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A new integrated morpho- and molecular systematic classification of Cenozoic radiolarians (Class Polycystinea) – suprageneric taxonomy and logical nomenclatorial acts

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A new integrated morpho- and molecular systematic classification of Cenozoic radiolarians (Class Polycystinea) – suprageneric taxonomy and logical nomenclatorial acts

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Cenozoic,
Radiolaria,
Molecular taxonomy,
Morphological taxonomy,
Taxonomic revision,
new synonyms,
new status,
new families.

ABSTRACT
A revised taxonomy of Cenozoic radiolarian families is of particular importance because exhaustive molecular phylogenetic analyses for Collodaria, Entactinaria, Nassellaria and Spumellaria have shown high level of confidence at family or higher taxonomic ranks. In this sense, this study presents a new comprehensive taxonomy at the family level that integrated a classification based on ribosomal taxonomic marker genes (rDNA) and classical morphological taxonomy. However, many family names commonly used in Cenozoic radiolarians (Polycystinea) are derived from genera whose type species were never illustrated at the time of the generic definition. Obviously, in the vast majority of those cases, the "Principle of Typification" regulated in the International Code of Zoological Nomenclature (ICZN 1999: Art. 61) cannot be logically applied. This has contributed to a century-long misunderstanding about the validity of Cenozoic taxa (species, genera and/or family-group names) erected without any illustration or drawing of their types, in particular the huge contribution of Ernst Haeckel from samples of the Challenger expedition (1872-1876). Reexamination of Haeckel's collection definitively confirmed that all the original types series (the specimens on which Haeckel established the nominal species-group taxon) being nonextant; in other words, all name-bearing specimens (the types) are restricted to the illustrations given in Haeckel's drawings. Because "types" in taxonomy are

precious things, a nominal species-group taxon lacking at all of illustration (or indication to a repository) do not ensure the recognition of the species. Following the rules and recommendations of the ICZN, these names should be excluded from all nomenclatorial and taxonomical acts. This revision presents the state of the art of all proposed family-group names (with full synonymy lists) for Cenozoic Polycystinea.

The list of family-group nominal taxa and their names was inventoried from 6694 publications (89% of the whole known references on radiolarians). The references were examined in order to clarify and fix the status of family names; hence these family-group names were rigidly classified as: valid, junior synonym, *nomen dubium*, *nomen nudum*, homonym, and invalid names. A total of 372 family-group names were proposed for the Cenozoic. These consist of 94 valid family-groups, 118 junior synonym family-groups, 111 *nomen dubium* family-groups (mainly artificially created in a hypothetical conceptual framework), 6 junior homonym family-groups, 19 *nomen nudum* family-groups, as well as 24 invalid names. In addition, one *nomen novum* et four new families are presented. The description of 25 families have been also emended.

This study also outlines the advantages of an integrated approach to taxonomy of Polycystinea by the combination of both morphological and molecular systematics. Based on molecular phylogenetic studies, the systematic classification proposed at suprageneric level is arranged as follows:

a) Order Spumellaria: three Phylogenetic Molecular Lineages (PM Lineages = suborders), 13 superfamilies and 42 families;
b) Order Entactinaria: one PM Lineage, five superfamilies and nine families;
c) Order Nassellaria: four PM Lineages, 16 superfamilies and 37 families;
d) Order Collodaria: three superfamilies and six families.

RÉSUMÉ

Une nouvelle classification systématique intégrée basée sur la phylogénèse moléculaire et le classement morphologique des radiolaires du Cénozoïque (Classe des Polycystinea) – taxonomie supragénérique et actes logiques de nomenclature.

Une révision de la taxonomie des familles de radiolaires du Cénozoïque est particulièrement importante, car de nouvelles analyses phylogénétiques moléculaires pour Collodaria, Entactinaria, Nassellaria et Spumellaria ont montré d'excellents résultats pour les rangs taxonomiques familiaux ou supérieurs. En ce sens, cette étude présente une nouvelle taxonomie complète au niveau familial, qui intègre une classification fondée sur les gènes marqueurs taxonomiques ribosomiques (ADNr) et la taxonomie classique fondée sur des caractéristiques morphologiques. De plus, de nombreux noms de familles communément utilisés pour les radiolaires polycystines du Cénozoïque dérivent de genres dont les espèces types n'ont jamais été illustrées au moment de la définition du genre. Apparemment, dans la plupart de ces cas, le « Principe de Typification » défini dans le Code international de Nomenclature zoologique (ICZN 1999: Art. 61) ne peut être logiquement utilisé. Cela a généré une longue incompréhension (un siècle) quant à la validité des taxa cénozoïques (noms d'espèces, genres, et/ou familles) érigés à partir de types non illustrés ou dessinés, en particulier dans l'immense travail de Ernst Haeckel sur les échantillons récoltés par l'Expédition du « Challenger » (1872-1876). Le réexamen de la collection d'Haeckel a définitivement confirmé que tous les originaux des espèces types d'Haeckel (les spécimens à partir desquels Haeckel a établi les taxa des groupes d'espèces) n'existent pas, en d'autres termes que les spécimen-types sont réduits aux illustrations des planches dessinées d'Haeckel. Comme les « types » sont indispensables, un taxon nominal du groupe espèce sans aucune illustration (ou sans indication du lieu de conservation) ne permet pas de confirmer la définition de l'espèce. D'après les règles et recommandations de l'ICZN, ces noms devraient être exclus de tous les actes de nomenclature et de taxonomie. Cette révision-ci présente un « état de l'art » de tous les noms du groupe famille (avec des listes complètes de synonymes) pour les Polycystines cénozoïques.

