrtis (Thyrsocyrtis) bromia Ehrenberg Kamikuri and Wade, pl. 1, figs. 8a, 8b.
- 2012b *Thyrsocyrtis (Thyrsocyrtis) bromia* Ehrenberg Kamikuri et al., p. 5, pl. P2, figs. 8a, 8b.
- 2015 Thyrsocyrtis (Thyrsocyrtis) bromia Ehrenberg Kamikuri, pl. 11, figs. 8a, 8b.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Thyrsocyrtis (Thyrsocyrtis) norrisi Sanfilippo and Blome, 2001 Plate II.19, Figure 12

2009 Thyrsocyrtis (Thyrsocyrtis) norrisi Sanfilippo and Blome, p. 207, figs. 7f–7j, 71, 7m.

2015 *Thyrsocyrtis (Thyrsocyrtis) norrisi* Sanfilippo and Blome – Kamikuri, pl. 7, figs. 7a–8b. Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Thyrsocyrtis (Thyrsocyrtis) robusta Riedel and Sanfilippo, 1970 Plate II.19, Figure 10

- 1970 Thyrsocyrtis hirsuta robusta Riedel and Sanfilippo, p. 526, pl. 8, fig. 1.
- 1971 Thyrsocyrtis hirsuta robusta Riedel and Sanfilippo Moore, p. 740, pl. 2, fig. 7.
- 1973 Thyrsocyrtis hirsuta robusta Riedel and Sanfilippo Foreman, p. 442, pl. 3, fig. 17.
- 1974 Thyrsocyrtis hirsuta robusta Riedel and Sanfilippo Nigrini, p. 1069, pl. 1J, figs. 3, 4.
- 1977 *Thyrsocyrtis hirsuta robusta* Riedel and Sanfilippo Riedel and Sanfilippo, pl. 6, fig.
 3.
- 2012b *Thyrsocyrtis (Thyrsocyrtis) robusta* Riedel and Sanfilippo Kamikuri et al., p. 5, pl. P2, figs. 1a, 1b.
- 2017 *Thyrsocyrtis (Thyrsocyrtis) robusta* Riedel and Sanfilippo de Souza et al., pl. 3, figs. 5a, 5b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Thyrsocyrtis (Pentalacorys) parvipes (Ehrenberg, 1874) Plate II.20, Figure 1

- 1874 Podocyrtis parvipes Ehrenberg, p. 252.
- 1876 Podocyrtis parvipes Ehrenberg Ehrenberg, p. 82, pl. 14, fig. 4.
- 1973 Thyrsocyrtis tetracantha (Ehrenberg) Dinkelman, p. 787, pl. 2, figs. 4, 5.
- 1973 Thyrsocyrtis cf. T. triacantha (Ehrenberg) Dinkelman, pl. 2, fig. 8.
- ? 1973 Thyrsocyrtis sp. aff. T. bromia Ehrenberg Dinkelman, pl. 3, fig. 5.
- 1974 Thyrsocyrtis tetracantha (Ehrenberg) Johnson, p. 549, pl. 5, fig. 15.
- 1977 Thyrsocyrtis tetracantha (Ehrenberg) Riedel and Sanfilippo, pl. 11, fig. 3 (part).
- 1978 Thyrsocyrtis tetracantha (Ehrenberg) Riedel and Sanfilippo, p. 81, pl. 10, fig. 9 (part).
- 1985 *Thyrsocyrtis (Pentalacorys) tetracantha* (Ehrenberg) Sanfilippo et al., p. 690, fig. 26.8b (part).
- 1982 Thyrsocyrtis (Pentalacorys) tetracantha (Ehrenberg) Sanfilippo and Riedel, p. 176 pl.
 1, fig. 11 (part).
- 1986 *Thyrsocyrtis (Pentalacorys) tetracantha* (Ehrenberg) Riedel and Sanfilippo, pl. 6, fig.
 3.
- 2000 *Thyrsocyrtis (Pentalacorys) tetracantha* (Ehrenberg) Nigrini and Sanfilippo, p. 74, pl. 1, fig. 2.
- 2001 Thyrsocyrtis (Pentalacorys) krooni Sanfilippo and Blome, p. 207, figs. 7a-7e.
- 2006 *Thyrsocyrtis (Pentalacorys) tetracantha* (Ehrenberg) Funakawa et al., p. 31, pl. P11, figs. 9a, 9b.
- 2009 Podocyrtis parvipes Ehrenberg Ogane et al., pl. 87, figs. 5a, 5b, pl. 90, figs. 6a, 6b.
- 2012 *Thyrsocyrtis (Pentalacorys) krooni* Sanfilippo and Blome Moore and Kamikuri, p. 11, pl. P8, figs. 7, 8.
- 2015 *Thyrsocyrtis (Pentalacorys) krooni* Sanfilippo and Blome Kamikuri, pl. 4, figs. 3a, 3b, 6a–7b.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Chapter II - Progress on middle Eocene radiolarian biodiversity

Thyrsocyrtis (Pentalacorys) schomburgkii (Ehrenberg, 1847) Plate II.19, Figures 14, 15

- 1847 Podocyrtis Schomburgkii [sic] Ehrenberg, p. 55, fig. 1.
- 1854a Podocyrtis Schomburgkii [sic] Ehrenberg Ehrenberg, pl. 36, fig. 22.
- 1854a Podocyrtis cothurnata Ehrenberg, pl. 36, fig. B21.
- 1862 Podocyrtis cothurnata Ehrenberg Bury, pl. 7, fig. 7.
- 1862 Anthocyrtis cothurnata (Ehrenberg) Haeckel, p. 310.
- 1862 Podocyrtis Schomburgki [sic] Ehrenberg Haeckel, p. 339.
- 1874 Podocyrtis bicornis Ehrenberg, p. 249.
- 1874 Podocyrtis Centriscus [sic] Ehrenberg, p. 249.
- 1874 Podocyrtis cothurnata Ehrenberg Ehrenberg, p. 250.
- 1874 Podocyrtis Dipus [sic] Ehrenberg Ehrenberg, p. 250.
- 1874 Podocyrtis Euceros [sic] Ehrenberg, p. 250.
- 1874 Podocyrtis Princeps [sic] Ehrenberg, p. 252.
- 1874 Podocyrtis radicata Ehrenberg, p. 253.
- 1874 Podocyrtis Schomburgkii [sic] Ehrenberg Ehrenberg, p. 253.
- 1874 Podocyrtis Triacantha [sic] Ehrenberg, p. 254.
- 1874 Podocyrtis ventricosa Ehrenberg, p. 254.
- 1876 Podocyrtis bicornis Ehrenberg Ehrenberg, p. 80, pl. 16, fig. 8.
- 1876 Podocyrtis Centriscus [sic] Ehrenberg Ehrenberg, p. 80, pl. 14, fig. 2.
- 1876 Podocyrtis cothurnata Ehrenberg Ehrenberg, p. 82, pl. 14, fig. 1.
- 1876 Podocyrtis Dipus [sic] Ehrenberg Ehrenberg, p. 82, pl. 12, fig. 11.
- 1876 Podocyrtis Euceros [sic] Ehrenberg Ehrenberg, p. 82, pl. 15, fig. 1.
- 1876 Podocyrtis Princeps [sic] Ehrenberg Ehrenberg, p. 82, pl. 13, fig. 1.
- 1876 Podocyrtis radicata Ehrenberg Ehrenberg, p. 82, pl. 13, fig. 5.
- 1876 Podocyrtis schomburgkii Ehrenberg Ehrenberg, p. 82, pl. 14, fig. 7.
- 1876 Podocyrtis Triacantha [sic] Ehrenberg Ehrenberg, p. 82, pl. 13, fig. 4.
- 1876 Podocyrtis ventricosa Ehrenberg Ehrenberg, p. 82, pl. 16, fig. 3.
- 1879 Dictyopodium moseleyi Haeckel, p. 706, pl. 16, fig. 10.
- 1882a Podocyrtis Princeps [sic] Ehrenberg Bütschli, p. 540, pl. 33, figs. 32a-32c.
- 1882b Podocyrtis cothurnata Ehrenberg Bütschli, pl. 30, fig. 13.
- 1882b Podocyrtis Princeps [sic] Ehrenberg Bütschli, pl. 30, figs. 14a–14b.
- 1887 Podocyrtis (Podocyrtecium) ventricosa Ehrenberg Haeckel, p. 1341.
- ? 1887 Podocyrtis (Podocyrtecium) flosculata Haeckel, p. 1341, pl. 72, fig. 9.
- 1887 Podocyrtis (Podocyrtecium) centriscus Ehrenberg Haeckel, p. 1341.
- 1887 Podocyrtis (Podocyrtecium) magnifica Haeckel, p. 1341.
- 1887 Podocyrtis (Podocyrtecium) princeps Ehrenberg Haeckel, p. 1342.
- 1887 Podocyrtis (Podocyrtecium) euceros Ehrenberg Haeckel, p. 1342.
- 1887 Podocyrtis (Podocyrtecium) cristata Haeckel, p. 1342, pl. 72, fig. 7.
- 1887 Podocyrtis (Podocyrtecium) schomburgkii Ehrenberg Haeckel, p. 1343.
- 1887 Podocyrtis (Podocyrtonium) tripus Haeckel, p. 1349.
- 1887 Podocyrtis (Podocyrtonium) triacantha Ehrenberg Haeckel, p. 1350.
- 1887 Thyrsocyrtis radicata (Ehrenberg) Haeckel, p. 1351.



Plate II.19. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic). (1, 2) Anthocyrtoma leptostyla (Ehrenberg, 1874): (1) ODP 1260A-13R-CC, 63–177 cm; (2) ODP 1260A-16R-1W, 55–57 cm. (3) Lamptonium fabaeforme fabaeforme (Krasheninnikov, 1960): ODP 1260A-20R-4W, 55-57 cm. (4) Lamptonium fabaeforme chaunothorax Riedel and Sanfilippo, 1970: ODP 1260A-20R-4W, 55-57 cm. (5) Theocotyle nigriniae Riedel and Sanfilippo, 1970: ODP 1051A-38X-5W, 55-57 cm. (6) Theocotyle cryptocephala (Ehrenberg, 1874): ODP 1260A-19R-CC, 63-177 cm. (7) Theocotyle conica Foreman, 1973: ODP 1260A-17R-CC, 63-177 cm. (8) Theocotyle venezuelensis Riedel and Sanfilippo, 1970: ODP 1260A-17R-CC, 63–177 cm. (9) Theocotylissa ficus (Ehrenberg, 1874): ODP 1260A-15R-2W, 55-57 cm. (10) Thyrsocyrtis (Thyrsocyrtis) robusta Riedel and Sanfilippo, 1970: ODP 1260A-20R-4W, 55–57 cm. (11) Thyrsocyrtis (Thyrsocyrtis) argulus (Ehrenberg, 1874): ODP 1260A-9R-3W, 55-57 cm. (12) Thyrsocyrtis (Thyrsocyrtis) norrisi Sanfilippo and Blome, 2001: ODP 1051A-13H-5W, 58–60 cm. (13) Thyrsocyrtis (Thyrsocyrtis) bromia Ehrenberg, 1874 group: ODP 1051A-2H-5W, 55-57 cm. (14, 15) Thyrsocyrtis (Pentalacorys) schomburgkii (Ehrenberg, 1847): (14) early morphotype, ODP 1260A-20R-1W, 55–57 cm; (15) ODP 1260A-10R-5W, 55–57 cm. (16) Thyrsocyrtis (Pentalacorys) tetracantha (Ehrenberg, 1874): ODP 1260A-6R-2W, 55–57 cm. All scale bars equal 50 µm.

- 1887 Dictyopodium scaphopodium Haeckel, p. 1353, pl. 73, fig. 8.
- 1887 Dictyopodium cothurnatum (Ehrenberg) Haeckel, p. 1353.
- 1887 Dictyopodium thyrsolophus Haeckel, p. 1354, pl. 73, fig. 7.
- 1944 Podocyrtis (Podocyrtecium) elegantissima Campbell and Clark, p. 29, pl. 7, fig. 25.
- 1957a Podocyrtis triacantha Ehrenberg Riedel, p. 260, pl. 63, fig. 9.
- 1958 Podocyrtis triacantha Ehrenberg Göke, pl. 1, fig. 6.
- 1970 Thyrsocyrtis triacantha (Ehrenberg) Riedel and Sanfilippo, p. 526, pl. 8, figs. 2, 3.
- 1971 Thyrsocyrtis triacantha (Ehrenberg) Riedel and Sanfilippo, p. 1596, pl. 3C, fig. 7.
- 1971 *Thyrsocyrtis triacantha* (Ehrenberg) Moore, p. 740, pl. 4, fig. 2.
- 1972 *Thyrsocyrtis triacantha* (Ehrenberg) Petrushevskaya and Kozlova, p. 542, pl. 32, fig. 9, pl. 34, fig. 6.
- 1973 Thyrsocyrtis triacantha (Ehrenberg) Dinkelman, p. 787, pl. 2, fig. 7.
- 1973 Thyrsocyrtis triacantha (Ehrenberg) Foreman, p. 442, pl. 12, figs. 9–11.
- 1974 Thyrsocyrtis triacantha (Ehrenberg) Nigrini, p. 1069, pl. 1J, figs. 5–7, pl. 2E, fig. 1.
- 1974 Thyrsocyrtis triacantha (Ehrenberg) Johnson, p. 549, pl. 5, fig. 16.
- 1975 Thyrsocyrtis triacantha (Ehrenberg) Holdsworth, p. 531, pl. 1, fig. 18.
- 1975 Thyrsocyrtis triacantha (Ehrenberg) Ling, p. 730, pl. 11, fig. 20.
- 1977 Thyrsocyrtis triacantha (Ehrenberg) Riedel and Sanfilippo, pl. 8, figs. 2, 3.
- 1978 Thyrsocyrtis triacantha (Ehrenberg) Riedel and Sanfilippo, p. 82, pl. 10, figs. 10, 11.
- 1982 Thyrsocyrtis (Pentalacorys) triacantha (Ehrenberg) Sanfilippo and Riedel, p. 176, pl. 1, figs. 8–10, pl. 3, figs. 3, 4, text-fig. 1.
- 1985 *Thyrsocyrtis (Pentalacorys) triacantha* (Ehrenberg) Sanfilippo et al., p. 690, figs. 26.7a, 26.7b.

- 1986 *Thyrsocyrtis (Pentalacorys) triacantha* (Ehrenberg) Riedel and Sanfilippo, pl. 4, fig. 18, pl. 6, fig. 2.
- 1993 Thyrsocyrtis (Pentalacorys) triacantha (Ehrenberg) Hull, p. 13, pl. 7, fig. 12, pl. 8, fig. 2.
- 2000 *Thyrsocyrtis (Pentalacorys) triacantha* (Ehrenberg) Nigrini and Sanfilippo, p. 74, pl. 1, figs. 13, 16, 17.
- 2006 *Thyrsocyrtis (Pentalacorys) triacantha* (Ehrenberg) Funakawa et al., p. 32, pl. P11, figs. 8a, 8b.
- 2009 Podocyrtis bicornis Ehrenberg Ogane et al., pl. 9, figs. 8a-8d, pl. 55, figs. 2a-2e.
- 2009 Podocyrtis euceros Ehrenberg Ogane et al., pl. 10, figs. 4a, 4b.
- 2009 Podocyrtis schomburgkii Ehrenberg Ogane et al., pl. 57, figs. 1a-1f.
- 2009 Podocyrtis dipus Ehrenberg Ogane et al., pl. 91, figs. 1a–1d.
- 2009 Podocyrtis triacantha Ehrenberg Ogane et al., pl. 91, figs. 2a-3c.
- 2009 Podocyrtis tetracantha Ehrenberg Ogane et al., pl. 91, figs. 4a–4c (part).
- 2012 *Thyrsocyrtis (Pentalacorys) triacantha* (Ehrenberg) Moore and Kamikuri, p. 11, pl. P9, figs. 1, 2.
- 2012 *Thyrsocyrtis (Pentalacorys) triacantha* (Ehrenberg) Kamikuri and Wade, pl. 1, figs. 2a, 2b.
- 2012b *Thyrsocyrtis (Pentalacorys) triacantha* (Ehrenberg) Kamikuri et al., p. 5, pl. P2, figs. 2a, 2b.
- 2013 *Thyrsocyrtis (Pentalacorys) triacantha* (Ehrenberg) Kamikuri et al., pl. 1, figs. 10a, 10b.
- 2015 Thyrsocyrtis (Pentalacorys) triacantha (Ehrenberg) Kamikuri, pl. 4, figs. 4a–5b, 8.
- 2017 Thyrsocyrtis (Pentalacorys) triacantha (Ehrenberg) de Souza et al., pl. 3, fig. 8.
- Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Thyrsocyrtis (Pentalacorys) tetracantha (Ehrenberg, 1874)

Plate II.19, Figure 16

1862 Podocyrtis Schomburgki [sic] Ehrenberg – Bury, pl. 17, fig. 2.

? 1874 Podocyrtis aculeata Ehrenberg, p. 248.

? 1874 Podocyrtis Pentacantha [sic] Ehrenberg, p. 252.

1874 Podocyrtis Tetracantha [sic] Ehrenberg, p. 254.

? 1876 Podocyrtis aculeata Ehrenberg – Ehrenberg, p. 80, pl. 13, fig. 3.

? 1876 Podocyrtis Pentacantha [sic] Ehrenberg – Ehrenberg, p. 82, pl. 17, fig. 1.

1876 Podocyrtis Tetracantha [sic] Ehrenberg – Ehrenberg, p. 82, pl. 13, fig. 2.

? 1882a *Podocyrtis aculeata* Ehrenberg – Bütschli, pl. 33, figs. 34a, 34b.

1887 Alacorys (Tetralacorys) tetracantha (Ehrenberg) – Haeckel, p. 1371.

1887 Alacorys (Hexalacorys) guilelmi Haeckel, p. 1372, pl. 65, fig. 2.

? 1887 Alacorys (Octalacorys) aculeata (Ehrenberg) – Haeckel, p. 1373.

1971 Thyrsocyrtis tetracantha (Ehrenberg) – Moore, p. 741, pl. 4, fig. 3.
- 1974 Thyrsocyrtis tetracantha (Ehrenberg) Nigrini, p. 1069, pl. 2E, fig. 2.
- 1975 Thyrsocyrtis tetracantha (Ehrenberg) Ling, p. 730, pl. 11, fig. 19.
- 1977 Thyrsocyrtis tetracantha (Ehrenberg) Riedel and Sanfilippo, pl. 11, fig. 4 (part).
- 1978 Thyrsocyrtis tetracantha (Ehrenberg) Riedel and Sanfilippo, p. 81, pl. 10, fig. 8 (part).
- 1982 *Thyrsocyrtis (Pentalacorys) tetracantha* (Ehrenberg) Sanfilippo and Riedel, p. 176, pl. 1, fig. 12, pl. 3, fig. 10, text-fig. 1 (part).
- 1985 *Thyrsocyrtis (Pentalacorys) tetracantha* (Ehrenberg) Sanfilippo et al., p. 690, fig. 26.8a (part).
- 2009 *Podocyrtis tetracantha* Ehrenberg Ogane et al., pl. 90, figs. 4a, 4b, pl. 92, figs. 1a–2b (part).
- 2001 Thyrsocyrtis (Pentalacorys) tetracantha (Ehrenberg) De Wever et al., p. 280, fig. 185.4.
- 2009 Podocyrtis aculeata Ehrenberg Ogane et al., pl. 92, figs. 3a–3d.
- 2009 Podocyrtis pentacantha Ehrenberg Ogane et al., pl. 93, figs. 1a–1d.
- 2012a Thyrsocyrtis (Pentalacorys) tetracantha (Ehrenberg) Kamikuri et al., p. 104, pl. 3, figs. 4a, 4b.
- Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Family Theoperidae Haeckel, 1882 emend. Riedel, 1967b Genus Artophormis Haeckel, 1882

Type species.— Artophormis horrida Haeckel, 1887, p. 1458, pl. 75, fig. 2.

Artophormis ? barbadensis (Ehrenberg, 1874)

Plate II.20, Figure 2

- 1874 Calocyclas barbadensis Ehrenberg, p. 217.
- 1874 Thyrsocyrtis anthophora Ehrenberg, p. 260.
- 1876 Calocyclas barbadensis Ehrenberg Ehrenberg, p. 66, pl. 18, fig. 8.
- 1876 Thyrsocyrtis anthophora Ehrenberg Ehrenberg, p. 84, pl. 12, fig. 9.
- 1887 Artophormis barbadensis (Ehrenberg) Haeckel, p. 1459.
- 1887 Eucyrtidium (Artocyrtis) anthophorum (Ehrenberg) Haeckel, p. 1491.
- 1970 Artophormis barbadensis (Ehrenberg) Riedel and Sanfilippo, p. 532, pl. 13, fig. 5.
- 1971 Artophormis barbadensis (Ehrenberg) Riedel and Sanfilippo, p. 1592, pl. 3B, figs. 8, 9.
- ? 1971 Artophormis barbadensis (Ehrenberg) Moore, p. 742, pl. 5, fig. 9.
- 1974 Artophormis barbadensis (Ehrenberg) Johnson, p. 547, pl. 5, fig. 6.
- 1975 Artophormis barbadensis (Ehrenberg) Ling, p. 728, pl. 9, figs. 9, 10.
- 1977 Artophormis barbadensis (Ehrenberg) Riedel and Sanfilippo, pl. 10, fig. 12.
- 1985 Artophormis barbadensis (Ehrenberg) Sanfilippo et al., p. 666, figs. 12.1a, 12.1b.
- 2006 Artophormis barbadensis (Ehrenberg) Funakawa et al., p. 21, pl. P4, figs. 1a, 1b.
- 2009 Thyrsocyrtis anthophora Ehrenberg Ogane et al., pl. 1, figs. 7a–7e.
- 2009 Calocyclas barbadensis Ehrenberg Ogane et al., pl. 96, fig. 3a–3c.
- 2012 Artophormis barbadensis (Ehrenberg) Moore and Kamikuri, p. 5, pl. P1, fig. 2.
- 2015 Artophormis barbadensis (Ehrenberg) Kamikuri, pl. 9, figs. 14a, 14b.
- 2017 Artophormis barbadensis (Ehrenberg) de Souza et al., pl. 2, figs. 2a, 2b.

Genus Calocyclas Ehrenberg, 1847

Type species.— *Calocyclas turris* Ehrenberg, 1847b, p. 218 (unfigured); Ehrenberg, 1876, p. 66, pl. 18, fig. 7.

Calocyclas aphradia Sanfilippo and Blome, 2001

Plate II.20, Figure 3

1974 Theoperid gen. et sp. indet. Sanfilippo and Riedel, pl. 3, figs. 5, 6.

1979 Unidentified theoperid Sanfilippo and Riedel, pl. 1, fig. 12.

2001 Calocyclas aphradia Sanfilippo and Blome, p. 202, figs. 6d-6f.

2015 Calocyclas aphradia Sanfilippo and Blome – Kamikuri, pl. 9, fig. 15.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Calocyclas ? chrysallis (Sanfilippo and Blome, 2001) Plate II.20, Figure 6

1975 Sethocyrtis sp. Chen, p. 459, pl. 1, fig. 5 (part).

1992 Sethocyrtis sp. Takemura, p. 747, pl. 7, figs. 14, 15.

1995 Sethocyrtis ? spp. Strong et al., p. 209, fig. 11W.

1997 Sethocyrtis sp. Takemura and Ling, p. 114, pl. 1, fig. 11.

1997 Sethocyrtis sp. A Hollis et al., p. 65, pl. 6, fig. 7.

2001 Sethocyrtis chrysallis Sanfilippo and Blome, p. 206, figs. 6j–6n.

2015 Sethocyrtis chrysallis Sanfilippo and Blome – Kamikuri, pl. 11, figs. 14–15b.

2020 Sethocyrtis chrysallis Sanfilippo and Blome – Hollis et al., pl. 10, figs. 20a, 20b.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Calocyclas hispida (Ehrenberg, 1874)

Plate II.20, Figure 4

1874 Anthocyrtis hispida Ehrenberg, p. 216.

1876 Anthocyrtis hispida Ehrenberg – Ehrenberg, p. 64, pl. 8, fig. 2.

1882a Anthocyrtis hispida Ehrenberg - Bütschli, pl. 33, figs. 30a, 30b.

1882b Anthocyrtis hispida Ehrenberg – Bütschli, pl. 31, fig. 5.

1887 Anthocyrtidium (Anthocyrtonium) hispidum (Ehrenberg) – Haeckel, p. 1275.

1957a ? Anthocyrtidium hispidum (Ehrenberg) - Riedel, p. 260, pl. 63, fig. 7.

1970 Anthocyrtidium hispidum (Ehrenberg) – Cita et al., p. 403, pl. 1, fig. G.

1970 Cycladophora hispida (Ehrenberg) – Riedel and Sanfilippo, p. 529, pl. 10, fig. 9.

1971 *Cycladophora hispida* (Ehrenberg) – Riedel and Sanfilippo, p. 1593, pl. 3B, figs. 10, 11.

1971 Cycladophora hispida (Ehrenberg) – Moore, p. 741, pl. 4, figs. 6, 7.

1973 Calocyclas hispida (Ehrenberg) – Foreman, p. 434, pl. 1, figs. 12–15, pl. 9, fig. 18.

1974 Calocyclas hispida (Ehrenberg) – Nigrini, p. 1067, pl. 1F, figs. 5-8.

1974 Calocyclas hispida (Ehrenberg) – Johnson, p. 547, pl. 4, fig. 1.
1975 Calocyclas hispida (Ehrenberg) – Chen, p. 459, pl. 3, fig. 10.
1975 Calocyclas hispida (Ehrenberg) – Ling, p. 728, pl. 9, fig. 12.
1977 Calocyclas hispida (Ehrenberg) – Riedel and Sanfilippo, pl. 9, fig. 10.
1978 Calocyclas hispida (Ehrenberg) – Riedel and Sanfilippo, p. 65, pl. 3, fig. 6.
1986 Calocyclas hispida (Ehrenberg) – Riedel and Sanfilippo, pl. 2, fig. 10.
1993 Calocyclas hispida (Ehrenberg) – Hull, p. 12, pl. 7, fig. 1.
1901 Calocyclas hispida (Ehrenberg) – Sanfilippo and Plame p. 210.

not 2001 *Calocyclas hispida* (Ehrenberg) s.s. – Sanfilippo and Blome, p. 210, fig. 6g.

2001 Calocyclas hispida (Ehrenberg) var. A – Sanfilippo and Blome, p. 211, fig. 8m.

2006 Calocyclas hispida (Ehrenberg) – Funakawa et al., p. 22, pl. P5, figs. 4a, 4b.

2008 Calocyclas hispida (Ehrenberg) – Jackett et al., p. 48, pl. 2, fig. 1.

2009 Anthocyrtis hispida Ehrenberg – Ogane et al., pl. 2, figs. 7a–9c, pl. 50, figs. 4a, 4b.

2012 Calocyclas hispida (Ehrenberg) – Moore and Kamikuri, p. 5, pl. P1, figs. 7, 8.

2012 Calocyclas hispida (Ehrenberg) – Kamikuri and Wade, pl. 1, figs. 1a, 1b.

2012b Calocyclas hispida (Ehrenberg) - Kamikuri et al., p. 3, pl. P1, figs. 8a, 8b.

2015 Calocyclas hispida (Ehrenberg) – Kamikuri, pl. 8, figs. 9a–10b.

2017 Calocyclas hispida (Ehrenberg) – de Souza et al., pl. 2, figs. 5a, 5b.

2020 Calocyclas hispida (Ehrenberg) – Hollis et al., pl. 9, figs. 5a, 5b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Calocyclas turris Ehrenberg, 1874

Plate II.20, Figure 5

1874 Calocyclas Turris [sic] Ehrenberg, p. 218.

1874 Cycladophora stiligera Ehrenberg, p. 223.

1876 Calocyclas Turris [sic] Ehrenberg – Ehrenberg, p. 66, pl. 18, fig. 7.

1876 Cycladophora stiligera Ehrenberg – Ehrenberg, p. 68, pl. 18, fig. 3.

1882a Calocyclas Turris [sic] Ehrenberg – Bütschli, p. 534.

1882b Cycladophora stiligera Ehrenberg – Bütschli, pl. 30, fig. 16.

1882b Calocyclas Turris [sic] Ehrenberg – Bütschli, pl. 31, fig. 9.

1887 Cycladophora (Cyclamptidium) fenestrata Haeckel, p. 1380, pl. 68, fig. 2.

1887 Calocyclas (Calocyclissa) turris Ehrenberg – Haeckel, p. 1383.

1957b Calocyclas turris Ehrenberg – Riedel, p. 89, pl. 3, fig. 8, pl. 4, figs. 1, 2.

1957a Calocyclas turris Ehrenberg - Riedel, p. 261, pl. 62, fig. 6.

1970 Cycladophora turris (Ehrenberg) – Riedel and Sanfilippo, p. 529, pl. 13, figs. 3, 4.

1971 Cycladophora turris (Ehrenberg) – Moore, p. 741, pl. 4, fig. 8.

1974 Calocyclas turris Ehrenberg – Nigrini, p. 1067, pl. 2C, fig. 6.

1974 Calocyclas turris Ehrenberg – Johnson, p. 547, pl. 5, fig. 2.

1975 Calocyclas turris Ehrenberg – Ling, p. 728, pl. 9, fig. 13.

1977 Calocyclas turris Ehrenberg – Riedel and Sanfilippo, pl. 11, fig. 1.

1978 Calocyclas turris Ehrenberg – Riedel and Sanfilippo, p. 65, pl. 3, figs. 7, 8.

1984 Calocyclas turris Ehrenberg – Saunders et al., p. 412, pl. 5, fig. 12.

1986 Calocyclas turris Ehrenberg – Riedel and Sanfilippo, pl. 2, fig. 11, pl. 5, fig. 3.

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2001 Calocyclas turris Ehrenberg – Sanfilippo and Blome, 2001, p. 211, figs. 8i–8k.

2006 Calocyclas turris Ehrenberg – Funakawa et al., p. 22, pl. P5, figs. 5a, 5b.

2009 Calocyclas turris Ehrenberg - Ogane et al., pl. 94, figs. 1a-7d.

2009 Cycladophora stiligera Ehrenberg - Ogane et al., pl. 10, figs. 2a-2d.

2012 Calocyclas turris Ehrenberg – Moore and Kamikuri, p. 5, pl. P1, figs. 9, 10.

2015 Calocyclas turris Ehrenberg - Kamikuri, pl. 5, figs. 4, 6a, 6b.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Calocycloma Haeckel, 1887

Type species.— Calocyclas (Calocycloma) casta Haeckel, 1887, p. 1384, pl. 73, fig. 10.

Calocycloma ampulla (Ehrenberg, 1854a)

Plate II.20, Figure 8

1854a Eucyrtidium Ampulla [sic] Ehrenberg, pl. 36, figs. 15a, 15b.

1874 Eucyrtidium Ampulla [sic] Ehrenberg – Ehrenberg, p. 225.

1876 Eucyrtidium Ampulla [sic] Ehrenberg – Ehrenberg, p. 70, pl. 10, figs. 11, 12.

1887 Sethamphora (Dictyoprona) ampulla (Ehrenberg) – Haeckel, p. 1251.

1958 Sethamphora ampulla (Ehrenberg) – Göke, pl. 2, fig. 4.

1970 Calocycloma ? ampulla (Ehrenberg) – Riedel and Sanfilippo, p. 524, pl. 6, fig. 1.

1971 Calocycloma ? ampulla (Ehrenberg) – Riedel and Sanfilippo, p. 1593, pl. 3B, fig. 4.

1973 Calocycloma ampulla (Ehrenberg) – Foreman, p. 434, pl. 1, figs. 1–5, pl. 9, fig. 20.

1974 Calocycloma ampulla (Ehrenberg) – Nigrini, p. 1067, pl. 1F, figs. 1–4.

1974 Calocycloma ampulla (Ehrenberg) – Johnson, p. 548, pl. 5, fig. 8.

1975 Calocycloma ampulla (Ehrenberg) – Ling, p. 728, pl. 9, fig. 14.

1987 Calocycloma castum (Ehrenberg) – Nishimura, p. 721, pl. 3, fig. 2.

1995 Calocycloma castum (Ehrenberg) – Strong et al., p. 208, figs. 9V–9X.

2008 Calocycloma ampulla (Ehrenberg) – Jackett et al., p. 50, pl. 2, fig. 2.

2009 Eucyrtidium ampulla Ehrenberg – Ogane et al., pl. 60, figs. 1a–3d.

2012 Calocycloma ampulla (Ehrenberg) – Moore and Kamikuri, p. 5, pl. P1, fig. 12.

2015 Calocycloma ampulla (Ehrenberg) – Kamikuri, pl. 10, figs. 10a, 10b.

not 2015 Calocycloma ampulla (Ehrenberg) – Hollis et al., pl. 9, figs. 7a, 7b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Calocycloma castum (Haeckel, 1887)

Plate II.20, Figure 7

1887 Calocyclas (Calocycloma) casta Haeckel, p. 1384, pl. 73, fig. 10.

1970 Calocyclas casta Haeckel – Cita et al., p. 404, pl. 2, fig. H.

1973 Calocycloma castum (Haeckel) – Foreman, p. 434, pl. 1, figs. 7, 9, 10.

1978 Calocycloma castum (Haeckel) – Weaver and Dinkelman, p. 868, pl. 5, fig. 11.

- 1978 Calocycloma castum (Haeckel) Riedel and Sanfilippo, p. 66, pl. 1, fig. 9, pl. 3, fig. 15.
- 1987 Calocycloma castum (Haeckel) Nishimura, p. 721, pl. 3, fig. 1.
- 1998a Calocycloma castum (Haeckel) Sanfilippo and Nigrini, p. 272, pl. 13.1, fig. 10.

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2008 Calocycloma castum (Haeckel) – Jackett et al., p. 50, pl. 2, fig. 3.

2001 Calocycloma castum (Haeckel) – Sanfilippo and Blome, p. 211, figs. 8n, 8o.

2017 Calocycloma ampulla (Ehrenberg) – de Souza et al., pl. 2, fig. 6.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Genus *Cyrtocapsa* Haeckel, 1881 emend. O'Connor, 1997a *Type species.— Cyrtocapsa ovalis* Rüst, 1885, p. 320, pl. 42, fig. 11.

Cyrtocapsa osculum O'Connor, 1997a

Plate II.21, Figure 1

1973 Theocorys sp. aff. Theocorys ? spongoconus Kling – Foreman, p. 440, pl. 11, fig. 14.

1997a *Cyrtocapsa osculum* O'Connor, p. 75, pl. 1, figs. 15–17, pl. 2, figs. 1, 2, pl. 8, figs. 3–10.

? 2003 ? Cyrtocapsa osculum O'Connor - Sanfilippo and Fourtanier, p. 11, pl. P2, figs. 19, 20.

2020 Cyrtocapsa osculum O'Connor – Hollis et al., pl. 9, figs. 17a, 17b.

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Eusyringium Haeckel, 1882

Type species.— *Eusyringium (Eusyringartus) conosiphon* Haeckel, 1887, p. 1496, pl. 78, fig. 10.

Eusyringium lagena (Ehrenberg, 1874)

Plate II.20, Figure 12

1874 Lithopera Lagena [sic] Ehrenberg, p. 241.

1876 Lithopera Lagena [sic] Ehrenberg – Ehrenberg, p. 78, pl. 3, fig. 4.

1882a Anthocyrtis Lagena [sic] Ehrenberg -, p. 533.

1887 Sethocapsa lagena (Ehrenberg) – Haeckel, p. 1310, pl. 57, fig. 2.

1970 ? Eusyringium lagena (Ehrenberg) – Riedel and Sanfilippo, p. 527, pl. 8, figs. 5–7.

1971 ? Eusyringium lagena (Ehrenberg) – Moore, p. 741, pl. 4, fig. 9.

1973 Eusyringium lagena (Ehrenberg) – Foreman, p. 435, pl. 11, figs. 4, 5.

1973 Eusyringium lagena (Ehrenberg) – Nigrini, p. 1067, pl. 1F, figs. 13, 14.

1974 ? Eusyringium lagena (Ehrenberg) – Johnson, p. 548, pl. 5, fig. 3.

1975 Eusyringium lagena (Ehrenberg) – Ling, p. 729, pl. 9, fig. 21.

1977 Eusyringium lagena (Ehrenberg) – Riedel and Sanfilippo, pl. 9, fig. 4.

1978 Eusyringium lagena (Ehrenberg) – Weaver and Dinkelman, p. 869, pl. 5, figs. 2, 3.

1978 Eusyringium lagena (Ehrenberg) – Riedel and Sanfilippo, p. 68, pl. 5, fig. 8.

1986 Eusyringium lagena (Ehrenberg) – Riedel and Sanfilippo, pl. 2, fig. 18.

1995 Eusyringium lagena (Ehrenberg) – Strong et al., p. 208, fig. 11C.

1997 Eusyringium lagena (Ehrenberg) – Hollis et al., p. 62, pl. 5, figs. 15, 16.

1999 Eusyringium lagena (Ehrenberg) – Kozlova, p. 155, pl. 27, figs. 17, 18, pl. 32, fig. 16.

2009 Lithocampe lagena [sic] Ehrenberg – Ogane et al., pl. 2, figs. 10a, 10b.

2009 Lithopera lagena Ehrenberg – Ogane et al., pl. 23, figs. 1a–2c.

2012a Eusyringium lagena (Ehrenberg) - Kamikuri et al., p. 102, pl. 3, fig. 13.

2012b Eusyringium lagena (Ehrenberg) - Kamikuri et al., p. 3, pl. P1, figs. 5a, 5b.



Plate II.20. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic). (1) *Thyrsocyrtis (Pentalacorys) parvipes* (Ehrenberg, 1874): ODP 1260A-6R-2W, 55–57 cm. (2) *Artophormis ? barbadensis* (Ehrenberg, 1874): ODP 1260A-9R-3W, 55–57 cm. (3) *Calocyclas aphradia* Sanfilippo and Blome, 2001: ODP 1051A-11H-5W, 59–61 cm. (4) *Calocyclas hispida* (Ehrenberg, 1874): ODP 1260A-11R-5W, 55–57 cm. (5) *Calocyclas turris* Ehrenberg, 1874: ODP 1051A-4H-5W, 56–58 cm. (6) *Calocyclas ? chrysallis* (Sanfilippo and Blome, 2001): ODP 1260A-9R-3W, 55–57 cm. (7) *Calocycloma castum* (Haeckel, 1887): ODP 1260A-17R-3W, 55–57 cm. (8) *Calocycloma ampulla* (Ehrenberg, 1854a): ODP 1260A-8R-2W, 55–57 cm. (9–11) *Eusyringium tubulus* (Ehrenberg, 1854a) group: (9) ODP 1260A-6R-CC, 63–177 cm; (10) ODP 1260A-11R-7W, 55–57 cm; (11): ODP 1260A-8R-6W, 54–56 cm. (12) *Eusyringium lagena* (Ehrenberg, 1874): ODP 1260A-14R-CC, 63–177 cm. (13) *Eusyringium ? ventricosum* (Ehrenberg, 1874): ODP 1051A-8H-5W, 53–55 cm. All scale bars equal 50 μm.

2017 *Eusyringium lagena* (Ehrenberg) – de Souza et al., pl. 3, figs. 12a, 12b.
2020 *Eusyringium lagena* (Ehrenberg) – Hollis et al., pl. 10, fig. 14.
Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Eusyringium tubulus (Ehrenberg, 1854a) group Plate II.20, Figures 9–11

1854a Eucyrtidium Tubulus [sic] Ehrenberg, pl. 36, fig. 19.

1862 Rhopalocanium ornatum Ehrenberg – Bury, pl. 6, fig. 3 (part).

- 1862 *Eucyrtidium tubulous* [sic] Ehrenberg Bury, pl. 11, fig. 2.
- 1862 Eucyrtidium tubulus Ehrenberg Bury, pl. 22, fig. 8.
- 1874 Eucyrtidium fistuligerum Ehrenberg, p. 229.
- 1874 Eucyrtidium Sipho [sic] Ehrenberg, p. 233.
- 1874 Eucyrtidium Tubulus [sic] Ehrenberg Ehrenberg, p. 233.
- 1876 Eucyrtidium fistuligerum Ehrenberg Ehrenberg, p. 70, pl. 9, fig. 3.
- 1876 Eucyrtidium Sipho [sic] Ehrenberg Ehrenberg, p. 72, pl. 9, fig. 2.
- 1876 Eucyrtidium Tubulus [sic] Ehrenberg Ehrenberg, p. 72, pl. 9, fig. 6.

1882a Lithopera fistuligera (Ehrenberg) – Bütschli, p. 532.

- 1882a Lithopera Sipho [sic] (Ehrenberg) Bütschli, p. 532.
- 1882a Lithopera Tubulus [sic] (Ehrenberg) Bütschli, p. 532.
- 1882b Lithopera Sipho [sic] (Ehrenberg) Bütschli, pl. 31, fig. 3.
- 1887 Theosyringium tibia Haeckel, p. 1409, pl. 68, fig. 4.
- 1887 Pterocorys (Pterosyringium) tubulosa Haeckel, p. 1419, pl. 68, fig. 6.
- 1887 Eusyringium (Eusyringartus) conosiphon Haeckel, p. 1496, pl. 78, fig. 10.
- 1887 Eusyringium (Eusyringartus) pachysiphon Haeckel, p. 1496, pl. 78, fig. 11.
- 1887 Eusyringium (Eusyringartus) macrosiphon Haeckel, p. 1497, pl. 78, fig. 12.
- 1887 Eusyringium (Eusyringartus) sipho (Ehrenberg) Haeckel, p. 1497.