La liste des familles ainsi que leurs noms sont fondés sur 6694 publications (89% de toutes les références connues sur les radiolaires). Ces références ont été revues afin de clarifier et définir le statut des noms de familles qui ont été classés comme : valides, synonymes juniors, *nomen dubium*, *nomen nudum*, homonymes et noms invalides. Un total de 372 noms de groupes familiaux a été proposé pour le Cénozoïque. Ils comprennent 94 noms de familles valides, 118 synonymes juniors de familles, 111 *nomina dubia* de familles (principalement artificiellement créés en ensembles hypothétiques), 6 groupes familiaux d'homonymes juniors, 19 groupes familiaux de *nomina nuda* et 24 noms invalides. Un *nomen novum* et quatre familles nouvelles sont aussi présentés. Les descriptions de 25 familles ont été également émendées.

Cette étude souligne les avantages d'une approche intégrée de la taxonomie des Polycystines par la combinaison d'analyses systématiques à la fois morphologiques et moléculaires. Sur la base d'analyses de séquences et phylogénies moléculaires, une systématique à un niveau supra-générique peut être ainsi proposée :

a) Ordre des Spumellaires : trois lignées phylogénétiques moléculaires (PM Lignées = sous-ordre), 13 superfamilles et 42 familles ;
b) Ordre des Entactinaires : un PM Lignée, cinq superfamilles et neuf familles ;
c) Ordre des Nassellaires : quatre PM Lignées, 16 superfamilles et 37 familles ;
d) Ordre des Collodaires : trois superfamilles et six familles.

MOTS CLÉS
Cénozoïque,
Radiolaria,
révision taxonomique,
taxonomie moléculaire,
taxonomie morphologique,
synonymes nouveaux,
statuts nouveaux,
familles nouvelles.

INTRODUCTION

There are generally fewer concerns regarding family-and-higher classification in micropaleontology since palaeoceanographic, evolutionary and biogeographic studies are largely based on species. The genus-level is equally unhelpful for these topics. By contrast, initial molecular phylogenetic analysis is considerably more sensitive at family and order levels as opposed to genus and species levels. An appropriate combination of genera and families is thus required for a combined study of morphological classification and molecular phylogenetic analysis. Despite this demand, the classification at the family level is far from reaching consensus, even in radiolarian study communities. Widely variable applied family schemes such those from Haeckel (1887), Campbell (1954), Riedel (1967a, b), Petrushevskaya (1971a, 1981), De Wever *et al.* (2001) and Matsuzaki *et al.* (2015) were used. It has been almost impossible to settle on a family and higher classification scheme as morphological characters of genera established by C.G. Ehrenberg (1795-1876) and Ernst Haeckel (1818-1910) were unclear. To resolve this challenge, the original samples and slides treated by Ehrenberg and Haeckel were searched for in Berlin, London and Jena by the Japan-Germany-Britain team with the support of the National Museum of Nature and Science, Tokyo (NMNS) (leader: Tanimura A.) in 2004 and 2009. Almost all name-bearing specimens from Ehrenberg were successfully recovered in the Museum für Naturkunde, Humboldt University, Berlin (NfM; see Ogane *et al.* 2009a, b; Suzuki *et al.* 2009c), part of *H.M.S. Challenger* plankton slides were found in the collections of the Natural History Museum, London (NHM; see Aita *et al.* 2009), and a few Messina slides from Haeckel (1861a, 1862) were unearthed in Ernst-Haeckel house, Jena (EHH; see Sakai *et al.* 2009). However, almost any slides of the *H.M.S. Challenger* sediments are fully missing. It was also unexpected that, despite the efforts, almost all "illustrated" species which should have been present in the examined plankton slides were not uncovered. Similar re-examination of legacy slides was carried out for collections of Cleve's (Bjørklund *et al.* 2014), Bailey's (Itaki & Bjørklund 2007), Campbell & Clark's (Blueford & Brunner 1984; Blueford 1988; Lazarus *et al.* 2005), Dogiel's (Petrushevskaya 1975), and Jørgensen's (Dolven *et al.* 2014), and consequently, more practical arrangements of genus combinations in families can be determined than in De Wever *et al.* (2001).

Re-arrangement of genus combination in families poses the problem of determining the validity of a family name in the sense of the International Code of Zoological Nomenclature (the Code, hereinafter): a) many families were established on genera with un-illustrated type species which is unviable and scientifically impossible; b) no useful list exists of the proposed family-groups for the Cenozoic; c) nomenclatural status such as "taxonomic available" and "*nomen dubium*" were not clarified in order not to determine the validity of a family; and d) un-appreciation for nomenclatural act at the family levels. Moreover, there is a strong wish to maintain accustomed usage of a family even if it results in disregard for the Code. In this sense, this paper summarizes: 1) the usage and applicability of the Code from various perspectives; 2) a guide to nomenclatural acts at the genus-level; 3) current systematics above the family-rank; 4) a policy for integrative morphological and molecular phylogenetic studies; and 5) the taxonomy hierarchy resulting from this revision work.

USAGE AND APPLICABILITY OF THE CODE: ACCUSTOMED USAGE VS RULED USAGE UNDER THE CODE

It should be noted that confusion in the genus and family taxonomy in radiolarians resulted from a general wish to preserve the accustomed usage. However, we must also be aware that this conservative disposition has been rejected, at least twice, by the International Commission on Zoological Nomenclature (the Commission here after). Plenary power decisions over the Code's provision must be ratified by the Commission as "Opinion" after public comments from zoologists for the accepted "Case" to be published in the *Bulletin of Zoological Nomenclature* (BZN). All the requested Cases are not always published in BZN. If a request is not accepted in BZN at the end of the process, the request itself must be solved under the Code ruling and the request is not formally recorded in BZN. As far as we know, two cases regarding radiolarian taxonomy were both rejected for Case in BZN. One argues that "Campbell (1954) should be excluded from the taxonomic work" (Deflandre 1960: 212, 215, 218; Lombari & Lazarus 1988: 100-101: Dumitrica 1995: 19-20). The major taxonomic confusion between accustomed and ruled usages is caused by the designation of un-illustrated type species for radiolarian genera by Campbell (1954), compelling almost all radiolarian specialists at the time to request a plenary power decision from the Commission (Petrushevskaya 1971a: 53-54; Merinfeld 1980; De Wever *et al.* 2001). Regardless of the consensus of the vast majority of specialists, Campbell's case was not included the Official Index of Rejected Works in Zoology by the Commission. The second case is the request for the suppression *Parafollicucullus* instead of a senior synonym *Pseudoalbaillella*. Obviously, the taxon name *Pseudoalbaillella* is of more common usage than *Parafollicucullus*, but this was also not presented in Case. These failures show us that it is impossible to keep "the habitual usage" even if almost all specialists have come to a consensus.

It is nonsensical if we refer to the famous arguments in fusulinids in 1930s. The genus *Schwagerina* is one of the most important taxon of the fusulinid. It was established by Möller (1878) for the species *Borelis princeps* Ehrenberg 1842 from the Russian platform. This species was the only taxa included in *Schwagerina* and was subsequently, automatically regarded as the type species. This designation leads to several problems in regards to taxonomic stability: 1) the type specimen illustrated pl. 37, figs X.C-X.C1 to C4 of Ehrenberg (1854c) cannot permit to distinguish the morphological characters important for the taxonomy; 2) Möller (1878) proposed the genus *Schwagerina* based on his own specimens; however, his identification was confirmed to be incorrect by subsequent studies; and furthermore 3) the diagnosis (definition) by Möller (1878) was based upon his mis-identified specimens. The name "*Schwagerina*" has been widely applied for many fusulinid species and the "*Schwagerina*" had been subdivided into several genera by 1930s. Under this scientific circumstance, the original material for this species from the Ehrenberg collection housed in Museum für Naturkunde, Berlin, was sectioned in order to observe its internal structures by Dunbar & Skinner (1936). The type specimen was poorly preserved but was sufficient in solving the "*nomen dubium*" condition (issue 1 listed above). Soon after this publication, Rauser-Chernoussova (1936) strongly disagreed with this paper's findings stating that "*the name of* Schwagerina *is so deeply rooted in geological literature and this genus is of such great stratigraphic importance, that in the given case it is necessary to admit an exception from the Rules of International Zoological Nomenclature*" and "*the species described by Moeller under the name of* Schwagerina princeps *Ehrenberg as the genotype of the genus* Schwagerina, *changing the name of the former to* Schwagerina moelleri *nom. nov.*". Rauser-Chernoussova (1936) insisted that issues 2 and 3 should be admitted for stability, that is, in favor of the habitual usage . This problem was legally treated by the Commission as Opinion 213 in 1954 (Hemming 1954). It was formally decided that the definition of the *Schwagerina* was based on the Ehrenberg's type specimen collections (Dunbar 1958). The arguments on *Schwagerina* demonstrate that: 1) the real type specimen is prioritized over the description; and that 2) the scientific importance as well as an accustomed usage have no value in considering taxonomic stability. Although the Article 80.5 of the Code states that "*An Opinion applies only to the particular case, no conclusions other than those expressly specified are to be drawn from it.*" The radiolarian case regarding Campbell (1954) was obviously not an applicable case that followed the "Use of Plenary Power defined in Article 81."

TREATMENT OF UN-ILLUSTRATED SPECIES IN HAECKEL (1887).