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1887 Eusyringium (Eusyringartus) fistuligerum (Ehrenberg) – Haeckel, p. 1498. 1957a ? Eusyringium aff. E. fistuligerum (Ehrenberg) – Riedel, p. 261, pl. 62, fig. 8. 1957b Eusyringium fistuligerum (Ehrenberg) – Riedel, p. 94, pl. 4, fig. 8. Eusvringium fistuligerum (Ehrenberg) – Riedel and Sanfilippo, p. 527, pl. 8, figs. 8, 9. 1970 1971 Eusyringium fistuligerum (Ehrenberg) - Riedel and Sanfilippo, p. 1594, pl. 3B, fig. 14. 1971 Eusyringium fistuligerum (Ehrenberg) – Moore, p. 741, pl. 4, figs. 10, 11. 1972 Eusyringium fistuligerum (Ehrenberg) – Petrushevskaya and Kozlova, p. 549, pl. 32, fig. 3. 1972 Eucyrtidium tubulus Ehrenberg – Petrushevskaya and Kozlova, p. 549, pl. 32, figs. 4, 5. 1973 Eusyringium fistuligerum (Ehrenberg) – Foreman, p. 435, pl. 11, fig. 6. 1974 Eusyringium fistuligerum (Ehrenberg) – Nigrini, p. 1067, pl. 1F, figs. 9–12, pl. 2C, fig. 9. 1974 Eusyringium fistuligerum (Ehrenberg) – Johnson, p. 548, pl. 5, fig. 4. 1975 Eusyringium fistuligerum (Ehrenberg) - Chen, p. 461, pl. 3, fig. 3. 1975 Eusyringium fistuligerum (Ehrenberg) – Ling, p. 728, pl. 9, figs. 19, 20. 1975 Eusyringium tubulus (Ehrenberg) – Ling, p. 729, pl. 9, fig. 22. Eusyringium fistuligerum (Ehrenberg) - Riedel and Sanfilippo, pl. 9, fig. 5. 1977 1977 ? Eusyringium fistuligerum (Ehrenberg) - Riedel and Sanfilippo, pl. 9, fig. 6. 1978 Eusyringium fistuligerum (Ehrenberg) – Weaver and Dinkelman, p. 869, pl. 5, fig. 1. 1978 Eusyringium fistuligerum (Ehrenberg) – Riedel and Sanfilippo, p. 68, pl. 5, figs. 6, 7. Eusyringium fistuligerum (Ehrenberg) – Sanfilippo et al., p. 672, figs. 17.2a-17.2c. 1985 Eusvringium fistuligerum (Ehrenberg) - Takemura, p. 746, pl. 7, figs. 5, 6. 1992 1995 Eusyringium fistuligerum (Ehrenberg) – Strong et al., p. 208, figs. 11D, 11E. 2000 Eusyringium fistuligerum (Ehrenberg) – Nigrini and Sanfilippo, p. 73, pl. 2, figs. 2, 3. Eusyringium fistuligerum (Ehrenberg) - Sanfilippo and Blome, p. 212, fig. 9a-9d. 2001 2001 Eusyringium conosiphon Haeckel – De Wever et al., p. 282, fig. 187.1. 2001 Pterosyringium tubulosum (Haeckel) – De Wever et al., p. 282, fig. 187.4. 2006 Eusyringium fistuligerum (Ehrenberg) – Funakawa et al., p. 35, pl. P12, figs. 1a-3. 2009b Eusyringium fistuligerum (Ehrenberg) - Suzuki et al., p. 262, pl. 22, figs. 14a, 14b. Eucyrtidium fistuligerum Ehrenberg - Ogane et al., pl. 47, figs. 3a-3f. 2009 2009 Eucyrtidium sipho Ehrenberg – Ogane et al., pl. 23, figs. 7a–7d, pl. 47, figs. 1a–1f, 4a, 4b, 6a, 6b. 2009 Eucyrtidium tubulus Ehrenberg – Ogane et al., pl. 47, figs. 2a, 2b, 5a–5d. 2012 Eusyringium fistuligerum (Ehrenberg) – Moore and Kamikuri, p. 8, pl. P5, fig. 1. 2012b Eusyringium fistuligerum (Ehrenberg) – Kamikuri et al., p. 3, pl. Pl, figs. 4a, 4b. 2015 Eusyringium fistuligerum (Ehrenberg) group – Kamikuri, pl. 12, figs. 22–24. 2017 Eusyringium fistuligerum (Ehrenberg) – de Souza et al., pl. 3, figs. 11a, 11b. Eusyringium fistuligerum (Ehrenberg) – Hollis et al., pl. 10, figs. 11–13. 2020 2021 Eusyringium fistuligerum (Ehrenberg) – de Souza et al., p. 15, pl. 3, fig. 5. Remarks. The great morphological disparity observed in Eusyringium tubulus (Ehrenberg) and E. fistuligerum (Ehrenberg), with a gradient of specimens displaying an intermediate morphology between these two morphospecies, leads us to consider them as a group of closely related species.

Eusyringium ? ventricosum (Ehrenberg, 1874)

Plate II.20, Figure 13

1874 Lithomelissa ventricosa Ehrenberg, p. 241.

1876 Lithomelissa ventricosa Ehrenberg – Ehrenberg, p. 78, pl. 3, fig. 11.

1887 Micromelissa ventricosa (Ehrenberg) – Haeckel, p. 1236.

2009 Lithomelissa ventricosa Ehrenberg - Ogane et al., pl. 96, figs. 1a-2d.

2012 Lychnocanoma turgidum Ehrenberg – Moore and Kamikuri, p. 9, pl. P7, fig. 4.

2015 Lithomelissa ? ventricosa Ehrenberg – Kamikuri, pl. 11, figs. 9a, 9b.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Genus *Rhopalocanium* Ehrenberg, 1846 *Type species.*—*Rhopalocanium ornatum* Ehrenberg, 1847, p. 55, fig. 3.

Rhopalocanium ornatum Ehrenberg, 1847

Plate II.21, Figure 2

- 1847 Rhopalocanium ornatum Ehrenberg, fig. 3.
- 1854a Lithornithium Loxia [sic] Ehrenberg, pl. 36, fig. 8.
- 1854a Rhopalocanium ornatum Ehrenberg Ehrenberg, pl. 36, fig. 9.
- 1862 Rhopalocanium ornatum Ehrenberg Bury, pl. 6, figs. 1, 2 (part).
- 1874 Lithornithium Loxia [sic] Ehrenberg Ehrenberg, p. 242.
- 1874 Lithornithium Luscinia [sic] Ehrenberg, p. 242.
- 1874 Rhopalocanium ornatum Ehrenberg Ehrenberg, p. 256.
- 1876 Lithornithium Loxia [sic] Ehrenberg Ehrenberg, p. 78, pl. 4, fig. 8.
- 1876 Lithornithium Luscinia [sic] Ehrenberg Ehrenberg, p. 78, pl. 4, fig. 9
- 1876 Rhopalocanium ornatum Ehrenberg Ehrenberg, p. 82, pl. 17, fig. 8.
- 1882b Lithornithium Luscinia [sic] Ehrenberg Bütschli, pl. 30, fig. 9.
- 1887 Theopera luscinia (Ehrenberg) Haeckel, p. 1358.
- 1887 Theopera cortina Haeckel, p. 1358, pl. 67, fig. 8.
- 1887 Rhopalatractus fenestratus (Haeckel) Haeckel, p. 1361, pl. 68, fig. 12.
- 1887 Artopera loxia (Ehrenberg) Haeckel, 1452.
- 1970 Gen. et sp. indet. Riedel and Sanfilippo, pl. 10, fig. 1.
- 1972 *Rhopalocanium ornatum* Ehrenberg Petrushevskaya and Kozlova, p. 552, pl. 27, figs. 13, 14.
- 1973 Rhopalocanium ornatum Ehrenberg Foreman, p. 439, pl. 2, figs. 8–10, pl. 12, fig. 3.
- 1974 Rhopalocanium ornatum Ehrenberg Nigrini, p. 1068, pl. 1H, figs. 6–10.
- 1974 Rhopalocanium ornatum Ehrenberg Johnson, p. 549, pl. 5, fig. 18.
- 1975 Rhopalocanium ornatum Ehrenberg Ling, p. 729, pl. 11, figs. 1–3.
- 1977 Rhopalocanium ornatum Ehrenberg Riedel and Sanfilippo, pl. 9, fig. 15.
- 1978 Theoperid gen. et sp. indet. Weaver and Dinkelman, pl. 9, fig. 12 (part).

- 1978 Rhopalocanium ornatum Ehrenberg Riedel and Sanfilippo, p. 72, pl. 9, fig. 5.
- 2001 Rhopalocanium ornatum Ehrenberg Sanfilippo and Blome, p. 217, figs. 10o, 10p.
- 2001 Rhopalocanium ornatum Ehrenberg De Wever et al., p. 282, fig. 187.5.
- 2001 Lithornithium loxia Ehrenberg De Wever et al., p. 282, fig. 187.6.
- 2009 Lithocorythium loxia Ehrenberg Ogane et al., pl. 24, figs. 1a–1d, 2a, 2b, 3a–3e.
- 2009 Lithornithium luscinia Ehrenberg Ogane et al., pl. 46, figs. 1a–1e.
- 2012 Rhopalocanium ornatum Ehrenberg Moore and Kamikuri, p. 10, pl. P7, fig. 13.
- 2015 Rhopalocanium ornatum Ehrenberg Kamikuri, pl. 1, figs. 2–3b.
- 2020 Rhopalocanium ornatum Ehrenberg Hollis et al., pl. 14, figs. 19, 20.

Rhopalocanium sphinx (Ehrenberg, 1874)

Plate II.21, Figure 3

- 1874 Pterocanium ? Sphinx [sic] Ehrenberg, p. 255.
- 1876 Pterocanium ? Sphinx [sic] Ehrenberg Ehrenberg, p. 82, pl. 17, fig. 5.
- 1882b Rhopalocanium Bombus [sic] (Ehrenberg) Bütschli, pl. 30, fig. 10.
- 1887 Pteropilium sphinx (Ehrenberg) Haeckel, p. 1443.
- 1972 Stichopilidium sphinx (Ehrenberg) Petrushevskaya and Kozlova, p. 552, pl. 27, fig. 1.
- 1977 Pteropilium sphinx (Ehrenberg) Riedel and Sanfilippo, pl. 7, fig. 10.
- not 2006 *Stichopilidium sphinx* Ehrenberg Funakawa et al., p. 31, pl. P11, figs. 1a, 1b.
- 2009 *Pterocanium sphinx* Ehrenberg Ogane, pl. 1, fis. 4a–4d, pl. 46, figs. 2a–3c, pl. 97, figs. 4a–4d.
- 2015 Stichopilidium sphinx Ehrenberg Kamikuri, pl. 5, figs. 5a, 5b.

Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Genus Pteropilium Haeckel, 1882

Type species.— Pteropilium (Clathropilium) stratiotes Haeckel, 1887, p. 1326, pl. 70, fig. 9.

Pteropilium aff. contiguum (Ehrenberg, 1874)

Plate II.21, Figure 4

- 1874 Pterocanium contiguum Ehrenberg, p. 255.
- 1876 Pterocanium contiguum Ehrenberg Ehrenberg, p. 82, pl. 17, fig. 7.
- 1882a Pterocyrtidium barbadense Ehrenberg Bütschli, pl. 33, figs. 28a, 28b.
- 1882b Pterocyrtidium barbadense Ehrenberg Bütschli, pl. 31, figs. 2a, 2b.
- 1887 Pterocanium (Pterocanarium) contiguum Ehrenberg Haeckel, p. 1330.
- 1887 Lithornithium ciconia Haeckel, p. 1354, pl. 67, fig. 3.
- 1972 *Pteropilium* ? sp. aff. *Pterocanium contiguum* Ehrenberg group Petrushevskaya and Kozlova, p. 553, pl. 29, figs. 8–10.
- 1977 Pterocanium contiguum Ehrenberg Riedel and Sanfilippo, pl. 4, fig. 7.
- 1991 Pteropilium sp. aff. Pterocanium contiguum (Ehrenberg) Caulet, p. 539, pl. 2, fig. 11.
- 1993 Pterocanium ? contiguum Ehrenberg Vitukhin, pl. 23, fig. 3.

- 1999a Pteropilium sp. O'Connor, p. 36, pl. 9, fig. 39.
- 1999 Pterocanium contiguum Ehrenberg Kozlova, p. 175, pl. 24, fig. 7.
- 2005 *Pteropilium* sp. aff. *Pterocanium contiguum* (Ehrenberg) Nigrini et al., p. 47, pl. P5, fig. 2.
- 2009 Pterocanium contiguum Ehrenberg Ogane et al., pl. 47, figs. 8a-8e.
- not 2012 *Pterocanium* sp. aff. *Pterocanium contiguum* Ehrenberg Moore and Kamikuri, p. 10, pl. P7, fig. 15.
- 2020 Pteropilium aff. contiguum (Ehrenberg) Hollis et al., pl. 14, figs. 16, 17 (part).
- 2021 Pteropilium aff. contiguum (Ehrenberg) de Souza et al., p. 15, pl. 3, figs. 7a, 7b.

Pteropilium ? melitta Haeckel, 1887

Plate II.21, Figure 5

- 1862 Rhopalocanium ornatum Ehrenberg Bury, pl. 6, fig. 4 (part).
- 1887 Pterocorys (Pterocyrtidium) melitta Haeckel, p. 1319.
- 1972 Pteropilium ? sp. Petrushevskaya and Kozlova, pl. 29, fig. 4.
- 1978 Theoperid gen. et sp. indet. Weaver and Dinkelman, pl. 1, fig. 3 (part).
- 1986 Pterocorys melitta Haeckel Göke, fig. 3.3.
- Remarks. The combination used here is derived from O'Dogherty et al. (2021).

Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

Genus Theocorys Haeckel, 1881

Type species.— Theocorys morchellula Rüst, 1885, p. 308, pl. 37, fig. 6.

Theocorys anaclasta Riedel and Sanfilippo, 1970

Plate II.21, Figure 6

- 1970 Theocorys anaclasta Riedel and Sanfilippo, p. 530, pl. 10, figs. 2, 3.
- 1971 Theocorys anaclasta Riedel and Sanfilippo Moore, p. 742, pl. 2, fig. 1.
- 1973 Theocorys anaclasta Riedel and Sanfilippo Foreman, p. 440, pl. 5, figs. 14, 15.
- 1977 Theocorys anaclasta Riedel and Sanfilippo Riedel and Sanfilippo, pl. 6, fig. 1.
- 1978 *Theocorys* sp. aff. *Theocorys anaclasta* Riedel and Sanfilippo Johnson, p. 784, pl. 2, figs. 12, 13.
- 1978 *Theocorys anaclasta* Riedel and Sanfilippo Weaver and Dinkelman, p. 873, pl. 7, figs. 1–3.
- 1978 *Theocorys anaclasta* Riedel and Sanfilippo Riedel and Sanfilippo, p. 76, plate 1, figs 6–8.
- 1978 *Theocorys* sp. aff. *Theocorys anaclasta* Riedel and Sanfilippo Foreman, p. 784, pl. 2, figs. 12, 13.
- 1985 Theocorys anaclasta Riedel and Sanfilippo Sanfilippo et al., p. 683, fig. 24.1a-24.1d.
- 2012a *Theocorys anaclasta anaclasta* Riedel and Sanfilippo Kamikuri et al., p. 94, pl. 1, figs. 7, 8.



Plate II.21. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic) and ODP Site 1051 (Blake Nose, western North Atlantic). (1) *Cyrtocapsa osculum* O'Connor, 1997a: ODP 1051A-8H-5W, 53–55 cm. (2) *Rhopalocanium ornatum* Ehrenberg, 1847: (1) ODP 1260A-6R-4W, 55–57 cm. (3) *Rhopalocanium sphinx* (Ehrenberg, 1874): ODP 1260A-6R-1W, 55–57 cm. (4) *Pteropilium* aff. *contiguum* Ehrenberg, 1874: ODP 1260A-9R-4W, 55–57 cm. (5) *Pteropilium*? *melitta* Haeckel, 1887: ODP 1051A-14H-5W, 52–54 cm. (6) *Theocorys anaclasta* Riedel and Sanfilippo, 1970: ODP 1260A-14R-1W, 55–57 cm. (7, 8) *Theocorys anapographa* Riedel and Sanfilippo, 1970: (7) ODP 1260A-14R-1W, 55–57 cm. (8): ODP 1260A-14R-CC, 63–177 cm. (9) *Theocorys anapographa* Riedel and Sanfilippo, 1970 var. A: ODP 1260A-6R-2W, 55–57 cm; (10, 11) *Theocorys ? scolopax* (Ehrenberg, 1874): (10) ODP 1260A-13R-4W, 55–57 cm;

(11) ODP 1260A-13R-4W, 55–57 cm. (12) *Valkyria pukapuka* O'Connor, 1997a: ODP 1051A-13H-2W, 52–54 cm. All scale bars equal 50 μm.

- 2012a Theocorys anaclasta clasta Riedel and Sanfilippo Kamikuri et al., p. 94, pl. 1, figs. 1a-4b.
- Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

Theocorys anapographa Riedel and Sanfilippo, 1970

Plate II.21, Figures 7, 8

- ? 1887 Lophoconus rhinoceros Haeckel, p. 1405, pl. 69, fig. 2.
- 1970 Theocorys anapographa Riedel and Sanfilippo, p. 530, pl. 10, fig. 4.
- 1971 Theocorys anapographa Riedel and Sanfilippo Moore, p. 742, pl. 2, fig. 1.
- 1973 Theocorys anapographa Riedel and Sanfilippo Dinkelman, pl. 2, fig. 2.
- 1973 *Theocorys anapographa* Riedel and Sanfilippo Foreman, p. 440, pl. 5, figs. 9, 10.
- 1974 Theocorys anapographa Riedel and Sanfilippo Nigrini, p. 1069, pl. 1I, figs. 9–13, pl. 2D, fig. 7.
- 1977 Theocorys anapographa Riedel and Sanfilippo Riedel and Sanfilippo, pl. 8, fig. 12.
- 1978 *Theocorys anapographa* Riedel and Sanfilippo Weaver and Dinkelman, p. 873, pl. 7, figs. 4, 5.
- 1978 Theocorys anapographa Riedel and Sanfilippo Riedel and Sanfilippo, p. 76, pl. 9, fig.
 15.
- 1999 Calocyclura sphaerophilum (Ehrenberg) Kozlova, pl. 31, figs. 7, 12, 17.
- 2012a *Theocorys anapographa* Riedel and Sanfilippo Kamikuri et al., p. 104, pl. 1, figs. 5a, 5b.
- ? 2020 Theocorys anapographa Riedel and Sanfilippo Hollis et al., pl. 11, figs. 4, 5.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Theocorys anapographa Riedel and Sanfilippo, 1970 var. A

Plate II.21, Figure 9

- 1973 *Theocorys anapographa* Riedel and Sanfilippo Riedel and Sanfilippo, p. 740, pl. 3, figs. 10, 11.
- 1975 Theocorys anapographa Riedel and Sanfilippo Ling, p. 730, pl. 11, figs. 11, 12.
- 2001 *Theocorys anapographa* Riedel and Sanfilippo var. A Sanfilippo and Blome, p. 219, figs. 11m, 11n.
- 2015 Theocorys sp. A Kamikuri, pl. 10, figs. 17a, 17b.

? 2015 Theocorys sp. B Kamikuri, pl. 10, figs. 18a, 18b.

2020 Theocorys anapographa Riedel and Sanfilippo var. A – Hollis et al., pl. 11, figs. 6a, 6b.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic) and ODP Site 1051 (Blake Nose; western north Atlantic).

Chapter II - Progress on middle Eocene radiolarian biodiversity

Theocorys ? scolopax (Ehrenberg, 1874)

Plate II.21, Figures 10, 11

1874 *Eucyrtidium Scolopax* [sic] Ehrenberg, p. 232.

1876 Eucyrtidium Scolopax [sic] Ehrenberg – Ehrenberg, p. 72, pl. 9, fig. 5.

1882a Eucyrtidium Scolopax [sic] Ehrenberg – Bütschli, p. 528.

1887 Theocorys (Theocoronium) scolopax (Ehrenberg) – Haeckel, p. 1416.

? 1977 ? Phormocyrtis embolum (Ehrenberg) - Riedel and Sanfilippo, pl. 8, fig. 13.

2002 Theocyrtis scolopax (Ehrenberg) – Popova et al., p. 50, fig. 14G.

2009 Eucyrtidium scolopax Ehrenberg – Ogane et al., pl. 58, figs. 3a-3f.

Occurrence. ODP Site 1260 (Demerara Rise; western equatorial Atlantic).

? Genus Valkyria O'Connor, 1997a

Type species.— Valkyria pukapuka O'Connor, 1997a, p. 74, pl. 2, figs. 15, 16.

Valkyria pukapuka O'Connor, 1997a

Plate II.21, Figure 12

1997a *Valkyria pukapuka* O'Connor, p. 74, pl. 2, figs. 15, 16, pl. 3, figs. 1, 2, pl. 7, figs. 11, 12, pl. 8, figs. 1, 2.

2015 *Valkyria pukapuka* O'Connor – Kamikuri, pl. 2, figs. 8a, 8b, pl. 3, figs. 7a, 7b. Occurrence. ODP Site 1051 (Blake Nose; western north Atlantic).

II.3. New radiolarian species from ODP Site 1260 (western equatorial Atlantic) and ODP Site 1051 (western North Atlantic)

This subchapter consists of two taxonomic papers published in the Journal of Paleontology. The first paper, titled **"Progress in understanding middle Eocene nassellarian (Rhizaria, Polycystinea) diversity; new insights from the western equatorial Atlantic Ocean"**, reports the description of 15 new nassellarian species from ODP Site 1260 (western equatorial Atlantic) and is available online at DOI: <u>https://doi.org/10.1017/jpa.2022.82</u>. The second paper, titled **"New middle Eocene radiolarian species (Rhizaria, Polycystinea) from Blake Nose, subtropical western North Atlantic Ocean"**, describes 21 new polycystine radiolarian species from ODP Site 1051 (western North Atlantic) and is currently in the final stages of production.

II.3.1. Progress in understanding middle Eocene nassellarian (Rhizaria, Polycystinea) diversity; new insights from the western equatorial Atlantic Ocean

Mathias Meunier* and Taniel Danelian

Univ. Lille, CNRS, UMR 8198 – Evo-Eco-Paleo, F-59000 Lille, France <mathias.meunier@univ-lille.fr>

*Corresponding author

Abstract.— Middle Eocene deep-sea sedimentary sequences cored at Ocean Drilling Program Site 1260 (Leg 207; equatorial Atlantic) yielded diverse and abundant radiolarian faunas that are conducive to biostratigraphic and paleoceanographic research, as well as to the study of radiolarian diversity dynamics during this epoch of dramatic climate change. However, many of the species found in these sediments have not been formally described and are therefore neglected in most biodiversity surveys. In an effort to improve the taxonomic resolution of middle Eocene radiolarians, 15 new nassellarian species are described and illustrated. The species are: Cymaetron? dilatatus n. sp., Eucyrtidium levisaltatrix n. sp. (Eucyrtidiidae), Siphocampe pollen n. sp., Spirocyrtis ? renaudiei n. sp. (Artostrobiidae), Pterocyrtidium eep n. sp. (Rhopalosyringiidae), Petalospyris cometa n. sp., Petalospyris castanea n. sp. (Cephalospyrididae), Velicucullus armatus n. sp. (Theophormididae), Lychnocanium nimrodi n. sp. (Lithochytrididae), Aphetocyrtis zamenhofi n. sp., Aphetocyrtis? columboi n. sp., Aphetocyrtis ? spheniscus n. sp. (Lophocyrtiidae), Albatrossidium regis n. sp., Albatrossidium annikasanfilippoae n. sp. and Phormocyrtis lazari n. sp. (Pterocorythidae). Stratigraphic range data are provided for each new species, as well as the orbitally tuned ages for their first and last occurrences. In addition to these new species, we also illustrated and documented the stratigraphic distribution of four species described in early radiolarian studies, which have rarely been observed since.

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II.3.1.1. Introduction

Reconstructing the paleodiversity dynamics of Eocene tropical radiolarians is hampered primarily by our incomplete taxonomic knowledge of these organisms. Indeed, despite being studied for nearly two centuries (Ehrenberg, 1839), we are still far from having fully documented and described all the species preserved in the Eocene fossil record. The first major contribution to the taxonomy of Eocene radiolarians is attributed to Ehrenberg (1874), who described 265 new species from middle Eocene to lower Oligocene pelagic sequences that crop out today on the Barbados Island (Saunders, 1984; Ogane et al., 2009), 85 of which were subsequently illustrated in Ehrenberg (1876). In his famous monograph, Haeckel (1887) also introduced ~200 middle Eocene radiolarian species from Barbados onshore samples, including illustrations for only half of them. In addition to this body of taxonomic work, several authors punctually published new species and genera throughout the late 19th century (Bury, 1862; Bütschli, 1882a, 1882b; Carter, 1893, 1895, 1896a, 1896b, 1896c, 1896d, 1896e; Sutton, 1896a, 1896b, 1896c, 1896d). However, many species described in these early radiolarian studies have not been observed since, and there are still many uncertainties about their stratigraphic range, biogeographic distribution, and the precise extent of their intraspecific variation (Ogane et al., 2009).

Although little taxonomic progress was achieved on tropical Eocene radiolarians during the first half of the 20th century (e.g., Brandt, 1935), two important publications by Clark and Campbell (1942, 1945) marked this period. They were devoted to the study of middle to late Eocene radiolarian faunas from three Californian shale formations and resulted in the description of 157 new species (Blueford, 1988). The subsequent advent of scientific ocean drilling in the 1960s and 1970s marked a turning point in the history of Cenozoic radiolarian taxonomy. Increased recovery of deep-sea sediments allowed extensive studies of radiolarian assemblages around the world and renewed interest in describing radiolarian diversity (e.g., Riedel and Sanfilippo, 1970, 1971, 1978; Petrushevskaya and Kozlova, 1972; Foreman, 1973; Sanfilippo and Riedel, 1973). The primary goal of these studies was biostratigraphy, and thus they tended to focus on a limited number of stratigraphically useful species that are often abundant in the Eocene fossil record. As a consequence, many rare morphotypes of no biostratigraphic value, or those belonging to morphologically complex taxa, remained undescribed and were neglected in most taxonomic surveys. Concurrently with this biostratigraphic work, some nassellarian families have also been the subject of more detailed taxonomic studies, leading to the establishment of several evolutionary lineages (e.g., Nigrini, 1977; Sanfilippo and Riedel, 1982, 1992; Sanfilippo and Caulet, 1998).

In an effort to improve the taxonomic resolution of tropical Eocene radiolarians, 15 new nassellarian species belonging to 11 genera and seven families are described and illustrated from the upper middle Eocene sequences drilled at Ocean Drilling Program Site 1260 (Leg 207; western Atlantic Ocean). Amongst the undescribed morphotypes encountered in this material, we chose to describe the most abundant and morphologically distinct ones, to best circumscribe the morphological diversity of each new species. As a consequence, a number of potentially new species that are represented by only one or a few isolated specimens have been excluded from this analysis. Information is also provided on the stratigraphic range of each new species, as well as the orbitally tuned ages for the first and last occurrences of most of them. Relationships with previously described species are also suggested. Finally, three species described in early radiolarian studies and rarely observed since are illustrated.

II.3.1.2. Materials and methods

Materials.— All samples examined in this study were collected from Leg 207 ODP Site 1260 (9°15'N, 54°32'W), located on the northwestern slope of Demerara Rise, a continental shelf off Suriname and French Guiana (Figure II.1). Today, the site lies between 9° and 10°N latitude,

but according to paleomagnetic data, its position during the middle Eocene is estimated to be paleolatitude ~1°N (Suganuma and Ogg, 2006). Two holes (1260A and 1260B) recovered Paleogene sediments at a water depth of 2549 mbsf, allowing the study of an expanded and nearly continuous sedimentary sequence extending from the lower Albian to the middle Eocene (Shipboard Scientific Party, 2004). The middle Eocene interval at ODP Site 1260 is composed of greenish-white foraminifer-nannofossil chalk that contain abundant and well-preserved radiolarians, and diatoms (Shipboard Scientific Party, 2004; Danelian et al., 2005, 2007; Renaudie et al., 2010). In this study, we focused on the richest radiolarian interval; a 91.72 m thick sequence ranging from 43.77 Ma to 39.83 Ma, corresponding to the late middle Eocene (middle Lutetian to middle Bartonian). A total of 55 samples were selected from 10 cores (15R to 6R) from Hole 1260A, resulting in an average inter-sample spacing of ~1.67 m and an average age resolution of ~71,600 years.



Figure II.1. Middle Eocene (ca. 40 Ma) paleogeographic map showing the location of Demerara Rise (ODP Leg 207) in the western equatorial Atlantic Ocean. The square shows the detailed location of ODP Site 1260 on a modern bathymetric map (modified after Wang et al., 2016). Paleogeographic reconstruction based on the ODSN Plate Tectonic Reconstruction Service (http://www.odsn.de/odsn/services/paleomap/paleomap.html).

A well-defined cyclostratigraphic framework has been developed for ODP Site 1260 using X-ray fluorescence core scanning (Westerhold and Röhl, 2013). Astrochronological calibration is available throughout the sequence at every 2 cm of sediment, allowing each sample to be dated with a high accuracy. Where calibration was not available for portions of Hole 1260A, the absolute ages of the corresponding samples were estimated based on the calibrated ages provided for samples at the same depth in Hole 1260B.

Methods.— Samples were processed according to the protocol described in Sanfilippo et al. (1985). First of all, ~1 cm² of untreated sediment was placed in a beaker and soaked in ~10 % hydrogen peroxide (H₂O₂) and ~30 % hydrochloric acid (HCl) to remove organic matter and carbonate fraction, respectively. The resulting residues were then washed through a 45 μ m sieve to remove clay, small diatom frustules, and radiolarian fragments. We chose this relatively fine mesh to improve the recovery of smaller radiolarian species that may be lost when using larger meshes. One to four slides were then prepared for each sample using a few mg of cleaned residue evenly distributed on a coverslip according to the preparation method described by Witkowski et al. (2012). When dry, the coverslips were mounted onto standard glass slides using Norland Optical Adhesive 61 (refractive index 1.56).

All slides were systematically examined for radiolarians by using a Zeiss Axio Imager.A2 as a transmitted light microscope equipped with a Zeiss AxioCam ERc5s digital camera. For each specimen illustrated, a series of five to ten images taken at different focus distances were z-stacked using Helicon Focus v.7.6.6 (HeliconSoft) to produce a fully focused composite image.

In the following section, dimensions are based on a maximum number of specimens observed at different depths in the sedimentary sequence, in order to represent, at best, the intraspecific variation throughout the stratigraphic range of the species. Measurements were made directly on the specimen pictures, using the image processing and analysis software ImageJ (Schneider et al., 2012).

The radiolarian biozonation used here is that introduced by Riedel and Sanfilippo (1970, 1971, 1978) and Sanfilippo et al. (1985), and recently refined by Meunier and Danelian (2022), with the introduction of some subzones. The stratigraphic occurrences of the species are shown in Figure II.2, and the associated bioevents are summarized in Table II.1, along with their tuned ages at ODP Site 1260.



Figure II.2. Range chart of 19 selected radiolarian species from the middle Eocene of ODP Site 1260 (Demerara Rise, western equatorial Atlantic). Geomagnetic timescale according to calibration of Suganuma and Ogg (2006), and radiolarian biozonations according to Meunier and Danelian (2022).

Repositories and institutional abbreviations.— All holotypes and figured specimens (Plates II.22–II.26) are housed in the public paleontological collection of the University of Lille (USTL), France. Specimens are indexed by hole number, core number, section number, interval depth, and England finder coordinates.

Table II.1. Summary of first occurrences (FO) and last occurrences (LO) at ODP Site 1260, drilled on Demerara Rise in the western equatorial Atlantic. Estimated ages and revised meter composite depths (rmcd) are from Westerhold and Röhl (2013).

ODP Site 1260			Tuned age (Ma)	
Radiolarian bioevents	Core, section, interval (cm) Base/top	Depth (rmcd) Base/top	Base/top	Midpoint
FO Petalospyris cometa n. sp.	6R-5W, 55–57/6R-4W, 55–57	44.75/43.25	40.11/40.04	40.08
LO Spirocyrtis ? renaudiei n. sp.	6R-5W, 55–57/6R-4W, 55–57	44.75/43.25	40.11/40.04	40.08
FO Aphetocyrtis ? columboi n. sp.	7R-6W, 54–56/7R-4W, 54–56	56.04/53.04	40.73/40.57	40.65
LO Eucyrtidium levisaltatrix n. sp.	7R-6W, 54–56/7R-4W, 54–56	56.04/53.04	40.73/40.57	40.65
LO Aphetocyrtis ? spheniscus n. sp.	8R-3W, 54–56/7R-6W, 54–56	61.24/56.04	40.96/40.73	40.85
LO Lychnocanium nimrodi n. sp.	8R-6W, 54–56/8R-5W, 54–56	65.74/64.24	41.12/41.07	41.10
LO Pterocyrtidium eep n. sp.	9R-1W, 55–57/8R-6W, 54–56	66.85/65.74	41.18/41.12	41.15
FO Lychnocanium nimrodi n. sp.	9R-5W, 55–57/9R-4W, 55–57	72.85/71.35	41.40/41.34	41.37
FO Spirocyrtis ? renaudiei n. sp.	9R-5W, 55–57/9R-4W, 55–57	72.85/71.35	41.40/41.34	41.37
FO Eucyrtidium levisaltatrix n. sp.	9R-7W, 55–57/9R-6W, 55–57	75.85/74.35	41.53/41.46	41.50
FO Petalospyris castanea n. sp.	9R-7W, 55–57/9R-6W, 55–57	75.85/74.35	41.53/41.46	41.50
LO Velicucullus armatus n. sp.	9R-7W, 55–57/9R-6W, 55–57	75.85/74.35	41.53/41.46	41.50
FO Phormocyrtis lazari n. sp.	10R-1W, 55–57/9R-7W, 55–57	77.33/75.85	41.59/41.53	41.56
LO Albatrossidium regis n. sp.	10R-5W, 55–57/10R-3W, 55–57	83.33/80.33	41.85/41.73	41.79
LO Corythomelissa galea (Ehrenberg) n. comb.	11R-3W, 55–57/11R-2W, 55–57	89.55/88.05	42.12/42.05	42.09
LO Aphetocyrtis zamenhofi n. sp.	14R-1W, 55–57/13R-6W, 54–56	116.02/112.74	43.16/43.06	43.11
FO Cymaetron ? dilatatus n. sp.	14R-2W, 55–57/14R-1W, 55–57	117.52/116.02	43.21/43.16	43.19
FO Pterocyrtidium eep n. sp.	14R-2W, 55–57/14R-1W, 55–57	117.52/116.02	43.21/43.16	43.19
FO Corythomelissa galea (Ehrenberg) n. comb.	14R-5W, 55–57/14R-4W, 55–57	122.02/120.52	43.39/43.33	43.36
FO Podocyrtis (L.) puellasinensis Ehrenberg	14R-5W, 55–57/14R-4W, 55–57	122.02/120.52	43.39/43.33	43.36
FO Albatrossidium annikasanfilippoae n. sp.	14R-7W, 55–57/14R-6W, 55–57	125.02/123.52	43.51/43.45	43.48
FO Aphetocyrtis ? spheniscus n. sp.	15R-1W, 55–57/14R-7W, 55–57	125.97/125.02	43.55/43.51	43.53
FO Siphocampe pollen n. sp.	15R-2W, 55–57/15R-1W, 55–57	127.47/125.97	43.63/43.55	43.59

II.3.1.3. Systematic paleontology

The higher-level classification used in this study is based on the most recent and comprehensive radiolarian classification provided by Suzuki et al. (2021). For previously described species, we used combinations derived from O'Dogherty et al. (2021).

The terminology used to designate the different parts of the fundamental nassellarian spicule is based on Petrushevskaya (1984). See also 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 features specific to the family Lophocyrtiidae.

Infrakingdom Rhizaria Cavalier-Smith, 2002 emend. Cavalier-Smith, 2003 Phylum Retaria Cavalier-Smith, 1999 Class Polycystinea Ehrenberg, 1839 Order Nassellaria Ehrenberg, 1876 Superfamily Eucyrtidioidea Ehrenberg, 1846 emend. Suzuki et al., 2021 Family Eucyrtidiidae Ehrenberg, 1846 emend. Suzuki et al., 2021 Genus *Cymaetron* Caulet, 1991

Type species.— Cymaetron sinolampas Caulet, 1991, p. 536, pl. 4, figs. 10–12; by monotypy.

Cymaetron ? dilatatus new species

Plate II.22, Figures 1-4

Holotype.— Plate II.22, Figure 1; collection number USTL 3483–1; coordinates V46/2; sample ODP 1260A-9R-4W, 55–57 cm; upper part of the *Podocyrtis* (*L.*) *mitra* Zone, in the *Podocyrtis* (*P.*) *apeza* Subzone (late Lutetian, middle Eocene).

Diagnosis.— Three-segmented eucyrtidiid with an abdomen constricted in two false segments.

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

Description.— Shell three-segmented, smooth and robust, with the collar and lumbar strictures marked externally by a change in the contour of the shell Cephalis proportionally small, globular, poreless or bearing a few small circular pores. Apical spine extending outward as a strong apical tribladed horn longer than the cephalis, and dorsal spine prolonged as thoracic rib on upper thorax. Thorax truncate conical to slightly inflated conical, with subcircular pores, hexagonally framed and quincuncially arranged. Abdomen conspicuously inflated in its proximal part, usually 1.5 to 2 times as wide as thorax, then subcylindrical to truncate conical. The two parts of the abdomen are not subdivided into segments by an inner-ring. Abdominal pores subcircular, hexagonally framed and quincuncially arranged, sometimes less regularly arranged in the most distal part of the segment. Aperture open wide. Abdominal termination invariably ragged along a row of pores.

Etymology.— The specific epithet refers to the expanded proximal part of the abdomen of the new species; *dilatatus* in Latin means 'dilated, expanded'. The specific epithet is to be treated as an adjective in the nominative singular.

Dimensions.— Based on 10 specimens (mean): total length without the apical horn 145–188 μ m (176), length of apical horn: 18–31 μ m (24), length of cephalothorax without the apical horn: 45–66 μ m (56), length of abdomen: 51–155 μ m (117), maximum breadth of abdomen 82–129 μ m (95).

Remarks.— Cymaetron ? dilatatus n. sp. is tentatively assigned to the genus *Cymaetron* based on the characteristic wavy outline of the shell, which is constricted in false segments. However, the generic assignment is doubtful because the genus *Cymaetron* was originally described by Caulet (1991) as a two-segmented eucyrtidiid, while *C. ? dilatatus* n. sp. clearly has a threesegmented shell. Furthermore, the new species differs from *C. sinolampas* Caulet, 1991, the only other species of the genus, by having only one abdominal constriction. In addition to the characters already mentioned, this new species is distinguished from all other eucyrtidiid species with an open abdomen in not having post-abdominal segments. Finally, *C. ? dilatatus* n. sp. superficially resembles *Theocorys anaclasta* Riedel and Sanfilippo, 1970, from which it differs in having a much more elongated shell, a bladed apical horn, and smaller abdominal pores which are regular in size.

Genus Eucyrtidium Ehrenberg, 1846

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

Eucyrtidium levisaltatrix new species

Plate II.22, Figures 5-8

Holotype.— Plate II.22, Figure 5; collection number USTL 3482–1; coordinates J52/2; sample ODP 1260A-9R-4W, 55–57 cm; upper part of the *Podocyrtis* (*L*.) *mitra* Zone, in the *Podocyrtis* (*P*.) *apeza* Subzone (late Lutetian, middle Eocene).

Diagnosis.— *Eucyrtidium* species with an elongated abdomen, which is the longer segment of the shell.

Occurrence.— This short-lived species is relatively rare from the uppermost part of the *Podocyrtis* (*L*.) *mitra* Zone, to the lower part of the *Podocyrtis* (*L*.) *chalara* Zone.

Description.— Shell multisegmented, conical-elongated and thick-walled. Cephalis relatively small, globular and sparsely pored, bearing a long conical apical horn. Collar stricture marked externally by a change in the contour of the shell. Thorax subspherical to campanulate, with circular pores quincuncially arranged. Dorsal spine of the initial spicule rarely protruding near the thoracic stricture as a reduced, curved thoracic wing (Plate II.22, Figure 8). Abdomen subcylindrical to campanulate, being the longest segment. Abdominal pores circular, slightly larger than thoracic pores, hexagonally framed and longitudinally aligned. First post-abdominal segment with pores of irregular size and shape. Abdomen and first post-abdominal segment separated by a slight external constriction and by a straight (Plate II.22, Figure 7) or wavy (Plate II.22, Figures 5, 6) internal ridge which appears externally as a thick dark band. Distal part of the abdomen invariably ragged along a row of pores.

Etymology.— From the Latin *levis*, meaning 'light, not heavy', and *saltatrix*, meaning 'female dancer, dancing girl'. The specific epithet is to be treated as a noun in the nominative singular standing in apposition to the generic name.

Dimensions.— Based on six specimens (mean): total length without the apical horn: 166–226 μ m (194), length of apical horn: 26–38 μ m (30), length of cephalothorax: 51–57 μ m (55), length of abdomen: 107–134 μ m (119), maximum breadth of shell: 101–127 μ m (118).

Remarks.— This distinctive species is differentiated from all other middle Eocene *Eucyrtidium* species by its long apical horn, its well-defined abdominal stricture, and by its more conical

shape due to the elongation of the abdomen compared to the other segments of the shell. In addition, unlike other large species of the genus *Eucyrtidium*, the shell of *E. levisaltatrix* n. sp. is usually broken at the first post-abdominal segment.

It is likely that the new species originated from a stock of late middle Eocene multisegmented *Eucyrtidium* by elongation of the abdomen. However, further phylogenetic affinities remain unclear due to the sudden appearance of *E. levisaltatrix* n. sp. in the fossil record.

Superfamily Artostrobioidea Riedel, 1967a

Family Artostrobiidae Riedel, 1967a 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 curta (Clark and Campbell, 1942)

Plate II.22, Figures 9–12

- 1942 Dictyocephalus (Dictyoprora) pulcherrimus curtus Clark and Campbell, p. 79, pl. 8, figs. 3, 6, 7.
- 1973 Theocampe pirum (Ehrenberg) Foreman, p. 432, pl. 9, fig. 11 (part).
- 1975 Theocampe urceolus (Haeckel) Chen, p. 456, pl. 3, fig. 7.
- ? 1994 Dictyoprora amphora (Haeckel) Weinheimer et al., p. 311, pl. 1, fig. 13.
- 1995 Dictyoprora amphora (Haeckel) Shilov, p. 126, pl. 2, figs. 7, 8.
- 1997 Theocampe amphora (Haeckel) Hollis et al., p. 56, pl. 4, figs. 38, 39.
- 2005 Dictyoprora spp. Nigrini et al., pl. P6, fig. 13 (part).
- 2006 Dictyoprora sp. A Funakawa et al., p. 18, pl. P2, figs. 10a, 10b.

Holotype.— As no type was designated by Clark and Campbell (1942) in their original publication, each of the three illustrated specimens (pl. 8, figs. 3, 6, 7) are candidate lectotypes; they are all housed in the University of California, Museum of Paleontology, San Francisco.

Occurrence.— This species is found throughout the studied interval. It occurs sporadically from the *Thyrsocyrtis* (*P*.) *triacantha*¹ Zone, to the upper part of the *Podocyrtis* (*L*.) *mitra* Zone, and becomes more consistent and abundant from the upper part of the *Podocyrtis* (*L*.) *mitra* Zone to the *Podocyrtis* (*L*.) *goetheana* Zone.