The un-illustrated species in Haeckel (1887) are automatically treated as "*nomen dubium*" due to the fact that there are no guarantees that the descriptions conform to the name-bearing specimens. In this case there are two possibilities: 1) the species was created by Haeckel; and 2) the real specimens did exist. As a significant part of Haeckel's work has been debunked and widely accepted as scientific forgery and fraud (e.g., Hopwood 2015), Haeckel (1887) can also be suspected as such. The National Museum of Nature and Science, Tokyo, Japan, organized a project named "*Reexamination of the Haeckel and Ehrenberg Microfossil Collections as a Historical and Scientific Legacy*" (Tanimura *et al.* 2009) in collaboration with Utsunomiya University (T. Sakai, Y. Aita) and Tohoku University (N. Suzuki, K. Ogane). The project was granted complete access to both Ehrenberg's and Haeckel's collections in the Museum für Naturkunde (D. Lazarus) and *H.M.S. Challenger* raw sediment samples in the Natural History Museum (J. Young), and EHH (O. Breidbach & T. Bach). Following the complete lack of all the microscopic slides originally produced from the *H.M.S. Challenger*'s sediments, this project examined newly prepared microscopic slides from the raw *H.M.S. Challenger* sediments housed in the Mineralogy Department, NHM. Our continuous efforts, however, failed to identify any possible un-illustrated species in these topotypic materials. These un-illustrated species are, thus, destabilizing the taxonomy as "invisible ghosts" for normal scientists. The best solution is to ignore them in accordance to the application of the Article 1.3.1 until a feasible rediscovery of real specimens in the future. According to Article 1.3.1, names proposed for hypothetical concepts are excluded from the provisions of the Code; however, there is an example of this usage. This is the famous case of the Platypus (*Ormithothynchus anatinus*). The real specimen was first provided to scientists by George Shaw in 1799, but it was designated as a fake. But as everyone knows, now there is no doubt about the Platypus' existence. If we consider the *nomen dubium* status, we must refer to Article 75.5. Article 75.5 saying "[...] *a nominal species-group taxon cannot be determined from its existing name-bearing type* [... a *nomen dubium*]*, and stability of universality is threatened; thereby, the author may request the Commission to set aside under its plenary power the existing name-bearing type and designate a neotype"*. However, it is not the case for "the un-illustrated species" in Haeckel (1887) as the name-bearing types do not exist. It is also noted that the glossary of the Code published in 1985 employed: "*Example: –* [...] *by Haeckel in 1886 for a hypothetical "missing link" between apes and man*" for explaining the terms of "hypothetical concept" (ICZN 1985: 252).

Do we have a right to condemn the application of hypothetical concept for "non-existent" name-bearing type? We should refer to the "principle" from the Introduction of the Code (ICZN 1985: XIX-XX). The principle sets forth two important items: 1) "*The device of name-bearing types allows names to be applied to taxa without infringing upon taxonomic judgement*"; and 2) "*Every name within the scope of the Code* [...] *is permanently attached to a name-bearing type."* The taxonomic availability of non-existent name-bearing types is not subject to the Code. Strictly, Haeckel's un-illustrated species are not "*nomen dubium*" but "non-existing name-bearing types" with "unavailable names".

Someone may intend to follow "the principle of the First Reviser" (Article 25) to retain the accustomed usage, but "the first reviser" rule has the tendency to be excessively applied for the sake of conservation of accustomed usage. This rule holds the first author responsible for the nomenclatural process in selecting the name, spelling, or acts that will best serve the stability and universality of the nomenclature (see Recommendation 24A). However, the principle of the first reviser can only be applied when "*the precedence between names or nomenclatural act cannot be objectively determined*" (Article 24.2.1) and is to be withdrawn "*if it is shown subsequently that the precedence of names, spellings or acts can be objectively determined*" (Article 24.2.5). Unfortunately, the principle of the first reviser is helpless in most cases in Polycystinea.

Finally, Article 23.3.5 cannot be considered because it denotes that "*The Principal of Priority requires if a name in use for a taxon is found to be unavailable and invalid it must be replaced by the recent oldest available name from among its synonyms* [...]" The difference between available or unavailable names can be likened to the cleavage between the scientific and unscientific world in paleontology.

CHALLENGE TO SAVE OUR ACCUSTOMED USAGE

First of all, our wish was not to discard what was accustomed for family and genus names. However, there is no hope for many Haeckel's taxon names, since we have not plenary power and because the hypothetical concept cannot be applied for no existing name-bearing type (over 1700 Haeckel's taxa in Polycystinea).

Commonly, we can think of employing the so-called "50-years-rule" to determine a "*nomen oblitum*". The rule is that "*an author will be required (without a ruling by the Commission) not to displace a name which has been used as valid by at least 10 authors in 25 publications during the past 50 years, and encompassing a span of not less than ten years, by an earlier synonym or homonym which has not been used as valid since 1899*" (ICZN 1999: XXVIII, Article 23.9.1.1). The application of this principle requires the condition that "*the senior synonym or homonym has not been used as a valid name after 1899*" (Article 23.9.1.1). This rule can be applied to available names; however, it cannot be applied to unavailable names, such as "hypothetical concept". Being that it is impossible to logically determine the synonymy of un-illustrated type species, genera based on un-illustrated type species cannot be employed for taxonomic evaluation.

If the junior synonym family is established upon an available name, the Code instructs to consider it as valid in Article 23.9.3. The Article 23.9.3 mentions that "*If the conditions of 23.9.1 are not met but nevertheless an author considers that the use of the older synonym or homonym would threaten stability or universality or cause confusion* [...] *he or she must refer the matter to the Commission for a ruling under the plenary power*." This article should have been applied for the case of *Pseudoalbaillella* and *Parafollicucullus,* but it failed because the term "hypothetical concept" in the case of Haeckel (1887) is not applicable.

Concerning the suppression of senior synonyms there is a misunderstood about the reading and application of Article 35.5 of the Code. Wrong lectures of this article leave open the possibility that older names after 1999 might be suppressed. The title of Article 35.5 is "*Precedence for names in use at higher rank*"; subsequently this article deals with the priorities between higher and lower ranks in family names. The full sentence of Article 35.5 is cited here, "*If after 1999 a name in use for a family-group taxon (e.g., for a subfamily) is found to be older than a name in prevailing usage for a taxon at higher rank in the same family-group taxon (e.g., for the family within which the older name is the name of a subfamily) the older name is not to displace the younger name*." This concerns taxon *"at higher rank in the same family-group*" after 1999, but not a simple "reversal of precedence" between an unused senior synonym and an accustomed junior synonym at the family level. This point is a complete mistake generated by the desire to uphold a junior synonym family-group name. Before Article 35.5, the "hypothetical concept" is not covered in the Code.

It might seem imaginable to designate a new type species from a valid species because a "non-existent" name-bearing type could be considered as an unavailable name. However, if we look to the case of "platypus", this policy is not advisable as we should consider that there is always a possibility to rediscover these particular specimens.

THE REQUIREMENT OF A FULL SYNONYMY LIST OF FAMILY-GROUP NAMES

We identified a serious problem with determining valid family-group names because no study has compiled the family-group synonymy thus far. Furthermore, the family-rank names have variable suffixes so the possibility to digitally search them is reduced. This obstacle would prevent a search for family-group names in the future. Thus, all accessible 6694 references about radiolarians in Tohoku University (89% of the known 7534 references) were manually checked through a page-by-page examination. Although some references are overlooked, the list provides sufficient information in order to apprehend the key details of family-group synonymy.

PREVAILING USAGE FOR FAMILY NAMES

The family group name is formed by adding suffix -OIDEA, -IDAE, -INAE, -INI, -INA, to the stem of the type genus name (Article 29.1). The stem of the type genus name for a family-group name is acquired by omitting the case ending of the appropriate genitive singular in Greek or Latin (Article 29.3.1). Some stems of polycystine genera are unexceptionally changed. In the case of *Pterocorys*, its genitive form is *Pterocorythos*, the stem is *Pterocoryth-* (see Moore 1972: 147). The genitive case of the Greek noun is essentially noted after the nominative case in the dictionary as in "κορυς, υθος", which is Latinized as "korys (corys), ythos" and thus; the stem of the genitive is "-yth" with the drop of "os". Therefore, the family name should be Pterocoryth-idae and not Pterocory-dae. Similar issue happens in the case of names such as *Plectopyramis* and *Lophospyris*. Another example of a commonly occurring erroneous forming of family is the case like *Euchitonia*. The genitive stem of such ending word is *Euchitoni-* but not *Euchiton-*. Subsequently, the name is formed as *Euchitoni-idae*.

Prevailing usage of family names should be maintained under certain rules. In this sense, the Article 29.3.1 sets that if the stem names formed ends in -id, those letters may be elided before adding the family-group suffixes (i.e. -corys,

-cyrtis, -pyramis, -spyris, etc.). If, however, the unelided form is in prevailing usage, that spelling is to be maintained, whether or not it is the original spelling. Regardless grammatical errors, the most important for of taxonomic stability is to maintain the prevalent usage (Article 29.5). All the aforementioned rules became effective only from 1961 onward (ICZN 1964).

MAJOR RULES FOR FAMILY NAMES

The final choice of a valid family name is a typical nomenclatural act under the Code. As applied rules are scattered throughout the Code in a very complex way, the important, but often forgotten rules are as follows (ICZN 1999):

Suffixes for family-group names are defined as -OIDEA, -IDAE, -INAE, -INI and -INA respectively for superfamily, family, subfamily, tribe and subtribe names (Article 29.2).

A family-group name is valid if it is based on an available genus-group name before 1931 (Article 12.2.4), if it is associated with a description (or reference), and based on a valid genus-group name after 1930 (Article 13.2).

If the family-group name is based on a genus-group name proposed after 1930, the type species for such a genus must be fixed (Article 13.5).

Any new taxon name including a family-group name after 1999 must be explicitly indicated as being intentionally new (e.g., n. fam.) (Article 16.1) and a new family-group name published after 1999 must be accompanied by the citation of the name of the type genus (Article 16.2).

When synonyms are established simultaneous, but proposed at different ranks, in the family group, genus group or species group, the name proposed at higher rank takes precedence as an automatic determination of precedence of names (Article 24.1).

The family-group name must not necessarily be replaced when the type genus of a nominal family-group taxon is considered to be a junior synonym of another genus-group name (Article 40.1).

The widely used spelling with grammatical errors should be maintained and does not needed to be corrected (Article 29.5), although the suffix of the family-group names must be one of following: -OIDEA, -IDAE, -INAE, -INI and -INA (Article 29.2).

The combination of genera in a family is determined by a comparison with its type genus only (Article 35.3).

Any names within a family-group (e.g., superfamily, family, subfamily, tribe, subtribe) hold the same authorship and date as the first describer of a family-group name (Article 36.1).

As genera with un-illustrated type species by Haeckel are regarded as "hypothetical concepts" they are excluded of any taxonomic act under the Code (Article 1.1, 1.3.1, the appendix figure just after the Glossary).

Prevailing usage of a grammatically wrong family name is maintained, even if the part of the grammatical stem "-id" was dropped in the orthography which deletes the case ending of the appropriate genitive singular from genus name in Greek or Latin (Articles 29.3.1, 29.4, 29.5). The implication of prevalent spelling is categorized later.