Description.— Ovoid shell consisting of three segments. Shell surface relatively smooth, but with fine surface sculpture on abdomen. Cephalis hemispherical, unarmed, with scattered subcircular pores. Ventral pore large and circular, but no ventral tube developed. Collar stricture externally not defined in most specimens observed. Thorax truncate conical, with irregularly arranged circular pores. Lumbar stricture slightly expressed externally by a change in the shell outline. Globular abdomen perforated by circular downwardly directed pores arranged in five to six transverse rows. Each abdominal pore opens into a furrow dug into the wall thickness and extending almost to the next row of pores. Shell narrows distally and terminates in a cylindrical poreless peristome with a smooth margin.

Dimensions.— Based on 15 specimens (mean): total length: 89–108 μ m (97), length of cephalothorax: 29–38 μ m (34), length of abdomen: 56–72 μ m (63).

¹ Thyrsocyrtis (Pentalocorys) schomburgkii (Ehrenberg, 1847) in Chapter II.2.



Plate II.22. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic). (1-4) Cymaetron ? dilatatus n. sp.: (1) holotype, ODP 1260A-9R-4W, 55-57 cm, USTL 3483-1, V46/2; (2) ODP 1260A-9R-4W, 55-57 cm, USTL 3481-1, H41/3; (3) ODP 1260A-9R-3W, 55-57 cm, USTL 3479-1, T47/1 (mirrored); (4) ODP 1260A-9R-4W, 55–57 cm, USTL 3481–2, J37/2. (5–8) Eucyrtidium levisaltatrix n. sp.: (5) holotype, ODP 1260A-9R-4W, 55-57 cm, USTL 3482-1, J52/2; (6) ODP 1260A-9R-4W, 55-57 cm, USTL 3484-1, V45/2; (7) ODP 1260A-9R-3W, 55-57 cm, USTL 3478-1, E48/4; (8) specimen showing thoracic wing (arrow), ODP 1260A-8R-3W, 54–56 cm, USTL 3462-3, Z63/4 (mirrored). (9-12) Dictyoprora curta (Clark and Campbell): (9) ODP 1260A-14R-1W, 55–57 cm, USTL 3530–1, J40/1; (10) ODP 1260A-6R-3W, 55–57 cm, USTL 3424– 1, H60/4; (11) ODP 1260A-9R-1W, 55-57 cm, USTL 2848-1, C46/2; (12) ODP 1260A-9R-1W, 55-57 cm, USTL 3473-1, L48/1. (13-16) Spirocyrtis ? renaudiei n. sp.: (13) holotype, showing apical tube (arrow), ODP 1260A-8R-3W, 54–56 cm, USTL 3462–1, Q53/1 (mirrored); (14) specimen showing ventral tube (arrow), ODP 1260A-8R-3W, 54–56 cm, USTL 3462–2, L48/1 (mirrored); (15) ODP 1260A-7R-6W, 54–56 cm, USTL 3454–1, X45/2; (16) ODP 1260A-7R-6W, 54-56 cm, USTL 3454-2, R43/2. All scale bars equal 50 µm.

Remarks.— We have judged it appropriate to re-illustrate this species because it has been rarely observed since its original description by Clark and Campbell (1942) from the upper middle Eocene strata of Mont Diablo, California. *Dictyoprora curta* (Clark and Campbell, 1942) is distinguished from all other dictyoprorids by its small globular abdomen (maximum length of the abdomen <80 µm). This species also differs from *D. pirum* (Ehrenberg, 1874) and *D. gibsoni* O'Connor, 1994 in having more closely spaced rows of pores, a well-developed peristome, and a thick-walled shell rather than a thin hyaline shell; from *D. urceolus* (Haeckel, 1887) by having a globular abdomen and its abdominal pores being downwardly directed; from *D. armadillo* (Ehrenberg, 1874) and *D. ovata* (Haeckel, 1887) in lacking a cephalic horn and in having less than seven rows of abdominal pores. Finally, it differs from *D. mongolfieri* (Ehrenberg, 1854a) in that the abdominal pores are regular in size and shape and aligned in transverse rows.

Genus Siphocampe Haeckel, 1882

Type species.— *Siphocampe annulosa* Haeckel, 1887, p. 1500, pl. 79, fig. 10; subsequent designation by Strelkov and Lipman (1959, p. 459).

Siphocampe pachyderma (Ehrenberg, 1874)

Plate II.23, Figures 1–4

- 1874 Eucyrtidium pachyderma Ehrenberg, p. 231.
- 1876 Eucyrtidium pachyderma Ehrenberg Ehrenberg, p. 72, pl. 11, fig. 21.
- 1882a Lithomitra Pachyderma [sic] (Ehrenberg) Bütschli, p. 529.
- 1882b Lithomitra Pachyderma [sic] (Ehrenberg) Bütschli, pl. 30, fig. 26.
- 1887 Lithomitra (Lithomitrella) pachyderma (Ehrenberg) Haeckel, p. 1483.
- 1976 Lithomitra ? sp. aff. Lithocampe minuta Clark and Campbell Dzinoridze et al., pl. 32, figs. 16, 17.
- 1991 Siphocampe pachyderma (Ehrenberg) Caulet, p. 539, pl. 3, fig. 12.
- 2009 Eucyrtidium pachyderma Ehrenberg Ogane et al., pl 21, figs. 1a–1d.
- 2013 Siphocampe ? sp. Kochhann et al., p. 542, pl. 3 fig. R.

Lectotype.— No holotype was designated by Ehrenberg in the original description of the species. The specimen drawn by Ehrenberg (1876, pl. 11, fig. 21) was re-illustrated by Ogane et al. (2009, pl. 21, figs. 1a-1d) during their re-examination of Ehrenberg's collection held at the Museum für Naturkunde, Humboldt-Universität (Berlin, Germany), and subsequently designated as a lectotype by O'Dogherty et al. (2021; p. 976).

Diagnosis.— Very thick-walled *Siphocampe* species, with an asymmetrically placed cephalis and widely spaced rows of abdominal pores.

Occurrence.— The record of this species is punctuated throughout the studied interval, from the *Thyrsocyrtis* (*P.*) *triacantha*² Zone to the *Podocyrtis* (*L.*) *goetheana* Zone.

Description.— Shell three-segmented, small, spindle-shaped, and very thick-walled. Cephalis hemispherical to subspherical, asymmetrically placed, poreless or with a few subcircular pores. Ventral pore present, but ventral tube not developed. Apical horn absent. Collar and lumbar stricture indistinct in most observed specimens. Thorax trapezoidal, with two to four transverse rows of circular pores. Thoracic wall thickened distally. Abdomen elongated, subcylindrical to barrel-shaped and very thick-walled, two to three times longer than the thorax. Abdominal pores small, circular, with tubular projections through the abdominal wall, arranged in three to five transverse rows of pores. Although the abdomen is externally smooth, internal indentations can be distinguished by transparency, the maximum thickness of the abdominal wall being reached between the rows of pores. Shell ends in a smooth, poreless peristome.

Dimensions.— Based on six specimens (mean): total length: 84–119 μ m (99), maximum breadth: 43–57 μ m (51).

Remarks.— Siphocampe pachyderma differs from all other species of the genus *Siphocampe* in having a very thick-walled and almost hyaline shell, and from *Plannapus aitai* O'Connor, 2000 in having a less elongated shell with less than 10 transverse rows of pores.

² Thyrsocyrtis (Pentalocorys) schomburgkii (Ehrenberg, 1847) in Chapter II.2.

Siphocampe pollen new species

Plate II.23, Figures 5-8

- 1975 Theocampe amphora (Haeckel) group Chen, p. 456, pl. 2, fig. 2 (part).
- 1976 Lithomitra ? sp. aff. Lithomitra minuta Clark and Campbell Dzinoridze et al., pl. 29, fig. 6.
- 1997 Siphocampe acephala (Ehrenberg) group Hollis et al., p. 54, pl. 4, fig. 8 (part).

Holotype.— Plate II.23, Figure 5; collection number USTL 2854–1; coordinates L48/1; sample 1260A-13R-4W, 55–56 cm; lowermost part of the *Podocyrtis* (*L.*) *mitra* Zone, in the *Artostrobus quadriporus* Subzone (late Lutetian, middle Eocene).

Diagnosis.— *Siphocampe* species with a symmetrically placed cephalis and a thick-walled abdomen pierced by closely spaced rows of transverse pores.

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

Description.— Shell of three segments, spindle-shaped and smooth-surfaced. Cephalis hemispherical, asymmetrically placed and partially embedded in the thorax. Apical horn absent. Ventral pore present, but ventral tube not developed. Cephalic pores subcircular, sparse and irregularly arranged. Collar stricture slightly dark on the outside, but not marked by a change in the contour of the shell. Thorax truncate conical with five to six closely spaced transverse rows of small subcircular to circular pores. Lumbar stricture usually dark on the outside. Abdomen elongated, barrel-shaped, and thick-walled, about twice the length of the

cephalothorax. Abdominal pores small, circular, cylindrical, arranged in nine to ten transverse rows. Distal part of the abdomen usually ragged (Plate II.23, Figures 6, 7), but in complete specimens the shell terminates in a thin, poreless peristome (Plate II.23, Figure 5).

Etymology.— From the Latin *pollen*, meaning 'flour flower', because of its resemblance to a pollen grain (i.e., the male reproductive particles produced by the anther lodges of flower stamens). The specific epithet is to be treated as a noun in the nominative singular standing in apposition to the generic name.

Dimensions.— Based on 24 specimens (mean): total length: $68-129 \mu m$ (91), maximum breadth: $30-55 \mu m$ (45).

Remarks.— The general shape of the shell of *Siphocampe pollen* n. sp. resembles that of *S. acephala* (Ehrenberg, 1874) and *S. missilis* O'Connor, 1994. It differs from these species in having a thicker abdominal and thoracic wall, and nine to ten transverse rows of pores on the abdomen, instead of four to eight rows in *S. acephala* and eight to seventeen rows in *S. missilis*. The new species also differs from *S. acephala* in having a spindle-shaped rather than subcylindrical abdomen, and from *S. missilis* in having an asymmetrical cephalis. It differs from *S. imbricata* (Ehrenberg, 1874), *S. lineata* (Ehrenberg, 1839) and *S. arachnea* (Ehrenberg, 1862) in the shorter length of the abdomen and the absence of abdominal indentations. The new species differs from the co-occurring species *S. pachyderma* (Ehrenberg, 1874) in having a thinner abdominal wall and closely spaced transverse rows of pores on the abdomen. Finally, *S. pollen* n. sp. differs from the enigmatic *Plannapus*? *aitai* O'Connor, 2000 in having an asymmetrically placed cephalis that never bears an apical horn, and a three-segmented shell with thinner walls. *S. pollen* n. sp. is probably related to *S. acephala* and *S. pachyderma*, which

also have an asymmetrical cephalis. The characteristic thickness of the shell wall also suggests a close relationship between the new species and *S. pachyderma*.

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 ? renaudiei new species

Plate II.22, Figures 13–16

Holotype.— Plate II.22, Figure 13; collection number USTL 3462–1; coordinates Q53/1; sample ODP 1260A-8R-3W, 54–56 cm; *Podocyrtis* (*L.*) *chalara* Zone, in the *Rhopalosyringium* ? *biauritum* Subzone (late Lutetian, middle Eocene).

Diagnosis.— Artostrobiid with a multisegmented pupoid shell, a short, truncated apical tube, and a flared ventral tube.

Occurrence.— From the uppermost part of the *Podocyrtis* (*L*.) *mitra* Zone, to the lowermost part of the *Podocyrtis* (*L*.) *goetheana* Zone.

Description.— Shell pupoid to spindle-shaped, thick-walled, and multisegmented, with the fourth segment being the widest (rarely the third). Strictures usually indistinct or only slightly dark externally. Cephalis truncate conical, with downwardly directed subcircular pores, bearing a short truncated apical tube (Plate II.22, Figure 13) and a robust, distally flared ventral tube that opens almost perpendicular to the axis of the shell (Plate II.22, Figure 14). Thorax truncate conical, half the length of the cephalis, with two to four transverse rows of subcircular pores.
Abdomen truncate conical or slightly campanulate, longer than thorax, with three to five transverse rows of pores. First post-abdominal segment short, cylindrical, and medially expanded, with its lower margin marked by a narrow hyaline band. Other post-abdominal segments short, truncate conical, broader proximally than distally. All post-abdominal segments with subcircular pores arranged in one to three transerve rows. Pores tend to be larger distally. Last segment terminating in a narrow hyaline peristome (Plate II.22, Figures 13, 14), ragged in most observed specimens (Plate II.22, Figures 15, 16).

Etymology.— This species is named after Dr. Johan Renaudie (Museum für Naturkunde – Humboldt-Universität, Berlin) in honor of his contribution to the study of Cenozoic radiolarians. The specific epithet is to be treated as a noun in the genitive case formed from a modern personal name.

Dimensions.— Based on 20 specimens (mean): total length without the apical tube: 173-216 µm (192), maximum breadth of shell: 66–98 µm (89), length of apical tube: 9–13 µm (10).

Remarks.— Spirocyrtis ? renaudiei n. sp. differs from all other *Spirocyrtis* species in having a pupoid rather than a conical shell. The new species is also distinguished from *Botryostrobus grantmackiei* (O'Connor, 1997a) and *B. hollisi* (O'Connor, 1997a) in having larger pores arranged in more closely spaced transverse rows and in lacking post-abdominal indentations; from *B. miralestensis* (Campbell and Clark, 1944) and *B. aquilonaris* (Bailey, 1856) in being more elongated and in lacking a hyaline peristome. Finally, it is also more elongated and lacks a hyaline peristome compared to *B. miralestensis* (Campbell and Clark, 1944) and *B. aquilonaris* (Bailey, 1856).



Plate II.23. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic). (1–4) Siphocampe pachyderma (Ehrenberg): (1) ODP 1260A-9R-3W, 55-57 cm, USTL 3477-3, V50/3; (2) ODP 1260A-12R-6W, 55-57 cm, USTL 3519-1, F39/4; (3) ODP 1260A-11R-7W, 55-57 cm, USTL 3506-1, M43/3; (4) ODP 1260A-12R-4W, 55-57 cm, USTL 3514-1, S45/4. (5-8) Siphocampe pollen n. sp.: (5) holotype, ODP 1260A-13R-4W, 55-56 cm, USTL 2854-1, X67/4; (6) ODP 1260A-14R-1W, 55-57 cm, USTL 3530-3, N41/3; (7) ODP 1260A-10R-6W, 55-57 cm, USTL 3498-1, L52/2; (8) ODP 1260A-14R-1W, 55–57 cm, USTL 3531–1, W56/1. (9–12) Pterocyrtidium eep n. sp.: (9) holotype, showing thoracic wing (arrow), ODP 1260A-12R-CC, 63-177 cm, USTL 3521-1, U59/2 (mirrored); (10) specimen showing thoracic wing (arrow), ODP 1260A-12R-1W, 55-57 cm, USTL 2851-5, L64/3 (mirrored); (11) ODP 1260A-12R-CC, 63-177 cm, USTL 3521-2, U53/3; (12) ODP 1260A-12R-CC, 63-177 cm, USTL 3520-1, H36/3 (mirrored). (13-16) Corythomelissa galea (Ehrenberg): (13) ODP 1260A-11R-3W, 55-57 cm, USTL 3502-1, W34/4 (mirrored); (14) ODP 1260A-11R-4W, 55-57 cm, USTL 3503-1, F36/3 (mirrored); (15) ODP 1260A-11R-4W, 55-57 cm, USTL 3503-2, X39/3 (mirrored); (16) specimen showing sagittal horn (arrow), ODP 1260A-12R-CC, 63-177 cm, USTL 3520-2, X33/2 (mirrored). All scale bars equal 50 µm.

The generic assignment of *S.*? *renaudiei* n. sp. is uncertain due to its affinity to both genera *Botryostrobus* and *Spirocyrtis*. The new species shares similarities with the genus *Botryostrobus*, as evidenced by the general pupoid shape of its shell, which tapers distally and widens at or before the fifth segment (O'Connor, 1997a). However, it can be distinguished from all *Botryostrobus* species by the presence of a short apical tube and a distally flared ventral tube, which are two diagnostic characteristics of the genus *Spirocyrtis* (Nigrini, 1977). The oldest known representatives of both genera have been found in upper Paleocene to lower Oligocene sequences: *B. joides* Petrushevskaya, 1975 (upper Eocene–lower Oligocene), *S.*? *hollisi* Renaudie and Lazarus, 2012 (upper Paleocene, see Hollis, 2002), *S. greeni* O'Connor, 1999a (upper Eocene) and *S. proboscis* O'Connor, 1994 (lower Oligocene). The middle Eocene species *S.*? *renaudiei* n. sp. is therefore one of the earliest known representatives of the genus *Spirocyrtis*, and its unique combination of features suggests a close relationship to the divergence between the genera *Botryostrobus* and *Spirocyrtis*.

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

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 eep new species

Plate II.23, Figures 9–12

Holotype.— Plate II.23, Figure 9; collection number USTL 3521–1; coordinates U59/2; sample ODP 1260A-12R-CC, 63–177 cm; lower part of the *Podocyrtis (L.) mitra* Zone, in the *Artostrobus quadriporus* Subzone (Lutetian, middle Eocene).

Diagnosis.— Pterocyrtidium species with a long apical horn and a roundish thorax that is larger than the abdomen.

Occurrence.— Rare, from the uppermost part of the *Podocyrtis (P.) ampla* Zone to the upper part of the *Podocyrtis (L.) mitra* Zone.

Description.— Shell three-segmented, subcylindrical. Cephalis relatively small and globular, penetrated with a few subcircular pores and bearing a remarkably strong apical horn, usually three times as long as the cephalis height. Two dimples are present at the base of the apical horn (Plate II.23, Figure 9). Collar stricture externally expressed as a constriction. Thorax roundish to inflated and penetrated by numerous subcircular pores that are quincuncially arranged and hexagonally framed. In some specimens, primary lateral spines outgrow from the lower thorax as one or two sharply pointed lateral wings (Plate II.23, Figures 9, 10). Lumbar stricture marked

by a change in the contour of the shell and a thick internal ridge. Abdominal pores subcircular and roughly aligned in longitudinal rows, and are less numerous in the distal part of the abdomen. Aperture open and bordered by a hyaline band, or ragged along a row of pores.

Etymology.— The specific epithet is to be treated as an arbitrary combination of letters derived from the acronym used to designate the Evolution, Ecology, Paleontology laboratory (EEP) of the University of Lille, as a token of gratitude for the assistance offered to the first author.

Dimensions.— Based on five specimens (mean): total length without the apical horn: 133–153 μ m (138), length of apical horn: 61–75 μ m (70), length of cephalothorax without the apical horn: 76–84 μ m (79), length of abdomen: 54–71 μ m (58).

Remarks.— *Pterocyrtidium eep* n. sp. is distinguished from *P. barbadense* (Ehrenberg, 1874) and *P. praebarbadense* Kozlova, 1983 by its long sharpely pointed apical horn, and from *P. borisenkoi* Nishimura, 1992 by possessing a roundish thorax instead of a pyramidal thorax. The new species also differs from *P. genrietta* Nishimura, 1992 by having a longer apical horn and a thorax wider than the abdomen. Finally, *P. eep* n. sp. differs from *P. zitteli* Bütschli, 1882a by having a simple, conical apical horn instead of a dichotomous, bladed apical horn, and by the absence of a ventral horn on the cephalis. Additionally, it differs from similarly shaped upper Paleogene Pterocorythids by having an unilobed cephalis.

Superfamily Acanthodesmioidea Haeckel, 1862

Family Cephalospyrididae Haeckel, 1882

Genus Petalospyris Ehrenberg, 1846

Type species.— Petalospyris diaboliscus Ehrenberg, 1847, p. 55, fig. 6; by monotypy.

Petalospyris cometa new species Plate II.24, Figures 1–3

Holotype.— Plate II.24, Figure 1; collection number USTL 3421–1; coordinates W42/3; sample ODP 1260A-6R-2W, 55–57 cm; lower part of the *Podocyrtis* (*L*.) *goetheana* Zone (early Bartonian, middle Eocene).

Diagnosis.— Spyrid with a tuberculate shell, large cephalic pores, and nine conical feet.

Occurrence.— At ODP Site 1260, this species appears in the lowermost part of the *Podocyrtis* (*L*.) *goetheana* Zone.

Description.— Lattice shell tuberculate, thick-walled, with a slight external sagittal stricture, and not extending below the basal ring. Sagittal ring D-shaped. Apical horn robust and triangular, with variable length, generally less than half the height of the lattice shell. Cephalic pores subcircular to quadrate, unequal in size, and arranged symmetrically with respect to the sagittal stricture. Vertical pore present, showing a strong vertical spine. Presence of nine conical feet with pointed ends that emerge directly from the basal ring. Each foot is well-individualized, straight or slightly divergent, with most of the curvature proximally.

Etymology.— From the Latin *cometa*, meaning 'comet'. The specific epithet is to be treated as a noun in the nominative singular standing in apposition to the generic name.

Dimensions.— Based on 15 specimens (mean): length of cephalis without the apical horn: 74–100 μ m (86), maximum breadth of cephalis: 104–132 μ m (118), length of apical horn: 33–85 μ m (62), length of lamellar feet: 70–180 μ m (129).

Remarks.— The new species differs from all *Dorcadospyris* species and from *Dendrospyris stylophora* (Ehrenberg, 1874) in having at least eight lamellar feet emerging from the basal ring, instead of a reduced number of curved or straight feet that are round in cross-section. Representatives of *Petalospyris cometa* n. sp. differ from those of *P. confluens* Ehrenberg, 1874 in having larger cephalic pores, and long and well-individualized lamellar feet (Plate II.24, Figure 8). *P. cometa* n. sp. differs from *P. inferispina* (Goll, 1968), *P. flabellum* Ehrenberg, 1874, *P. platyacantha* Ehrenberg, 1874, and *Dendrospyris* ? *golli* Nishimura, 1992 in having larger pores, a rougher surface, and an apical horn that is shorter than the lattice shell. *P. cometa* n. sp. differs also from *P. diaboliscus* Ehrenberg, 1847 and *P. castanea* n. sp. by the absence of two lateral spines on the cephalis. Additionally, the new species is distinguished from *P. argiscus* (Plate II.24, Figure 4), *P. carinata* Ehrenberg, 1874, and *P. eupetala* Ehrenberg, 1874 by having less than 10 pores on the circumference of the cephalis at its widest part, a robust apical horn shorter than the lattice shell, and a wide vertical pore.

The origin of *P. cometa* n. sp. is to be found within a number of middle Eocene spyrids introduced by Ehrenberg (1874) as distinct species: *P. argiscus*, *P. carinata* and *P. eupetala*. These species exhibit a cephalis with a pebbly surface and numerous teeth surrounding the cephalic aperture. *P. argiscus* is abundant throughout the studied interval and displays high intraspecific variability, as well as in the length and inclination of the lamellar teeth. At ODP Site 1260, we also observed specimens with proximally carinate lamellar teeth, especially in the *Podocyrtis* (*L.*) *mitra* Zone. These different morphotypes do not form homogeneous groups distinct from typical *P. argiscus* (Plate II.24, Figure 4), therefore we chose to include them all

under this species. Our enlarged concept of *P. argiscus* encompasses morphotypes previously assigned to *P. eupetala* and *P. carinata*, so the latter are considered as synonyms of *P. argiscus*. In this revised taxonomic framework, *P. cometa* n. sp. is regarded as an offshoot of *P. argiscus* (Figure II.3).

Petalospyris castanea new species

Plate II.24, Figures 5–7

Holotype.— Plate II.24, Figure 5; collection number USTL 3477–1; coordinates H33/3; sample ODP 1260A-9R-3W, 55–57 cm; upper part of the *Podocyrtis* (*L*.) *mitra* Zone, in the *Podocyrtis* (*P*.) *apeza* Subzone (late Lutetian, middle Eocene).

Diagnosis.— Spyrid with two lateral spines on the cephalis and a latticed thorax that terminates in long teeth.

Occurrence.— This species occurs sporadically from the upper part of the *Podocyrtis* (*L*.) *mitra* Zone until the end of the studied interval, which falls in the lowermost part of the *Podocyrtis* (*L*.) *goetheana* Zone.

Description.— Shell dicyrtid, smooth, with a bilobed cephalis and a short latticed thorax. Cephalis globular, separated into two lobes by a weak sagittal constriction, bearing a short needle-like apical horn and two short lateral spines. Lateral spines developed directly from the latticed shell. Cephalic and thoracic pores subcircular, of different sizes, and randomly distributed. Thorax terminating in a ring of teeth that are as long as the thorax or slightly longer (although they are usually broken). These teeth point distally and are slightly curved inward. *Etymology.*— From the Latin *castanea*, meaning 'chestnut', for its resemblance to the fruit of the sweet chestnut tree (*Castanea sativa* Mill.). The specific epithet is to be treated as an adjective in the nominative singular.

Dimensions.— Based on five specimens (mean): length of cephalis without the apical horn: 33–45 μ m (40), maximum breadth of cephalis: 61–70 μ m (65), maximum length of lamellar feet: 26–64 μ m (36).

Remarks.— *Petalospyris castanea* n. sp. is characterized by two lateral spines on the cephalis, distinguishing it from most other species in the genus *Petalospyris*. It can be differentiated from *P. diaboliscus* Ehrenberg, 1847 by its latticed thorax and shorter, straight lateral spines on the cephalis. Additionally, *P. castanea* n. sp. has a shorter thorax than the cephalis height, larger pores, and fewer perioral teeth than *P. tricornis* (Haeckel, 1887).

P. castanea n. sp. appears to have evolved from *P. confluens* Ehrenberg, 1874 in the upper part of the *Podocyrtis* (*L.*) *mitra* Zone, with which it co-occurred afterward throughout the analyzed stratigraphic interval (Figure II.3). *P. diaboliscus*, on the other hand, is thought to have evolved from a stock of *P. castanea* n. sp. in the lower part of the *Podocyrtis* (*L.*) *goetheana* Zone. One major trend in this evolutionary lineage is the appearance and lengthening of two lateral horns on the cephalis, which developed directly from the latticed shell. Additionally, there was resorption of the thoracic pores and lengthening of the perioral teeth. The origin of *P. confluens* remains unclear, and there are no known descendants of *P. diaboliscus*.

Superfamily Archipilioidea Haeckel, 1882 sensu Sandin et al., 2019

Family Theophormididae Haeckel, 1882 emend. Suzuki et al., 2021

Genus Velicucullus Riedel and Campbell, 1952

Type species.— *Soreuma (Soreumium ?) magnificum* Clark and Campbell, 1942, p. 51, pl. 4, fig. 15; by monotypy.

Velicucullus armatus new species

Plate II.24, Figures 13–14

1973 Velicucullus sp. Sanfilippo and Riedel, p. 530, pl. 20, figs. 2, 3 (part).

Holotype.— Plate II.24, Figure 13; collection number USTL 3277–1; coordinates Q41/1; sample ODP 1260A-14R-5W, 55–57 cm; *Podocyrtis* (*P*.) *ampla* Zone, in the lower part of the *Coccolarnacium periphaenoides* Subzone (late Lutetian, middle Eocene).

Diagnosis.— *Velicucullus* species with four collar pores subequal in size, and a thorax terminating in ~20 well-individualized radial spines.

Occurrence.— This species occurs sporadically from the *Thyrsocyrtis* (*P*.) *triacantha*³ Zone, to the upper part of the *Podocyrtis* (*L*.) *mitra* Zone.

Description.— Shell two-segmented, consisting of a large cephalis and a flat extended discoidal thorax. We did not find any specimens in our material that display an entirely developed cephalis. Therefore, the anatomical details of the cephalis remain unknown. Basal ring

³ Thyrsocyrtis (Pentalocorys) schomburgkii (Ehrenberg, 1847) in Chapter II.2.

composed of the dorsal spine, the ventral spine, and two primary lateral spines. The four rods intersect orthogonally at angles of 90°, delimiting four collar pores that are subequal in size. Thoracic pores subcircular to quadrangular, roughly aligned longitudinally and increasing in size toward the periphery. Thorax ending in a narrow hyaline band that is armed with ~20–25 radial spines. Each spine spaced by three or four pores and ventrally connected to the velum. Very reduced velum positioned under the most distal row of thoracic pores and not extending on the oral surface of the thorax (Plate II.24, Figure 14).

Etymology.— From the Latin *armatus*, meaning 'armed'. The specific epithet is to be treated as an adjective in the nominative singular.

Dimensions.— Based on the only two complete specimens found: shell diameter: 251–293 µm.

Remarks.— The fossil record of ODP Site 1260 contains highly fragmented remains of this species, including isolated portions of the thorax. However, the distinct shape of the distal margin of its thorax allows for easy identification, even in the form of small fragments. *Velicucullus armatus* n. sp. can be differentiated from *V. discoides* (Ehrenberg, 1874) and *V. fragilis* O'Connor, 1999a by the presence of radial spines on the distal margin of the thorax. The new species also differs from *V. magnificum* (Clark and Campbell, 1942) in having larger and fewer thoracic pores and well-individualized radial spines, and from *V. palaeocenica* Nishimura, 1992 in having collar pores that are equal in size and an almost flat thorax. Finally, *V. armatus* is found alongside a massive unidentified *Velicucullus* species throughout its observed stratigraphic range. However, this species is only is represented only by fragments in our material, and thus cannot be formally described. This species is distinguished by its larger

size (>300 μ m), the absence of radial spines, and by its smaller and more numerous thoracic pores.

Superfamily Plagiacanthoidea Hertwig, 1879

Family Pseudodictyophimidae Suzuki in Suzuki et al., 2021

Genus Corythomelissa Campbell, 1951

Type species.— Lithomelissa corythium Ehrenberg, 1874, p. 240 (unfigured); Ehrenberg, 1876,

p. 78, pl. 3, fig. 12; subsequent designation by Campbell (1951, p. 529).

Corythomelissa galea (Ehrenberg, 1874) new combination

Plate II.23, Figures 13–16

- 1874 Halicalyptra Galea [sic] Ehrenberg, p. 234.
- 1876 Halicalyptra Galea [sic] Ehrenberg Ehrenberg, p. 74, pl. 2, fig. 10.
- 1887 Tripocalpis galea (Ehrenberg) Haeckel, p. 1136.
- 2009 Halicalyptra galea Ehrenberg Ogane et al., pl. 44, figs. 2a-2g.

Holotype.— No holotype was designated by Ehrenberg in the original description of the species. However, the specimen he drew (1876, pl. 2, fig. 10), which was later re-illustrated by Ogane et al. (2009, pl. 44, figs. 2a–2g) during their reexamination of Ehrenberg's collection kept in the Museum für Naturkunde, Humboldt University (Berlin, Germany), is a potential lectotype.

Diagnosis.— *Corythomelissa* species with a proportionally small cephalis bearing a strong apical horn and sometimes an inconspicuous ventral horn, a closed thorax, and three straight, downwardly directed feet.

Occurrence.— This species has a discontinuous range at ODP Site 1260, extending from the upper part of the *Podocyrtis* (*P*.) *ampla* Zone, to the lower part of the *Podocyrtis* (*L*.) *mitra* Zone.

Description.— Shell composed of two segments, globular and thick-walled. Cephalis subspherical to hemispherical, partially embedded in the thorax, and penetrated by randomly distributed subcircular pores. Apical spine free in the cephalic cavity, extending outside as a stout, bladed apical horn. In some specimens, the ventral spine protrudes as a small sagittal horn (Plate II.23, Figure 16). Dorsal and primary lateral spines elongated as strong ribs or ridges on the thorax, and protruding as three straight bladed feet. Thorax globular, asymmetrical in lateral view due to the development of the dorsal spine. Distal end of the thorax either round or closed. Thoracic pores subcircular to elongated around the thoracic ribs, irregular in size, and generally larger than the cephalic ones.

Dimensions.— Based on five specimens (mean): length of cephalothorax without the apical horn: $82-105 \mu m$ (90), length of apical horn: $21-35 \mu m$ (29), length of feet: $53-86 \mu m$ (64).

Remarks.— *Corythomelissa galea* (Ehrenberg, 1874) n. comb. was assigned to the genus *Corythomelissa* on the basis of its closed thorax, its hemispherical cephalis bearing an apical and a ventral spine, and its dorsal and primary lateral spines prolonged as three straight, downwardly directed feet. The combination recently suggested by O'Dogherty et al. (2021): *Phaenocalpis galea* (Ehrenberg, 1874), was not selected because the species belonging to the



Plate II.24. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic). (1–3) *Petalospyris cometa* n. sp.: (1) holotype, ODP 1260A-6R-2W, 55–57 cm, USTL 3421–1, W42/3; (2) ODP 1260A-6R-1W, 55–57 cm, USTL 2847–1, X45/1; (3) ODP 1260A-6R-1W, 55–57 cm, USTL 2847–2, D39/2; (4) *Petalospyris argiscus* Ehrenberg: ODP 1260A-13R-4W, 55–56 cm, USTL 2854–4, M38/4. (5-7) *Petalospyris castanea* n. sp.: (5) holotype, ODP 1260A-9R-3W, 55–57 cm, USTL 3477–1, H33/3; (6) ODP 1260A-8R-2W, 54–56 cm, USTL 3461–1, R55/3; (7) ODP 1260A-9R-3W, 55–57 cm, USTL 3479–2, S42/1. (8) *Petalospyris confluens* Ehrenberg: ODP 1260A-9R-3W, 55–57 cm, USTL 3478–3, U43/3. (9–12) *Lychnocanium nimrodi* n. sp.: (9) holotype, ODP 1260A-9R-4W, 55–57 cm, USTL 3483–2, L38/2; (10) ODP 1260A-9R-4W, 55–57 cm, USTL 3481–4, U38/3 (mirrored); (11) ODP 1260A-9R-4W, 55–57 cm, USTL 3484–2, L36/9; (12) ODP 1260A-9R-2W, 55–57 cm, USTL 3474–2, O38/3. (13, 14) *Velicucullus armatus* n. sp.: (13) holotype, ODP 1260A-14R-5W, 55–57 cm, USTL 3277–1, Q41/1; (14) ODP 1260A-13R-4W, 55–56 cm, USTL 2854–3, T61/3. All scale bars equal 50 μm.

genus *Phaenocalpis* are all composed of a single segment. *C. galea* (Ehrenberg, 1874) n. comb differs from *C. horrida* (Petrushevskaya, 1975) group, *C. omoprominentia* Funakawa, 1995a, and *C. spinosa* Funakawa, 1995a in having a smooth-surfaced cephalis bearing shorter apical and ventral horns. It also differs from *C. pachyostraca* Funakawa, 1995a in having a smaller cephalis with shorter apical and ventral horns and a closed thorax. Amongst similar-looking *Pseudodictyophimus* species, *C. galea* (Ehrenberg, 1874) n. comb. differs from *Ps. bicornis* (Ehrenberg, 1874), *Ps. leptoretis* Funakawa, 1995b, *Ps. pyramidalis* Funakawa, 1995b, and *Ps. tanythorax* Funakawa, 1994 in having a shorter ventral horn, three straight, downwardly directed feet, and a closed thorax. It is also distinguished from *Ps. ? sphaerothorax* Funakawa, 1995b in having a smaller ventral horn and a proportionally larger thorax, and from *Ps. ? charlestonensis* (Clark and Campbell, 1945) in having three straight feet and a cephalis that is conspicuously embedded in the thorax. Finally, *C. galea* (Ehrenberg, 1874) n. comb. differs from *Spongomelissa cucumella* Sanfilippo and Riedel, 1973 in having larger pores, a cephalis that is distinctly smaller than the thorax, and three longer feet.

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 (O'Dogherty et al., 2021).

Lychnocanium nimrodi new species

Plate II.24, Figures 9–12

1985 Sethochytris babylonis (Clark and Campbell) group – Sanfilippo et al., fig. 17.8a (part).

Holotype.— Plate II.24, Figure 9; collection number USTL 3483–2; coordinates L38/2; sample ODP 1260A-9R-4W, 55–57 cm; upper part of the *Podocyrtis* (*L*.) *mitra* Zone, in the *Podocyrtis* (*P*.) *apeza* Subzone (late Lutetian, middle Eocene).

Diagnosis.— *Lychnocanium* species with a stout, distally dilated apical horn, and three long subparallel feet that are rectangular in cross-section.

Occurrence.—*Lychnocanium nimrodi* n. sp. ranges from the upper part of the *Podocyrtis* (*L*.) *mitra* Zone to the lowermost part of the *Podocyrtis* (*L*.) *chalara* Zone.

Description.— Cephalis subspherical, thick-walled, and poreless. Apical horn longer than the cephalis, stout, and distally dilated, with a hammered surface. Collar stricture well-defined externally by a change in the contour of the shell. Thorax pyriform, with subcircular pores of different sizes, quincuncially or irregularly arranged. Three long and subparallel feet emerging

from the base of the thorax, rectangular in cross section and dilated at the end in heavy silicified specimens (Plate II.24, Figures 9, 11). Feet smooth-surfaced over a large part of their length, then rough when they are dilated.

Etymology.— Named after Nimrod, the ancient king of Babylon who commissioned the construction of the Tower of Babel. The specific epithet is to be treated as a noun in the genitive case formed from a personal name.

Dimensions.— Based on 20 specimens (mean): length of cephalothorax without the apical horn: $81-107 \mu m$ (91), length of apical horn: $35-59 \mu m$ (46), length of feet: $88-140 \mu m$ (117).

Remarks.— *Lychnocanium nimrodi* n. sp. is undoubtedly related to the *L. babylonis* (Clark and Campbell, 1942) group⁴. It is distinguished from all morphotypes grouped under this name in having a rounded thorax rather than a pyramidal thorax with sharp angles, and in having three long subparallel feet, which are rectangular in cross-section and usually distally dilated. A distally dilated apical horn is also a characteristic feature of *L. nimrodi* n. sp. This short-lived species is considered as an offshoot from the *L. babylonis* group⁴ (Figure II.3).

Superfamily Pterocorythoidea Haeckel, 1882 emend. Suzuki et al., 2021 Family Lophocyrtiidae Sanfilippo and Caulet *in* De Wever et al., 2001 Genus *Aphetocyrtis* Sanfilippo and Caulet, 1998

Type species.— Aphetocyrtis gnomabax Sanfilippo and Caulet, 1998, p. 16, pl. 7, fig. 10.

⁴ Lychnocanium tribulus (Ehrenberg, 1874) group in Chapter II.2.

Aphetocyrtis zamenhofi new species Plate II.25, Figures 1–4, 8

1977 Theocorys sp. Riedel and Sanfilippo, pl. 7, fig. 9.

2006 Lophocyrtis (Apoplanius) aspera (Ehrenberg) – Funakawa et al., p. 25, pl. P7, figs. 5a, 5b (part).

Holotype.— Plate II.25, Figure 1; collection number USTL 3543–1; coordinates Q37/4; sample 1260A-15R-2W, 55–57 cm; lowermost part of the *Podocyrtis* (*P.*) *ampla* Zone, in the *Dictyomitra parva* Subzone (late Lutetian, middle Eocene).

Diagnosis.— *Aphetocyrtis* species with an apical spine that is completely free in the cephalic cavity, an inflated hemispherical thorax and an abdomen divided in two by a constriction.

Occurrence.— From the beginning of the studied interval, which is situated in the *Thyrsocyrtis* (*P.*) *triacantha* Zone, to the upper part of the *Podocyrtis* (*P.*) *ampla* Zone.

Description.— Shell three-segmented, thick-walled and, almost cylindrical. Cephalis proportionally small, spherical and globular, porous. Apical spine fused with the cephalic wall, protruding outside as a small, simple apical horn. Collar constriction expressed externally by a sharp change in the contour of the shell, giving the impression that the cephalis merely rests on the thorax. Thorax inflated hemispherical, perforated by subcircular pores of regular size and shape, that are quincuncially arranged and hexagonally framed by high, sharp ridges, that give the thorax its thorny contour. Lumbar stricture marked by a thick internal ridge that appears externally as a dark band. Abdomen shaped like an hourglass, with an inflated proximal portion

followed by a constriction and then an enlargement of the shell. Abdominal pores subcircular to ovoid, unequal in size, randomly distributed or roughly aligned longitudinally. In the proximal part of the abdomen, pores separated by weak ridges, sometimes fused, and arranged longitudinally according to the alignment of the pores. Abdominal termination lacks a peristome or terminal feet.

Etymology.— Named after the Polish ophthalmologist Ludwik Lejzer Zamenhof, who is the creator of Esperanto, one of the most widely used constructed international auxiliary languages. The specific epithet is to be treated as a noun in the genitive case formed from a modern personal name.

Dimensions.— Based on 30 specimens (mean): total length: 120–258 μ m (188), length of cephalothorax: 61–107 μ m (84), length of abdomen: 59–157 μ m (104).

Remarks.— The new species shows strong morphological similarities to early representatives of *Aphetocyrtis gnomabax* Sanfilippo and Caulet, 1998 which can have a constricted abdomen (e.g., Sanfilippo and Caulet, 1998, pl. 2, figs. 14–17). However, *A. zamenhofi* n. sp. is distinguished from *A. gnomabax* by having an apical spine that is completely free in the cephalic cavity, a more globular cephalis that is well-separated from the thorax, and an inflated hemispherical thorax rather than an inflated campanulate thorax. In addition to the organization of its initial spicule, *A. zamenhofi* n. sp. differs from the Southern Ocean species *A. rossi* Sanfilippo and Caulet, 1998 and *A. catalexis* Sanfilippo and Caulet, 1998, and from the tropical species *A. ? columboi* n. sp. in having a constricted abdomen. The new species is separated from *A. ? bianulus* (O'Connor, 1997a) by its shorter abdomen with only one constriction. In part of

its range, *A. zamenhofi* n. sp. co-occurs with *Lophocyrtis alauda* (Ehrenberg, 1874), , which is easily distinguished by its stronger apical horn and its subcylindrical abdomen perforated by pores of regular size and shape. Amongst the Lophocyrtiids, *Apoplanius klydus* (Sanfilippo and Caulet, 1998) also has a wavy abdomen, but this species differs from *A. zamenhofi* n. sp. in having a spiny thorax, an apical spine partially included within the cephalis wall, and a stronger apical horn.

Under the original description of the genus *Aphetocyrtis*, Sanfilippo and Caulet (1998) described three species (*A. gnomabax*, *A. rossi* and *A. catalexis*), which were all included in the *A. gnomabax* lineage. One of the major trends in this evolutionary lineage during the late Paleogene is the gradual inclusion of the apical spine in the cephalic wall. In *A. gnomabax*, the earliest morphospecies of this lineage, known during the earliest middle Eocene, the apical spine is loosely attached to the cephalic wall. Then, the apical spine becomes completely included in the cephalic wall in the youngest Oligocene morphospecies *A. rossi* and *A. catalexis*. The apical spine of *A. zamenhofi* n. sp., which is completely merged in the cephalic wall (Plate II.25, Figure 8), prevents the inclusion of this species in the *A. gnomabax*, in spite of their great morphological proximity; it probably belongs to another evolutionary lineage within the genus *Aphetocyrtis*. In any case, the documentation of this new species allows us to firmly place the origin of the genus *Aphetocyrtis* at the low latitudes since the middle Eocene, before its migration to the high latitudes during the late Eocene (Sanfilippo and Caulet, 1998).

Aphetocyrtis ? *columboi* new species Plate II.25, Figures 5–7, 9

Holotype.— Plate II.25, Figure 5; collection number USTL 3438–1; coordinates J31/1; sample ODP 1260A-6R-6W, 55–57 cm; lowermost part of the *Podocyrtis* (*L*.) *goetheana* Zone (early Bartonian, middle Eocene).

Diagnosis.— Spindle-shaped shell with a tapered abdomen, ending in a horn-like structure.

Occurrence.— From the upper part of the *Podocyrtis* (*L*.) *chalara* Zone to the *Podocyrtis* (*L*.) *goetheana* Zone.

Description.— Shell three-segmented, spindle-shaped, and thick-walled, with the collar and lumbar strictures expressed externally as a slight change in the contour of the shell. Cephalis spheroidal to flattened ovoid, partially embedded in the thorax, poreless or with a few small and irregularly distributed pores. Apical spine included in the cephalic wall, projecting outward as a reduced apical horn, shorter than the cephalis height. Mitral arches leave the apical spine in the middle of the cephalis, and diverge rapidly at a large angle. Thorax hemispherical to inflated campanulate, as wide as, or wider than the abdomen, with subcircular pores quincuncially arranged. Dorsal and primary lateral spines prolonged in the thoracic wall as externally indistinct ribs, protruding outside the shell as three inconspicuous conical wings usually broken and difficult to see (Plate II.25, Figure 5). Abdomen inverted conical, with subcircular pores roughly arranged in longitudinal rows. Abdomen terminating in a horn-like structure, usually longer than the apical horn (Plate II.25, Figure 5), but ragged along a row of pores in most observed specimens (Plate II.25, Figures 6, 7).

Etymology.— Named after the iconic cigar smoking Lieutenant Columbo of the eponymous American crime drama series Columbo, due to the resemblance of this species to a cigar. The specific epithet is to be treated as a noun in the genitive case formed from a modern personal name.

Dimensions.— Based on 11 specimens (mean): total length: $191-207 \mu m$ (193), length of cephalothorax: $71-84 \mu m$ (77), length of abdomen: $101-121 \mu m$ (116).

Remarks.— This species is tentatively assigned to the genus *Aphetocyrtis* because of the general morphology of its shell and the organization of its initial spicule. Its phylogenetic relationships with other members of the A. gnomabax lineage are difficult to determine at this time; however, it can be noted that this new species has reached an advanced stage in the inclusion of the apical spine in the cephalic wall early in the history of the genus (Plate II.25, Figure 9). A. ? columboi n. sp. differs from A. gnomabax Sanfilippo and Caulet, 1998, A. rossi Sanfilippo and Caulet, 1998, A. catalexis Sanfilippo and Caulet, 1998 and A. zamenhofi n. sp. in having a tapered abdomen terminating in a horn-like structure and a thorax flanked by three small wings. This new species is morphologically close to Pterosyringium hamata O'Connor, 1999a, from which it differs in being larger, and in having more regularly arranged abdominal pores. A. ? columboi n. sp. is also distinguished from Lophocyrtis versipellis (Ehrenberg, 1874) in having a flattened ovoid cephalis and smaller abdominal pores. In its general form, A. ? columboi n. sp. superficially resembles some species of the genus *Glomaria*, especially the middle Miocene species G. thornburgi (Sanfilippo and Riedel, 1970) and G. baueri (Sanfilippo and Riedel, 1970). However, the thorax of A. columboi n. sp. does not consist of a loose spongy network, which allows it to be easily distinguished from all species of the genus Glomaria.

The origin of *A*. ? *columboi* n. sp. remains unclair; it is probably closely related to the late Eocene species *P. hamata* (O'Connor, 1999a) described from the Oamaru diatomite.

Aphetocyrtis ? spheniscus new species

Plate II.25, Figures 10–13

Holotype.— Plate II.25, Figure 10; collection number USTL 2851–2; coordinates Y49/1; sample ODP 1260A-12R-1W, 55–57 cm; lower part of the *Podocyrtis* (*L.*) *mitra* Zone, in the *Artostrobus quadriporus* Subzone (late Lutetian, middle Eocene).

Diagnosis.— *Aphetocyrtis* species with an elongated shell, a slight abdominal constriction, and an open aperture.

Occurrence.— From the lowermost part of the *Podocyrtis (P.) ampla* Zone, to the lower part of the *Podocyrtis (L.) chalara* Zone.

Description.— Shell of three segments, subcylindrical to fusiform and thick-walled. Cephalis subspherical, perforated by a few subcircular pores, and bearing a strong bladed apical horn. Collar stricture expressed as a change in the contour of the shell. Thorax thick-walled, campanulate to truncate conical, with circular pores quincuncially arranged. Thoracic stricture marked externally by a slight constriction of the shell and lined by an internal ridge that appears externally as a dark band. The pores on the thoracic stricture are slightly elongated longitudinally. Abdomen subcylindrical, with circular pores longitudinally aligned, although pore alignment tends to be less regular in the distal part of the abdomen. Short longitudinal

ridges may sometimes separate rows of abdominal pores (Plate II.25, Figure 11). Aperture sometimes slightly constricted, and always ragged.

Etymology.— From the Latin *spheniscus*, meaning 'penguin', for its resemblance to the great penguins. The specific epithet is to be treated as a noun in the nominative singular standing in apposition to the generic name.

Dimensions.— Based on 30 specimens (mean): total length: 130–214 μ m (159), length of apical horn: 12–23 μ m (15), length of cephalothorax: 70–102 μ m (80), length of abdomen: 62–144 μ m (80).

Remarks.— This species is tentatively assigned to the genus *Aphetocyrtis* because of the absence of a ventral horn, or of any external extensions associated with the dorsal and the primary lateral spines, and because the abdomen terminates in a simple peristome. The new species is morphologically close to the specimen designated as holotype of the species *A. catalexis* Sanfilippo and Caulet, 1998 (pl. 7, figs. 14a, 14b), but it differs in having a truncate conical thorax rather than a hemispherical thorax, and less pronounced abdominal and collar constrictions. *A. ? spheniscus* n. sp. differs also from *Theocorys saginata* Takemura and Ling, 1998 in having smaller thoracic and abdominal pores, and a less pronounced constriction between the thorax and the abdomen; from *T. minuta* Takemura and Ling, 1998 and *T. perforalvus* (O'Connor, 1997a) in being more elongated, with a truncate conical thorax instead of a hemispherical to spherical thorax, and in having a stronger apical horn; from *T. spongoconus* (Kling, 1971) in having a latticed abdomen instead of a spongious abdomen; and from *T. kerguelensis* Takemura and Ling, 1998 in having a shorter apical horn, and regular

abdominal pores in size and shape. *A.*? *spheniscus* n. sp. is also distinguished from *Theocyrtis diabloensis* Clark and Campbell, 1942 and *Th. robusta* Clark and Campbell, 1942 in having a less pronounced lumbar stricture, a shorter apical horn and regularly arranged pores. Finally, the new species can be distinguished from *Th.*? *scolopax* (Ehrenberg, 1874) by its shorter apical horn, its smaller thoracic and abdominal pores, and by the absence of well-defined longitudinal ridges separating the rows of abdominal pores.

Family Pterocorythidae Haeckel, 1882

Genus Albatrossidium Sanfilippo and Riedel, 1992

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

Albatrossidium regis new species

Plate II.25, Figures 14–17

Holotype.— Plate II.25, Figure 14; collection number USTL 2851–1; coordinates Y54/2; sample 1260A-12R-1W, 55–57 cm; lower part of the *Podocyrtis* (*L*.) *mitra* Zone, in the *Artostrobus quadriporus* Subzone (late Lutetian, middle Eocene).

Diagnosis.— *Albatrossidium* species with a cylindrical shell, a large triangular apical horn, and spaced, irregularly arranged pores in the distal part of the abdomen.

Occurrence.— From the beginning of the studied interval, which is situated in the *Thyrsocyrtis* (*P.*) *triacantha*⁵ Zone, to the upper part of the *Podocyrtis* (*L.*) *mitra* Zone

⁵ Thyrsocyrtis (Pentalocorys) schomburgkii (Ehrenberg, 1847) in Chapter II.2.



Plate II.25. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic). (1-4, 8) Aphetocyrtis zamenhofi n. sp.: (1) holotype, ODP 1260A-15R-2W, 55-57 cm, USTL 3543-1, O37/4; (2) ODP 1260A-14R-CC, 63–117 cm, USTL 3540–1, P37/1; (3) ODP 1260A-15R-1W, 55–57 cm, USTL 3541–1, N47/2; (4) ODP 1260A-15R-1W, 55-57 cm, USTL 3541-2, Q54/1; (8) focus on the cephalis, ODP 1260A-15R-2W, 55-57 cm, USTL 3543-2. (5-7, 9) Aphetocyrtis? columboi n. sp.: (5) holotype, showing thoracic wing (arrow), ODP 1260A-6R-6W, 55-57 cm, USTL 3438-1, J31/1; (6) specimen showing thoracic wing (arrow), ODP 1260A-6R-6W, 55-57 cm, USTL 3438-2, G46/1; (7) ODP 1260A-6R-6W, 55-57 cm, USTL 3438-3, L38/3; (9) focus on the cephalis of the specimen illustrated as Figure 10. (10-13) Aphetocyrtis ? spheniscus n. sp.: (10) holotype, ODP 1260A-12R-1W, 55-57 cm, USTL 2851-2, Y49/1; (11) ODP 1260A-9R-3W, 55-57 cm, USTL 3478-2, S52/4; (12) ODP 1260A-12R-1W, 55-57 cm, USTL 2851-3, G45/2 (mirrored); (13) ODP 1260A-12R-3W, 55–57 cm, USTL 3512–2, H58/1. (14–17) Albatrossidium regis n. sp.: (14) holotype, ODP 1260A-12R-1W, 55-57 cm, USTL 2851-1, Y54/2 (mirrored); (15) ODP 1260A-13R-5W, 54–56 cm, USTL 3525–1, W56/2 (mirrored); (16) ODP 1260A-14R-1W, 55-57 cm, USTL 3530-2, M38/1 (mirrored); (17) ODP 1260A-12R-5W, 55-57 cm, USTL 3516-1, N49/1 (mirrored). All scale bars equal 50 µm.

Description.— Shell three-segmented, cylindrical and thick-walled. Cephalis hemispherical and trilobate, with a strong pyramidal apical horn and sometimes a few small accessory spines on the margin of the cephalic hole. Cephalic pores subcircular, few in number, and randomly arranged. Inconspicuous collar stricture. Thorax subcylindrical to campanulate, with subcircular pores hexagonally framed and quincuncially arranged. The boundary between the thorax and abdomen is marked by an internal ring, that appears externally as a dark band. Abdomen cylindrical, with subcircular pores longitudinally aligned in the proximal part, then smaller, irregularly arranged, and more widely spaced. Abdomen ending in a simple, almost hyaline peristome, or in three inconspicuous shovel-shaped feet.

Etymology.— This species is named after the late radiolarian specialist Dr. William Rex Riedel, who actively participated in the renewal of radiolarian studies in the second half of the 20th century. The specific epithet is to be treated as a noun in the genitive case formed from a personal name that is Latin.

Dimensions.— Based on 14 specimens (mean): total length without the apical horn: 76–167 μ m (121), length of apical horn: 26–38 μ m (31), length of cephalothorax without the apical horn: 62–93 μ m (70), length of abdomen: 39–85 μ m (55).

Remarks.— Albatrossidium regis n. sp. is distinguished from the holotype of *A. minzok* (Sanfilippo and Riedel, 1992, pl. 2, fig. 7) in having a large triangular apical horn, and three shovel-shaped feet. The new species differs from *A. cylindricum* (Ehrenberg, 1874) and *A. tenellum* (Foreman, 1973) in having a more elongated apical horn, which is typically accompanied by a few accessory spines near its base, and by the proportion of thoracic length to abdominal length: 1:1 to 1:1.5 in the former, while it is greater than 1:2 for the other two species mentioned. Finally, *A. regis* n. sp. differs from *A. annikasanfilippoae* n. sp. in being much more cylindrical, with a reduction in the number of pores in the distal part of the abdomen, in having smaller accessory spines, and in not having any perforation in the apical horn.

A. minzok is considered to be the ancestral species of the genus (Sanfilippo and Riedel, 1992). Given its stratigraphic position (early Eocene to middle Eocene), this species represents a potential ancestor for the late middle Eocene species *A. regis* n. sp. However, due to the absence of *A. minzok* at ODP Site 1260, the phylogenetic relationship between these two species could not be determined in this study. A few specimens with a large triangular apical horn and a long cylindrical abdomen perforated by regularly arranged pores were observed in the *Podocyrtis* (*L.*) *goetheana* Zone after the last occurrence of *A. regis* n. sp. They correspond well to *A. cylindricum* as described by Ehrenberg (1874, p. 227) and illustrated by Ogane et al. (2009, pl. 84, figs. 5a–5d, pl. 85, figs. 1a–1d). These specimens may represent the descendants of *A. regis* n. sp. due to their morphological resemblance and stratigraphic position.

Albatrossidium annikasanfilippoae new species Plate II.26, Figures 1–4

1992 Albatrossidium minzok Sanfilippo and Riedel, p. 18, pl. 1, fig. 18 (part).

Holotype.— Plate II.26, Figure 1; collection number USTL 3512–1; coordinates Y39/1; sample ODP 1260A-12R-3W, 55–57 cm; lower part of the *Podocyrtis* (*L*.) *mitra* Zone, in the *Artostrobus quadriporus* Subzone (late Lutetian, middle Eocene).

Diagnosis.— *Albatrossidium* species with a large, triangular, and perforated apical horn, surrounded by several accessory spines.

Occurrence.— From the lower part of the *Podocyrtis* (*P*.) *ampla* Zone, to the end of the studied interval, which is situated in the lower part of the *Podocyrtis* (*L*.) *goetheana* Zone.

Description.— Shell three-segmented, smooth, and thick-walled. Cephalis trilobate, hemispherical, with a strong triangular apical horn and usually two or four accessory spines on the rim of the cephalic hole. Proximal half of the apical horn usually perforated by several subcircular pores. Cephalic pores subcircular and randomly arranged. Collar stricture expressed externally as a slight change in the contour of the shell. Thorax campanulate to inflated campanulate, with subcircular pores with polygonal pore-frames, and quincuncially arranged. Thorax and abdomen separated by an internal septum that is marked externally by a slight change in the contour of the shell. Abdomen subcylindrical, with subcircular pores arranged roughly in longitudinal rows. Abdominal termination undifferentiate, invariably ragged along a row of pores.

Etymology.— The species is named after Dr. Annika Sanfilippo, in recognition of her pioneering work on Paleogene radiolarians. The specific epithet is to be treated as a noun in the genitive case formed from a modern personal name.

Dimensions.— Based on 26 specimens (mean): total length without the apical horn: 110–174 μ m (126), length of apical horn: 30–47 μ m (39), length of cephalothorax without the apical horn: 61–100 μ m (77), length of abdomen: 29–87 μ m (49).

Remarks.— *Albatrossidium annikasanfilippoae* n. sp. is distinguished from the holotype of *A*. *minzok* (Sanfilippo and Riedel, 1992, pl. 2, fig. 7), *A. cylindricum* (Ehrenberg, 1874), and *A. tenellum* (Foreman, 1973) by its perforated apical horn surrounded by several accessory spines, and an abdomen shorter than the thorax. *A. annikasanfilippoae* n. sp. differs from *A. regis* n. sp. as described under this species.

Since *A. minzok* is the earliest member of the genus *Albatrossidium*, known from the early Eocene to the middle Eocene (Sanfilippo and Riedel, 1992), it seems to be a possible ancestor of the late middle Eocene species *A. annikasanfilippoae* n. sp. However, *A. minzok* was not found at ODP Site 1260, and therefore, it is currently impossible to confirm this phylogenetic hypothesis. The cephalic hole observed in *A. annikasanfilippoae* n. sp. resembles the open cephalis of Neogene and Quaternary species of the genus *Lamprocyrtis* (see for example Sanfilippo and Riedel, 1992, pl. 4, figs. 7–9). However, the rest of the cephalis of *Lamprocyrtis* species differs in being longitudinally elongated and indistinctly trilobed. Although the two genera are related (Sanfilippo and Riedel, 1992), it is likely that this remarkable cephalic structure appeared twice independently.

Genus Phormocyrtis Haeckel, 1887

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

Phormocyrtis lazari new species

Plate II.26, Figures 5-8

- 1957b Phormocyrtis embolum (Ehrenberg) Riedel, p. 88, pl. 2, fig. 7 (part).
- 1972 Phormocyrtis embolum (Ehrenberg) group Petrushevskaya and Kozlova, p. 537, pl.
 22, figs. 8, 9.
- 1974 Phormocyrtis embolum (Ehrenberg) Kruglikova, fig. 3.10.
- 1975 ? Phormocyrtis proxima Clark and Campbell Chen, p. 456, pl. 2, fig. 6.
- ? 1999 Phormocyrtis embolum (Ehrenberg) Kozlova, p. 148, pl. 31, fig. 14.
- ? 1999 Phormocyrtis sp. cf. P. embolum (Ehrenberg) Kozlova, pl. 35, fig. 16.

Holotype.— Plate II.26, Figure 5; collection number USTL 3474–1; coordinates T40/4; sample

1260A-9R-2W, 55-57 cm; uppermost part of the Podocyrtis (L.) mitra Zone, in the Podocyrtis

(P.) apeza Subzone (late Lutetian, Middle Eocene).

Diagnosis.— *Phormocyrtis* species with a subcylindrical hyaline abdomen that is terminated by lamellar feet.

Occurrence.— From the upper part of the *Podocyrtis* (*L*.) *mitra* Zone, to the end of the studied interval, which is situated in the lower part of the *Podocyrtis* (*L*.) *goetheana* Zone.



Plate II.26. Composite light micrographs of new radiolarian species from ODP Site 1260 (Demerara Rise, western equatorial Atlantic). (1–4) *Albatrossidium annikasanfilippoae* n. sp.: (1) holotype, ODP 1260A-12R-3W, 55–57 cm, USTL 3512–1, Y39/1; (2) ODP 1260A-13R-4W, 55–57 cm, USTL 2854–5, X67/4; (3) ODP 1260A-13R-4W, 55–57 cm, USTL 2854–2, O66/1; (4) ODP 1260A-9R-3W, 55–57 cm, USTL 3477–2, L56/3. (5–8) *Phormocyrtis lazari* n. sp.: (5) holotype, ODP 1260A-9R-2W, 55–57 cm, USTL 3474–1, T40/4; (6) ODP 1260A-9R-3W, 55–57 cm, USTL 3480–1, M35/1; (7) ODP 1260A-9R-4W, 55–57 cm, USTL 3482–2, W36/3; (8) ODP 1260A-9R-4W, 55–57 cm, USTL 3481–3, E38/3. (9–12) *Podocyrtis (Lampterium) puellasinensis* (Ehrenberg): (9) ODP 1260A-6R-2W, 55–57 cm, USTL 3420–1, U56/1; (10) ODP 1260A-9R-4W, 55–57 cm, USTL 3484–3, D47/3; (11) ODP 1260A-12R-1W, 55–57 cm, USTL 2851–4, C47/4 (mirrored). (12) *Podocyrtis (Lampterium) goetheana*

(Haeckel), focus on the cephalothorax, ODP 1260A-8R-2W, 54–56 cm, USTL 3461–2, S49/1 (mirrored). All scale bars equal 50 μ m.

Description.— Shell three-segmented, smooth, and thick-walled, with slight collar and lumbar constrictions. Cephalis hemispherical, poreles,s or with a few small subcircular pores, bearing a short conical horn that is weakly bladed, at least in the proximal part. Thorax truncate conical to subcylindrical, with pores in longitudinal rows (six to seven in a row), separated by strong longitudinal ribs. Lower margin of the thorax marked by a well-defined internal septal band. Abdomen subcylindrical to truncate conical, either hyaline or sparsely pored in its upper portion, thence surrounded by ~20 lamellar feet that point distally and vary in length (about 1/2 to 2 length of the hyaline part). If present, abdominal pores are either subcircular or longitudinally elongated, and can be up to three times as long as the thoracic ones.

Etymology.— This species is named in honor of Dr. David Lazarus (Museum für Naturkunde – Humboldt-Universität, Berlin) in recognition of his contribution to the study of Cenozoic radiolarians. The specific epithet is to be treated as a noun in the genitive case formed from a personal name that is Latin.

Dimensions.— Based on 30 specimens (mean): total length without the apical horn: 69–180 μ m (129), length of apical horn (when present): 7–15 μ m (12), length of cephalothorax without the apical horn: 51–84 μ m (72), length of the hyaline proximal part of the abdomen: 18–40 μ m (27), length of lamellar feet: 6–68 μ m (33).

Remarks.— This species differs from *Phormocyrtis embolum* (Ehrenberg, 1874), *P. ligulata* Clark and Campbell, 1942 and *P. striata* Brandt, 1935 by having a subcylindrical sparsely pored abdomen that terminates in lamellar feet, instead of an inverted truncate conical abdomen with

numerous pores and a simple peristome. Additionally, *P. lazari* n. sp. is unique among all *P. striata* subspecies due to the presence of an internal septal band at the lower margin of the thorax. The new species is finally distinguished from *P. proxima* Clark and Campbell, 1942 by its nearly hyaline abdomen terminated by lamellar feet, and from *Phormocyrtis alexandrae* O'Connor, 1997b, *P. ? cubense* Riedel and Sanfilippo, 1971, and *P. turgida* (Krasheninnikov, 1960) in lacking a fourth segment.

According to the stratigraphic data collected at ODP Site 1260, it is suggested that P. lazari n. sp. originated from P. embolum. The latter species disappeared shortly after the first occurrence of P. lazari n. sp. (Figure II.3). The two species share many morphological similarities: towards the end of its age range, P. embolum tends to become more cylindrical, with a subcylindrical to slightly tapered abdomen. This late morphotype of P. embolum corresponds well to the original description of *P. proxima*, supporting the synonymization of these two species. This suggestion was already made by Riedel (1957b), who also included specimens with an abdomen terminated by lamellar teeth, although the original description of P. proxima does not mention the presence of such perioral appendages. A few specimens with an intermediate morphology between P. embolum and P. lazari n. sp. have also been observed at ODP Site 1260, as well as in the Southern Ocean (Hollis et al., 2020, pl. 10, fig. 18). These specimens have a subcylindrical porous abdomen terminated by short lamellar teeth. P. ligulata is also likely related to these taxa. Unfortunately, this species has only been reported from the Pacific Ocean (Clark and Campbell, 1942, 1945; Blueford, 1988) and from the Southern Ocean (O'Connor, 1999b; Hollis et al., 2020), and we were therefore unable to clarify its phylogenetic relationships with *P. embolum* and *P. lazari* n. sp.

Genus Podocyrtis Ehrenberg, 1846

Type species.— *Podocyrtis papalis* Ehrenberg, 1847, p. 55, fig. 2; subsequent designation by Campbell (1954, p. D130).

Podocyrtis (Lampterium) puellasinensis Ehrenberg, 1874

Plate II.26, Figures 9–11

1874 Podocyrtis Puella sinensis [sic] Ehrenberg, p. 252.

1876 Podocyrtis Puella sinensis [sic] Ehrenberg – Ehrenberg, p. 82, pl. 14, fig. 3.

1882a Cycladophora Puella sinensis [sic] Ehrenberg – Bütschli, p. 527.

1887 Clathrocyclas (Clathrocyclia) puella [sic] (Ehrenberg) – Haeckel, p. 1387.

2009 Podocyrtis puella-sinensis [sic] Ehrenberg – Ogane et al., pl. 48, figs. 9a–9f.

Holotype.— No holotype was designated by Ehrenberg in the original description of the species. However, the specimen he drew (1876, pl. 14, fig. 3), which was later re-illustrated by Ogane et al. (2009, pl. 48, figs. 9a–9f) during their re-examination of Ehrenberg's collection kept in the Museum für Naturkunde, Humboldt University (Berlin, Germany), is a potential lectotype.

Diagnosis.—*Podocyrtis* species with a two-segmented shell, and a well-defined cephalic hole that is delimited by a thick hyaline rim.

Occurrence.— From the upper part of the *Podocyrtis* (*P*.) *ampla* Zone, to the end of the studied interval, which is situated in the lower part of the *Podocyrtis* (*L*.) *goetheana* Zone.

Description.— Shell two-segmented and robust. Cephalis trilobed, with one large unpaired eucephalic lobe, and two small paired lobes dorsally positioned. Cephalic pores subcircular to quadrate, irregular in size and randomly arranged. Apical horn as long as the cephalis, triangular, with a large cephalic hole circumscribed by a thick hyaline rim. Thorax truncate conical to globular, perforated by subcircular pores of various sizes, usually hexagonally framed, and much larger than the cephalic ones. Thorax ending in a smooth hyaline peristome that is doubled by an internal septum, or more rarely in a crown of very short spines (Plate II.26, Figure 11).



Figure II.3. Stratigraphic ranges and evolutionnary relationships to previously described species of four of the new species described at ODP Site 1260 (Demerara Rise, western equatorial Atlantic). The stratigraphic ranges of *Petalospyris argiscus*, *Petalospyris confluens*, *Petalospyris diaboliscus*, *Lychnocanium babylonis* group¹, and *Phormocyrtis embolum* at ODP Site 1260 are presented according to Meunier and Danelian (2022). Geomagnetic timescale after calibration of Suganuma and Ogg (2006), and radiolarian biozonation after Meunier and Danelian (2022). (1 – Lychnocanium tribulus (Ehrenberg, 1874) group in Chapter II.2).
Dimensions.— Based on 18 specimens (mean): length of cephalothorax without the apical horn: 65–90 μ m (78), length of apical horn 27–51 μ m (41), maximum breadth of shell: 66–92 μ m (78).

Remarks.— *Podocyrtis* (*L*.) *puellasinensis* Ehrenberg, 1874 is distinguished from all other *Podocyrtis* species by its two-segmented shell, and its well-developed cephalic hole.

We have decided to retain P. (L.) puellasinensis in the genus Podocyrtis, despite the absence of an abdominal segment in this species, which contradicts the diagnosis of the genus (O'Dogherty et al., 2021). This decision was based on the strong morphological similarities between P. (L.) puellasinensis and the cephalothorax of the latter members of the subgenus Lampterium, such as P. (L.) chalara Riedel and Sanfilippo, 1970 and P. (L.) goetheana [Haeckel, 1887]). See Plate II.26, Figure 12 for a comparison with a typical *P*. (*Lampterium*) cephalothorax. This unexpected resemblance is noteworthy, especially considering that the first occurrence of P. (L.) puellasinensis dates back to 43.36 Ma at ODP Site 1260, about 2.2 Ma earlier than the first occurrence of P. (L.) chalara (41.15 Ma; Meunier and Danelian, 2022). Therefore, the origin of P. (L.) puellasinensis is difficult to decipher. The most suitable candidate is likely P. (L.) sinuosa Ehrenberg, 1874, despite its thorax being more campanulate and penetrated by smaller pores. In this case, P. (L.) puellasinensis would be an offshoot of the lineage from P. (L.) sinuosa to P. (L.) mitra, and for this reason, it is placed in the subgenus Lampterium. In their taxonomic review, O'Dogherty et al. (2021) recognized the subgenus Lampterium as a distinct genus and suggested the following combinations: Lampterium chalara (Riedel and Sanfilippo, 1970) and L. (L.) goetheana (Haeckel, 1887). We disagree with this view because the Lampterium evolutionary lineage that leads from P. (L.) acalles Sanfilippo and Riedel, 1992 to P. (L.) goetheana has been amply demonstrated in previous studies (e.g., Riedel and Sanfilippo, 1970; Sanfilippo and Riedel, 1992), and this taxonomic change would imply that the genus *Podocyrtis* is paraphyletic. An alternative hypothesis to explain the particular morphology of *P*. (*L*.) *puellasinensis* is that this species is the expression of an early stage in the development of the *Podocyrtis* shell, known as neoteny.

II.3.1.4. Conclusions

Examination of middle Eocene sedimentary sequences from the equatorial Atlantic Ocean allowed the description of 15 new radiolarian species and the re-illustration of ffour species that have been rarely seen since their original description in early radiolarian studies. With the exception of a few sporadic species (*Petalospyris castanea* n. sp., *Pterocyrtidium eep* n. sp., *Cymaetron*? *dilatatus* n. sp. and *Velicucullus armatus* n. sp.), the taxa reported here have a continuous range in the studied interval and can therefore be included in future biostratigraphic studies. Although the studied interval is relatively limited and did not allow the total range of most of these species to be determined, a total of 23 radiolarian bioevents are documented, including 14 first occurrences and nine last occurrences. Orbitally tuned ages are provided for these bioevents through direct calibration to the Astronomical Time Scale, increasing the number of biostratigraphic tiepoints available for the equatorial Atlantic Ocean.

Several new species described here show strong morphological similarities to previously described species, allowing us to suggest phylogenetic hypotheses by integrating stratigraphic data. Despite being fragmentary, these observations are important for establishing new evolutionary lineages, and better understanding the evolutionary dynamics of nassellarians. The documentation of new species has also improved our understanding of the origins of some genera. This is the case of the genus *Aphetocyrtis*, which is now clearly rooted in the tropics, with three new tropical species reported here (*A. zamenhofi* n. sp., *A. ? columboi* n. sp. and *A. ? spheniscus* n. sp.). Likewise, the documentation of *Spirocyrtis ? renaudiei* n. sp.,

an Artostrobiid species with a mixture of characters borrowed from the genera *Botryostrobus* and *Spirocyrtis*, allows to locate the divergence of these two genera shortly before the late middle Eocene. Finally, this study contributed to the addition of new species to the monotypic genera *Albatrossidium* and *Cymaetron*, which have been poorly known and rarely observed since their original description.

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II.3.2. New middle Eocene radiolarian species (Rhizaria, Polycystinea) from Blake Nose, subtropical western North Atlantic Ocean

Mathias Meunier* and Taniel Danelian

Univ. Lille, CNRS, UMR 8198 – Evo-Eco-Paleo, F-59000 Lille, France

<mathias.meunier@univ-lille.fr>

*Corresponding author

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. Are described herein: Periphaena petrushevskavae n. sp. (Phacodiscidae), Stylodictva 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), *Thyrsocyrtis kamikuri* n. sp. (Theocotylidae). Biostratigraphic information is provided for each new species. In addition, we redescribe and illustrate the morphological variability of a remarkable Pterocyrtidium species formerly published by Bütschli (1882a).

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II.3.2.1. 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.

radiolarians were the first to Eocene receive sustained attention from micropaleontologists, with the description of several hundred species from siliceous-rich chalk beds cropping on the Barbados Island (Ehrenberg, 1839; 1846; 1847; 1874, 1876; Haeckel, 1887; Bütschli, 1882a, 1882b). 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 20th 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, many rare morphotypes that are of no interest for biostratigraphic correlations, or those belonging to poorly defined genera and families, were not documented and remain undescribed until recently (i.e., Meunier and Danelian, 2023).

To contribute to our understanding of Paleogene radiolarian diversity, 21 new species distributed amongst 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 they were left in open nomenclature. Biostratigraphic information is provided for each new species, and stratophenetic relationships to previously described species are suggested.

II.3.2.2. 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 at the edge of the Blake Plateau, in the western North Atlantic Ocean (Figure 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/kyr (Norris et al., 1998; Edgar et al., 2010).

The species described in this paper are 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 cm² 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 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 (H₂O₂) to remove organic material. The siliceous residues were finally sieved through a 45 μ m 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).



Figure II.4. 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.

Observation and identification of radiolarians were performed using a Zeiss Axio Imager.A2 transmitted light microscope at 20x 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 \sim 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 species are shown in Figure II.5, and the associated bioevents are summarized in Table II.2.



Figure II.5. 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) and geomagnetic timescale after calibration of Ogg and Bardot (2001). Radiolarian biostratigraphy according to Sanfilippo and Blome (2001), planktonic foraminiferal biostratigraphy according to Norris et al. (1998) and Edgar et al. (2010), and calcareous nannofossil biostratigraphy according to Mita (2001). Abbreviations: mcd, meters composite depth.

Repositories and institutional abbreviations.— All holotypes and figured specimens (Figures 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.

Table II.2. 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)	
	Core - section - interval (cm)	mbsf	mcd
Radiolarian bioevents	Base/top	Base/top	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

II.3.2.3. 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 the different parts of the fundamental nassellarian spicule follows that of Petrushevskaya (1984). See also 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

Genre Periphaena Ehrenberg, 1874

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

Periphaena petrushevskayae new species

Plate II.27, Figures 1-4

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

Holotype.— Plate II.27, Figure 1; collection number USTL 4525–1; coordinates K55/2; sample ODP 171B-1051A-9H-2W, 53–55 cm; *Podocyrtis (L.) chalara* Zone (RP15; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.— Phacodiscid species with a thick equatorial hyaline girdle bearing six to 10 triangular spines of variable length.

Occurrence.— This species 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 welldeveloped 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 (about 10 pores in a radius). Medullary shell double, globular, attached to the cortical shell by a few thick rods.

Etymology.— The specific epithet honours 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), length of equatorial spines: 34–156 μm (76).

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 less 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 Genre *Stylodictya* Ehrenberg, 1846

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

Stylodictya oligodonta new species Plate II.27, Figures 5–8

Holotype.— Plate II.27, Figure 5; collection number USTL 4536–2; coordinates R52/1; sample ODP 171B-1051A-11H-2W, 62–64 cm; lower part of the *Podocyrtis* (*L*.) *chalara* Zone (RP15; Sanfilippo and Blome, 2001); middle Eocene.

Diagnosis.— Small trematodiscid species with less 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 (Plate II.27, Figure 8) to three (Plate II.27, Figure 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 and less numerous on the marginal ring.

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

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

Remarks.— The new species is placed in the genus *Stylodictya* because it has 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 μ m), as well as its short triangular to rounded spines, allow it to be distinguished from all other middle Eocene flattened spumellarians 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

Plate II.27, Figures 9–12

Holotype.— Plate II.27, Figures 9, 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.— 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.— 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 projecting from 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 μ m (13), of outer medullary shell: 38–44 μ m (41), of third shell: 61–73 μ m (67), of cortical shell: 102–118 μ m (108), length of cortical spines: 15–46 μ m (23).

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; figs. 11a, 11b) or 1:7 (Haeckel, 1887; pl. 29, fig. 2). The new species is also distinguished from the middle Miocene specimens illustrated as *E. sphaeroncha* by Sugiyama and Furutani (1992; pl. 12, figs. 1, 2, pl. 16, fig. 3) in having a spherical outer medullary shell.



Plate II.27. 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-9H-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 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 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.

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, Figure 27; subsequent designation by Frizzell and Middour, 1951, p. 33.

Eucyrtidium granatum new species

Plate II.28, Figures 1–4

2015 Eucyrtidium sp. A Kamikuri, pl. 9, figs. 6a, 6b.

Holotype.— Plate II.28, Figure 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 lower part of the *Podocyrtis* (*P*.) *chalara* Zone (RP15) to the lower part of the *Podocyrtis* (*L*.) *goetheana* Zone (RP16).

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 μ m (162), length of apical horn: 12–17 μ m (15), length of cephalothorax: 41–48 μ m (44), length of abdomen: 86–116 μ m (96), length of first post-abdominal segment: 31–45 μ m (38).

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 Plate II.28, Figures 5–8

1973 Theocampe amphora (Haeckel) group – Foreman, p. 431, pl. 9, fig. 8 (part).

2015 Dictyoprora sp. E Kamikuri, pl. 12, figs. 11a, 11b.

Holotype.— Plate II.28, Figure 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 shape and an abdominal segment perforated by 8 to ten closely spaced rows of pores.

Occurrence.— This species is abundant 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, ovoid, and externally smooth. Cephalis subspherical to hemispherical, unarmed, deeply embedded in the thorax. Cephalic pores circular and closely spaced. Ventral pore relatively large, circular to ovoid (Plate II.28, Figures 7, 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 to 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 anteater (echidna), for the shell ornamentation of the new species, which resembles the texture of the back of these animals covered by spines.

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

Remarks.— *Dictyoprora echidna* n. sp. differs from other *Dictyoprora* species in having a large cephalis that 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 three-segmented 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*. These specimens are 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

Plate II.28, Figures 9–12

Holotype.— Plate II.28, Figure 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 upper 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 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 a 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 μ m (164), length of cephalothorax: 38–43 μ m (40), length of apical tube: 8–23 μ m (14), length of abdomen: 20–35 μ m (27); length of all post-abdominal segments: 77–133 μ m (98); maximum breadth of shell: 56–69 μ m (63).

Remarks.— The new species 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 less 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, giving 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, 1882a

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, 1882a

Plate II.28, Figures 13–16

1882a Pterocyrtidium Zitteli [sic] Bütschli, p. 531, pl. 33, figs. 28a, 28b.
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° to 90°. Ventral spine 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 variabke in number and size,



Plate II.28. 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. (13–15) 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, O53/1; (15) hvaline 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.

scattered over the surface (Plate II.28, Figure 13) or quincuncially arranged (Plate II.28, Figure 14). 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 μ m (64), length of secondary branch of the apical horn (when present): 14–51 μ m (32), length of ventral horn (when present): 18–55 μ m (33), length of wings (when present): 13–67 μ m (36), total length without the apical horn: 87–192 μ m (127), length of cephalothorax without the apical horn: 57–88 μ m (76), length of abdomen: 31–114 μ m (60).

Remarks.— Pterocyrtidium zitteli Bütschli, 1882a 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 examinated (see Plate II.28, Figures 15, 16), possibly represeting juvenile specimens or aberrant forms.

Superfamily Acanthodesmioidea Haeckel, 1862

Family Cephalospyrididae Hackel, 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

Plate II.29, Figures 1–4

Holotype.— Plate II.29, Figure 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.

Diagnosis.— Cephalospyridid species with a smooth-surfaced shell pierced 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.— Shell quadrate to cordiform, smooth-surfaced, with a slight sagittal constriction. The sagittal ring appears by transparency as a thick opaque band. Cephalis with a short apical horn and two reduced lateral ones. Ventral side of the cephalis pierced 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 μ m (50), maximum breadth of cephalis: 65–86 μ m (76), length of apical horn (when present): 4–12 μ m (8), length of lateral cephalic horns (when present): 3–6 μ m (4), length of feet: 27–60 μ m (38).

Remarks.— This species is placed in 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 the genus *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 *D. acuta* (Goll, 1968) or *D. lata* (Goll, 1969).

Elaphospyris quadricornis new species

Plate II.29, Figures 5-8

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

Holotype.— Plate II.29, Figure 5; collection number USTL 4517–2; coordinates T47/2; 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.— Cephalospyridid species with a latticed shell and two pairs of lateral cephalic spines.

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 unisegmented, thick-walled, and weakly tuberculate. Sagittal ring D-shaped, dividing the cephalis into two lobes. Cephalis with 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 $\sim 30^{\circ}$ with the sagittal ring; second pair of lateral horns usually longer and stronger, forming an angle of $\sim 90^{\circ}$ 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: $45-103 \mu m$ (74), maximum breadth of cephalis: $58-99 \mu m$ (80), length of apical horn: $6-49 \mu m$ (25), length of first pair of

lateral cephalic horns: $8-50 \ \mu m$ (33), length of second pair of lateral cephalic horns: $19-58 \ \mu m$ (39), length of feet: $27-116 \ \mu m$ (69).

Remarks.— Elaphospyris quadricornis n. sp. is placed in the genus *Elaphospyris* because of the general morphology of its shell, which is very similar to that of *E. didiceros* (Ehrenberg, 1874). *E. 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, 1882a, 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

Plate II.30, Figures 1-4

Holotype.— Plate II.30, Figure 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 roughened by slender spines arising from the intervening pore bars (e.g., Plate II.30, Figure 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 (Plate II.30, Figures 2–4) or flanked by a few long conical spines (Plate II.30, Figure 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: $121-227 \ \mu m$ (159), length of apical horn: $8-41 \ \mu m$ (22), maximum breadth of cephalothorax: $57-163 \ \mu m$ (93).

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. The new species 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

Plate II.29, Figures 9–12

Holotype.— Plate II.29, Figure 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 (Plate II.29, Figure 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 (Plate II.29, Figure 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 7 specimens (mean): length of cephalothorax without the cephalic spines: $97-78 \ \mu m$ (88), length of eucephalic lobe: $28-33 \ \mu m$ (31), length of ante-cephalic lobe: $36-40 \ \mu m$ (38), length of cephalic spines: $13-39 \ \mu m$ (25), length of thorax: $42-61 \ \mu m$ (51).

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

Plate II.29, Figures 13-16

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.



Plate II.29. 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 μ m.

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 μ m (27), height of antecephalic lobe without the apical tube: 20–26 μ m (23), length of apical tube: 8–33 μ m (22), length of ventral tube: 14–42 μ m (29), length of thorax: 33–60 μ m (48).

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

Plate II.30, Figures 5-8

1975 Lychnocanium sp. Chen, p. 462, pl. 1, figs. 8, 9.

2020 Lychnocanium tripodium Ehrenberg – Hollis et al., pl. 14, figs. 8–10b.

Holotype.— Plate II.30, Figure 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.— This species 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 crosssection. They are more than twice as long as the thorax and extend from the peristome.

Etymology.— This species is 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 μ m (32), length of cephalis without the apical horn: 21–33 μ m (27), length of thorax: 45–72 μ m (56), length of feet: 131–256 μ m (164).

Remarks.— Lychnocanium cheni n. sp. is distinguishable 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 or 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 larger 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

Plate II.30, Figures 9–12

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

Holotype.— Plate II.30, Figure 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.— This species 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 height of the cephalis. Collar stricture distinct. Thorax subspherical, pierced 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.

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 μ m (36), length of cephalis without the apical horn: 19–30 μ m (24), length of thorax: 46–80 μ m (61), thickness of peristome: 5–12 μ m (8), length of feet: 44–121 μ m (84).

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

Plate II.31, Figures 1-4

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

Holotype.— Plate II.31, Figure 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.— This species 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, with 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 (Plate II.31, Figure 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: $101-123 \ \mu m \ (112)$, length of cephalis without the apical horn: $19-26 \ \mu m \ (23)$, length of apical horn: $7-23 \ \mu m \ (16)$, length of thorax: $79-98 \ \mu m \ (89)$, maximum breadth of thorax: $67-78 \ \mu m \ (73)$, length of feet (when present): $10-12 \ \mu m \ (11)$.