CONSTRUCTION OF A HIGHER CLASSIFICATION SYSTEM

Radiolaria vs Radiozoa: current status at the order and higher levels

Polycystinea and molecular phylogenetically close taxa are named "Radiolaria" or "Radiozoa". Radiolaria was coined by Müller (1859b: 16) and Radiozoa by Cavalier-Smith (1987: 20). Are they identical or not? Which one should be used? There is a variety of higher classification systems in the history (Appendix 1).

An accurate Linnean hierarchy system in Eukaryotes seems highly improbable and thus it has recently been abandoned (e.g., Adl *et al.* 2019: 77). However, the Linnaean hierarchy still provides a high communication benefit in fossils studies. We owe much to the series proposed by Cavalier-Smith as his work was always concerned with the Linnaean hierarchy. However, it is unfortunate that the author and year reports for several nomenclatural acts appear as incorrect in many cases. For example, Cavalier-Smith *et al.* (2018: 1528-1529) wrongly cited Cavalier-Smith (1993), and not Levine *et al.* (1980: 43), as the first nomenclatural act to elevate the Polycystinea at a taxonomic class rank. The years of publication of the papers from "Ehrenberg 1838", "Haeckel 1881" and "Ehrenberg 1875" have been a matter of dispute. The Haeckel-Ehrenberg Project corrected the publication years of these papers by respectively changing and confirming as 1839, 1882 and 1876, (see Lazarus & Suzuki 2009: 26, table 1). A series of Cavalier-Smith's papers indicated that the Sticholonchea were first considered a taxonomic class by Petrushevskaya 1977: 1448.

Another serious issue is "Radiolaria" versus "Radiozoa". Radiolaria initially included Acantharia, Polycystinea and Phaeodaria (Haeckel 1887; Campbell 1954). Poche (1913: 206-224) first included the Taxopodia (originally Sticholonchidea) into the subclass Radiolaria. Initially, Radiolaria was grouped with the Acantharia, Polycystinea, Phaeodaria and Taxopodia. Honigberg *et al.* (1964: 13-14) following a consensus of the committee on Taxonomy and Taxonomic Problems of the Society of Protozoologists excluded the Acantharia from the Radiolaria. Later, Levine *et al.* (1980: 43-44) following a consensus of the committee on Systematic and Evolution of the Society of Protozoologists considered the word "Radiolaria" as obsolete and grouped the classes Acantharea, Polycystinea, Phaeodarea and Heliozoea into the superclass Actinopoda. "Radiozoa" first appeared as a branch between the subkingdom and subphylum in Cavalier-Smith (1987: 20) to include Acantharia and "Radiolaria". The term "Radiolaria" for Cavalier-Smith (1987) includes Spumellaria, Nassellaria and Phaeodaria in the sense of Suzuki & Not (2015). The "Radiozoa" is equivalent to "Radiolaria" in the sense of Haeckel (1887). As Cavalier-Smith (1987) kept the name "Radiolaria" in the sense of Honigberg *et al.* (1964), the uses of "Radiozoa" and "Radiolaria" were acceptable for that time.

After Cavalier-Smith (1987), two major proposals to the so-called protistans were proposed and revised by Adl *et al.* (2005, 2012, 2019) as well as a series of Cavalier-Smith's papers (Cavalier-Smith 1993, 1998, 1999, 2002, 2003; Cavalier-Smith *et al.* 2018). The word "Radiolaria" appeared in Adl *et al.* (2005: 419-420), disappeared in Adl *et al.* (2012: 474-475), and reappeared in Adl *et al.* (2019: 77). These changes were largely related to the confusion around monophyletic or polyphyletic opinions in molecular phylogenetic studies.

The series of Cavalier-Smith's papers have a history different from the series of Adl *et al.* (2019). Cavalier-Smith (1993: 972) extended the concept of "Phylum Radiozoa" to include the Class Sticholonchea, and used the "subphylum Radiolaria" which is subdivided into the classes Polycystinea and Phaeodarea. Thus, "Radiozoa" is the same as "Radiolaria" in the sense of Poche (1913); whereas "Radiolaria" in the sense of Cavalier-Smith (1993) is the same as "Radiolaria" in the sense of Honigberg *et al.* (1964). After the Phaeodarea became known as a separated group within the molecular phylogeny, the term "Radiozoa" disappeared; "Radiolaria" changed to include the acantharians and "euradiolarians" which is the same as Polycystinea (Cavalier-Smith 1999: 349; 2002: 326). One year later, Cavalier-Smith (2003: 347) abandoned "Radiolaria" and revived "Radiozoa" for the Sticholonchea, Acantharea and Polycystinea. It was noted that the Phaeodaria were clearly excluded from the "Radiolaria", but the "Radiozoa" in the sense of Cavalier-Smith (2003) were the same as "Radiolaria" in the sense of Adl *et al.* (2005). However, Cavalier-Smith *et al.* (2018) changed the concept of the "Radiozoa" to include only the Acantharea and Polycystinea. This concept became the same as the "Radiolaria" of Cavalier-Smith (1999, 2002), because Cavalier-Smith (1999, 2002) did not include the group "Phaeodaria".