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 Plate II.30, Figures 13–16

Holotype.— Plate II.30, Figure 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.— This species 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, inwardly curved, and 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 name of the European earwig (*Forficula auricularia* L.), whose male forceps are curved like the feet of the new species.



Plate II.30. 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 4536-3, Q70/4; (15) 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.

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

Remarks.— Lychnocanium forficula n. sp. differs from the similar-looking species *L. cypselus* Ehrenberg, 1874 in having a truncate conical thorax instead of 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). *L. 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 instead of four divergent feet, and from *L. cheni* n. sp., *L. cingulatum* n. sp. and *L. tripodium* Ehrenberg, 1874 in having curved feet instead of straight, subparallel feet. The new species also differs

from *L. carinatum* Ehrenberg, 1874, *L. continuum* Ehrenberg, 1874 and *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

Plate II.31, Figures 5–8

2015 Eucyrtidium ? sp. D Kamikuri, pl. 9, figs. 9a, 9b.

Holotype.— Plate II.31, Figure 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, with 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 the same length the thorax, or slightly shorter. Abdominal pores less regular in size and shape compared to the thoracic ones, tending toward longitudinal arrangement. All observed specimens have an abdomen that terminates in an undifferentiated, ragged margin.

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

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

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

Plate II.31, Figures 9–12

not 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.— Plate II.31, Figure 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 (Plate II.31, Figures 10, 11). The thickness of the shell and the poorly developed external

furrows can make the cephalic lobes difficult to distinguish. The cephalis is also slightly embedded in the thorax, giving the species the appearance of a carpocaniid. A short, broadbased 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 judokas.

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

Remarks.— 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.

The new species differs from the lectotype of *Cr. ornatum* (Ehrenberg, 1874) designated by O'Dogherty et al. (2021) in having a symmetrical cephalis with a short apical horn instead of a hornless asymmetrically placed cephalis, and in having more thoracic pores (~10 in a longitudinal row). *Cr.* ? *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



Plate II.31. 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.

Sanfilippo, 1971 by having a subcylindrical thorax and abdomen, instead of an inflated thorax and a tapered abdomen, and from *Ca. bramlettei* Riedel and Sanfilippo, 1971 by having a porous abdomen. *Cr.*? *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

Plate II.31, Figures 13–16

Holotype.— Plate II.31, Figure 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.— This species 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 pierced by a few subcircular pores, with 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 (Plate II.31, Figures 15, 16) or surrounded by a few short, triangular, or rectangular spines (Plate II.31, Figures 13, 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 μ m (10), length of cephalis without the apical horn: 16–29 μ m (23), length of thorax: 36–67 μ m (51), length of lamellar teeth: 11–30 μ m (19).

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

Plate II.32, Figures 1–4

Holotype.— Plate II.32, Figure 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.— This species 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 (Plate II.32, Figures 1, 2). Mitral arches depart from the apical spine in the middle of the cephalis and quickly diverge at a great angle (Plate II.32, Figure 4). The collar stricture is indicated by a change in the contour of the shell. Thorax hemispherical to inflated, penetrated by subcircular pores that are irregular in size and shape 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 μ m (103), length of cephalis without the apical horn: 17–25 μ m (14), length of apical horn: 7–18 μ m (14), length of ventral horn (when present): 4–10 μ m (7), length of thorax: 27–40 μ m (32), maximum breadth of thorax: 47–60 μ m (56), length of abdomen: 33–60 μ m (49), maximum breadth of abdomen: 62–81 μ m (68).

Remarks.— Apoplanius cryptodirus n. sp. is assigned to the genus *Apoplanius* on the basis of its simple, short apical horn without three proximal openings, and its apical spine, which is partially embedded in the cephalic wall (Sanfilippo and Caulet, 1998; O'Dogherty et al., 2021). The new species differs from *A. asperus* (Ehrenberg, 1874) and *A. nomas* (Sanfilippo and Caulet, 1998) in having a less swollen 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 instead of 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

Plate II.32, Figures 5–7

Holotype.— Plate II.32, Figure 5; collection number USTL 4566–2; coordinates N61/4; 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.— 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*.) *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 (Plate II.32, Figure 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, variable 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 μ m (133), length of cephalis without the apical horn: 19–26 μ m (22), length of apical horn: 32–47 μ m (37), length of thorax: 32–47 μ m (37), maximum breadth of thorax: 47–72 μ m (54), length of abdomen: 55–90 μ m (74).

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). This new species differs from all other documented lophocyrtiid species in having a thick-walled hyaline thorax. *A. hyalinus* n. sp. shares many characteristics with *A. kerasperus* (Sanfilippo and Caulet, 1998) (Plate II.32, Figure 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* Riedel and Sanfilippo, 1970 var. A (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

Plate II.32, Figures 9–12

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

Holotype.— Plate II.32, Figure 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 with three short, perforated feet.

Chapter II - Progress on middle Eocene radiolarian biodiversity



Plate II.32. 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 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.

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, conical to campanulate. Cephalis small, hemispherical, sparsely perforated, 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 by a constriction and a thin internal ridge. Abdomen inflated to truncate conical, wider and longer than the thorax, with 8–10 pores per 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.— This species 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 μ m (194), length of apical horn: 13–55 μ m (45), length of cephalis without the apical horn: 20–29 μ m (24), length of thorax: 41–75 μ m (63), maximum breadth of thorax: 90–125 μ m (102),

length of abdomen: 76–138 μ m (106), maximum breadth of abdomen: 114–193 μ m (153), length of feet: 34–70 μ m (56).

Remarks.— Thyrsocyrtis kamikuri n. sp. differs from *T. lochites* (Sanfilippo and Riedel, 1982), *T. orthotenes* Nigrini et al., 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. *T. kamikuri* n. sp. also differs from *T. norrisi* Sanfilippo and Blome, 2001 in not having a flared peristome and an unserrated apical horn. Finally, the new species 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.

II.3.2.4. Conclusions

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 redescribe 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. A total of 14 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 *L. cheni* n. sp. which is known from the Naturaliste Plateau (DSDP Site 264), the new species described here have never been reported before 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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Chapter III – Progress on late middle Eocene radiolarian biostratigraphy

This chapter consists of a single article titled "Astronomical calibration of late middle Eocene radiolarian bioevents from ODP Site 1260 (equatorial Atlantic, Leg 207) and refinement of the global tropical radiolarian biozonation", published in the Journal of Micropalaeontology, and available online at DOI: <u>https://doi.org/10.5194/jm-41-1-2022</u>.

Astronomical calibration of late middle Eocene radiolarian bioevents from ODP Site 1260 (equatorial Atlantic, Leg 207) and refinement of the global tropical radiolarian biozonation

Mathias Meunier* and Taniel Danelian

Univ. Lille, CNRS, UMR 8198 – Evo-Eco-Paleo, F-59000 Lille, France <mathias.meunier@univ-lille.fr> *Corresponding author

Abstract

The middle Eocene sedimentary sequence drilled at Ocean Drilling Program Site 1260 (Leg 207), Demerara Rise, western equatorial Atlantic, yielded a rich and diverse radiolarian fauna. The expanded and complete sedimentary record of this site, as well as the existence of an orbital chronological framework, allowed us to study a series of radiolarian bioevents with a very fine temporal resolution. We have compiled a well-resolved sequence of 71 radiolarian bioevents and provided calibrations to the geomagnetic polarity timescale and the astronomical timescale. Comparison of the radiolarian successions at ODP Site 1260A with the northwestern Atlantic IODP Site U1403 and the IODP Sites U1331, U1332, and 1333, situated in the eastern equatorial Pacific, allowed the demonstration of the synchroneity of primary radiolarian bioevents that underpin the middle Eocene zonal scheme. Several secondary bioevents were also found to be synchronous between the two oceans and were therefore used to define seven new subzones for the low-latitude middle Eocene sequences: Dictyomitra parva interval subzone (RP13a), Coccolarnacium periphaenoides interval subzone (RP13b), Artostrobus quadriporus interval subzone (RP14a), Sethochytris triconiscus interval subzone (RP14b), Podocyrtis (P.) apeza interval subzone (RP14c), Rhopalosyringium? biauritum interval subzone (RP15a), and Thyrsocyrtis (P.) krooni¹ interval subzone (RP15b). This refined radiolarian biozonation has significantly improved stratigraphic resolution and age control for the late middle Eocene interval (an average of two subzones per 1.5 million years). A substantial diachronism was also found in 20 secondary radiolarian bioevents between the two oceans. The majority of radiolarian species appear to have evolved first in the equatorial Atlantic Ocean and subsequently in the equatorial Pacific. However, the reasons for this pattern of diachroneity are currently uncertain and would require a greater sampling coverage to be elucidated.

¹ Thyrsocyrtis (Pentalocorys) parvipes (Ehrenberg, 1874) in Chapter II.2.

III.1. Introduction

Accurate chronostratigraphic frameworks are essential to decipher past Earth system processes and events, as well as the complex history of life on Earth. Amongst the biostratigraphically important Cenozoic marine microfossils, polycystine radiolaria offer major advantages for dating and correlating marine sediments because they are commonly preserved in the fossil record, they are globally distributed, and have experienced high rates of evolution (De Wever et al., 2001). They are particularly useful in oceanic basins where carbonate fossils are absent or poorly preserved (Lazarus, 2005). Due to old misconceptions about their evolution, radiolarians have long been neglected as they were considered to be long-ranging species of no biostratigraphic value. Riedel (1957b) was the first to emphasize the value of Cenozoic radiolarians for biostratigraphy, based on the study of deep-sea cores collected during the Swedish Deep-Sea Expedition. The subsequent advent of scientific ocean drilling campaigns improved deep-sea sediment recovery and allowed extensive studies of radiolarian assemblages, leading to the establishment of the first tropical radiolarian biozonation for the Cenozoic (Riedel and Sanfilippo, 1970, 1971, 1978; Foreman, 1973; Sanfilippo and Riedel, 1973; Nigrini, 1974; Sanfilippo et al., 1985). Paleocene zones and subzones were later added by Nishimura (1987, 1992) and Hollis (1993) based on material from higher latitudes. Sanfilippo and Nigrini (1998b) revised the tropical biozonation and introduced an alphanumeric code for the Cenozoic (RP1-RP22 for the Paleogene) to facilitate correlation with other microfossil groups.

Radiolarian bioevents defining the Paleogene zones were finally calibrated to the geomagnetic polarity timescale (Kamikuri et al., 2012a; de Souza et al., 2017, 2021; Hollis et al., 2020). Absolute ages were provided by Kamikuri et al. (2012a) for 226 early Eocene to late Oligocene radiolarian bioevents recorded in the equatorial Pacific Ocean by using age-depth models based on magnetostratigraphy. For their part, Hollis et al. (2020) provided absolute ages

for 99 middle Paleocene to middle Eocene radiolarian bioevents by using age-depth models based on magnetobiochronology. The recent development of an orbitally calibrated stratigraphy for the Paleogene (Westerhold et al., 2012, 2014, 2015; Westerhold and Röhl, 2013; Boulila et al., 2018) opens new prospects for precise calibration of radiolarian bioevents, especially for the equatorial Atlantic, which remains less well documented and calibrated than the equatorial Pacific.

Here, we present a detailed biostratigraphic analysis of the middle Eocene radiolarian record from Ocean Drilling Program (ODP) Site 1260, drilled on Demerara Rise (western equatorial Atlantic Ocean). This site provided a remarkably complete and continuous middle Eocene sedimentary sequence containing a rich record of both siliceous and carbonate microfossils. A very well-defined framework in terms of both magnetostratigraphy and cyclostratigraphy is now available for this site (Westerhold and Röhl, 2013). Thus, the main objective of this study was to refine the absolute ages of middle Eocene radiolarian bioevents through high-resolution faunal analysis of ODP Site 1260 and direct correlation with the geomagnetic polarity and astronomical timescales. We documented the stratigraphic distribution of radiolarian species at this site, including some species described in very early studies (i.e., Ehrenberg, 1874) and rarely reported since. The absolute ages of radiolarian bioevents derived from ODP Site 1260 were then compared to previous biostratigraphic studies conduced at three low-latitude sites in the Pacific (Kamikuri et al., 2012a) and one mid-latitude site in the Atlantic (Hollis et al., 2020) to assess the degree of synchroneity of radiolarian bioevents between the equatorial Atlantic and Pacific oceans, and between the low and middle latitudes of the Atlantic Ocean.

III.2. Material and methods

All observed samples were collected at ODP Site 1260 (9°16'N, 54°32'W) located on the northwestern margin of Demerara Rise, a submarine plateau off the coast of Suriname and French Guiana (Figure III.1). The site is inferred to have been closer to the equator during the middle Eocene than it is today (paleolatitude of ~1°N; Suganuma and Ogg, 2006). Two closely spaced holes (1260A and 1260B) were drilled using rotary coring, starting at a modern water depth of 2549 m below sea level. A nearly continuous record of an expanded Albian–Oligocene



Figure III.1. Middle Eocene (ca. 40 Ma) paleogeographic map showing the location of Demerara Rise (ODP Site 1260, Leg 207) (solid circle) and the four equatorial Pacific and North Atlantic IODP sites used for comparison (open circles). Paleogeographic reconstruction drawn after ODSN Plate Tectonic Reconstruction Service (<u>http://www.odsn.de/odsn/services/p</u> <u>aleomap/paleomap.html</u>, last access: 8 January 2021).

sequence was recovered (Shipboard Scientific Party, 2004). The middle Eocene interval of the site is characterized by nannofossil chalk, rich in biogenic silica (i.e., opal), with abundant and well-preserved radiolarian fauna (Danelian et al., 2005, 2007) and some other siliceous microfossil groups, including diatoms (Renaudie et al., 2010), ebridians, silicoflagellates, and sponge spicules. The studied sequence is 91.72 m thick and accumulated in only 3.94 million years, between 43.78 and 39.84 Ma (sedimentation rate estimated at ~2.3 cm/kyr), during the

late middle Eocene (middle Lutetian to early Bartonian). A total of 55 samples were selected from hole 1260A. Sampling was as regular as possible in order to avoid any bias associated with heterogeneous bin durations. The average sample spacing is approximately 1.67 m, and the average age difference between two consecutive samples is ~71 600 years.

An excellent age control for ODP Site 1260 was provided by Westerhold and Röhl (2013), who developed a high-resolution astronomical timescale for this site based on iron (Fe) intensity data obtained by X-ray fluorescence core scanning. Orbitally tuned ages were used to date each sample, and for intervals where no data were available from hole 1260A, the absolute sample ages were estimated from tuned ages provided for samples situated at the same depth in hole 1260B.

Sample preparation followed the protocol described in Sanfilippo et al. (1985). Samples were first soaked in hydrogen peroxide (H₂O₂), and then in hydrochloric acid (HCl) to remove organic matter and carbonate content, respectively. Residues were washed several times through a 45 μ m sieve to remove clay, small radiolarian fragments, and diatom frustules, and then dried overnight at ~40°C. For each sample, one to four slides were prepared by homogeneously spreading ~5 mg of cleaned residue on a coverslip according to the method described by Witkowski et al. (2012). After drying, the coverslips were mounted on standard glass slides using Norland Optical Adhesive 61 (refractive index 1.56). Species identification was perforemed using a Zeiss Axio Imager.A2 as a light microscope (20× objective lens) equipped with a Zeiss AxioCam ERe5s digital camera. For each specimen illustrated, a series of 5 to 10 images taken at slightly different focal depths were stacked using Helicon Focus v.7.6.6 (HeliconSoft) in order to obtain a composite image of the entire shell. Specimens mounted on a slide were identified to species level where possible. However, as many of the morphotypes encountered have not yet been formally described, most of them were not included in this study.

III.3. Results

III.3.1. Radiolarian bioevents at hole 1260A

Radiolarians are abundant and well-preserved throughout the studied middle Eocene sequence. The assemblages are taxonomically diverse, with at least 29 families recognized according to the latest classification provided by Suzuki et al. (2021). The stratigraphic distribution of 61 species, whose first or last occurrence falls within the studied interval, is shown in Figure III.2, and all species are illustrated in Plates III.1–III.3. A total of 71 bioevents were recognized in hole 1260A (~1.8 events per 100 kyr), including 38 first occurrences (FOs), 29 last occurrences (LOs), and four evolutionary transitions (ETs). These bioevents are summarized in Table III.1, with their calibrated age in hole 1260A.



Figure III.2. Range chart of 61 selected radiolarian species from the middle Eocene of ODP hole 1260A. Geomagnetic timescale after calibration of Suganuma and Ogg (2006). (1 – *Lithochytris pyramidalis* Ehrenberg in Chapter II.2; 2 – *Lychnocanium tribulus* (Ehrenberg) group in Chapter II.2; 3 – *Histiastrum coronatum* Haeckel in Chapter II.2; 4 – *Thyrsocyrtis (P.) parvipes* (Ehrenberg) in Chapter II.2).

Table III.1. Summary of first occurrences (FOs), last occurrences (LOs), and evolutionary transitions (ETs) at ODP Site 1260, drilled on Demerara Rise in the western equatorial Atlantic. Estimated ages and revised meter composite depth (rmcd) are after Westerhold and Röhl (2013). Primary bioevents that define the boundaries of radiolarian zones and subzones, are shown in bold.

		(0		Kamikuri et al., 2012 (IODP Sites U1331-1333)		Hollis et al., 2020 (IODP Site U1403)		
Zones	Padialarian bioavants	Core - section - interval (cm)	Depth (rmcd)	Tuned age (Ma)		Age (Ma)*	Revised age (Ma)**	Age (Ma)
Zones	Kaulolai lan blocvents	Base / Top	Base / Top	Base / Top	Midpoint			
RP16	FO Dictyopodium aff. oxylophus	6R-2W, 55-57 / 6R-1W, 55-57	40.25 / 38.75	39.91 / 39.84	39.87	-	-	-
	FO Dorcadospyris anastasis	6R-2W, 55-57 / 6R-1W, 55-57	40.25 / 38.75	39.91 / 39.84	39.87	39.30	40.20	-
	FO Thyrsocyrtis (P.) tetracantha	6R-3W, 55-57 / 6R-2W, 55-57	41.75 / 40.25	39.97 / 39.91	39.94	38.10	39.10	-
	FO Petalospyris diaboliscus	6R-4W, 55-57 / 6R-3W, 55-57	43.25 / 41.75	40.04 / 39.97	40.01	-	-	-
	LO Podocyrtis (L.) mitra	6R-4W, 55-57 / 6R-3W, 55-57	43.25 / 41.75	40.04 / 39.97	40.01	39.20	40.00	-
	LO Lychnocanium babylonis group ¹	6R-4W, 55-57 / 6R-3W, 55-57	43.25 / 41.75	40.04 / 39.97	40.01	-	-	-
	LO Anthocyrtoma spp.	6R-5W, 55-57 / 6R-4W, 55-57	44.75 / 43.25	40.11 / 40.04	40.08	37.90	38.20	-
	LO Dictyophimus craticula	6R-5W, 55-57 / 6R-4W, 55-57	44.75 / 43.25	40.11 / 40.04	40.08	38.30	39.10	-
	LO Histiastrum quaternarium	6R-5W, 55-57 / 6R-4W, 55-57	44.75 / 43.25	40.11 / 40.04	40.08	-	-	-
	LO Lithochytris vespertilio ²	6R-5W, 55-57 / 6R-4W, 55-57	44.75 / 43.25	40.11 / 40.04	40.08	39.10	39.80	-
	FO Periphaena pentasteriscus	6R-5W, 55-57 / 6R-4W, 55-57	44.75 / 43.25	40.11 / 40.04	40.08	-	-	-
	LO Theocotylissa ficus	6R-6W, 55-57 / 6R-5W, 55-57	46.25 / 44.75	40.19 / 40.11	40.15	37.90	38.20	-
	FO Podocyrtis (L.) goetheana	7R-1W, 54-56 / 6R-6W, 55-57	48.54 / 46.25	40.32 / 40.19	40.26	39.30	40.10	-
RP15	FO Lithocyclia aristotelis group	7R-3W, 54-56 / 7R-2W, 54-56	51.54 / 50.04	40.48 / 40.40	40.44	38.80	39.60	-
	LO Rhopalosyringium? auriculaleporis	7R-4W, 54-56 / 7R-3W, 54-56	53.04 / 51.54	40.57 / 40.48	40.52	-	-	-
	FO Thyrsocyrtis (P.) krooni ³	7R-6W, 54-56 / 7R-4W, 54-56	56.04 / 53.04	40.73 / 40.57	40.65	38.10	39.10	-
	LO Rhopalosyringium ? biauritum	8R-3W, 54-56 / 7R-6W, 54-56	61.24 / 56.04	40.96 / 40.73	40.84	40.00	40.40	40.73
	FO Apoplanius klydus	8R-3W, 54-56 / 7R-6W, 54-56	61.24 / 56.04	40.96 / 40.73	40.84	-	-	-
	LO Petalospyris flabellum	8R-5W, 54-56 / 8R-3W, 54-56	64.24 / 61.24	41.07 / 40.96	41.02	-	-	-
	FO Dictyoprora armadillo group	8R-6W, 54-56 / 8R-5W, 54-56	65.74 / 64.24	41.12 / 41.07	41.10	-	-	-
	FO Dorcadospyris ombros	8R-6W, 54-56 / 8R-5W, 54-56	65.74 / 64.24	41.12 / 41.07	41.10	41.40	42.10	-
	FO Dictyopodium aff. eurylophus	9R-1W, 55-57 / 8R-6W, 54-56	66.85 / 65.74	41.18 / 41.12	41.15	-	-	-
	FO Podocyrtis (L.) chalara	9R-1W, 55-57 / 8R-6W, 54-56	66.85 / 65.74	41.18 / 41.12	41.15	41.00	41.90	-
	ET Podocyrtis mitra \rightarrow P. chalara	9R-1W, 55-57 / 8R-6W, 54-56	66.85 / 65.74	41.18 / 41.12	41.15	40.50	41.20	-
RP14	LO Phormocyrtis embolum	9R-5W, 55-57 / 9R-4W, 55-57	72.85 / 71.35	41.40 / 41.34	41.37	-	-	-
	LO Podocyrtis (L.) trachodes	9R-5W, 55-57 / 9R-4W, 55-57	72.85 / 71.35	41.40 / 41.34	41.37	40.60	40.80	41.13
	LO Theocorys ? scolopax	9R-6W, 55-57 / 9R-5W, 55-57	74.35 / 72.85	41.46 / 41.40	41.43	-	-	-
	FO Dendrospyris fragoides	10R-3W, 55-57 / 10R-1W, 55-57	80.33 / 77.33	41.73 / 41.59	41.66	-	-	-
	LO Lychnocanium pileatum	10R-5W, 55-57 / 10R-3W, 55-57	83.33 / 80.33	41.85 / 41.73	41.79	-	-	-
	LO Lophocyrtis alauda	10R-5W, 55-57 / 10R-3W, 55-57	83.33 / 80.33	41.85 / 41.73	41.79	-	-	-
	LO Podocyrtis (P.) ampla	10R-5W, 55-57 / 10R-3W, 55-57	83.33 / 80.33	41.85 / 41.73	41.79	41.20	41.50	-
	FO Podocyrtis (P.) apeza	10R-5W, 55-57 / 10R-3W, 55-57	83.33 / 80.33	41.85 / 41.73	41.79	41.00	41.90	41.94
	LO Podocyrtis (L.) fasciolata	10R-5W, 55-57 / 10R-3W, 55-57	83.33 / 80.33	41.85 / 41.73	41.79	41.20	41.80	42.11
	LO Zealithapium anoectum	10R-5W, 55-57 / 10R-3W, 55-57	83.33 / 80.33	41.85 / 41.73	41.79	41.20	41.50	42.11
	FO Zealithapium mitra	10R-5W, 55-57 / 10R-3W, 55-57	83.33 / 80.33	41.85 / 41.73	41.79	41.00	41.60	-
	FO Dictyoprora ovata group	11R-3W, 55-57 / 11R-2W, 55-57	89.55 / 88.05	42.12 / 42.05	42.08	-	-	-

(Table III.1. continued)

	- Radiolarian bioevents	(Kamikuri et al., 2012 (IODP Sites U1331-1333)		Hollis et al., 2020 (IODP Site U1403)			
Zones		Core - section - interval (cm)	Depth (rmcd)	Tuned age (Ma)		Age (Ma)*	Revised age (Ma)**	Age (Ma)
		Base / Top	Base / Top	Base / Top	Midpoint			
RP14	FO Sethochytris triconiscus	11R-3W, 55-57 / 11R-2W, 55-57	89.55 / 88.05	42.12 / 42.05	42.08	41.30	42.10	-
	LO Podocyrtis (L.) sinuosa	11R-4W, 55-57 / 11R-3W, 55-57	91.05 / 89.55	42.18 / 42.12	42.15	42.40	41.90	43.06
	LO Pterocyrtidium barbadense	11R-6W, 55-57 / 11R-5W, 55-57	94.05 / 92.55	42.30 / 42.24	42.27	-	-	-
	FO Histiastrum sp. A ⁴	11R-7W, 55-57 / 11R-6W, 55-57	95.55 / 94.05	42.37 / 42.30	42.33	-	-	-
	FO Podocyrtis (L.) fasciolata	12R-1W, 55-57 / 11R-7W, 55-57	96.15 / 95.55	42.41 / 42.37	42.39	42.90	43.60	43.80
	FO Podocyrtis (L.) trachodes	12R-1W, 55-57 / 11R-7W, 55-57	96.15 / 95.55	42.41 / 42.37	42.39	41.90	43.00	42.65
	FO Theocorys anapographa var. A	12R-1W, 55-57 / 11R-7W, 55-57	96.15 / 95.55	42.41 / 42.37	42.39	-	-	-
	LO Eusyringium lagena	12R-1W, 55-57 / 11R-7W, 55-57	96.15 / 95.55	42.41 / 42.37	42.39	41.40	41.80	42.32
	LO Zealithapium plegmacantha	12R-1W, 55-57 / 11R-7W, 55-57	96.15 / 95.55	42.41 / 42.37	42.39	41.20	41.80	42.11
	FO Dorcadospyris confluens	12R-3W, 55-57 / 12R-2W, 55-57	99.15 / 97.65	42.54 / 42.48	42.51	-	-	-
	FO Dictyoprora pirum	12R-6W-55-57 / 12R-5W-55-57	103.65 / 102.15	42.73 / 42.66	42.69	-	-	-
	LO Dendrospyris golli	13R-1W, 54-55 / 12R-6W-55-57	105.24 / 103.65	42.79 / 42.73	42.76	-	-	-
	LO Coccolarnacium periphaenoides	13R-2W, 54-55 / 13R-1W, 54-55	106.74 / 105.24	42.86 / 42.79	42.82	-	-	-
	LO Entapium regulare	13R-2W, 54-55 / 13R-1W, 54-55	106.74 / 105.24	42.86 / 42.79	42.82	-	-	-
	FO Apoplanius asperus group	13R-2W, 54-55 / 13R-1W, 54-55	106.74 / 105.24	42.86 / 42.79	42.82	-	-	-
	FO Apoplanius kerasperus	13R-2W, 54-55 / 13R-1W, 54-55	106.74 / 105.24	42.86 / 42.79	42.82	-	-	-
	FO Artophormis ? barbadensis	13R-5W, 54-56 / 13R-4W, 55-56	111.24 / 109.75	43.01 / 42.96	42.98	-	-	-
	FO Carpocanopsis ornata	13R-5W, 54-56 / 13R-4W, 55-56	111.24 / 109.75	43.01 / 42.96	42.98	40.90	41.60	41.86
	FO Podocyrtis (L.) mitra	13R-5W, 54-56 / 13R-4W, 55-56	111.24 / 109.75	43.01 / 42.96	42.98	43.20	43.90	44.29
	ET Podocyrtis sinuosa \rightarrow P. mitra	13R-5W, 54-56 / 13R-4W, 55-56	111.24 / 109.75	43.01 / 42.96	42.98	42.50	43.20	-
RP13	FO Artostrobus quadriporus	13R-6W, 54-56 / 13R-5W, 54-56	112.74 / 111.24	43.05 / 43.01	43.03	-	-	-
	LO Podocyrtis (P.) diamesa	13R-6W, 54-56 / 13R-5W, 54-56	112.74 / 111.24	43.05 / 43.01	43.03	-	-	-
	FO Pteropilium ? contiguum	13R-6W, 54-56 / 13R-5W, 54-56	112.74 / 111.24	43.05 / 43.01	43.03	-	-	-
	LO Stylosphaera ? agdaraensis	13R-6W, 54-56 / 13R-5W, 54-56	112.74 / 111.24	43.05 / 43.01	43.03	-	-	-
	FO Semantidium haeckelii	14R-2W, 55-57 / 14R-1W, 55-57	117.52 / 116.02	43.21 / 43.16	43.18	-	-	-
	FO Siphocampe ? elegans	14R-2W, 55-57 / 14R-1W, 55-57	117.52 / 116.02	43.21 / 43.16	43.18	-	-	-
	FO Lychnocanium pileatum	14R-3W, 55-57 / 14R-2W, 55-57	119.02 / 117.52	43.26 / 43.21	43.24	-	-	-
	FO Lithostrobus picus	14R-5W, 55-57 / 14R-4W, 55-57	122.02 / 120.52	43.39 / 43.33	43.36	-	-	-
	FO Lophophaena radians	14R-5W, 55-57 / 14R-4W, 55-57	122.02 / 120.52	43.39 / 43.33	43.36	-	-	-
	LO Dictyomitra parva	14R-5W, 55-57 / 14R-4W, 55-57	122.02 / 120.52	43.39 / 43.33	43.36	-	-	-
	FO Coccolarnacium periphaenoides	14R-7W, 55-57 / 14R-6W, 55-57	125.02 / 123.52	43.51 / 43.45	43.48	-	-	-
	FO Pterocyrtidium barbadense	14R-7W, 55-57 / 14R-6W, 55-57	125.02 / 123.52	43.51 / 43.45	43.48	-	-	-
	LO Podocyrtis (P.) phyxis	14R-7W, 55-57 / 14R-6W, 55-57	125.02 / 123.52	43.51 / 43.45	43.48	42.90	43.60	-
	ET Podocyrtis phyxis $\rightarrow P$. ampla	15R-3W, 55-57 / 15R-2W, 55-57	128.97 / 127.47	43.70 / 43.63	43.67	43.20	43.90	-

* Absolute ages provided by Kamikuri et al. (2012) based on age-depth models that integrate the geomagnetic time scale of Lourens et al. (2004).

** Revised ages based on age-depth models which integrate the geomagnetic time scale of Speijer et al. (2020).

(1 – Lychnocanium tribulus (Ehrenberg, 1874) group in Chapter II.2; 2 – Lithochytris pyramidalis Ehrenberg, 1874 in Chapter II.2; *Thyrsocyrtis (Pentalocorys) parvipes* (Ehrenberg, 1874) in Chapter II.2; *Histiastrum coronatum* Haeckel, 1887 in Chapter II.2).

III.3.2. Correlation between the equatorial Atlantic and Pacific Oceans

Middle Eocene radiolarian bioevents were correlated between ODP Site 1260 and three lowlatitude sites located in the eastern equatorial Pacific: IODP Sites U1331, U1332, and 1333 (Kamikuri et al., 2012a), which were considered by these authors as a single site, due to their geographical proximity (<300 km). Of the aforementioned 71 radiolarian bioevents mentioned above, documented between zones RP12 and RP16, 31 are common to the equatorial Pacific record and were therefore used for correlation (Figure III.3). The absolute ages for these radiolarian bioevents provided by Kamikuri et al. (2012a) were obtained after correlation with the geomagnetic polarity timescale (GPTS) provided by Lourens et al. (2004). However, because the calibration of the GPTS has since changed, we have revised the age–depth models for these Pacific sites by using new models generated here (Supplementary Figure III.1) based on the most recent geomagnetic polarity reversal ages provided by Speijer et al. (2020).

Amongst the primary bioevents, the FO of *Podocyrtis (L.) goetheana* and the ET of *Podocyrtis (L.) mitra* to *Podocyrtis (L.) chalara* are nearly isochronous (less than 160 kyr difference) between the equatorial Atlantic and Pacific oceans, whereas the ET of *Podocyrtis (L.) sinuosa* to *Podocyrtis (L.) mitra* and the ET of *Podocyrtis (P.) phyxis* to *Podocyrtis (P.) ampla* are slightly diachronous (~220 and ~230 kyr difference, respectively). Seven secondary bioevents are also shown to be nearly synchronous (less than 250 kyr difference) and thus reliable for interoceanic correlations. Moreover, since the order of these bioevents is coherent between the Atlantic and the Pacific Oceans they are used to define new subzones (see Section III.3.4). These bioevents concern the FOs of *Podocyrtis (P.) apeza, Sethochytris triconiscus*, and *Zealithapium mitra* and the LOs of *Podocyrtis (L.) fasciolata, Podocyrtis (L.) mitra*, *Podocyrtis (L.) sinuosa*, and *Podocyrtis (P.) phyxis*.

On the other hand, 20 secondary bioevents are shown to be moderately diachronous (between 250 kyr and 1 Ma difference) to highly diachronous (more than 1 Myr difference)

between the Atlantic and the Pacific Oceans. Moderately diachronous bioevents include the FOs of *Dorcadospyris anastasis*, *Lithocyclia aristotelis* group, *Podocyrtis* (*L*.) *chalara*, *Podocyrtis* (*L*.) *mitra*, *Podocyrtis* (*L*.) *trachodes*, and *Thyrsocyrtis* (*P*.) *tetracantha* and the LOs of *Rhopalosyringium* ? *biauritum*, *Dictyophimus craticula*, *Eusyringium lagena*, *Lithochytris vespertilio*², *Podocyrtis* (*L*.) *trachodes*, *Podocyrtis* (*P*.) *ampla*, *Zealithapium anoectum*, and *Zealithapium plegmacantha*. Highly diachronous bioevents include the FOs of *Cryptocarpium ornatum*, *Dorcadospyris ombros*, *Podocyrtis* (*L*.) *fasciolata*, and *Thyrsocyrtis* (*P*.) *krooni*³ and the LOs of *Anthocyrtoma* spp. and *Theocotylissa ficus*. Except for the FOs of *Dorcadospyris anastasis*, *Dorcadospyris ombros*, *Podocyrtis* (*L*.) *chalara*, *Podocyrtis* (*L*.) *fasciolata*, and *Podocyrtis* (*L*.) *trachodes*, all these diachronous bioevents occurred earlier in the Atlantic Ocean.

III.3.3. Correlation between low- and middle-latitude sequences in the North Atlantic Ocean

Radiolarian bioevents recorded at ODP Site 1260 were also correlated with the northwestern Atlantic IODP Site U1403 (Hollis et al., 2020). A total of 298 radiolarian bioevents were documented at this site, 29 of which are common to the record in the equatorial Atlantic sequence and were therefore used for correlation (Figure III.4). The absolute ages provided by Hollis et al. (2020) for these radiolarian bioevents were obtained by calibration to the latest version of the GTS Paleogene timescale (Speijer et al., 2020) using calcareous nannofossil biostratigraphy and magnetostratigraphy.

Three secondary bioevents are found to be nearly isochronous (less than 160 kyr difference) between low and mid–latitudes in the North Atlantic Ocean, including the FO of

² Lithochytris pyramidalis Ehrenberg, 1874 in Chapter II.2.

³ Thyrsocyrtis (Pentalocorys) parvipes (Ehrenberg, 1874) in Chapter II.2.



Figure III.3. Correlation of radiolarian bioevents between ODP hole 1260A (this study) and IODP Sites U1331, U1332, and U1333 (Kamikuri et al., 2012a). Black lines represent nearly synchronous bioevents, blue lines represent diachronous bioevents first occurring in the Atlantic Ocean, and red lines represent diachronous bioevents first occurring in the Pacific Ocean. The geomagnetic timescale is after Speijer et al. (2020). (1 – *Thyrsocyrtis (P.) parvipes* (Ehrenberg) in Chapter II.2; 2 – *Lithochytris pyramidalis* Ehrenberg in Chapter II.2).

Podocyrtis (P.) apeza and the LOs of Rhopalosyringium ? biauritum and Eusyringium lagena.

On the other hand, nine secondary bioevents are shown to be moderately (250 kyr to 1 Myr
difference) to highly diachronous (more than 1 Myr difference) between low and mid– latitudes. Moderately diachronous bioevents include the FO of *Podocyrtis* (*L*.) *trachodes* and the LOs of *Podocyrtis* (*L*.) *fasciolata*, *Podocyrtis* (*L*.) *trachodes*, *Zealithapium mitra*, and *Zealithapium plegmacantha*. Highly diachronous bioevents include the FOs of Carpocanopsis ornata, *Podocyrtis* (L.) *fasciolata*, and *Podocyrtis* (*L*.) *mitra*, and the LO of *Podocyrtis* (*L*.) *sinuosa*.



Figure III.4. Correlation of radiolarian bioevents between ODP Site 1260 (this study) and IODP Site U1403 (Hollis et al., 2020). Black lines represent nearly synchronous bioevents, blue lines represent diachronous bioevents that first occur at ODP Site 1260, and red lines represent diachronous bioevents that first occur at IODP Site U1403. The geomagnetic timescale is from Speijer et al. (2020).

III.3.4 Established radiolarian biozones and new subzones

Five biozones of the tropical radiolarian biozonation of Sanfilippo and Nigrini (1998b) were recognized for our studied sequence; they correspond to the upper part of Zone RP12, the entire Zones RP13, RP14 and RP15, and the lower part of Zone RP16. As mentioned above, the correlation of a number of common bioevents between the Atlantic (ODP Site 1260 and IODP Site U1403, see Figure III.4) and the Pacific (IODP Sites U1331, U1332 and U1333, see Figure III.3) allows us to subdivide the RP13 zone into two subzones: *Dictyomitra parva* Subzone (RP13a) and *Coccolarnacium periphaenoides* Subzone (RP13b), and the RP14 zone into three subzones: *Artostrobus quadriporus* Subzone (RP14a), *Sethochytris triconiscus* Subzone (RP14b), and *Podocyrtis (Podocyrtopsis) apeza* Subzone (RP14c), and the RP15 zone into two subzones: *Rhopalosyringium ? biauritum* Subzone (RP15a) and *Thyrsocyrtis (Pentalocorys) kroont*⁴ Subzone (RP15b) (Figure III.5). The pre-established radiolarian zones and the newly defined subzones are given below in stratigraphic order, with their formal definitions, their magnetostratigraphic calibrations, and their absolute age obtained by the orbital time framework provided for ODP Site 1260 (Westerhold and Röhl, 2013). The first occurrences are shown as FO, the last occurrences as LO, and the evolutionary transitions as ET.

RP16 - Podocyrtis (Lampterium) goetheana Interval Zone

(Moore, 1971 emend. Riedel and Sanfilippo, 1978)

Definition: Biostratigraphic interval between the FO of *Podocyrtis (Lampterium) goetheana* (Haeckel, 1887) (base) and the FO of *Cryptocarpium azyx* (Sanfilippo and Riedel, 1973) (top).

⁴ Thyrsocyrtis (Pentalocorys) parvipes (Ehrenberg, 1874) in Chapter II.2.

Occurrence at Hole 1260A: The base of this zone is located between samples ODP 1260A-7R-1W, 54–56 cm (48.54 rmcd) and ODP 1260A-6R-6W, 55–57 cm (46.25 rmcd).

Estimated age: The base of the zone is dated to 40.26 Ma in the equatorial Atlantic (Westerhold and Röhl, 2013) and 40.1 Ma in the equatorial Pacific (Kamikuri et al., 2012a; revised age in this study); middle Eocene (early Bartonian).

Magnetostratigraphic calibration: The base of this zone is placed within the uppermost part of Chron C18r at both the Atlantic (this study, in combination with Suganuma and Ogg, 2006) and Pacific sites (Kamikuri et al., 2012a; revised calibration in this study).

Secondary bioevents: Five FOs (*Dictyopodium* aff. *oxylophus*, *Dorcadospyris anastasis*, *Thyrsocyrtis* (*P*.) *tetracantha*, *Petalospyris diaboliscus*, and *Periphaena pentasteriscus*), and seven LOs (*Podocyrtis* (*L*.) *mitra*, *Lychnocanium babylonis* group⁵, *Anthocyrtoma* spp., *Dictyophimus craticula*, *Histiastrum quaternarium*, *Lithochytris vespertilio*,⁶ and *Theocotylissa ficus*).

Remarks: The record of Zone RP16 is truncated at Hole 1260A. It corresponds to the entire core 6R, above which (>38.2 rmcd) samples contain only rare and/or non-diagnostic radiolarian fragments. Thus, most of the Zone RP16 and associated bioevents are missing, including the FOs of *Cryptocarpium azyx* and *Thyrsocyrtis (T.) bromia*, some short-lived *Dorcadospyris* species found in the equatorial Pacific (e.g., *Dorcadospyris copelata*; Nigrini et al., 2005), and the acme of *Podocyrtis (L.) goetheana*. At ODP Hole 1260A, the base of Zone RP16 correlates with the upper part of the planktic foraminiferal Zone P13, and the basal datum is approximately synchronous with the LO of the nannofossil species *Chiasmolithus solitus*, which defines the base of the *Discoaster saipanensis* Zone (NP17).

⁵ Lychnocanium tribulus (Ehrenberg, 1874) group in Chapter II.2.

⁶ Lithochytris pyramidalis Ehrenberg, 1874 in Chapter II.2.



Chapter III - Progress on late middle Eocene radiolarian biostratigraphy

Plate III.1. Composite light micrographs of selected radiolarians from ODP Site 1260. (1) *Dictyomitra parva* (Kim), ODP 1260A-15R-4W, 55–57 cm, USTL 3549; (2) *Siphocampe* ? *elegans* (Ehrenberg), ODP 1260A-6R-3W, 55–57 cm, USTL 3424; (3) *Dictyoprora ovata* (Haeckel) group, ODP 1260A-9R-3W, 55–57 cm, USTL 3477; (4) *Dictyoprora armadillo* (Ehrenberg) group, ODP 1260A-6R-3W, 55–57 cm, USTL 3426; (5) *Dictyoprora pirum* (Ehrenberg), ODP 1260A-6R-2W, 55–57 cm, USTL 3421; (6) *Rhopalosyringium* ? *biauritum*

(Ehrenberg), ODP 1260A-9R-3W, 55–57 cm, USTL 3477; (7) Rhopalosyringium ? auriculaleporis (Clark and Campbell), ODP 1260A-9R-4W, 55-57 cm, USTL 3481; (8) Theocorys anapographa Riedel and Sanfilippo var. A, ODP 1260A-6R-3W, 55–57cm, USTL 3424; (9) Artostrobus quadriporus Bjørklund, ODP 1260A-6R-3W, 55-57 cm, USTL 3424; (10) Eusyringium lagena (Ehrenberg), ODP 1260A-15R-4W, 55-57 cm, USTL 3550; (11) Dictyopodium eurylophus Ehrenberg, ODP 1260A-6R-2W, 55-57 cm, USTL 3423; (12) Dictyopodium aff. oxylophus Ehrenberg, ODP 1260A-6R-1W, 55–57 cm, USTL 3419; (13) *Lychnocanium babylonis* (Clark and Campbell) group (= *Lychnocanium tribulus* (Ehrenberg) group in Chapter II.2), ODP 1260A-11R-1W, 55-57 cm, USTL 3500; (14) Lychnocanium pileatum (Ehrenberg), ODP 1260A-11R-7W, 55-57 cm, USTL 3506; (15) Sethochytris triconiscus Haeckel, ODP 1260A-9R-6W, 55-57 cm, USTL 3489; (16) Lophocyrtis alauda (Ehrenberg), ODP 1260A-13R-6W, 54–56 cm, USTL 3527; (17) Pterocyrtidium barbadense (Ehrenberg), ODP 1260A-13R-5W, 55-56 cm, USTL 3524; (18) Apoplanius asperus (Ehrenberg), ODP 1260A-10R-4W, 55-57 cm, USTL 3496; (19) Apoplanius kerasperus (Sanfilippo and Caulet), ODP 1260A-13R-5W, 55-56 cm, USTL 3524; (20) Apoplanius klydus (Sanfilippo and Caulet), ODP 1260A-6R-6W, 55-57 cm, USTL 3436; (21) Zealithapium plegmacantha (Riedel and Sanfilippo), ODP 1260A-14R-1W, 55-57 cm, USTL 3530; (22) Zealithapium anoectum (Riedel and Sanfilippo), ODP 1260A-12R-3W, 55–57 cm, USTL 3512; (23) Zealithapium mitra (Ehrenberg), ODP 1260A-7R-4W, 54-56 cm, USTL 3451; (24) Pteropilium aff. contiguum (Ehrenberg), ODP 1260A-9R-4W, 55-57 cm, USTL 3481; (25) Theocyrtis ? scolopax (Ehrenberg), ODP 1260A-10R-6W, 55-57 cm, USTL 3498. All scale bars equal 50 µm.

RP15 – Podocyrtis (Lampterium) chalara Lineage Zone

(Riedel and Sanfilippo, 1970, 1978)

Definition: Biostratigraphic interval between the ET of *Podocyrtis (Lampterium) mitra* Ehrenberg, 1854 to *Podocyrtis (Lampterium) chalara* Riedel and Sanfilippo, 1970 (base) and the FO of *Podocyrtis (Lampterium) goetheana* (Haeckel, 1887) (top).

Occurrence at Hole 1260A: Base: from sample ODP 1260A-8R-6W, 54–56 cm (66.85 rmcd)

to sample ODP 1260A-9R-1W, 55-57 cm (65.74 rmcd). Top: from sample ODP 1260A-7R-

1W, 54–56 cm (48.54 rmcd) to sample ODP 1260A-6R-6W, 55–57 cm (46.25 rmcd).

Estimated age: From 41.15 Ma to 40.26 Ma in the equatorial Atlantic (Westerhold and Röhl,

2013), and from 41.2 Ma to 40.1 Ma in the equatorial Pacific (Kamikuri et al., 2012a; revised ages); middle Eocene (late Lutetian to early Bartonian).

Magnetostratigraphic calibration: The basal datum is placed within Chron C19n in the equatorial Atlantic (this study in combination with Suganuma and Ogg, 2006), while it falls within the uppermost part of Chron C19r in the equatorial Pacific (Kamikuri et al., 2012a; revised calibration in this study). The top of the zone is placed within the uppermost part of Chron C18r at both the Atlantic (this study in combination with Suganuma and Ogg, 2006) and Pacific sites (Kamikuri et al., 2012a; revised calibration in this study).

Secondary bioevents: Seven FOs (*Lithocyclia aristotelis* group, *Thyrsocyrtis* (*P.*) *krooni*⁷, *Apoplanius klydus*, *Dictyoprora armadillo* group, *Dorcadospyris ombros*, *Dictyopodium* aff. *eurylophus* and *Podocyrtis* (*L.*) *chalara*), and three LOs (*Rhopalosyringium* ? *auriculaleporis*, *Rhopalosyringium* ? *biauritum* and *Petalospyris flabellum*).

Remarks: At ODP Hole 1260A, this zone is correlated with the uppermost part of the planktic foraminiferal Zone P12 to the lower part of Zone P13, and to the upper part of the nannofossil Zone NP16. The Lutetian/Bartonian boundary is placed within this zone at ~63.17 rmcd (41.03 Ma), between samples ODP 1260A-8R-6W, 54–56 cm (65.74 rmcd) and ODP 1260A-8R-5W, 54–56 cm (64.24 rmcd). This zone is subdivided into lower (a) and upper (b) subzones.

RP15b – Thyrsocyrtis (Pentalocorys) krooni⁷ Interval Subzone

new subzone

Definition: Biostratigraphic interval between the LO of *Rhopalosyringium* ? *biauritum* (Ehrenberg, 1874) (base) and the FO of *Podocyrtis (Lampterium) goetheana* (Haeckel, 1887) (top).

Occurrence at Hole 1260A: Base: from sample ODP 1260A-8R-3W, 54–56 cm (61.24 rmcd) to sample ODP 1260A-7R-6W, 54–56 cm (56.04 rmcd). Top: from sample ODP

⁷ Thyrsocyrtis (Pentalocorys) parvipes (Ehrenberg, 1874) in Chapter II.2.

1260A-7R-1W, 54–56 cm (48.54 rmcd) to sample ODP 1260A-6R-6W, 55–57 cm (46.25 rmcd).

Estimated age: From 40.84 Ma to 40.26 Ma in the equatorial Atlantic (Westerhold and Röhl, 2013), and from 40.4 Ma to 40.1 Ma in the equatorial Pacific (Kamikuri et al., 2012a; revised ages in this study); middle Eocene (early Bartonian).

Magnetostratigraphic calibration: The new subzone falls entirely within Chron C18r at both the Atlantic (this study in combination with Suganuma and Ogg, 2006) and Pacific sites (Kamikuri et al., 2012a; revised calibration in this study).

Remarks: The basal datum is nearly isochronous between ODP Hole 1260A (40.84 Ma) and IODP Site U1403 (40.73 Ma), while it is moderately diachronous between ODP Hole 1260A (40.84 Ma) and IODP Sites U1331, U1332 and U1333 (40.40 Ma). However, at each equatorial site, the FO of *Rhopalosyringium ? biauritum* is close to the FO of *Orbulinoides beckmanni*, which defines the base of the planktic foraminiferal Zone P13. Futhermore, the FO of *Rhopalosyringium ? biauritum* appears to be synchronous on the scale of the eastern equatorial Pacific (Nigrini et al., 2005). As mentioned above, this subzone is correlated in ODP Hole 1260A with the uppermost part of the planktic foraminiferal Zone P12 to the lower part of Zone P13, and the upper part of the nannofossil Zone NP16.

RP15a – Rhopalosyringium ? biauritum Interval Subzone

new subzone

Definition: Biostratigraphic interval between the ET from *Podocyrtis (Lampterium) mitra* Ehrenberg, 1854 to *Podocyrtis (Lampterium) chalara* Riedel and Sanfilippo, 1970 (base) and the LO of *Rhopalosyringium ? biauritum* (Ehrenberg, 1874) (top).



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Plate III.2. Composite light micrographs of selected radiolarians from ODP Site 1260. (1) *Podocyrtis (Lampterium) sinuosa* Ehrenberg, ODP 1260A-15R-4W, 55–57 cm, USTL 3552;
(2) *Podocyrtis (Lampterium) mitra* Ehrenberg, ODP 1260A-9R-3W, 55–57 cm, USTL 3477;
(3) *Podocyrtis (Lampterium) trachodes* Riedel and Sanfilippo, ODP 1260A-10R-6W, 55–57 cm, USTL 3498;
(4) *Podocyrtis (Lampterium) chalara* Riedel and Sanfilippo, ODP 1260A-6R-6W, 55–57 cm, USTL 3436;
(5) *Podocyrtis (Lampterium) goetheana* (Haeckel), ODP 1260A-6R-6W, 55–57 cm, USTL 3436;

6R-2W, 55-57 cm, USTL 3420; (6) Podocyrtis (Lampterium) fasciolata Nigrini, ODP 1260A-11R-7W, 55-57 cm, USTL 3506; (7) Podocyrtis (Podocyrtoges) diamesa Riedel and Sanfilippo, ODP 1260A-15R-2W, 55–57 cm, USTL 3543; (8) Podocyrtis (Podocyrtoges) phyxis Sanfilippo and Riedel, ODP 1260A-15R-2W, 55-57 cm, USTL 3543; (9) Podocvrtis (Podocyrtoges) ampla Ehrenberg, ODP 1260A-10R-6W, 55-57 cm, USTL 3498; (10) Podocyrtis (Podocyrtopsis) apeza Sanfilippo and Riedel, ODP 1260A-6R-2W, 55-57 cm, USTL 3421; (11) Dorcadospyris anastasis Sanfilippo in Nigrini et al., ODP 1260A-6R-1W, 55-57 cm, USTL 3419; (12) Phormocyrtis embolum (Ehrenberg), ODP 1260A-13R-1W, 54-55 cm, USTL 3522; (13) Thyrsocyrtis (Pentalocorys) tetracantha (Ehrenberg), ODP 1260A-6R-2W, 55-57 cm, USTL 3420; (14) Thyrsocyrtis (Pentalocorys) krooni Sanfilippo and Blome (= Thyrsocyrtis (P.) parvipes (Ehrenberg) in Chapter II.2), ODP 1260A-6R-2W, 55-57 cm, USTL 3421; (15) Lithostrobus picus (Ehrenberg), ODP 1260A-13R-4W, 55-57 cm, USTL 2854; (16) Dendrospyris fragoides Sanfilippo and Riedel, ODP 1260A-9R-3W, 55-57 cm. USTL 3478; (17) Dendrospyris golli Nishimura, ODP 1260A-15R-4W, 55-57 cm, USTL 3550; (18) Semantidium haeckelii (Bütschli), ODP 1260A-9R-3W, 55-57 cm, USTL 3477; (19) Dorcadospyris ombros Sanfilippo in Nigrini et al., ODP 1260A-7R-6W, 54-56 cm, USTL 3454; (20) Dorcadospyris confluens (Ehrenberg), ODP 1260A-6R-1W, 55–57 cm, USTL 3419; (21) Petalospyris flabellum Ehrenberg, ODP 1260A-10R-6W, 55-57 cm, USTL 3498; (22) Petalospyris diaboliscus Ehrenberg, ODP 1260A-6R-1W, 55-57 cm, USTL 3419; (23) Artophormis barbadensis (Ehrenberg), ODP 1260A-6R-2W, 55-57 cm, USTL 3420. All scale bars equal 50 μm.

Occurrence at Hole 1260A: Base: from sample ODP 1260A-8R-6W, 54–56 cm (66.85 rmcd)

to sample ODP 1260A-9R-1W, 55-57 cm (65.74 rmcd). Top: from sample ODP 1260A-8R-

3W, 54–56 cm (61.24 rmcd) to sample ODP 1260A-7R-6W, 54–56 cm (56.04 rmcd).

Estimated age: From 41.15 Ma to 40.84 Ma in the equatorial Atlantic (Westerhold and Röhl,

2013), and from 41.2 Ma to 40.4 Ma in the equatorial Pacific (Kamikuri et al., 2012a; revised ages in this study); middle Eocene (late Lutetian to early Bartonian).

Magnetostratigraphic calibration: The base of the zone falls within Chron C19n, and the top within Chron C18r at both the Atlantic (this study in combination with Suganuma and Ogg, 2006) and Pacific sites (Kamikuri et al., 2012a; revised calibration in this study).

Remarks: The basal datum is synchronous with the FOs of *Dictyopodium* aff. *eurylophus* in ODP Hole 1260A. This subzone corresponds to the uppermost part of the planktic foraminiferal

Zone P12, and the nannofossil Zone NP16. The Lutetian–Bartonian boundary is found in this subzone.

RP14 – Podocyrtis (Lampterium) mitra Lineage Zone

(Riedel and Sanfilippo, 1970, 1978)

Definition: Biostratigraphic interval between the ET from *Podocyrtis (Lampterium) sinuosa* Ehrenberg, 1874 to *Podocyrtis (Lampterium) mitra* Ehrenberg, 1854 (base) and the ET from *Podocyrtis (Lampterium) mitra* Ehrenberg, 1854 to *Podocyrtis (Lampterium) chalara* Riedel and Sanfilippo, 1970 (top).

Occurrence at Hole 1260A: Base: from sample ODP 1260A-13R-5W, 54–56 cm (111.24 rmcd) to sample ODP 1260A-13R-4W, 55–56 cm (109.75 rmcd). Top: from sample ODP 1260A-9R-1W, 55–57 cm (66.85 rmcd) to sample ODP 1260A-8R-6W, 54–56 cm (65.74 rmcd).

Estimated age: From 42.98 Ma to 41.15 Ma in the equatorial Atlantic (Westerhold and Röhl, 2013), and from 43.2 Ma to 41.2 Ma in the equatorial Pacific (Kamikuri et al., 2012a; revised ages in this study); middle Eocene (late Lutetian).

Magnetostratigraphic calibration: The base of the zone is placed within Chron C20n, and the top within Chron C19n at both the Atlantic (this study in combination with Suganuma and Ogg, 2006) and Pacific sites (Kamikuri et al., 2012a; revised calibration in this study).

Secondary bioevents. Sixteen FOs (*Dendrospyris fragoides*, *Podocyrtis* (*P.*) *apeza*, Zealithapium mitra, *Dictyoprora ovata* group, *Sethochytris triconiscus*, *Histiastrum* sp. A⁸, *Podocyrtis* (*L.*) *fasciolata*, *Podocyrtis* (*L.*) *trachodes*, *Theocorys anapographa* var. A, *Dorcadospyris confluens*, *Dictyoprora pirum*, *Apoplanius asperus*, *Apoplanius kerasperus*,

⁸ Histiastrum coronatum Haeckel, 1887 in Chapter II.2.

Artophormis barbadensis, Carpocanopsis ornatum and Podocyrtis (L.) mitra), fifteen LOs (Phormocyrtis embolum, Podocyrtis (L.) trachodes, Theocorys? scolopax, Lophocyrtis alauda, Lychnocanium pileatum, Podocyrtis (P.) ampla, Podocyrtis (L.) fasciolata, Zealithapium anoectum, Podocyrtis (L.) sinuosa, Pterocyrtidium barbadense, Eusyringium lagena, Zealithapium plegmacantha, Dendrospyris golli, Coccolarnacium periphaenoides, Entapium regulare).

Remarks: This zone is the longest in ODP Hole 1260A, covering 46% of the studied interval and containing nearly half of the recognized bioevents. The radiolarian Zone RP14 correlates with the planktic foraminiferal Zone P12 and the nannofossil Zone NP16. This zone is subdivided into three subzones.

RP14c – Podocyrtis (Podocyrtopsis) apeza Interval Subzone

new subzone

Definition: Biostratigraphic interval between the FO of *Podocyrtis (Podocyrtopsis)* apeza Sanfilippo and Riedel, 1992 (base) and the ET from *Podocyrtis (Lampterium) mitra* Ehrenberg, 1854 to *Podocyrtis (Lampterium) chalara* Riedel and Sanfilippo, 1970 (top).

Occurrence at Hole 1260A: Base: from sample ODP 1260A-10R-5W, 55–57 cm (83.33 rmcd) to sample ODP 1260A-10R-3W, 55–57 cm (80.33 rmcd). Top: from sample ODP 1260A-9R-1W, 55–57 cm (66.85 rmcd) to sample ODP 1260A-8R-6W, 54–56 cm (65.74 rmcd).

Estimated age: From 41.79 Ma to 41.15 Ma in the equatorial Atlantic (Westerhold and Röhl, 2013), and from 41.6 Ma to 41.2 Ma in the equatorial Pacific (Kamikuri et al., 2012a; revised ages in this study); middle Eocene (late Lutetian).

Magnetostratigraphic calibration: The base of the zone is within Chron C19r, and the top is within Chron C19n at both the Atlantic (this study in combination with Suganuma and Ogg, 2006) and Pacific sites (Kamikuri et al., 2012a; revised calibration in this study).



Chapter III - Progress on late middle Eocene radiolarian biostratigraphy

Plate III.3. Composite light micrographs of selected radiolarians from ODP hole 1260A. (1) *Lophophaena radians* Ehrenberg, ODP 1260A-9R-3W, 55–57 cm, USTL 3477; (2) *Carpocanopsis ornata* (Ehrenberg), ODP 1260A-6R-2W, 55–57 cm, USTL 3420; (3) *Theocotylissa ficus* (Ehrenberg), ODP 1260A-15R-2W, 55–57 cm, USTL 3543; (4) *Lithochytris vespertilio* Ehrenberg (= *Lithochytris pyramidalis* Ehrenberg in Chapter II.2), ODP 1260A-16R-1W, 55–57 cm, USTL 3558; (5) *Stylosphaera*? *agdaraensis* (Mamedov), ODP 1260A-15R-2W, 55–57 cm, USTL 3551; (7) *Anthocyrtoma* spp., ODP 1260A-13R-4W, 55–57 cm, USTL 3551; (7) *Anthocyrtoma* spp., ODP 1260A-13R-4W, 55–57 cm, USTL 3525; (9) *Histiastrum quaternarium* Ehrenberg, ODP 1260A-13R-5W, 54–56 cm, USTL 3525; (9) *Histiastrum* sp. A (= *Histiastrum coronatum* Haeckel in Chapter II.2), ODP 1260A-6R-2W, 55–57 cm, USTL 3422; (11) *Lithocyclia aristotelis* (Ehrenberg) group, ODP 1260A-6R-3W, 55–57 cm, USTL 3425; (12) *Coccolarnacium periphaenoides* Dumitrică, ODP 1260A-13R-2W, 54–55 cm, USTL 2852; (13) *Entapium regulare* Sanfilippo and Riedel, ODP 1260A-14R-6W, 55–57 cm, USTL 3537. All scale bars equal 50 μm.

Remarks: The base of the subzone is characterized by the FO of *Podocyrtis (P.) apeza*, which is isochronous between ODP Hole 1260A (41.79 Ma), IODP Sites U1331, U1332, and U1333

(41.6 Ma), and IODP Site U1403 (41.94 Ma). The basal datum is approximately synchronous with a significant faunal turnover involving the FOs of *Podocyrtis* (*P.*) *apeza* and *Zealithapium mitra*, and the LOs of *Lophocyrtis alauda*, *Lychnocanium pileatum*, *Podocyrtis* (*P.*) *ampla*, *Podocyrtis* (*L.*) *fasciolata* and *Zealithapium anoectum*. This subzone correlates with the upper part of planktic foraminiferal Zone P12 and the nannofossil Zone NP16 in ODP Hole 1260A.

RP14b - Sethochytris triconiscus Interval Subzone

new subzone

Definition: Biostratigraphic interval between the FO of *Sethochytris triconiscus* Haeckel, 1887 (base) and the FO of *Podocyrtis (Podocyrtopsis) apeza* Sanfilippo and Riedel, 1992 (top).

Occurrence at Hole 1260A: Base: from sample ODP 1260A-11R-3W, 55–57 cm (89.55 rmcd) to sample ODP 1260A-11R-2W, 55–57 cm (88.05 rmcd). Top: from sample ODP 1260A-10R-5W, 55–57 cm (83.33 rmcd) to sample ODP 1260A-10R-3W, 55–57 cm (80.33 rmcd).

Estimated age: 42.08 Ma to 41.79 Ma in the equatorial Atlantic (Westerhold and Röhl, 2013), and 42.1 Ma to 41.9 Ma in the equatorial Pacific (Kamikuri et al., 2012a; revised ages in this study); middle Eocene (Lutetian).

Magnetostratigraphic calibration: The new subzone falls completely whithin Chron C19r at both the Atlantic (this study in combination with Suganuma and Ogg, 2006) and Pacific sites (Kamikuri et al., 2012a; revised calibration in this study).

Remarks: The base of the subzone is characterized by the FO of *Sethochytris triconiscus*, which is isochronous between ODP Hole 1260A (42.08 Ma) and IODP Sites U1331, U1332 and U1333 (42.1 Ma). The basal datum is synchronous with the FO of *Dictyoprora ovata* group in ODP Hole 1260A. The *Sethochytris triconiscus* Subzone is correlated with the planktic foraminiferal Zone P12 and the nannofossil Zone NP16.

RP14a – Artostrobus quadriporus Interval Subzone

new subzone

Definition: Biostratigraphic interval between the ET from *Podocyrtis (Lampterium) sinuosa* Ehrenberg, 1874 to *Podocyrtis (Lampterium) mitra* Ehrenberg, 1854 (base) and the FO of *Sethochytris triconiscus* Haeckel, 1887 (top).

Occurrence at Hole 1260A: Base: from sample ODP 1260A-13R-5W, 54–56 cm (111.24 rmcd) to sample ODP 1260A-13R-4W, 55–56 cm (109.75 rmcd). Top: from sample ODP 1260A-11R-3W, 55–57 cm (89.55 rmcd) to sample ODP 1260A-11R-2W, 55–57 cm (88.05 rmcd).

Estimated age: From 42.98 Ma to 42.08 Ma in the equatorial Atlantic (Westerhold and Röhl, 2013), and from 43.2 Ma to 42.1 Ma in the equatorial Pacific (Kamikuri et al., 2012a; revised ages in this study); middle Eocene (Lutetian).

Magnetostratigraphic calibration: The base of the zone is located within Chron C20n, and the top is whithin Chron C19r at both the Atlantic (this study in combination with Suganuma and Ogg, 2006) and Pacific sites (Kamikuri et al., 2012a; revised calibration in this study).

Remarks: The basal datum is nearly synchronous with the FO of *Artostrobus quadriporus* in ODP Hole 1260A. This subzone correlates with the planktic foraminiferal Zone P12 and the lower part of the nannofossil Zone NP16.

RP13 – Podocyrtis (Podocyrtoges) ampla Lineage Zone

(Riedel and Sanfilippo, 1970, 1978)

Definition: Biostratigraphic interval between the ET from *Podocyrtis (Podocyrtoges) physis* Sanfilippo and Riedel, 1973 to *Podocyrtis (Podocyrtoges) ampla* Ehrenberg, 1874 (base) and the ET from *Podocyrtis (Lampterium) sinuosa* Ehrenberg, 1874 to *Podocyrtis (Lampterium) mitra* Ehrenberg, 1854 (top).

Occurrence at Hole 1260A: Base: from sample ODP 1260A-15R-3W, 55–57 cm (128.97 rmcd) to sample ODP 1260A-15R-2W, 55–57 cm (127.47 rmcd). Top: from sample ODP 1260A-13R-5W, 54–56 cm (111.24 rmcd) to sample ODP 1260A-13R-4W, 54–56 cm (109.75 rmcd).

Estimated age: From 43.67 Ma to 42.98 Ma in the equatorial Atlantic (Westerhold and Röhl, 2013), and from 43.9 Ma to 43.2 Ma in the equatorial Pacific (Kamikuri et al., 2012a; revised ages in this study); middle Eocene (middle Lutetian).

Magnetostratigraphic calibration: The base of this zone lies within the upper part of Chron C20r, and the top within the lower part of Chron C20n at both the Atlantic (this study in combination with Suganuma and Ogg, 2006) and Pacific sites (Kamikuri et al., 2012a; revised calibration in this study).

Secondary bioevents: Nine FOs (*Artostrobus quadriporus*, *Coccolarnacium periphaenoides*, Lithostrobus picus, Lophophaena radians, Lychnocanium pileatum, Pterocyrtidium barbadense, Pteropilium ? contiguum, Semantidium haeckelii and Siphocampe ? elegans) and four LOs (*Dictyomitra parva*, *Podocyrtis* (*P*.) diamesa, *Podocyrtis* (*P*.) phyxis and Stylosphaera ? agdaraensis).

Remarks: The basal datum is approximately synchronous with the LO of the planktic foraminiferal species *Morozovella aragonensis*, which defines the base of Zone P12. The *Podocyrtis* (*P.*) *ampla* Zone corresponds to the lowermost part of the planktic foraminiferal Zone P12, and to the uppermost part of the nannofossil Zone NP15 to the lowermost part of Zone NP16. This zone is divided into a lower (a) and a upper (b) subzones.

RP13b - Coccolarnacium periphaenoides Interval Subzone

new subzone

Definition: Biostratigraphic interval between the LO of *Podocyrtis (Podocyrtoges) physis* Sanfilippo and Riedel, 1973 (base) and the ET from *Podocyrtis (Lampterium) sinuosa* Ehrenberg, 1874 to *Podocyrtis (Lampterium) mitra* Ehrenberg, 1854 (top).

Occurrence at Hole 1260A: Base: from sample ODP 1260A-14R-7W, 55–57 cm (125.02 rmcd) to sample ODP 1260A-14R-6W, 55–57 cm (123.52 rmcd). Top: from sample ODP 1260A-13R-5W, 54–56 cm (111.24 rmcd) to sample ODP 1260A-13R-4W, 55–56 cm (109.75 rmcd).

Estimated age: From 43.48 Ma to 42.98 Ma in the equatorial Atlantic (Westerhold and Röhl, 2013), and from 43.6 Ma to 43.2 Ma in the equatorial Pacific (Kamikuri et al., 2012a; revised ages in this study); middle Eocene (middle Lutetian).

Magnetostratigraphic calibration: The subzone falls completely within Chron C20n at both the Atlantic (this study in combination with Suganuma and Ogg, 2006) and Pacific sites (Kamikuri et al., 2012a; revised calibration in this study).

Remarks: This subzone roughly corresponds to the stratigraphic extension of *Coccolarnacium periphaenoides* in ODP Hole 1260A. The FO of the nannofossil species *Nannotetrina fulgens*, which defines the base of Zone NP16 is recorded in this subzone. This subzone correlates with the lowermost part of planktic foraminiferal Zone P12, and the uppermost part of the nannofossil Zone NP15 correlates with the lowermost part of Zone NP16.

RP13a – Dictyomitra parva Interval Subzone

new subzone

Definition: Biostratigraphic interval between the ET from *Podocyrtis (Podocyrtoges) physis* Sanfilippo and Riedel, 1973 to *Podocyrtis (Podocyrtoges) ampla* Ehrenberg, 1874 (base) and the LO of *Podocyrtis (Podocyrtoges) physis* Sanfilippo and Riedel, 1973 (top).

Occurrence at Hole 1260A: Base: from sample ODP 1260A-15R-3W, 55–57 cm (128.97 rmcd) to sample ODP 1260A-15R-2W, 55–57 cm (127.47 rmcd). Top: from sample ODP 1260A-14R-7W, 55–57 cm (125.02 rmcd) to sample ODP 1260A-14R-6W, 55–57 cm (123.52 rmcd).

Estimated age: From 43.67 Ma to 43.48 Ma in the equatorial Atlantic (Westerhold and Röhl, 2013), and from 43.9 Ma to 43.6 Ma in the equatorial Pacific (Kamikuri et al., 2012a; revised ages in this study); middle Eocene (middle Lutetian).

Magnetostratigraphic calibration: The subzone falls completely within Chron C20r at both the Atlantic (this study in combination with Suganuma and Ogg, 2006) and Pacific sites (Kamikuri et al., 2012a; revised calibration in this study).

Remarks: This subzone corresponds to the interval where *Podocyrtis* (*P.*) *phyxis* and its descendant *Podocyrtis* (*P.*) *ampla* occur together. The artostrobiid *Dictyomitra parva* was abundant throughout this subzone, before its sudden extinction in the lower part of the *Coccolarnacium periphaenoides* Subzone. This subzone correlates with the uppermost part of the planktic foraminiferal Zone P11 to the lowermost part of Zone P12, and to the nannofossil Zone NP15.

RP12 – Thyrsocyrtis (Pentalocorys) triacantha⁹ Lineage Zone

(Riedel and Sanfilippo, 1970 emend. Riedel and Sanfilippo, 1978)

Definition: Biostratigraphic interval between the FO of *Eusyringium lagena* (Ehrenberg, 1874) (base) and the ET from *Podocyrtis (Podocyrtoges) physis* Sanfilippo and Riedel, 1973 to *Podocyrtis (Podocyrtoges) ampla* Ehrenberg, 1874 (top).

Occurrence at Hole 1260A: The top of this zone is located between samples ODP 1260A-15R-3W, 55–57 cm (128.97 rmcd) and ODP 1260A-15R-2W, 55–57 cm (127.47 rmcd).

Estimated age: The top of the zone is dated 43.67 Ma in the equatorial Atlantic (Westerhold and Röhl, 2013) and 43.9 Ma in the equatorial Pacific (Kamikuri et al., 2012a; revised age in this study); middle Eocene (Lutetian).

Magnetostratigraphic calibration: The top of this zone is placed within the upper part of Chron C20r at both the Atlantic (this study in combination with Suganuma and Ogg, 2006) and Pacific sites (Kamikuri et al., 2012a; revised calibration in this study).

Remarks: Only the very end of Zone RP12 was found in the studied interval, and it contains no secondary bioevents. Due to the poor recovery of cores 16R and 17R (10.2% and 50.5%, respectively), we decided to stop the sampling at 130.47 rmcd (ODP sample 1260A-15R-4W, 55–57 cm). The end of the radiolarian Zone RP12 correlates with the upper part of the planktic foraminiferal Zone P11 and the nannofossil Zone NP15.

III.4. Discussion

A total of 71 radiolarian bioevents have been identified in the middle Eocene of the equatorial Atlantic Ocean, and calibrated to the Geomagnetic Polarity and Astronomical Time Scales. Our study represents the first attempt to directly calibrate radiolarian bioevents to the Astronomical

⁹ Thyrsocyrtis (Pentalacorys) schomburgkii (Ehrenberg, 1847) in Chapter II.2.

Time Scale and to assign absolute ages to middle Eocene radiolarian bioevents with an unprecedented resolution. Some species described in very early studies (e.g., Ehrenberg, 1874) are calibrated for the first time in this study. We chose to include them in our analysis in order to increase the number of well-constrained calibration points available to produce age-depth models for the equatorial Atlantic. However, given the limited information available on these species, the assessment of their usefulness for correlations could not be evaluated here; this task requires additional biostratigraphic studies over a broad geographic area.

Comparison of our results with the equatorial Pacific radiolarian record demonstrates the synchronicity of primary radiolarian bioevents that underpin the middle Eocene tropical zonal scheme by means of independent correlational techniques (i.e., paleomagnetic stratigraphy and cyclostratigraphy). These observations reinforce the robustness of the previously established low-latitude radiolarian biozonation and demonstrate its reliability over a large oceanic area. Seven secondary bioevents are also found to be synchronous between the equatorial regions of the Atlantic and Pacific Oceans, and three secondary bioevents between the low and mid-latitudes of the North Atlantic Ocean, making them valuable for correlations. Four of these synchronous bioevents were used for the subdivision of zones RP13, RP14, and RP15 into seven new subzones. The selection of the bioevents used to define these new subzones was motivated by the abundance of associated marker species, their ease of identification, and the overall consistency of their stratigraphic range accros different lowlatitude sections (Riedel and Sanfilippo, 1970; Moore, 1971; Dinkelman, 1973; Nigrini et al., 2005). Although the FO of *Podocyrtis (P.) apeza*, which defines the base of Subzone RP14c, and the LO of Rhopalosyringium ? biauritum, which defines the base of Subzone RP15b, are synchronous between low et mid-latitudes in the North Atlantic Ocean, the new biostratigraphic scheme is restricted to the low latitudes. As a consequence of biogeographically controlled variations in the stratigraphic range of the species, no primary

bioevents for the late Middle Eocene were observed at IODP Site U1403, and the degree of synchroneity of these bioevents with the low latitudes of the Atlantic Ocean could not be tested. In addition, *Podocyrtis (P.) phyxis*, the first occurrence of which serves as the basal datum for Subzone RP13b, is also a species with tropical affinities. To date, it has only been reported from a few low-latitude sites (e.g., Riedel and Sanfilippo, 1973; Sanfilippo and Riedel, 1973; Johnson, 1974; Renz, 1984; Nigrini et al., 2005) and a single mid-latitude site located in the South Atlantic Ocean (de Souza et al., 2017).



Figure III.5. Biostratigraphic summary of calcareous and siliceous microfossils at ODP Site 1260 after the biostratigraphic results of the Shipboard Scientific Party (2004) and of this study, including the newly defined radiolarian subzones. The geomagnetic timescale used is from Suganuma and Ogg (2006). FO: first occurrence, LO: last occurrence, ET: evolutionary transition.

The new biostratigraphic scheme proposed here allows a substantial increase in the stratigraphic resolution that can be offered in the low latitudes for the middle Eocene. The mean

duration of a biostratigraphic unit is about 525 kyr for a middle Eocene biozonation based on radiolarian bioevents, while it is about 1.28 Ma for biozonations based on planktic foraminifera (Wade et al., 2011) and 1.27 Ma for biozonations based on nannofossils (Agnini et al., 2014). Radiolarians are therefore amongst the most accurate biostratigraphic microfossils for the period of interest. Future advances in astronomical dating will allow the extension of the astronomical calibration of radiolarian bioevents to the entire Cenozoic era to obtain a global and consistent biochronological framework, as it has already been achieved for planktic foraminifera (Wade et al., 2011). The development of such a high-resolution temporal framework for Cenozoic radiolarians will benefit a wide range of macroevolutionary studies, including the search for changes in radiolarian diversity or disparity, as well as the study of their ecological response to past climatic events.

On the other hand, two-thirds of the studied radiolarian bioevents were found to be moderately to highly diachronous between the equatorial regions of the Atlantic and Pacific Oceans, as well as three-quarters of the studied bioevents between the low and mid–latitudes of the North Atlantic Ocean. In contrast to previous biostratigraphic analyses carried out in the Indo-Pacific, we found no asymetric distribution of diachronous events between first occurrences and last occurrences (Johnson and Nigrini, 1985a; Nigrini and Caulet, 1992). Hence, among radiolarian datums, first occurrences do not seem to be less reliable for correlations than last occurrences.

The diachroneity of bioevents between sedimentary sections is a common phenomenon in biostratigraphy. In addition to reasons related to the biogeographic dynamics, diachroneity may be the result of a number of different other factors, including differences in sampling intensity, in quality of stratigraphic and age controls, as well as biases in preservation, bioturbation, or errors in species identification. These factors are largely independent of radiolarian biogeography and could lead to an apparent diachronism that is not due to differences in the stratigraphic range of species between different geographic areas. Diachronous bioevents may also be subject to ecological control as it has been amply demonstrated at different scales in radiolarians (e.g., Johnson and Nigrini, 1985a, b; Spencer-Cervato et al., 1993, 1994). In some well-constrained cases, diachronism has been explained by particular environmental conditions, such as in upwelling zones (Nigrini and Caulet, 1992), by large-scale changes in the boundaries of oceanic currents (Moore et al., 1993), or by the discontinuous nature of the stratigraphic range of some species due to local shifts in environmental conditions (Nigrini et al., 2005). The observed patterns of diachroneity between ODP Site 1260, IODP Site U1403, and IODP Sites U1331, 1332, and 1333 are difficult to explain in terms of ecological or paleoceanographic processes, due to the complexity of disentangling radiolarian migration pathways from such a limited spatial coverage. Although a number of radiolarian species first appear in the equatorial Atlantic Ocean and then in the equatorial Pacific, there is no convincing evidence for diachroneity due to interoceanic migration.

III.5. Conclusions

This study examined the stratigraphic range of 61 middle Eocene radiolarian species from the equatorial ODP Site 1260, which preserves an expanded and well-preserved siliceous record. Taking advantage of the unique time framework provided by previous magnetostratigraphic and cyclostratigraphic work conduced on the studied site, our results are placed in a very precise astronomical time frame. The absolute ages of 71 radiolarian bioevents were refined, improving the age control of equatorial Atlantic sections of middle Eocene age and providing new calibration points for the application of age-depth models in future studies. Future

macroevolutionary studies of Eocene radiolarians may also benefit from this well-constrained temporal framework.

Subsequently, by comparison with the equatorial Pacific record, we demonstrated the synchronicity of primary radiolarian bioevents that underpin the middle Eocene zonal scheme, thereby reinforcing the robustness of the tropical radiolarian biozonation. Several secondary bioevents were also found to be synchronous between the equatorial regions of the Atlantic and Pacific Oceans and between low and mid–latitudes of the Atlantic Ocean. These bioevents were used to subdivide zones RP13, RP14 and RP15 into seven new subzones: *Dictyomitra parva* Interval Subzone (RP13a), *Coccolarnacium periphaenoides* Interval Subzone (RP13b), *Artostrobus quadriporus* Interval Subzone (RP14a), *Sethochytris triconiscus* Interval Subzone (RP14b), *Podocyrtis (Podocyrtopsis) apeza* Interval Subzone (RP14c), *Rhopalosyringium ? biauritum* Interval Subzone (RP15a) and *Thyrsocyrtis (Pentalocorys) krooni*¹⁰ Interval Subzone (RP15b). On the other hand, numerous bioevents are shown to be highly diachronous between the two oceans, with generally older appearance and disappearance dates in the Atlantic. Although it is difficult to fully explain the observed patterns of diachroneity, recognition of age-transgressive bioevents in radiolarians could have implications for our understanding of plankton migration pathways between the Atlantic and Pacific Oceans.

Data availability.

Illustrated specimens are housed in the paleontological collection of the University of Lille, Villeneuve-d'Ascq, France.

¹⁰ Thyrsocyrtis (Pentalocorys) parvipes (Ehrenberg, 1874) in Chapter II.2.

Author contribution.

T.D. designed and directed the project. **M.M.** was responsible for the data acquisition, analysis, and drawing of figures. The interpretation of data and discussion of results were conducted by both authors. **M.M.** wrote the manuscript, in consultation with **T.D.**

Competing interests.

The authors declare that they have no conflict of interest.

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Supplementary Figure III.1. Revised age–depth models for the IODP Sites U1331, U1332, and U1333 (eastern equatorial Pacific, expedition 320, "Pacific Equatorial Age Transect I").

Chapter IV – Biotic impacts of the Middle Eocene Climate Optimum (MECO)

This chapter includes two distinct articles. The first article, titled "No dramatic changes observed in subtropical radiolarian plankton assemblages during the Middle Eocene Climatic Optimum (MECO); evidence from the North Atlantic ODP Site 1051" was published in the journal Marine Micropaleontology, and is available online at DOI: https://doi.org/10.1016/j.marmicro.2023.102272. The second article, submitted to the journal Palaeogeography, Palaeoclimatology, Palaeoecology, is an original manuscript titled "Morphological responses of the plankton to the Middle Eocene Climatic Optimum (MECO): The case of the radiolarian species *Podocyrtis papalis* from the western equatorial Atlantic (ODP Site 1260)".

IV.1. No dramatic changes observed in subtropical radiolarian plankton assemblages during the Middle Eocene Climatic Optimum (MECO); Evidence from the North Atlantic ODP Site 1051

Mathias Meunier* and Taniel Danelian

Univ. Lille, CNRS, UMR 8198 – Evo-Eco-Paleo, F-59000 Lille, France

<mathias.meunier@univ-lille.fr>

*Corresponding author

Abstract

The Middle Eocene Climatic Optimum (MECO; ca. 40 Ma) was a prominent global warming event that lasted 400 kyr and was characterized by a 4-6 °C increase in high-latitude surface and deep-water temperatures. Since the radiolarian plankton response to this warming event is largely unknown, whole-assemblage quantitative analyses were performed on well-preserved radiolarian assemblages from ODP Site 1051 (western North Atlantic). Although radiolarians at site site apparently benefited from an increase in oceanic fertility induced by the MECO, this event does not appear to have had a severe impact on subtropical radiolarian fauna. No significant faunal turnover was found in the studied interval, suggesting that subtropical radiolarians are relatively resilient to transient warming events. Similarly, variations in radiolarian assemblage composition indicate weak ecological responses to ocean warming. One of the most striking faunal changes associated with the MECO is the clear increase in radiolarian diversity (taxic richness), as a result of the northward migration of warm tropical radiolarian species. Likewise, several typical middle Eocene tropical species are found to be more abundant in the warmest interval. In addition to these poleward migrations, we identified three radiolarian clusters composed of warm-water or cool-water species, as well as two abundant artostrobiid species that may represent nutrient opportunists.

IV.1.1. Introduction

The Eocene epoch (ca. 56–34 million years ago; Ma) is a key period for the understanding of the Cenozoic climate dynamics and the transition from a "warmhouse" to a "coolhouse" climate state. After the early Eocene warmhouse (ca. 56–47 Ma), during which global temperatures were more than 5°C higher than they are today, the Earth underwent a long-term gradual cooling that culminated in a shift to coolhouse conditions around the Eocene-Oligocene boundary (ca. 34 Ma; Zachos et al., 2008; Westerhold et al., 2020; Hutchinson et al., 2021). This middle–late Eocene transitional interval was characterized by the formation of nascent ice sheets in eastern Antarctica and several short-lived warming events (Edgar et al., 2007; Westerhold and Röhl, 2013).

One of them, the Middle Eocene Climatic Optimum (MECO; Bohaty and Zachos, 2003; Bohaty et al., 2009) was a global warming event that occurred during the late middle Eocene (around 40 Ma); it lasted ~400 kyr and resulted to a significant perturbation of the carbon cycle (Edgar et al., 2010; Westerhold and Röhl, 2013). The MECO signature has been identified in the isotopic record of many oceanic sites as a negative shift of ~1.0–1.5‰ in the oxygen isotope (δ^{18} O) values of both benthic foraminiferal and bulk carbonate sediments, which is interpreted as a ~4–6°C rise in high latitude surface and deep water temperatures (Bohaty and Zachos, 2003; Bohaty et al., 2009; Bijl et al., 2010). The warmer interval is marked by a sharp decrease in δ^{18} O values at ca. 40 Ma (Edgar et al., 2010; Westerhold and Röhl, 2013), and is accompanied at some sites by a weak negative excursion (~0.05‰) in carbon isotope (δ^{13} C) values (Giorgioni et al., 2019). The peak warming phase of the MECO lasted <100 kyr and it was followed by a rapid return to pre-event temperatures (Bohaty et al., 2009; Edgar et al., 2010; Westerhold and Röhl, 2013). The MECO differs from other Paleogene global warming events, such as the Paleocene-Eocene Thermal Maximum (Kennett and Stott, 1991) or the early Eocene hyperthermal events (Lourens et al., 2005; Stap et al., 2010; Sexton et al., 2011) by its relatively long duration, the abruptness of its return to pre-event conditions and the spatial inconsistency of its carbon isotope signature (Giorgioni et al., 2019; Henehan et al., 2020). All these peculiar features make the MECO difficult to interpret, as a result, its triggering mechanism is poorly understood. It is possible that the conjunction of different factors, including volcanic outgassing and a favorable orbital configuration due to a very long eccentricity minimum, played an important role in the rise of the MECO (Henehan et al., 2020). Moreover, the latter occurred between two major carbonate accumulation events (CAE3 and CAE4, Lyle et al., 2005, 2008; Pälike et al., 2012), and is marked by worldwide carbonate dissolution in the deep-sea record, considered to be the result of increased levels of pCO2, which then induced seawater acidification through the entire water column and a deepening of the carbonate compensation depth (Bohaty et al., 2009; Cornaggia et al., 2020).