The common points between Cavalier-Smith *et al.* (2018) and Adl *et al.* (2019) are that Polycystinea and Acantharia should be placed at the same taxonomic level as the Foraminifera under the Retaria. Conversely, the major difference between them is the placement of "Taxopodia" (see Appendix 1). Some years earlier, Krabberød *et al.* (2017) summarized the Rhizaria genetic and morphological evolution. This paper recognized three large groups in the Retaria: the Taxopodia, the "Radiolaria" (including Acantharia and Polycystinea) and Foraminifera. As the concept "Radiolaria" is sensitive to differences among authors, it is not necessary to keep the retain the term "Radiozoa" until a change in the conception is permanently fixed. In fact, the name "Radiozoa" only appeared in 0.68% of the papers on radiolarians (23 of 3388 papers, including review) between 1994 and 2019.

Cavalier-Smith *et al.* (2018) proposed a new subphylum: Ectoreta to include Foraminifera, Polycystinea and Taxopodia. As the tight grouping among these taxa was reported frequently, the Ectoreta is presumably acceptable. In consideration of the historical changes, the principle of the first reviser, as well as the taxonomic stability, the following high classification system is a genuine and reasonable arrangement:

- Infrakingdom Rhizaria Cavalier-Smith, 2002 *sensu* emend. Cavalier-Smith (2003);
  - Phylum Retaria Cavalier-Smith, 1999 stat. Cavalier-Smith (2002);
    - Subphylum Ectoreta Cavalier-Smith *in* Cavalier-Smith Chao & Lewis, 2018;
      - Infraphylum Foraminifera Eichwald, 1830 stat. Cavalier-Smith *et al.* (2018);
      - Infraphylum Radiolaria Müller, 1859b *sensu* Krabberød *et al.* (2017);
        - Class Acantharea Haeckel, 1882, stat. Cavalier-Smith (1993);
        - Class Polycystinea Ehrenberg, 1839, stat. Levine *et al.* (1980);
          - Order Spumellaria Ehrenberg, 1876, stat. Haeckel (1884);
          - Order Collodaria Haeckel, 1882;
          - Order Entactinaria Kozur & Mostler, 1982;
          - Order Nassellaria Ehrenberg, 1876, stat. Haeckel (1884);
      - Infraphylum Sticholonchia Poche, 1913 stat. Cavalier-Smith *et al.* (2018), *sensu* Krabberød *et al.* (2017);
        - Class Sticholonchea Poche, 1913 stat. Petrushevskaya (1977);
          - Order Taxopodia Fol, 1883.

For consistency in the higher classification scheme for the protist by Adl *et al.* (2019), we placed Collodaria, Entactinaria, Nassellaria and Spumellaria at the order-rank in the same way as Matsuzaki *et al.* (2015) and Suzuki & Not (2015). It is also noted that higher classification has been changing at shorter intervals, often every year. Several publications conceived Acantharea and Taxopodia as an order of Radiolaria, such formulation was consistent with the current knowledge at the time (Suzuki & Aita 2011; Suzuki & Not 2015); however, this should be replaced in the revised system proposed above until a more realistic one is proposed. Some papers placed the "Nassellaria", "Spumellaria" and "Collodaria" in the sense of Suzuki & Not (2015) at a higher level, above order or even higher ranks. These proposals are unacceptable with the accepted higher-level classification of eukaryotes (e.g., Cavalier-Smith *et al.* 2018; Adl *et al.* 2019) and all living organisms' classification (e.g., Ruggiero *et al.* 2015).

Molecular phylogeny and higher classification system above families

Molecular phylogenetic studies have been performed for Collodaria (Biard *et al.* 2015), Entactinaria and Spumellaria (Nakamura *et al.* 2020; Sandin *et al.* 2021) and Nassellaria (Sandin *et al.* 2019) taking into account the most recent morphology-based taxonomic knowledge. These procedures have shown the potential benefits of combining the molecular phylogeny and the morphological taxonomy in a single scheme. Morphology-based taxonomy at the family level is largely based on the commonality of the central structure or the configuration of the cephalic internal spicular system. This was hypothesized early on by Bütschli (1882) who suggested its importance at the family level. Its usability was proved at the family level by molecular phylogenetic studies (Sandin *et al.* 2019, 2021; Nakamura *et al.* 2020). Molecular phylogenetic studies with 18s rDNA and 28S rDNA are key determinants in objectively establishing the phylogenetic relationship at the family-rank, order-rank and higher ranks. The family-level has already been established by morphological study (e.g., Petrushevskaya 1971a; De Wever *et al.* 2001; Matsuzaki *et al.* 2015) and this categorization corresponds well with molecular phylogenetic results. In consideration of these two restrictions regarding the taxonomic rank, "Lineage" in Nassellaria and Spumellaria (Sandin *et al.* 2019, 2021) is relevant to the suborder level and the "Clade" within a Lineage is should be perceived as a superfamily level. Molecular analysis for Collodaria (Biard *et al.* 2015) used the term of "Clade". These clades are concordant with the family classification by morphological analysis. Collodaria are traditionally divided into "solitary Collodaria" and "colonial Collodaria" (e.g., Suzuki & Aita 2011) but the solitary Collodaria are scattered in clades A, B and C (Biard *et al.* 2015). This presumably implies a life stage of colonial Collodaria for solitary Collodaria but it is unhelpful for real samples. Accordingly, the "solitary Collodaria" group was kept as an artificial superfamily in this catalogue. "Living" Entactinaria in the sense of De Wever *et al.* (2001) was proved, beyond doubt, to be a polyphyletic group (Nakamura *et al.* 2020) but some families are grouped under "Entactinaria" as request of one of us (PD).