Significant assemblage changes across the MECO are recorded in several microfossil groups, including planktic and benthic foraminifera (Edgar et al., 2013; Luciani et al., 2010; Boscolo Galazzo et al., 2013, 2015; Moebius et al., 2014, 2015; D'Onofrio et al., 2021), coccolithophorids (Villa et al., 2008; Toffanin et al., 2011), dinocysts (Bijl et al., 2010; Cramwinckel et al., 2019) and diatoms (Renaudie et al., 2010; Witkowski et al., 2014). In contrast, the radiolarian biotic response to the MECO is still very poorly known. Witkowski et al. (2012) documented a high-latitude siliceous plankton assemblage dominated by ebridians and radiolarians (ODP Sites 748 and 749, Kerguelen Plateau) that showed an increase in biosiliceous sedimentation across the MECO interval. Witkowski et al. (2014) have also reported at the mid-latitude ODP Site 1051 (western Atlantic) an increase in the relative abundance of radiolarian skeletons associated with the warmest phase of the MECO event. However, in none of these studies, radiolarians were identified at the species level, hindering any understanding of faunal changes. Only two species-level radiolarian studies have been conducted previously in relation to the MECO, but none of them concerned the mid-latitudes

and especially the Blake Nose sediments, which are particularly rich in well-preserved siliceous microfossils. Kamikuri et al. (2013) investigated early to middle Eocene radiolarian assemblages from the eastern equatorial Pacific Ocean (ODP Site U1331), highlighting a decrease in cool-water radiolarian species across the MECO. In addition, Pascher et al. (2015) studied radiolarians from the southwest Pacific Ocean (DSDP Site 277, Campbell Plateau), where they recognized the migration of several tropical radiolarian species to the high latitudes during the MECO. However, only very few stratigraphic levels were investigated in this study and counting was only limited to abundant or biostratigraphically relevant taxa.

Based on a whole assemblage quantitative study of radiolarians from ODP Site 1051 (subtropical Atlantic), this study aims to describe in detail changes in the abundance and assemblage structure of radiolarians across the MECO. The observed changes will be interpreted within the stable isotope paleoclimatic framework established previously for this site and discussed in conjunction with the known record of other microfossil groups.

IV.1.2. Stratigraphic and paleoclimatic framework

ODP Site 1051 (30°03'N, 76°21'W) was drilled on Blake Nose, a submerged peninsula extending from the eastern margin of the Blake Plateau, in the subtropical western North Atlantic Ocean (Figure IV.1.1). A 630 m-thick Paleogene sequence was recovered at this site from two adjacent holes (1051A and 1051B) drilled at a current water depth of ~1983 m below sea level (mbsl) (Norris et al., 1998). During the middle Eocene, the paleodepth of this site was lower bathyal (~1000–2000 mbsl; Norris et al., 1998), with a palaeolatitude of ~25°N (Ogg and Bardot, 2001). The middle Eocene interval of ODP Site 1051 (~370 m-thick) is dominated by nannofossil ooze rich in siliceous microfossils, including abundant and well-preserved radiolarians, diatoms and sponge spicules, and a few rare ebridians, silicoflagellates and endoskeletal dinoflagellates (Norris et al., 1998; Witkowski et al., 2014). Age control for the

middle Eocene interval of ODP Site 1051 is provided by biostratigraphy (Norris et al., 1998; Mita, 2001; Sanfilippo and Blome, 2001; Edgar et al., 2010; Witkowski et al., 2020) and magnetostratigraphy (Ogg and Bardot, 2001).



Figure IV.1.1. 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.

The middle Eocene sedimentary sequence at ODP Site 1051 is characterized by an overall high sedimentation rate, estimated to be ~4 cm/kyr (Norris et al., 1998; Edgar et al., 2010). A total of 11 samples were selected from hole 1051A, with an average sample spacing of approximately 4.8 m in the MECO interval and an average age difference between two consecutive samples of ~120 kyr. Each sample was approximately 1 cm wide, respresenting an interval of ~250 years. Sampling was as regular as possible to avoid any bias associated with time bins of unequal duration.

At ODP Site 1051, noticeable shifts in both the δ^{13} C and δ^{18} O stable isotope records occur within the studied interval and are correlated with the two major phases of the MECO event (Figure IV.1.2; Bohaty et al., 2009; Edgar et al., 2010). The onset of the MECO occurs in the lower part of magnetochron C18r, around 118 mcd (Edgar et al., 2010). Subsequently, the benthic foraminiferal δ^{18} O record gradually decreased, reaching a brief minimum in the upper part of the magnetochron C18r (ca. 86 mcd), which coincides with an abrupt decrease in δ^{13} C values (Bohaty et al., 2009; Edgar et al., 2010). This minimum is interpreted as the peak warming condition of the MECO (Figure IV.1.2).

IV.1.3. Material and methods

IV.1.3.1. Sampling interval and sample preparation

Samples were processed according to the method described by Sanfilippo et al. (1985) and Tetard et al. (2020). A small amount (~2 cm2) of unprocessed sediment was collected from each sample and dried overnight at 50 °C to remove any residual water. After weighing, sediment samples were soaked for two hours in a 500 mL polypropylene beaker containing 30 mL of 30% hydrochloric acid (HCl) to dissolve their carbonate content and concentrate siliceous microfossils. A few mL of HCl was added at the end of this stage to ensure the end of the reaction. The residues resulting from acidification were then washed by adding ~200 mL of distilled water. After decanting for two hours, the excess water was carefully removed with a pipette. The residues were then soaked for two hours in 30 mL of 10% hydrogen peroxide (H2O2) to remove organic matter. The resulting residues were finally washed through a 45 µm sieve with distilled water and transferred to a storage vial using ethanol. After evaporation, the vial was weighed and the mass of the residues was calculated by subtracting the mass of the empty vial. One slide per sample was prepared from ~3 mg of dry residues randomly settled on a coverslip, following the method described by Witkowski et al. (2012). After drying, the coverslips were mounted on standard glass slides using Eukitt mounting medium (refractive index = 1.49). The weight of the residue used to prepare each slide was then calculated by subtracting the weight of the storage vial before and after sampling.



Figure IV.1.2. Variation of geochemical proxies across the MECO interval of ODP Site 1051 (Blake Nose, western North Atlantic). The darker orange zone highlights the peak-MECO interval. Stable isotope data are from Bohaty et al. (2009) for the fine carbonate fraction and from Edgar et al. (2010) for the benthic foraminiferal carbonate record. Magnetostratigraphy follows Ogg and Bardot (2001), the radiolarian biozonation is from Sanfilippo and Blome (2001), the planktic foraminiferal zonation is from Norris et al. (1998) and Edgar et al. (2010), and the calcareous nannofossil biostratigraphy is from Mita (2001). Abbreviations: Foram., planktic foraminifera; mcd, meters composite depth; Nanno., calcareous nannofossils; Rad., radiolarians; VPBD, Vienna Pee Dee Belemnite.

IV.1.3.2. Biodiversity survey

In order to examine variations in radiolarian assemblages across the MECO interval, we documented the entire radiolarian fauna preserved at ODP Site 1051. Rare taxa were thus taken into account, including numerous unknown morphospecies, that were left in open nomenclature (see online appendix: <u>https://doi.org/10.1016/j.marmicro.2023.102272</u>). Most of the enumerated classes were resolved to the species level, but occasionally higher taxonomic levels were used to record broken or unidentifiable specimens. The latter were not included in our diversity analyses. Species identification was performed using a Zeiss Axio Imager.A2 as a light microscope equipped with a Zeiss AxioCam ERc5s digital camera.

Approximately 6,000 specimens were recorded for each sample (see Supplementary Table 1) using a stratified procedure inspired by Renaudie and Lazarus (2013b) and Trubovitz et al. (2020). All specimens were first counted along vertical traverses until ~500 specimens were reached. All specimens mounted on a slide were then counted, excluding species representing >5% of the assemblage in the first sampling step. At the end of the count, the abundance of these common species was extrapolated by using the number of specimens observed in the first sampling step. To assess the robustness of our taxonomic sampling, sample completeness based on Good's U estimator (Good, 1953; Chao et al., 2020) was calculated using the scientific environment R (version 4.1.3; R Core Team, 2022), using the iNext package (version 3.0.0; Hsieh et al., 2016).

IV.1.3.3. Quantitative analyses

To describe the radiolarian response to the paleoenvironmental changes that occurred during the MECO, we calculated several indices of taxonomic richness based on species-level count data. Because many taxonomic inconsistencies remain in Cenozoic radiolarians, we have avoided using genus-level data. First, we determined the sampled-in-bin diversity (SIB), which is the raw count of taxa actually observed in each sample. Since the number of species encountered is expected to increase with the number of individuals sampled, the SIB may be biased by heterogeneous sampling effort between samples (Simpson, 1949; Raup, 1972; Bunge and Fitzpatrick, 1993; Gotelli and Colwell, 2001; Chao et al., 2014). We therefore computed the shareholder quorum subsampling (SQS) diversity (Alroy, 2010a, 2010b, 2010c) to correct for any possible bias introduced by unequal sampling. This coverage-based rarefaction approach draws randomly selected taxa from a sample until the sum of the relative frequencies of these taxa reaches a pre-specified coverage level (the 'quorum'). In this study, SQS diversity was estimated using a quorum level of 0.9, and by including dominant and single-interval taxa.

Several biodiversity indices commonly used in paleoenvironmental reconstructions were also calculated, including the Shannon–Wiever index, which was used as a measure of radiolarian diversity that integrates the relationship between the number of species and the number of individuals in an assemblage (Shannon and Weaver, 1949): $H' = \Sigma pi$ lnpi, where pi is the relative frequency of species i. This index varies between 0 and 1, with 0 representing minimum diversity and 1 representing maximum diversity. In addition to metrics of species diversity, we also included the Pielou equitability index (Pielou, 1966), which is a measure of species distribution within a sample derived from the Shannon–Wiener index: J = H'/log(SIB). Low equitability scores indicate an imbalance where only one or a few species dominate the community, while high scores indicate almost evenly distributed species.

In order to group species with similar distributions, a hierarchical cluster analysis (HCA) was performed on the most abundant taxa representing >1% of the total assemblage in at least three samples. We used the UPGMA linkage method (Sokal and Michener, 1958) and the Morisita similarity index (Morisita, 1959), which has the major advantage of being independent of sample size and diversity.
Finally, a one-way Analysis of similarity (ANOSIM) was used to test for significant differences in radiolarian assemblages between the MECO event, and the pre- and post-MECO cooling intervals. ANOSIM was run on a dissimilarity matrix (Bray–Curtis dissimilarity index) computed from raw counts of radiolarian species, using 9999 random permutations of group membership (Clarke, 1993). This type of analysis produces an R statistic ranging from 0 to 1, which indicates the degree of separation between groups. A large positive R indicates dissimilarity in assemblages between groups. Differences between each pair of groups were then assessed using ANOSIM post-hoc tests with p-value adjustments for multiple comparisons. When ANOSIM revealed significant differences between groups, we used the SIMPER (for 'Similarity Percentage') analysis to determine the relative contribution of each species to the overall average dissimilarity observed between groups (Clarke, 1993).

ANOSIM and SIMPER analyses were computed using the R package vegan (version 2.6–4; Oksanen et al., 2013), while all the other biodiversity indices and clustering analysis were calculated using the Paleontological Statistics Software Package (PAST; version 4.12; Hammer et al., 2001).

IV.1.4. Results

At ODP Site 1051, radiolarian assemblages are diverse and remarkably well-preserved across the ~80 m-thick interval investigated. Skeleton fragmentation is moderate and signs of corrosion are rare, with the more delicate skeletal elements being generally preserved (e.g., thin external processes, spumellarian spongy meshwork). The absolute abundance of radiolarian skeletons is characterized by low to moderate values in the pre-MECO interval and during the long-term MECO warming phase (average of 9.3 x 10^5 radiolarian skeletons per gram of sediment). An exceptionally high abundance (28.5 x 10^5 g⁻¹) is observed in one sample located in the warmest interval (peak-MECO), around 86.3 mcd (Figure IV.1.3). The post-MECO cooling interval shows decreased radiolarian abundance values (average of 7.1 x 10^5 g⁻¹) that are close to those observed before the MECO.

A total of 326 radiolarian species were identified at ODP Site 1051 (average of 216 species per sample), including most of the typical middle Eocene species found in tropical to warm-subtropical latitudes. A few potentially reworked specimens of the early Eocene species *Buryella tetradica* Foreman and *Phormocyrtis striata striata* Brandt were found. However, they represent a very small fraction of the assemblage and were usually broken in our material, allowing them to be easily distinguished from the in situ fauna. In the considered interval, nassellarians are both very diverse and abundant, accounting for ~80% of the total radiolarian diversity and 70% to 80% of the total counted specimens. A relatively high proportion of species (~27%) are present in all samples. Analysis of sample completeness indicates that all samples have excellent coverage, ranging between 98% and 99%.

IV.1.4.1. Diversity changes across the MECO

Radiolarian paleobiodiversity curves constructed using sampled-in-bin values (SIB; measure of raw taxonomic diversity) and diversity corrected for sampling bias are shown in Figure IV.1.3. The SIB diversity is ~30% higher during the MECO interval, with the highest values recorded in the warmest interval (peak-MECO). The diversity values are lower during the post-MECO cooling phase, although they are slightly higher than those observed during the pre-MECO phase. Rarefied diversity shows similar broad trends to the SIB diversity, suggesting that the observed diversity is not heavily distorted by sampling biases. The most striking difference is a more pronounced decrease in rarefied diversity in the middle part of the MECO interval (98.68 mcd) and a shift of the diversity peak towards the post-MECO interval.

At ODP Site 1051, the species diversity (H') was calculated from the Shannon-Wiener index ranged from 3.92 to 4.31 (average 4.20) throughout the study interval (Figure IV.1.3).

The lowest value is recorded in the lower part of the MECO event, around 98.68 mcd. The evenness is also stable and high throughout the studied interval, with values ranging between 0.75 and 0.8, and with only two samples (located at 113.78 and 98.68 mcd) characterized by an evenness value lower than the average lower of 0.78 (Figure IV.1.3). These samples are dominated by two small artostrobiids: *Siphocampe acephala* (Ehrenberg) and *S. ? paupera* (Ehrenberg), together representing between 16% and 24% of the total assemblage.



Figure IV.1.3. Radiolarian diversity patterns across the MECO interval of ODP Site 1051 (Blake Nose, western North Atlantic), plotted against magnetostratigraphy (Ogg and Bardot, 2001), radiolarian biostratigraphy (Sanfilippo and Blome, 2001), planktic foraminiferal biostratigraphy (Norris et al., 1998; Edgar et al., 2010), and calcareous nannofossil biostratigraphy (Mita, 2001). The darker orange zone highlights the peak-MECO interval, and black dots represent the samples examinated (each one of which is 1 cm–thick). Abbreviations: Foram., planktic foraminifera; mcd, meters composite depth; Nanno., calcareous nannofossils; Rad., radiolarians; SQS, Shareholder Quorum Subsampling.

IV.1.4.2. Changes in faunal composition across the MECO

The clustering analysis performed on the 28 most abundant radiolarian species highlights the presence of three well-defined clusters (Figure IV.1.4). These species are shown in Plates IV.1.1 and IV.1.2, and their stratigraphic distribution and abundance fluctuations are given in Figure IV.1.5. Cluster A consists of seven species, including notably *Carpocanopsis ornata* (Ehrenberg) and *Rhopalosyringium ? biauritum* (Ehrenberg). This cluster accounts for 2% to 18% of the total assemblage, with the highest values recorded in the pre-MECO and showing a decline during the MECO (Figure IV.1.6).



Figure IV.1.4. Hierarchical cluster analysis (UPGMA linkage and Morisita similarity index) of the 28 most abundant radiolarian species from ODP Site 1051 (Blake Nose, western North Atlantic). (1 – Described as *Spirocyrtis matsuokai* Meunier and Danelian n. sp. in Chapter II.3; 2 – Described as *Dictyoprora echidna* Meunier and Danelian n. sp. in Chapter II.3; 3 – Described as *Apoplanius hyalinus* Meunier and Danelian n. sp. in Chapter II.3; 4 – Described as *Phormocyrtis microtesta* Meunier and Danelian n. sp. in Chapter II.3; 5 – *Dictyoprora crassiceps* (Ehrenberg) group in Chapter II.2).

Cluster B consists of two species (*Apoplanius* sp. A¹ and *Theocorys anapographa* Sanfilippo and Riedel var. A) and shows a marked increase throughout the studied interval (Figure IV.1.6), although it represents only 0.2% to 4% of the total assemblage. Cluster C is the largest cluster with 19 taxa, including inter alia *Phormocyrtis lazari* Meunier and Danelian, *Siphocampe acephala* (Ehrenberg), *S.* ? *paupera* (Ehrenberg), and *Stylosphaera laevis* (Ehrenberg). This cluster is the major component of the radiolarian assemblages (33% to 49%) in the late middle Eocene interval of ODP Site 1051 (Figure IV.1.6).

The results of the one-way ANOSIM analysis indicated statistically significant differences in the taxonomic composition between the sample groups (R = 0.75, p-value = 0.001). Pairwise ANOSIM tests showed significant differences between the MECO interval and the pre-MECO and post-MECO intervals (p-values = 0.025 and 0.027, respectively), but not between the pre-MECO and post-MECO intervals (p-value = 0.331). SIMPER analysis allows the examination of the species that contribute the most to the dissimilarity between groups (Table IV.1). SIMPER analyses show that the radiolarian assemblage of the pre-MECO interval differs from those of the MECO interval in being characterized by a higher abundance of *Larcopyle hayesi hayesi* (Chen), *Rhopalosyringium* ? *biauritum* (Ehrenberg), and *Stylosphaera laevis* Ehrenberg, whereas the MECO interval is mostly defined by the predominance of *Apoplanius* sp. A², *Siphocampe acephala* (Ehrenberg), *S.* ? *paupera* (Ehrenberg), and *Theocorys anapographa* Riedel and Sanfilippo var. A. According to SIMPER analyses, the most significant differences between the post-MECO and the MECO intervals are the high abundance of *Carpocanopsis ornata* (Ehrenberg), *Cornutella circularis* Ehrenberg, *Dictyoprora* sp. D, *Elaphospyris* cf. *didiceros*, *Spirocyrtis* sp. A³ and *R.* ? *biauritum* throughout the MECO interval.

¹ Described as Apoplanius hyalinus Meunier and Danelian in Chapter II.3.

² Described as Apoplanius hyalinus Meunier and Danelian n. sp. in Chapter II.3.

³ Described as Spirocyrtis matsuokai Meunier and Danelian n. sp. in Chapter II.3.



Chapter IV – Biotic effects of the Middle Eocene Climate Optimum (MECO)

Figure IV.1.5. Relative abundance (%) variations of the 28 most abundant radiolarian species recognized for the MECO interval of ODP Site 1051 (Blake Nose, western North Atlantic) plotted against magnetostratigraphy (Ogg and Bardot, 2001), radiolarian biostratigraphy (Sanfilippo and Blome, 2001), planktic foraminiferal biostratigraphy (Norris et al., 1998; Edgar et al., 2010) and calcareous nannofossil biostratigraphy (Mita, 2001). Abbreviations: Foram., planktic foraminifera; mcd, meters composite depth; Nanno., calcareous nannofossils; Rad., radiolarians. The colors refer to the three clusters found by the hierarchical cluster analysis.

(1 – Described as *Spirocyrtis matsuokai* Meunier and Danelian n. sp. in Chapter II.3; 2 – Described as *Dictyoprora echidna* Meunier and Danelian n. sp. in Chapter II.3; 3 – Described as *Apoplanius hyalinus* Meunier and Danelian n. sp. in Chapter II.3; 4 –*Dictyoprora crassiceps* (Ehrenberg) group in Chapter II.2; 5 – Described as *Phormocyrtis microtesta* Meunier and Danelian n. sp. in Chapter II.3).

IV.1.5. Discussion

The radiolarian skeletons observed in our material exhibit an excellent quality of preservation, suggesting that the diagenetic influence on radiolarian biogenic silica, abundance, and assemblage structure is negligible. However, Witkowski et al. (2014) found that middle Eocene diatoms from ODP Site 1051 showed a rather moderate degree of dissolution (i.e., absence of delicate parts on valves). This difference of preservation may be due to the delicate and finely perforated diatom frustule as compared to the largely more robust radiolarian skeleton, which was particularly silica-rich for Paleogene radiolarians (Lazarus et al., 2009). Radiolarian abundance appears to be higher within the MECO, which is consistent with the planktic foraminiferal and diatom record from the same site, supporting increased eutrophication during the MECO warming interval (Edgar et al., 2013; Witkowski et al., 2014).

In addition to siliceous plankton, spicules from epibenthic siliceous sponges are also a major component of middle Eocene siliceous microfossils from ODP Site 1051 (Norris et al., 1998). However, their abundance could not be precisely quantified due to the difficulty of counting broken monaxons. It is likely that the pinakid-type sponge spicules observed in our material from ODP Site 1051 (Plate IV.1.2, Figure 15) belong to shallow-water demosponges of the order Astrophorida, and that they were probably redeposited from shallower shelf environments (Bąk et al., 2015).

As discussed above, the middle Eocene sedimentary sequences recovered at ODP Site 1051 are characterized by diverse radiolarian fauna. A total of 321 radiolarian species were identified in this study (with an average of 216 species per sample), while only 41 species were **Table IV.1.** Summary of the SIMPER (similarity percentage) analysis. The first column shows taxa contributing the most to the average dissimilarities between groups, ranked in order of importance. A cut-off of a cumulative percentage of dissimilarity of 50% was applied. The second and third columns represent the individual and cumulative contributions of each taxon to the average dissimilarities between groups. The last columns show the mean relative abundance of taxa per group. (1 – Described as *Phormocyrtis microtesta* Meunier and Danelian n. sp. in Chapter II.3; 2 – *Dictyoprora crassiceps* (Ehrenberg) group in Chapter II.2; 3 – Described as *Apoplanius hyalinus* Meunier and Danelian n. sp. in Chapter II.3; 4 – Described as *Spirocyrtis matsuokai* Meunier and Danelian n. sp. in Chapter II.3).

Frequency

Taxon	Average dissimilarity	Contribution (%)	Cumulative (%)	post-MECO	MECO	pre-MECO
Siphocampe ? paupera	2.06	6.36	6.36	8.82	5.99	2.02
Rhopalosyringium ? biauritum	1.92	5.94	12.29	0.01	1.87	6.84
Siphocampe acephala	1.32	4.09	16.38	7.79	7.53	4.52
Carpocanopsis ornata	1.08	3.33	19.71	1.68	4.39	5.03
Stylosphaera laevis	0.98	3.04	22.76	5.46	5.41	8.20
<i>Phormocyrtis</i> cf. <i>lazari</i> ¹	0.81	2.52	25.28	4.87	3.43	2.42
<i>Dictyoprora urceolus</i> group ²	0.77	2.37	27.65	4.93	3.75	2.25
Lithomelissa macroptera	0.71	2.21	29.86	2.90	3.32	2.10
Apoplanius sp. A^3	0.67	2.08	31.93	1.95	1.39	0.02
Phormocyrtis lazari	0.62	1.91	33.84	4.53	5.27	5.56
Dictyoprora sp. D	0.62	1.91	35.75	0.67	1.62	2.83
Dictyoprora ovata group	0.54	1.66	37.41	2.32	1.44	1.12
Dictyoprora pirum	0.48	1.50	38.90	3.62	3.15	2.86
Cornutella circularis	0.43	1.33	40.23	0.29	1.04	1.66
Dictyoprora mongolfieri	0.43	1.32	41.55	2.40	2.64	2.38
Theocorys anapographa var. A	0.42	1.30	42.85	1.66	1.22	0.33
<i>Spirocyrtis</i> sp. A ⁴	0.41	1.28	44.13	0.23	1.11	1.49
Zygocircus butschlii	0.37	1.14	45.27	2.22	2.19	2.17
Elaphospyris cf. didiceros	0.36	1.11	46.38	0.09	1.03	1.37
Stylodictya inaequalispina group	0.35	1.09	47.47	1.25	0.06	0.05
Larcopyle hayesi hayesi	0.35	1.07	48.54	0.41	0.75	1.58
Apoplanius kerasperus	0.34	1.05	49.58	0.37	0.84	0.61
Podocyrtis papalis	0.33	1.01	50.59	1.38	1.80	1.43

previously reported by Sanfilippo and Blome (2001) from the same stratigraphic interval. Radiolarians are more diverse than diatoms at ODP Site 1051, where a total of 137 diatom species were recorded in the MECO interval, with an average of 28 diatom species per sample (Witkowski et al., 2014). The most abundant radiolarian taxa rarely account for >5% of the total assemblage; numerous species are rather rare and represented by only a few specimens in our material, as this is also the case in some other recent detailed radiolarian studies (Renaudie and Lazarus, 2013b; Trubovitz et al., 2020).



Figure IV.1.6. Relative abundance (%) variations of the three radiolarian clusters recognized across the MECO interval of ODP Site 1051 (Blake Nose, western North Atlantic) plotted against magnetostratigraphy (Ogg and Bardot, 2001), radiolarian biostratigraphy (Sanfilippo and Blome, 2001), planktic foraminiferal biostratigraphy (Norris et al., 1998; Edgar et al., 2010) and calcareous nannofossil biostratigraphy (Mita, 2001). The MECO interval is indicated by two dotted horizontal lines. Abbreviations: Foram., planktic foraminifera; mcd, meters composite depth; Nanno., calcareous nannofossils; Rad., radiolarians. Colors refer to the three clusters found by the hierarchical cluster analysis.

At ODP Site 1051, the total number of species per sample is relatively constant across the studied interval, although a ~30% increase in taxonomic richness was observed in samples coming from the warmest interval of the MECO. This increased richness is probably due to an influx of warm, low-latitude taxa that temporarily expanded their geographic range to higher latitudes, such as Podocyrtis chalara Riedel and Sanfilippo, whose occurrence coincides with the peak warming phase of the MECO. These migration events appear to be triggered by climate warming, and it is likely that they were facilitated by changes in surface ocean circulation that altered water mass boundaries during the Eocene (Vahlenkamp et al., 2018; Cramwinckel et al., 2020). Similarly, the acme of several emblematic tropical middle Eocene species lies in the warmest interval of the MECO, including P. mitra Ehrenberg, P. papalis Ehrenberg, *Thyrsocyrtis triacantha* Ehrenberg⁴, and *T. rhizodon* Ehrenberg⁵. With the exception of these few well-known species, it is difficult to specify the latitudinal affinity of most of the taxa encountered, as nearly half of them are new to science, and most of the others are known only from their type locality. Nevertheless, the radiolarian fauna of ODP Site 1051 can be compared to the equatorial record of ODP Site 1260 (Demerara Rise, ~3500 km southeast of the Blake Plateau), which has recently been the subject of a detailed biostratigraphic study (Meunier and Danelian, 2022). Several species commonly found in upper middle Eocene sediments of the equatorial Atlantic ODP Site 1260 are missing from ODP Site 1051, including notably Apoplanius klydus (Sanfilippo and Caulet), Dorcadospyris ombros Sanfilippo in Nigrini et al., Lithochytris vespertilio Ehrenberg⁶, P. trachodes Sanfilippo and Riedel, and Theocorys ? scolopax (Ehrenberg). Although the boundaries of the geographic range of radiolarian species are roughly explained by sea-surface temperature (e.g., Boltovskoy et al., 2010), their latitudinal

⁴ Thyrsocyrtis (Pentalacorys) schomburgkii (Ehrenberg, 1847) in Chapter II.2.

⁵ Thyrsocyrtis (Thyrsocyrtis) argulus (Ehrenberg, 1874) in Chapter II.2.

⁶ Lithochytris pyramidalis Ehrenberg, 1874 in Chapter II.2.

distribution is also controlled by other abiotic and biotic factors, including salinity, dissolved oxygen, nutrient availability, and interspecific interactions (Lazarus et al., 2021). The lack of poleward migration for some other tropical radiolarian species may be related to the difference in sampling effort between the two sites, or the result of a combination of some unknown environmental parameters. Similarly, some abundant species at ODP Site 1260 are found to be rare at ODP Site 1051, including the biostratigraphically important species *Sethochytris triconiscus* Haeckel and *Lychnocanium babylonis* (Clark and Campbell) group⁷, and *Rhopalosyringium*? *auriculaleporis* (Clark and Campbell), which is replaced at this subtropical site by *R*. ? *biauritum* (Ehrenberg).

It is noteworthy that Pascher et al. (2015), who studied the southern high-latitude radiolarian fauna of DSDP Site 277 (southwest Pacific, paleolatitude ~55°S), also found an increased taxonomic richness during the MECO, and a shift to higher latitudes of several tropical taxa, including the spumellarian species *Amphicraspedula murrayana* (Haeckel) and *A. prolixa* (Sanfilippo and Riedel) group. However, important middle Eocene tropical species of the genera *Podocyrtis* and *Thyrsocyrtis* appear to be absent from the southwest Pacific (Pascher et al., 2015; Hollis et al., 2020), suggesting that their ability to track their preferred thermal habitat is either limited to mid-latitudes or that temperatures were not sufficiently elevated in this part of the ocean during the MECO. Poleward migrations of tropical radiolarian species have also been observed in the Southern Hemisphere during the Paleocene-Eocene Thermal Maximum (Hollis et al., 2005a, 2005b; Hollis, 2006), as well as in other planktic groups such as the planktic foraminifera (Thomas and Shackleton, 1996; Arenillas et al., 1999; Lu and Keller, 1995; Berggren and Ouda, 2003) and the dinoflagellates (Bujak and Brinkhuis, 1998; Crouch et al., 2001, 2003; Sluijs et al., 2005, 2006).

⁷ Lychnocanium tribulus (Ehrenberg, 1874) group in Chapter II.2.



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Plate IV.1.1. Composite light micrographs of selected radiolarians from ODP Site 1051. All scale bars equal 50 µm. (1) Cornutella circularis Ehrenberg, 171B-1051A-14H-5W, 52-54 cm, L1, USTL 4554; (2) Carpocanopsis ornata (Ehrenberg) group, 171B-1051A-9H-5W, 53-55 cm, L2, USTL 4528; (3) Dictyoprora mongolfieri (Ehrenberg), 171B-1051A-8H-5W, 61-63 cm, L1, USTL 4521; (4) Dictyoprora ovata (Haeckel) group, 171B-1051A-9H-5W, 53-55 cm, L3, USTL 4529; (5) Dictyoprora pirum (Ehrenberg), 171B-1051A-9H-5W, 53-55 cm, L3, USTL 4529; (6) *Dictyoprora urceolus* (Haeckel) group (= *Dictyoprora crassiceps* (Ehrenberg) group in Chapter II.2), 171B-1051A-9H-5W, 53-55 cm, L2, USTL 4528; (7) Dictvoprora sp. A (described as Dictyoprora echidna Meunier and Danelian n. sp. in Chapter II.3), 171B-1051A-6H-5W, 53-55 cm, L1, USTL 4518; (8) Dictyoprora sp. D, 171B-1051A-9H-5W, 53-55 cm, L2, USTL 4528; (9) Siphocampe acephala (Ehrenberg), 171B-1051A-9H-5W, 53-55 cm, L2, USTL 4528; (10) Siphocampe ? paupera (Ehrenberg), 171B-1051A-14H-5W, 52-54 cm, L1, USTL 4554; (11) Spirocyrtis sp. A (described as Spirocyrtis matsuokai Meunier and Danelian n. sp. in Chapter II.3), 171B 1051A-14H-5W, 52-54 cm, L1, USTL 4554; (12) Rhopalosyringium ? biauritum (Ehrenberg), 171B-1051A-14H-5W, 52-54 cm, L1, USTL 4554; (13) Ceratospyris clavata Bütschli group, 171B-1051A-14H-5W, 52–54 cm, L1, USTL 4554; (14) Elaphospyris cf. didiceros (Ehrenberg), 171B-1051A-14H-5W, 52-54 cm, L1, USTL 4554; (15) Liriospyris clathrata (Ehrenberg) group, 171B-1051A-9H-2W, 53-55 cm, L1, USTL 4524; (16) Zvgocircus butschlii Haeckel, 171B-1051A-14H-5W, 52-54 cm, L1, USTL 4554.

In addition to this influx of tropical species, quantitative analysis of microfossil assemblages revealed only minor changes in the radiolarian faunal composition throughout the studied interval. Similarly, few changes in radiolarian assemblages have been documented at ODP Site 1051 during the PETM event (Sanfilippo and Blome, 2001), suggesting that subtropical radiolarians are relatively resilient to transient warming events.

The radiolarian fauna of the pre-MECO interval is characterized by a high abundance of cluster A species, especially *Larcopyle hayesi hayesi* (Chen) and *R*. ? *biauritum* (Ehrenberg). Since the relative abundance of Cluster A species tends to decrease over the study interval, they may represent species associated with colder water masses. A similar decline in cool-water taxa has also been observed in the eastern equatorial Pacific Ocean during the MECO (Kamikuri et al., 2013).



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Plate IV.1.2. Composite light micrographs of selected radiolarians from ODP Site 1051. All scale bars equal 50 µm. (1) Anthocyrtis mespilus Ehrenberg group, 171B-1051A-9H-5W, 53-55 cm, L2, USTL 4528; (2) Lophophaena radians Ehrenberg, 171B-1051A-9H-2W, 53-55 cm, L1, USTL 4524; (3) Lithomelissa macroptera Ehrenberg, 171B-1051A-9H-5W, 53-55 cm, L3, USTL 4529; (4) Apoplanius sp. A (described as Apoplanius hyalinus Meunier and Danelian n. sp. in Chapter II.3), 171B-1051A-8H-5W, 61-63 cm, L1, USTL 4521; (5) Lophocyrtis microtheca (Ehrenberg), 171B-1051A-9H-5W, 53-55 cm, L2, USTL 4528; (6) Phormocyrtis lazari Meunier and Danelian, 171B-1051A-9H-2W, 53-55 cm, L1, USTL 4524; (7) Phormocyrtis cf. lazari Meunier and Danelian (described as Phormocyrtis microtesta Meunier and Danelian n. sp. in Chapter II.3), 171B-1051A-9H-2W, 53-55 cm, L3, USTL 4526; (8) Podocyrtis (Podocyrtis) papalis Ehrenberg, 171B-1051A-9H-5W, 53-55 cm, L3, USTL 4529; (9) Podocyrtis (Lampterium) mitra Ehrenberg, 171B-1051A-9H-5W, 53-55 cm, L3, USTL 4529; (10) Podocyrtis (Lampterium) chalara Riedel and Sanfilippo, 171B-1051A-9H-5W, 53-55 cm, L3, USTL 4529; (11) Theocorys anapographa Riedel and Sanfilippo var. A, 171B-1051A-9H-2W, 53-55 cm, L3, USTL 4526; (12) Stylosphaera coronata Ehrenberg, 171B-1051A-9H-2W, 53-55 cm, L3, USTL 4526; (13) Stylosphaera laevis Ehrenberg, 171B-1051A-9H-5W, 53-55 cm, L2, USTL 4528; (14) Larcopyle havesi havesi (Chen), 171B-1051A-9H-2W, 53-55 cm, L1, USTL 4524; (15) Pinakid (demosponge spicule), 171B-1051A-9H-2W, 53-55 cm, L3, USTL 4526; (16) Verticillated acanthostrongyle (demosponge spicule), 171B-1051A-9H-2W, 53-55 cm, L2, USTL 4525.

On the other hand, the MECO interval is mainly characterized by the dominance of cluster B species (*Apoplanius* sp. A⁸ and *Theocorys anapographa* Riedel and Sanfilippo var. A), as well as two very abundant artostrobiid species: *Siphocampe acephala* (Ehrenberg) and *S. ? paupera* (Ehrenberg). Since the genus *Apoplanius* is considered to have originated in the tropics (Sanfilippo and Caulet, 1998), and *Theocorys anapographa* var. A is known only from tropical and subtropical localities (Ling, 1975; Sanfilippo and Blome, 2001; Hollis et al., 2020; Meunier and Danelian, 2022), cluster B is interpreted as a group of warm-water tropical species. The stratigraphic and geographic distributions of *S. acephala* and *S. ? paupera* are not well known, probably because these two species are relatively small for Eocene radiolarians (total length: ~80–100 μ m) and can be therefore easily lost during sample preparation. This

⁸ Described as Apoplanius hyalinus Meunier and Danelian n. sp. in Chapter II.3.

emphasizes the need to use narrow mesh sieves (45 µm or less) in order to obtain reliable data for analyses of the entire radiolarian fauna. At ODP Site 1051, *S. acephala* and *S. ? paupera* are the most abundant species, representing on average 10% (up to 18%) of the total radiolarian assemblage. They may thus represent nutrient opportunists (r-strategists). In addition, these two species have a relatively simple morphology (see Plate 1, Plate 1.9 1.0), which is known to be a characteristic feature of opportunistic planktic species (e.g., Bé, 1982; Hemleben et al., 1989).

Finally, the major differences between the MECO and the post-MECO intervals are the abundance of *Carpocanopsis ornata* (Ehrenberg) group, *Cornutella circularis* Ehrenberg, *Dictyoprora* sp. D, *Elaphospyris* cf. *didiceros*, *Spirocyrtis* sp. A⁹, and *R*. ? *biauritum* throughout the MECO interval. Interestingly, these cluster C species continue to decline in relative abundance during the post-MECO cooling phase, when recovery of cool-water species is expected. However, a better sampling of the post-MECO interval is needed to be conclusive.

IV.1.6. Conclusions

Our results on mid-latitude radiolarian assemblages from ODP Site 1051 are in good agreement with previous studies conducted on diatoms and planktic foraminifera from the same site, suggesting increased eutrophication during the MECO. Although radiolarians have apparently benefited from an increase in oceanic fertility induced by the MECO, this global warming event does not appear to have profoundly altered subtropical radiolarian fauna. Indeed, a detailed quantitative study of the entire radiolarian fauna preserved at Blake Nose did not reveal any significant faunal turnover during the MECO. On the contrary, we find here establish that radiolarian taxonomic richness increased during the warmest interval, a likely result of the northward incursion of several tropical radiolarian species. The biogeographic expansion of

⁹ Described as Spirocyrtis matsuokai Meunier and Danelian n. sp. in Chapter II.3.

low-latitude radiolarian species appears to have been initiated by the MECO global warming and is likely associated with changes in oceanic current circulation. Similarly, our quantitative analyses of the composition of the entire radiolarian assemblage indicate that ocean warming induced only a weak ecological response in radiolarian plankton. Indeed, the radiolarian fauna observed during MECO differs only slightly from the radiolarian fauna observed before and after the MECO, and this difference is mainly due to variations in the relative abundance of a small number of species. We have also identified two very abundant artostrobiid species (*Siphocampe acephala* and *S. ? paupera*) that may represent nutrient opportunists (r-strategists).

Finally, the MECO appears to be a minor event in the history of Paleogene radiolarians. It may be best considered as a poleward migration event of tropical radiolarians, as this is also the case for planktic foraminifera. However, the faunal changes reported here may have only a regional significance (i.e., the western subtropical Atlantic), and may not be representative of the effects of the MECO on radiolarian faunas at higher latitudes.

Author contributions

Mathias Meunier: Methodology, Investigation, Data curation, Software, Visualization, Writing – original draft, Writing – review and editing. **Taniel Danelian**: Conceptualization, Supervision, Resources, Writing – original draft, Writing – review and editing.

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I.V.2. Morphological responses of the plankton to the Middle Eocene Climatic Optimum (MECO): The case of the radiolarian species *Podocyrtis papalis* from the western equatorial Atlantic (ODP Site 1260)

Mathias Meunier*, Claude Monnet, Rémi Habert, José Francisco Pínto Cabrera, Marie Cueille, Taniel Danelian

Univ. Lille, CNRS, UMR 8198 – Evo-Eco-Paleo, F-59000 Lille, France

<mathias.meunier@univ-lille.fr>

*Corresponding author

Abstract

The Middle Climatic Optimum (MECO) was a major event and carbon cycle perturbation that occurred at ca. 40 Ma and reversed the long-term Cenozoic cooling trend. Previous studies have highlighted changes in microfossil assemblages during the MECO interval, mainly affecting the relative abundance and biogeographic distribution of species, but very little is known about the morphological response of plankton species to this warming event. In this study, we apply a geometric morphometric approach to document and quantify, for the first time, variations in radiolarian disparity and morphological space occupancy in response to oceanographic perturbations induced by the MECO. Investigations were conducted on the nassellarian species *Podocyrtis papalis*, and a closely related morphotype (*P. cf. papalis*) that is particularly abundant during the MECO interval, as preserved at ODP Site 1260 (western equatorial Atlantic). Comparison of the quantified morphological variations with geochemical proxies recorded throughout the MECO establishes a differential response of the two studied taxa: P. papalis locally disappeared during the climatic interval, while P. cf. papalis became dominant and showed a wide range of morphological variability. The morphological diversification of P. cf. papalis expanded on pre-existing morphologies of P. papalis and culminated with the appearance of extreme shapes during the warmest interval of the MECO. Interestingly, the upheavals induced by the MECO event appear to be reversible; indeed, after the reappearance of *P. papalis* during the post-MECO cooling phase, the morphospace occupation returned to the original pre-MECO conditions. Our study highlights the great potential of geometric morphometrics to decipher subtle changes in radiolarian morphology in relation to climate change.

IV.2.1. Introduction

The Middle Eocene Climatic Optimum (MECO; Bohaty and Zachos, 2003; Bohaty et al., 2009) is one of the most significant global warming events of the Cenozoic. It occurred during the Bartonian (ca. 40 Ma) and temporarily interrupted the long-term cooling trend initiated at the end of the early Eocene climate optimum (Westerhold and Röhl, 2013; Westerhold et al., 2020). The MECO has been recognized in the marine and continental record by a negative oxygen isotope excursion, which is interpreted as a ~4-6°C rise in seawater temperature (Bohaty and Zachos, 2003; Bohaty et al., 2009; Bijl et al., 2010; Edgar et al., 2010). However, in contrast to what is usually observed for other Paleogene hyperthermal events, the MECO corresponds to only a weak shift in carbon isotope values (Bohaty and Zachos, 2003; Bohaty et al., 2009; Bijl et al., 2010; Giorgioni et al., 2019). Although the actual triggering mechanisms of the MECO are still poorly understood, modeling of the carbon cycle suggests an imbalance in long-term carbon fluxes, resulting in elevated carbon dioxide levels in the ocean-atmosphere system and a shoaling of the carbonate saturation profile (Edgar et al., 2007; Bohaty et al., 2009; Sluijs et al., 2013; Cornaggia et al., 2020; Henehan et al., 2020). Previous studies investigating changes in plankton biodiversity during the MECO have found different types of changes in assemblages, mainly affecting the taxonomic richness, relative abundance, and biogeographic distribution of species (Villa et al., 2008; Bijl et al., 2010; Luciani et al., 2010; Renaudie et al., 2010; Toffanin et al., 2011; Witkowski et al., 2012, 2014; Edgar et al., 2013; Kamikuri et al., 2013: Pascher et al., 2015; Cramwinckel et al., 2019; D'Onofrio et al., 2021; Meunier and Danelian, 2023a). However, no major extinction event and/or prominent taxonomic turnover was observed in any of the plankton microfossil groups during the MECO warming event. In contrast, relatively little is known about the impact of this event on plankton morphology. As species richness and morphological disparity are known to be two distinct components of biodiversity that are often decoupled from each other (Foote, 1991, 1993; Hopkins, 2013),

analysis of morphology may prove to be a valuable approach to the assessement of the impact of environmental perturbations that did not result in species extinctions. In addition, size changes and increased morphological disparity in planktic organisms have been reported in association with older Paleogene environmental perturbations, such as the Paleocene-Eocene Thermal Maximum (PETM) (Clay Kelly et al., 1996; Kaiho et al., 2006; Luciani et al., 2007; Yamaguchi et al., 2012; Gibbs et al., 2018; Westacott et al., 2023). These morphological changes induced by environmental forcing may have a significant impact on marine plankton because body size and shape are closely linked to many physiological, ecological, and life history traits.

Therefore, the main objective of this study is to evaluate radiolarian shape variation during environmental perturbations associated with the MECO. To date, the morphology of radiolarian shells has been quantified by biometric analyses, typically based on linear measurements mainly to differentiate closely related species (e.g. Kellogg, 1975, 1983; Lazarus, 1986; Granlund, 1990; Cortese and Bjørklund, 1997, 1998). In recent decades, advances in geometric morphometric methods have driven forward paleobiology by revealing previously unexplored aspects of the fossil record. In particular, quantitative approaches have benne used to extract evolutionary, ecological, and phylogenetic signals from fossils (e.g. Smith and Hendricks, 2013; Parins-Fukuchi, 2018; Bault et al., 2022, 2023; De Mendoza and Gómez, 2022) or to separate cryptic taxa (e.g. Danelian and MacLeod, 2019; Viertler et al., 2022). However, the more recent and powerful methods of geometric morphometrics have been used only occasionally (Sanfilippo and Riedel, 1990; Danelian and MacLeod, 2019).

As a case study, investigations were conducted here on the nassellarian species *Podocyrtis papalis* which is a prominent component of Eocene tropical radiolarian assemblages, from which the biostratigraphically important evolutionary lineages *Podocyrtoges* and *Lampterium* arose (Sanfilippo and Riedel, 1992). Although *P. papalis* is

considered as a long-lived species that has experienced morphological stasis, it exhibits highly variable shell morphology throughout the MECO. This interval is marked by the proliferation of specimens with an atypical morphology, classified here as *P*. cf. *papalis*, which are characterized by a less spindle-shaped shell with a well-defined lumbar constriction (see Appendix 1. for a more detailed taxonomic description of the two studied taxa). In this study, we aim to 1) quantify the morphological variability of *P. papalis* and its related morphotypes by using geometric morphometrics on their shell outline, and 2) compare the evolution of the morphological disparity with stable isotope data to assess the effect of environmental perturbations on shape variation of *P. papalis* and its related morphotypes.

IV.2.2. Material and methods

IV.2.2.1. Stratigraphic and paleoclimatic framework

This study is based on Eocene sediment cores drilled at Ocean Drilling Program (ODP) Site 1260 (9°15'N, 54°32'W) on the northern slope of Demerara Rise, a submarine plateau off the coast of South America, on the French Guiana-Suriname margin (Figure IV.2.1). Two holes (1260A and 1260B) situated 50 m apart were drilled at a modern water depth of 2,549 m below sea level (mbsl) (Shipboard Scientific Party, 2004). A 325 m thick Paleogene sequence was recovered from ODP Site 1260, including a ~180 m thick middle Eocene interval dominated by nannofossil chalk rich in siliceous microfossils (Danelian et al., 2005, 2007; Renaudie et al., 2010; Meunier and Danelian, 2022, 2023a, 2023b). During the middle Eocene this site was situated even closer to the equator than it is today, at a paleolatitude of ~1°N (Suganuma and Ogg, 2006).

At ODP Site 1260, significant shifts were recorded in both oxygen (δ^{18} O) and carbon (δ^{13} C) stable isotope records were recorded (Bohaty et al., 2009; Edgar et al., 2007) and



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Figure IV.2.1. Geographic location of Demerara Rise and location of studied ODP Site 1260. Bathymetric map modified fromShipboard Scientific Party (2004) and the paleogeographic reconstruction form ODSN Plate Tectonic Reconstruction Service (http://www.odsn.de/odsn/services/paleomap/paleomap.html, last accessed: 14 May, 2023).

correlated with the MECO event (Figure IV.2.2). The onset of the MECO is located at about 52 rmcd, in the upper part of the magnetochron C18r (Edgar et al., 2007); benthic foraminiferal δ^{18} O values subsequently decreased (~1.0 ‰) toward the peak warming interval of the MECO at 44 rmcd (Figure IV.2.2). The warmer interval is also marked at this site by a negative excursion (~0.5‰) in benthic foraminiferal δ^{13} C values (Edgar et al., 2007). The peak warming phase was followed by a rapid return to the conditions that prevailed prior to the MECO (Bohaty et al., 2009; Edgar et al., 2010; Westerhold and Röhl, 2013). A high-resolution cyclostratigraphic framework also been developed for ODP Site 1260 (Westerhold and Röhl, 2013). Astrochronological calibration allowed us to date the onset of the MECO at ~40.50 ±

0.02 Ma, the peak warming at \sim 40.07 \pm 0.02 Ma, and the end of the MECO at \sim 40.05 \pm 0.02 Ma (Westerhold and Röhl, 2013).

The studied sequence has a thickness of 15.22 m and is estimated to have been accumulated between 40.66 Ma and 39.84 Ma, during the late middle Eocene (Bartonian). A total of 15 samples covering the MECO interval were selected from hole 1260A (Figure IV.2.2). Mean sample spacing is approximately 1.67 m and the mean age difference between two consecutive samples is ~58 kyr.



Figure IV.2.2. Variation of geochemical proxies through the MECO interval of ODP Site 1260 (Demerara Rise, equatorial Atlantic Ocean). The darker orange zone highlights the peak warming MECO interval. Stable isotope data are from Edgar et al. (2007), magnetostratigraphy from Suganuma and Ogg (2006), calcareous nannofossil and planktc foraminiferal biostratigraphy from the Shipboard Scientific Party (2004), and radiolarian biozonation is from Meunier and Danelian (2022).

IV.2.2.2. Sample preparation

Samples were processed according to the procedures described in Sanfilippo et al. (1985) and Tetard et al. (2020). Approximately 2 cm² of unprocessed sediment was first soaked for 2 hours in a polypropylene beaker containing 30 mL of 30% hydrochloric acid (HCl) to dissolve the carbonate content and to concentrate siliceous microfossils. The residues were then washed with distilled water. After decantation, the excess water was slowly removed with a pipette, and the residues were soaked in 30 mL of 10% hydrogen peroxide (H₂O₂) for two hours to remove organic matter. The resulting residues were finally washed through a 63 μ m sieve to remove clay and small radiolarian fragments and transferred to a storage vial.

IV.2.2.3. Morphometric data and analyses

To describe the morphological response of *Podocyrtis papalis* to the paleoenvironmental changes that occurred during the MECO, we applied a landmark-based geometric morphometric approach to study shell shape variation (Bookstein, 1991; Rohlf and Marcus, 1993; Rohlf, 1999; Mitteroecker and Gunz, 2009; Zelditch et al., 2012; Adams et al., 2013). A total of 491 complete specimens of *P. papalis* were manually collected under a Zeiss SteREO Discovery V20 binocular microscope. The shells were positioned in lateral view using the trilobate pterocorythid cephalis (see Petrushevskaya, 1971, pl. 9, figs. I, II), with the longitudinal axis oriented parallel to the glass slide. The right side of the shell was selected for this study, and the left-sided shells were mirrored for analysis. Each specimen was photographed in the sagittal plane of the shell, allowing the entire shell contour to be seen in a single image. Based on these photos, two-dimensional landmark coordinates were extracted using TpsDig, version 2.31 (Rohlf, 2010, 2015). The shape of the shell was described by a set of six anatomical landmarks placed at the collar and lumbar strictures, and at the intersection of the abdomen and the feet, as well as by four curves of 10 equidistant semilandmarks

describing the thoracic and abdominal outlines (Figure IV.2.3). The cephalis was not included in this analysis because previous studies suggest its low taxonomic value for species discrimination within the genus *Podocyrtis* (Sanfilippo and Riedel, 1992; Danelian and MacLeod, 2019).



Figure IV.2.3. Diagrammatic representation of a *Podocyrtis* shell in lateral view, including the location of the six selected landmarks (Arabic numerals) and the four semi-landmark curves (Roman numerals, with the number of points per curve indicated in parentheses).

The acquired 2D landmark coordinates of the studied specimens were then superimposed using a generalized Procrustes analysis (GPA; Rohlf and Slice, 1990). Next, a morphological space (Dryden and Mardia, 1998; Kendall et al., 1999; Klingenberg, 2020) was constructed by means of a principal component analysis (PCA; Ringnér, 2008; Abdi and Williams, 2010). This morphospace allows the description and quantification of the morphological disparity of the two studied taxa through time (Ciampaglio et al., 2001; Wills,

2001; Guillerme et al., 2020). Here, morphospace occupancy is estimated by the sum of ranges (SoR), which refers to the total range of morphospace occupancy (Foote, 1991), as well as the sum of variances (SoV), which measures the variance in distance between examined specimens in the morphospace (Van Valen, 1974; Foote, 1991, 1993; Wills, 2001). In order to assess the effect of sample size variation overtime, confidence intervals for the computed disparity values were calculated using a bootstrap approach by iteratively calculating SoR and SoV (1000 times) from random resampling with replacement of the individual points in the morphospace (Foote, 1993). Finally, the measurement error associated with the precision of landmark digitization was evaluated by comparing the distribution of the Procrustes distances among all specimens with those of 10 specimens digitized each by two different observers. Here, a permutational ANOVA test indicated that this replicability error accounted for ~12% of the total variance and, therefore, had a reduced impact (Appendix IV.2.2).

All shape analyses were performed in the scientific environment R (v. 4.1.3; R Core Team 2022), using the packages geomorph (v. 4.0.3; Adams and Otárola-Castillo, 2013), MASS (v. 7.3-60; Ripley et al., 2013), vegan (v. 2.5-6; Oksanen et al., 2019), and epaleo (v. 1.0.0; Monnet, unpub.).

IV.2.3. Results

IV.2.3.1. Global morphological space

Thefirst two principal components (PCs) of the morphospace explain 78.8% of the total variance in shell shape variation for the radiolarians *Podocyrtis papalis* and *P*. cf. *papalis* (PC1 = 63.3%; PC2 = 15.5%; Figure IV.2.4). The morphological interpretation of the shape changes associated with each axis of the morphospace can be investigated by plotting reconstructed virtual shapes at different locations along the principal components. The first axis of the PCA, which accounts for more than half of the total variation in intraspecific shell morphology of the

two studied taxa, clearly shows a gradient in the transversal asymmetry and lateral thickness of the abdominal segment (Figure IV.2.4). On the one hand, high PC1 values show typical *P*. *papalis* morphotypes with a relatively short abdomen, giving the shell a spindle-shaped to pyriform overall shape. In addition, the shell is widest just above the lumbar stricture, which is not usually expressed externally, and the thorax/abdomen ratio is greater than 1. On the other hand, low PC1 scores indicate a longer abdomen, giving the shell a more elongated appearance, sometimes with a slight lumbar constriction and a thorax/abdomen ratio closer to 1 (Figure IV.2.4). The second axis of the PCA shows variations in thorax elongation. Morphotypes situated on the positive side of the axis show a relatively short and swollen thoracic segment, whereas negative PC2 values reflect a much more slender thorax (Figure IV.2.4).



Figure IV.2.4. Results of the first two axes of the Principal Component Analysis (PCA) performed on the superimposed landmark coordinates. Above the PC plot are illustrated the reconstructed virtual shapes obtained after a back-transformating of the PC scores of the first axis.

The morphospace overlaid with the two studied taxa (Figure IV.2.4) shows that they both cover the major shape changes discussed above. Also, the significant overlap between *P*. *papalis* and *P*. cf. *papalis* shows that these major shape changes (transversal asymmetry, lateral thickness, and thoracic elongation) are at the intraspecific level and are not discriminatory at the species level. However, *P*. cf. *papalis* shows the greatest disparity, occupying almost the entire morphospace, while *P. papalis* is more restricted to the 'right' half of the morphospace, lacking the most elongate and symmetrical shapes.

IV.2.3.2. Morphospace occupancy and morphological disparity through time

Changes in morphospace occupancy and morphological disparity through time for the two studied taxa are shown in FigureS IV.2.5 and IV.2.6, respectively. During the pre-MECO interval (Figures IV.2.5A–5C), the morphospace was characterized by a reduced occupancy, with low SoR and SoV values (Figures IV.2.6A–6B). The oldest sample examined (Figures IV.2.5A) contains only stypical *Podocyrtis papalis* specimens packed into a relatively compact point cloud whose center is in the positive part of PC1. The first appearance of *P. cf. papalis* around 40.57 Ma (~110 kyr before the onset of the MECO) marks the first changes in the morphospace occupancy. The point cloud corresponding to *P. cf. papalis* extends around the origin, occupying part of the morphological space previously occupied by *P. papalis* (Figures IV.2.5B), while the specimens corresponding to *P. papalis* are completely relegated to the positive part of PC1 (Figures IV.2.5B, 5C). It is noteworthy that *P. cf. papalis* was abundantsince its emergence, representing up to ~50% of the specimens examinedprior the onset of the MECO.

The MECO interval coincided with a protracted increase in morphological disparity indices (Figures IV.2.6A, 6B), corresponding to the spread of *P*. cf. *papalis*, which completely invaded the 'left' half of the morphospace (Figures IV.2.5D–5I). The maximal spread of *P*. cf.

papalis is observed during the warmest interval of the MECO (Figures IV.2.5J–5L). This increase in the occupancy of the morphospace is illustrated by the SoR values that begin to increase slowly at 40.2 Ma and peak at 40.05 Ma (Figures IV.2.6A). The SoV also showed a



Figure IV.2.5. Changes in morphospace occupancy through time, with the typical morphotype of *Podocyrtis papalis* represented by red dots, and *P*. cf. *papalis* represented by blue squares. Estimated tuned ages are taken from Westerhold and Röhl (2013). The darker orange rectangles, highlight the peak warming MECO interval.

global increase peaking during the warmest interval of the MECO but, unlike the SoR, this global increase was interrupted by low values between ~40.3 and 40.1 Ma (Figures IV.2.6B).



Figure IV.2.6. Evolution of *Podocyrtis* shell morphological disparity through the Middle Eocene Climate Optimum (MECO). The magnetostratigraphy follows Suganuma and Ogg (2006) and the radiolarian biozonation is from Meunier and Danelian (2022). Estimated tuned ages are taken from Westerhold and Röhl (2013). The darker orange zone highlights the peak warming MECO interval.

The post-MECO interval is marked by the recovery of typical *P. papalis* (ca. 39.9 Ma) and a striking concomitant decrease in the morphological disparity of *P.* cf. *papalis* , reflected in both SoR and SoV values (Figures IV.2.6A, 6B). Furthermore, this post-MECO pattern is clearly a return to the initial pre-MECO state of coexistence of the two taxa (compare Figures IV.2.5B–5C and 5M–5O), with the point cloud of *P.* cf. *papalis* extending around the morphospace origin and the specimens of *P. papalis* remaining confined to the positive part of PC1.

IV.2.4. Discussion

The major pattern revealed by the geometric analysis of the Podocyrtis shell outline is a profound, differential ecological response of Podocyrtis papalis and P. cf. papalis to environmental perturbations that did not cross the extinction threshold. Figure IV.2.7 shows an adaptive model derived from the temporal sequence of morphological space occupancy. First, the incidence of P. cf. *papalis* increased dramatically during the MECO interval (> 90% of the sampled specimens), while the typical *P. papalis* became increasingly rare until the end of the climatic event. Since P. papalis was found to be more abundant at mid-latitude ODP Site 1051 (North Atlantic) during the MECO interval (Meunier and Danelian, 2023a), its disappearance from equatorial ODP Site 1260 can be explained by a poleward migration that was triggered by the warming event. P. papalis would then have found refuge in the mid-latitudes by tracking its preferred temperature conditions. Interestingly, the migration of tropical radiolarian species to higher latitudes has also been documented in the Southern Hemisphere during the Paleocene-Eocene Thermal Maximum (Hollis et al., 2005a, b; Hollis 2006), as well as in paleoceanographic studies based on planktic foraminifera (Thomas and Shackleton, 1996; Arenillas et al., 1999; Lu and Keller, 1995; Berggren and Ouda, 2003) and dinoflagellates (Bujak and Brinkhuis, 1998; Crouch et al., 2001, 2003; Sluijs et al., 2005, 2006). The observed pattern of migration in response to environmental change appears to be a common biotic response of tropical/subtropical planktic species to Paleogene global warming events.



Figure IV.2.7. Adaptive model derived from the temporal sequence of morphological space occupancy by *Podocyrtis papalis* and *P.* cf. *papalis* through the Middle Eocene Climate Optimum (MECO). The darker orange zone highlights the peak warming MECO interval.

On the contrary, *P*. cf. *papalis* remains abundant at ODP Site 1260 throughout the MECO interval and appears to behave as an opportunistic species, taking advantage of the local disappearance of *P*. *papalis* to occupy the entire morphospace. A combination of range- and variance-based disparity metrics shows that the morphological diversification of *P*. cf. *papalis* culminated during the warmest interval of the MECO with the appearance of extreme shapes (see Appendix IV.2.1, Plate IV.2.2, Figures 13–16). Morphological instability has long been

hypothesized to be indicative of environmental stress on the physiology of an organism during its development (Klingenberg et al., 2003), so it is likely that this increase in P. cf. papalis shell disparity is indicative of ecological stress induced by the warming event. In addition, it has been shown in several taxa that populations under environmental stress can respond by increasing trait variation, allowing species to persist under global change (e.g. Charmantier et al., 2008; Polechova and Storch, 2008; Nicotra et al., 2010). Thus, we can thus hypothesize that the specimens assigned to P. cf. papalis may have developed a diverse shell morphology to overcome transient MECO-associated environmental perturbations. Such events of morphological diversification in response to Paleogene environmental forcing have also been documented in the fossil record of planktonic foraminifera. For example, the genera Morozovella and Acarinina show increasing test variation during the PETM (Luciani et al., 2007). This transient diversification gave rise to several short-lived morphospecies, the socalled 'excursion taxa', whose stratigraphic range is limited to the climatic interval (Clay Kelly et al., 1996; Luciani et al., 2007, 2010; Ouda, 2018). Since the total range of P. cf. papalis exceeds the limits of the MECO, this morphotype cannot be considered as a, strictly speaking, excursion taxon, although the most extreme forms occurred only during the peak warming interval.

Although the disparity peak coincides with the temperature peak, the exact mechanism leading to the diversification of shell morphologies remains elusive. The isotopic data used to identify the MECO interval and to construct the temperature curve are a simplification of the perturbations that actually occurred during this climatic event, and reflect only one aspect of this complex phenomenon generated by the interactions of numerous abiotic parameters (Henehan et al., 2020). In previous studies, foraminiferal test deformations associated with the MECO warming have been tentatively linked to increased productivity and/or low oxygen levels in surface waters, although changes in temperature, pH, or salinity cannot be discarded

(Luciani et al., 2007, 2010). Similarly, in silicoflagellates, which are close to radiolarians in terms of morphology and skeletal composition, high morphological variability has been attributed to fluctuations in salinity (Dumitrică, 1972; McCartney and Wise, 1990) or to heavy metal contamination (Thomas et al., 1980). Variations in the composition of siliceous plankton assemblages at ODP Site 1260 indicate higher productivity in surface waters throughout the MECO interval (Renaudie et al., 2010; Meunier and Danelian, 2023a), which may have favored the morphological diversification of *P*. cf. *papalis*. However, the hypothetical effects of environmental parameters on the skeletogenesis of polycystine radiolarians are intricate and not well-documented because these pelagic organisms are too sensitive to be cultured under laboratory conditions (Anderson et al., 1986, 1989a, b). This technical problem, combined with an incomplete knowledge of the ecology of modern radiolarians, remains a serious obstacle to our understanding of radiolarian paleoecology.

Geometric morphometric shape analyses illustrate two possible responses of planktic organisms to global warming: either migrate to follow their preferred temperature conditions, or adapt by producing additional morphologies. This allows us to gain a deeper understanding of the impact of climate change on oceanic plankton, especially in the case of low-magnitude climatic events that did not result in taxonomic extinctions. In a world threatened by global changes induced by human activities, this information may be of significant importance for characterizing how biological systems respond to environmental perturbations, in order to better model and anticipate future upheavals. It is also interesting to note that the perturbations in the morphological space occupancy observed at ODP Site 1260 during the MECO warming ended with the recovery of *P. papalis* around 40 Ma. The two taxa returned to a balanced occupation of the morphological space, similar to pre-MECO conditions, highlighting the resilience of radiolarians to global change.

IV.2.5. Conclusions

The morphological response of radiolarians to the Middle Eocene Climatic Optimum (ca. 40 Ma) is examined for the first time in this study. Using geometric morphometric methods, we document variation in morphological disparity of the nassellarian species *Podocyrtis papalis* and a closely related taxon classified as *P*. cf. *papalis*, which is particularly abundant during the MECO interval.

Changes in morphospace occupancy through the MECO showed that the two studied taxa reacted differently to the environmental forcing. On the one hand, *P. papalis* almost completely disappeared from low latitudes during the climatic interval. The concurrent increase in the relative abundance of this species at mid-latitude ODP Site 1051 suggests that it has sought refuge at higher latitudes by tracking its optimal habitat. On the other hand, *P. cf. papalis* remains abundant at ODP Site 1260 during the MECO and exihits a wide range of morphological variability, culminating in the appearance of extreme shapes during the warmest interval of the MECO. The high morphological variability expressed by *P. cf. papalis* is interpreted as an indicator of the biological stress induced by the MECO. These results illustrate two possible responses of planktic organisms to global warming, either migration or adaptation through the production of additional morphologies. Despite the profound changes induced by the warming event, a return to pre-event conditions is observed at ODP Site 1260 following the recovery of *P. papalis* during the post-MECO cooling phase, highlighting the resilience of radiolarian species to climate change.

Finally, this study demonstrates that the application of modern geometric morphometrics to quantify variation in radiolarian shell morphology can be used as a reliable baseline for further paleontological research on radiolarians. This approach appears to be more sensitive than the traditional taxonomic richness to the study of low-magnitude climatic events that have not crossed the threshold to drive extinction in planktic species.
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Author contributions

Mathias Meunier: Conceptualization, Methodology, Investigation, Visualization, Writing-Original draft, Writing-Reviewing and Editing. Claude Monnet: Conceptualization, Methodology, Software, Data Analysis, Writing-Reviewing and Editing. Rémi Habert: Data collection, Data curation. José Francisco Pínto Cabrera: Methodology, Investigation, Data Curation. Marie Cueille: Visualization. Taniel Danelian: Conceptualization, Supervision, Resources, Writing-Original draft, Writing-Reviewing and Editing.

Appendix IV.2.1. Taxonomic framework

The text follows the morphological terminology of Sanfilippo and Riedel (1992) to designate the various parts of the Podocyrtis shell.

Class Polycystinea Ehrenberg, 1839

Order Nassellaria Ehrenberg, 1876

Superfamily Pterocorythoidea Haeckel, 1882 emend. Suzuki et al., 2021

Family Pterocorythidae Haeckel, 1882

Genus Podocyrtis Ehrenberg, 1846

Type species.—*Podocyrtis papalis* Ehrenberg, 1847, p. 55, fig. 2.

Podocyrtis (Podocyrtis) papalis Ehrenberg, 1847

Plate IV.2.1, Figures 1-6

- 1847 Podocyrtis papalis Ehrenberg, p. 55, fig. 2.
- 1854a Podocyrtis papalis Ehrenberg Ehrenberg, pl. 36, fig. 23.
- 1874 Podocyrtis papalis Ehrenberg Ehrenberg, p. 251.
- 1973 *Podocyrtis (Podocyrtis) papalis* Ehrenberg Sanfilippo and Riedel, p. 531, pl. 20, figs. 11–14, pl. 36, figs. 2, 3.
- 1974 Podocyrtis (Podocyrtis) papalis Ehrenberg Nigrini, p. 1069, pl. 1K, figs. 7–10.
- 2009 Podocyrtis papalis Ehrenberg Ogane et al., pl. 58, figs. 1a–1f.

Description.— The shell is spindle-shaped, thick-walled, and trisegmented. The cephalis is trilobate, with a large eucephalic lobe that can be sub-hemispherical or longitudinally elongated, and two smaller subspherical lateral lobes. The apical spine protrudes as a moderately to well-developed apical horn, which is usually three-bladed, sometimes conical. The collar stricture is marked by a slight change in shell contour and underlined by a thin V-shaped dark line. Well-preserved specimens usually have a short axobate. The thorax is truncate-conical to inflated and

perforated by circular, longitudinally arranged pores, which are separated by weak longitudinal costae. The shell is widest just above the lumbar stricture, which is not expressed externally but marked by a relatively thick internal ridge. The abdomen is inverted truncate-conical, short, and noticeably less voluminous than the thorax (with a thorax/abdomen ratio of approximately 2:1 for the typical morphotype of *Podocyrtis papalis*). The proximal part of the abdomen is perforated by pores that are similar in shape and size to those found on the thorax. The distal part, on the other hand, lacks pores and terminates in three broad, shovel-shaped feet.

Remarks.— *Podocyrtis papalis* is the earliest pterocorythid species found in the fossil record. Its first occurrence is near the Paleocene-Eocene boundary (Sanfilippo and Riedel, 1992), and its stratigraphic range extends from the late *Bekoma bidartensis* Zone (early Eocene) to the *Calocyclas bandyca* Zone (middle-late Eocene).

P. aphorma Riedel and Sanfilippo, 1970 can be distinguished from *P. papalis* by its less regular abdominal pores and the presence of a slight lumbar constriction. Similarly, *P. acalles* Sanfilippo and Riedel, 1992 is distinguished from *P. papalis* by the presence of a slight external lumbar constriction. Additionally, while the shell of *P. papalis* is widest above the lumbar stricture, *P. acalles* is widest at or slightly below the lumbar stricture (Sanfilippo and Riedel, 1992). In *P. acalles*, the size of abdominal pores is irregular and not always strictly aligned longitudinally. This results in more discrete and discontinuous longitudinal ridges between pore rows. Additionally, the thorax/abdomen ratio in both *P. aphorma* and *P. acalles* tends towards 1. Unfortunately, no differential diagnosis was provided to differentiate *P. acalles* from *P. aphorma*, which appears to be morphologically indistinguishable based on the photographs published along with their original descriptions.



Plate IV.2.1. Composite light micrographs of analyzed radiolarian specimens from ODP Site 1260 (Demerara Rise, western equatorial Atlantic). (1-6) Typical *Podocyrtis papalis* Ehrenberg, 1847: (1) ODP 1260A-7H-5W, 70–72 cm; (2) ODP 1260A-7H-5W, 70–72 cm; (3) ODP 1260A-7H-5W, 70–72 cm; (4) ODP 1260A-7H-3W, 69–71 cm; (5) ODP 1260A-7H-1W, 22–24 cm; (6) specimen showing a reduced abdomen, ODP 1260A-6H-6W, 57–59 cm. (7-12) *Podocyrtis* cf. *papalis* Ehrenberg, 1847: (7) ODP 1260A-7H-2W, 19–21 cm; (8) ODP 1260A-6H-6W, 20–22 cm; (9) ODP 1260A-6H-6W, 57–59 cm; (10) ODP 1260A-6H-6W, 57–59 cm; (11) ODP 1260A-6H-4W, 119–121 cm; (12) ODP 1260A-6H-4W, 119–121 cm; (13) ODP 1260A-6H-3W, 18–20 cm; (16) ODP 1260A-6H-4W, 68–70 cm. All scale bars equal 50 μm.

Podocyrtis (Podocyrtis) cf. papalis Ehrenberg, 1847

Plate IV.2.1, Figures 7-16, Plate IV.2.2, Figures 1-16

- 1993 Podocyrtis (Podocyrtis) sp. aff. P. (P.) papalis Ehrenberg Hull, pl. 8, fig. 3.
- ? 1999 Podocyrtis mitrella Ehrenberg Kozlova, p. 174, pl. 18, fig. 24.
- 2006 Podocyrtis (Podocyrtis) papalis Ehrenberg Funakawa et al., p. 29, pl. P9, figs. 13a, 13b.
- 2012 *Podocyrtis (Podocyrtoges) diamesa* Sanfilippo and Riedel Kamikuri and Wade, pl. 1, figs. 7a, 7b.
- 2015 Podocyrtis (Podocyrtis) papalis Ehrenberg Kamikuri, pl. 9, figs. 1a, 1b (part).

Remarks.— This morphotype is similar to *Podocyrtis papalis*, but it has a more elongated shape and a less pronounced lumbar constriction. It also has a thinner shell wall and a reduced tribladed apical horn, which is usually the same height as the cephalis. The attachment area of the horn on the cephalis appears to be relatively fragile, as the apical horn was broken in most of the observed specimens. The specimen illustrated by Kamikuri and Wade (2012) from ODP Site 1051 cannot be assigned to *P. diamesa* due to its small size. Additionally, its stratigraphic position in the upper part of the *P. goetheana* Zone (RP16) does not correspond to the known stratigraphic range of *P. diamesa*, whose last occurrence lies in the *P. ampla* Zone (Nigrini et al., 2005; Kamikuri et al., 2012a; Meunier and Danelian, 2022).



Plate IV.2.2. Composite light micrographs of analyzed radiolarian specimens from ODP Site 1260 (Demerara Rise, western equatorial Atlantic). (1-16) Podocyrtis cf. papalis Ehrenberg, 1847: (1) ODP 1260A-6H-6W, 20-22 cm; (2) ODP 1260A-6H-6W, 20-22 cm; (3) ODP 1260A-6H-6W, 57-59 cm; (4) ODP 1260A-6H-4W, 119-121 cm; (5) ODP 1260A-6H-4W, 68-70 cm; (6) ODP 1260A-6H-4W, 119-121 cm; (7) ODP 1260A-6H-6W, 57-59 cm; (8) ODP 1260A-6H-5W, 63-65 cm; (9) ODP 1260A-6H-4W, 119-121 cm; (10) ODP 1260A-6H-6W, 20-22 cm; (11) ODP 1260A-6H-6W, 57-59 cm; (12) ODP 1260A-6H-3W, 18-20 cm; (13) ODP 1260A-6H-4W, 68-70 cm; (14) ODP 1260A-6H-5W, 63-65 cm; (15) ODP 1260A-6H-4W, 119–121 cm; (16) ODP 1260A-6H-4W, 119–121 cm. All scale bars equal 50 µm.

Appendix IV.2.2. Evaluation of the measurement process bias (measurement error).



Within-group distribution of the Procrustes distance among specimens

Chapter V – General conclusions and perspectives

Polycystine radiolarians represent one of the most diverse groups of marine plankton during the Eocene. A total of 245 morphospecies were identified in this study in a ~5.4 Ma stratigraphic interval spanning the late middle Eocene (early Lutetian to middle Bartonian). However, this astonishing diversity is far from being fully documented. Indeed, although radiolarians have attracted the attention of micropaleontologists since the nineteenth century, numerous rare morphotypes of no biostratigraphic value, or those belonging to morphologically complex taxa, remained undescribed. At ODP Site 1051, where we achieved the catalog of the whole radiolarian assemblage, unknown morphotypes account for 48% of the total diversity. This knowledge gap at the most basic level of species description is probably one of the main obstacles to the development of radiolarian research. To address this issue, 36 new radiolarian species have been formally described, including 32 nassellarians and four spumellarians. This represents an increase of ~14% to the total diversity inventoried during our taxonomic survey. Some of these new species are major components of radiolarian assemblages (e.g., Apoplanius hyalinus Meunier and Danelian and Dictyoprora echidna Meunier and Danelian at ODP Site 1051) and could prove to be good stratigraphic markers, or display interesting combinations of character states that improve our understanding of the evolution of some genera (e.g., Aphetocyrtis zamenhofi Meunier and Danelian and Spirocyrtis? renaudiei Meunier and Danelian). Biostratigraphic information was also provided for each new taxon, and stratophenetic relationships to previously described species were proposed, leading to the establishment of four new evolutionary lineages.

Alpha-taxonomic studies are a prerequisite for developing radiolarian research, but a robust taxonomic framework at higher levels should also support the description of biodiversity. In Cenozoic radiolarians, the superfamily and family levels are relatively consistent, notably through the latest synthesis by Suzuki et al. (2021), who achieved an integrated classification

of Cenozoic radiolarians based on morphological and molecular data. In the current state of Cenozoic radiolarian taxonomy, the main hurdle is at the genus level, which is poorly defined in most cases. Consequently, genus assignment is highly subjective and proceeds almost entirely based on the opinion of the author. A thorough revision of the descriptions and diagnoses of Cenozoic radiolarian genera is therefore urgently needed. This work was initiated by O'Dogherty et al. (2021), but unfortunately, the diagnoses they provide are often vague and too general for accurate identification and are unusable in the daily practice of taxonomy.

Our detailed inventory of late middle Eocene radiolarian species served as a starting point for a high-resolution biostratigraphic study at ODP Site 1260 (western equatorial Atlantic). Taking advantage of the precise cyclostratigraphic framework developed at this site, we calibrated astronomically the absolute ages of 71 radiolarian bioevents, including bioevents related to abundant species that are usually neglected in biostratigraphic studies. By comparison of our results with the equatorial Pacific record, we subsequently demonstrated the synchroneity of primary radiolarian bioevents that underpin the middle Eocene zonal scheme. This demonstration achieved by means of two independent dating methods was (magnetostratigraphy and astronomical calibration), reinforcing the robustness of the tropical radiolarian biozonation, and demonstrating that radiolarians are amongst the most accurate middle Eocene biostratigraphic microfossils.

After adjusting the taxonomic and biostratigraphic framework, the main aim of this thesis was to study the effects of global warming on polycystine radiolarians. Two categories of metrics were used to achieve this goal. On the one hand, diversity metrics were calculated to unravel the impact of the MECO at a large, macroevolutionary scale. This quantitative analysis of the entire radiolarian assemblage was conducted at subtropical ODP Site 1051. On the other

hand, geometric morphometrics approaches were applied for the first time to quantify the morphological disparity of radiolarian shells. This latter study was focused on a single biostratigraphically important nassellarian species from tropical ODP Site 1260.

Firstly, the detailed examination of the radiolarian fauna at ODP Site 1051 did not reveal any significant turnover during the MECO. These results show that a rapid rise of \sim 4–6°C in sea surface temperature did not exceed the threshold to drive extinction in radiolarians. On the contrary, we documented an increase of \sim 30 % in radiolarian richness, coinciding with the warmest interval of the MECO (around 40 Ma). This increase is due to the poleward migration of several warm tropical radiolarian species that expanded their geographical ranges to higher latitudes during the warming event. Similarly, several typical middle Eocene tropical species, such as *Podocyrtis (L.) chalara* Riedel and Sanfilippo and *Podocyrtis (L.) mitra* Ehrenberg, have peak abundances during the warmest interval. Apart from these observations, quantitative analyses showed that ocean warming elicited only a weak response in radiolarians, with assemblages observed during the MECO interval differing sightly from those of the pre- and post-MECO intervals.

In terms of total radiolarian diversity, the MECO warming only represents a minor event that did not profoundly alter radiolarian assemblages. Since poleward migrations of planktic tropical species appear to be the most striking ecological feature of this event, we stated that the MECO is probably best classified as a migration event. It is should be noted, however, that the faunal changes documented in our study only have a local relevance (i.e., the western subtropical Atlantic) and may not be representative of the effects of the MECO on radiolarian assemblages in all oceanic regions. Given the climate sensitivity of polar planktic faunas (Trubovitz et al., 2020; Penn and Deutsch, 2022), different responses can be expected at higher latitudes. These aspects have already been studied in the Southern Ocean (DSDP Site 277, Campbell Plateau) by Pascher et al. (2015). However, this study examined too few stratigraphic

levels to be conclusive, and more importantly, counts were only limited to a subset of abundant or biostratigraphically important species. An exhaustive study of high-latitude radiolarian assemblages is needed to obtain an accurate depiction of the biotic changes induced by the MECO warming.

The study of morphological disparity seems to be a valuable complement to traditional taxonomic richness analyses, especially for assessing the impact of low-magnitude environmental perturbations that did not result in extinctions. In the case of the MECO, geometric morphometric shape analyses have revealed two possible responses of planktic organisms to global warming: either migrate to track their preferred temperature conditions, or adapt by producing additional morphologies. Our results have also shown that fluctuations in the morphological disparity of radiolarian shells coincide with a shift in the stable isotope record. The peak of morphological disparity falls in the warmest interval of the MECO and is interpreted as an indicator of biological stress induced by the climatic event. However, further ecological function is intricate and not well-established in radiolarians. Finally, this pilot morphometric study can be seen as a first step in the investigation of previously unexplored aspects of the radiolarian fossil record. An interesting development would be to apply this method to a larger panel of species, in order to gain a better understanding of the general rules that shape plankton morphological diversity.

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Abstract

The Middle Eocene Climatic Optimum (MECO) is a global warming event that occurred ca. 40 Ma and temporarily interrupted the long-term Eocene cooling trend. Although the MECO represents one of the major climatic perturbations of the Paleogene, its impact on the biosphere is still poorly understood. Based on a wide range of quantitative methods, this thesis aims to study the radiolarian paleodiversity dynamics and morphological disparity through the MECO, to better understand the biotic perturbations associated with this climatic event. The taxonomic framework of the middle Eocene radiolarian was first clarified by documenting at the species level two well-preserved radiolarian faunas recovered from two distinct geographic regions: the equatorial Atlantic (ODP site 1260) and the North Atlantic (ODP site 1051). A total of 281 species were identified, including 36 new to science. Taking advantage of the cyclostratigraphic framework developed at Site 1260, we refined the global tropical radiolarian biozonation. The absolute ages of 71 radiolarian bioevents were calibrated and, by comparison with the equatorial Pacific record, the synchroneity of primary bioevents was demonstrated. Once the taxonomic and biostratigraphic frameworks were clarified, the main aim of this thesis was to assess the biotic sensitivity of radiolarians to climate change. Two categories of metrics were used to achieve this objective. First, we performed a quantitative analysis of the entire assemblage at ODP Site 1051. This detailed investigation of the radiolarian fauna did not reveal any prominent turnover during the MECO but only a slight increase in radiolarian taxic richness due to the poleward migration of several tropical radiolarian species. Then, we applied geometric morphometric approaches to quantify the morphological disparity of radiolarian shells through the MECO interval. This study was focused on a single species (Podocyrtis papalis) from Site 1260 and showed that fluctuations in morphological disparity coincide with the warmest interval of the MECO. This signal is interpreted as an indicator of biological stress induced by the warming event.

Keywords - Radiolarians, middle Eocene, biostratigraphy, diversity, disparity, ODP, Atlantic Ocean

Résumé

L'Optimum Climatique de l'Éocène Moyen (MECO) est un évènement de réchauffement climatique qui s'est produit il y a 40 Ma, interrompant temporairement la tendance générale au refroidissement observée durant l'Éocène. Bien que le MECO soit l'une des perturbations climatiques les plus importantes du Paléogène, son impact sur la biosphère demeure encore mal connu. Via un large éventail de méthodes quantitatives, cette thèse vise à étudier la dynamique de la paléodiversité et la disparité morphologique des radiolaires au cours du MECO, afin de mieux comprendre les bouleversements biotiques qui lui sont associés. La première étape de ce travail a consisté à dresser la liste taxinomique exhaustive des espèces de radiolaires éocènes rencontrés dans deux domaines géographiques distincts : l'Atlantique équatorial (ODP Site 1260) et l'Atlantique septentrional (ODP Site 1051). Au total, 281 taxons ont été identifiés, dont 36 nouvelles espèces. S'appuyant sur le cadre cyclostratigraphique développé au Site 1260, nous avons également affiné la biozonation des radiolaires tropicaux. Les âges absolus de 71 bioévènements ont été calibrés et, par comparaison avec l'enregistrement fossilifère du Pacifique équatorial, nous avons démontré la synchronicité des bioévènements qui définissent les limites des biozones de l'Éocène moyen. Une fois les cadres taxonomique et biostratigraphique clarifiés, l'objectif de cette thèse était d'évaluer l'impact du réchauffement climatique sur les radiolaires. Pour ce faire, deux grandes catégories de mesures ont été utilisées. D'une part, nous avons effectué une analyse quantitative de l'assemblage fossile du site 1051. Cette étude détaillée n'a révélé aucun changement de faune important au cours du MECO. Seule une légère augmentation de la richesse taxinomique a été documentée, due à la migration de certaines espèces tropicales vers les hautes latitudes durant le MECO. D'autre part, nous avons employé des méthodes de géométrie morphométrique pour quantifier la disparité morphologique du squelette des radiolaires. Cette étude s'est concentrée sur une espèce de nassellaire (Podocyrtis papalis) du Site 1260. Nous avons montré que les fluctuations de la disparité morphologique du contour du squelette coïncidaient avec le pic de température du MECO. Ce signal est interprété comme un indicateur de stress biologique induit par le réchauffement climatique.

Mots-clefs - Radiolaires, Éocène moyen, biostratigraphie, diversité, disparité, ODP, Océan Atlantique