Several people strongly object the use of molecular phylogenetic results as these schemes are not consistent with their own results and because the phylogenetic trees are continuously changed. Very often, these molecular phylogenetic results are denied, but the reason for this is purely based upon a conceptual refusal. They have never trusted the quality and reliability of molecular studies. This suspicion might have been justified during the early stages of the study given the few samples available in the early 2000s, but the quality and reliability of molecular phylogenetic trees are quantitatively evaluated in all published works. The key point in reading phylogenetic trees is to check for: 1) the correct identification of specimens; 2) the purpose of the tree; 3) the examined position of DNA; 4) the taxa omitted in the tree; 5) the presence of long branching taxa; and 6) the statistic scores, such as bootstrap values with the number of replicates (BS) and posterior probabilities (PP). It is quite common to misunderstand that a branch is the direct ancestor between two taxa at the same taxonomic level. It goes without saying that the branch is represented by a group with extinct taxa as well as the concerned taxon and, thus, the branch may reflect a higher taxonomic level than the highest level of the concerned taxa. In summary, results with small BS and PP supports should not be blindly trusted.

The corresponding relationship between molecular phylogeny and morphological classification in studies on Polycystinea is initially determined by the species examined in molecular phylogeny. As almost all skeletal and living photos referring to molecular studies are accessible, their identification was updated under modern taxonomic schemes to determine the appropriate genus (e.g., Matsuzaki *et al.* 2015). These genera are not always the type genus of a family. Nevertheless, the family for these genera was arranged into the proposed Clade and Lineage of Collodaria (Biard *et al.* 2015), Nassellaria (Sandin *et al.* 2019) and Spumellaria and Entactinaria (Nakamura *et al.* 2020; Sandin *et al.* 2021) with a meticulous evaluation of the quality and reliability of their molecular morphological trees. The superfamily position of the extinct families was classed into morphologically similar extant families due to the fact that the combination of extant families within a superfamily was globally in accordance with the knowledge of morphology-based classification.

Higher rank system

The current higher classification system for the Cenozoic polycystine genera is summarized in Appendix 1 and, an exhaustive synonymy list of family-group names is presented in Appendix 2. This inventory also includes junior synonyms, *nomina dubia, nomina nuda* and invalid names. To simplify the table, all these families are written as a family name with the suffix -IDAE. A total of 372 family-group names were proposed for the Cenozoic. They consist of 94 valid names, 118 junior synonym names, 111 *nomen dubium* (largely established with "hypothetical concept"), 6 family names from junior homonym genera, and 19 *nomen nudum* family-groups. In addition, 24 invalid names were proposed without genera or species known or described.

The systematic classification proposed at suprageneric level is arranged as follows (see Appendices 3 and 4):

a) Order Spumellaria: three Phylogenetic Molecular Lineages (PM Lineages = suborders), 13 superfamilies and 42 families;
b) Order Entactinaria: one PM Lineage, five superfamilies and nine families;
c) Order Nassellaria: four PM Lineages, 16 superfamilies and 37 families;
d) Order Collodaria: three superfamilies and six families.

As explained before, the "Entactinaria" are placed in Lineage III of spumellarian phylogenetic results by Sandin *et al.* (2021).

CONTENTS IN SYSTEMATICS

Systematics include: 1) a full synonym list of family-rank with some higher ranks; 2) a valid genera list with junior synonyms; 3) an unavailable name due to homonymy; 4) *nomina dubia* with the names which must be excluded from any nomenclature act due to "hypothetical concept" without preserving name-bearing specimens; 5) a short diagnosis; 6) remarks; 7) the validity of the included genera; and 8) the stratigraphic occurrence of the family based on the group of taxa which were validated after several years of extensive revision work (see Appendix 4 for a quick view). The family names in Appendix 4 are tied to the revised dataset by a permanent link to ninety-seven PDF files (see the appendix 2 in the revision article of genera, O'Dogherty *et al.* in press). Each family file includes those genera considered as valid with a list of the species and their objective synonyms; the stratigraphic occurrences assigned in the original papers are also documented.

The diagnosis section includes important characters for quick identification, and important analytical characters for a critical case of identification. For convenience, the diagnosis does not include the complete description of families. As for remarks, the following points are included when possible.

1. Reasons for higher classification (Lineage, superfamily);
2. Morpho- and phylogenetic distinctions between easily recognizable families;
3. Major differences from previous family concepts;
4. Source of evidence regarding the internal structure;
5. Topics not discussed in this revision;
6. The protoplasm and the presence of algal symbionts and parasites.

1. Reasons for higher classification (lineage, superfamily)

Although different opinions still remain, synthesized higher taxonomic classification system for the entirety of Eukaryotes has moved a step towards consensus in the International Society of Protistologists (Adl *et al.* 2019; Ruggiero *et al.* 2015; Cavalier-Smith *et al.* 2018). As "Polycystinea" is placed in "Class" for consistency in the rank system of Eukaryotes and all living organisms, the best place for "Collodaria", "Entactinaria", "Nassellaria" and "Spumellaria" is within the order-rank. Afanasieva & Amon (2006) regarded "Polycystinea" as a subphylum, but this opinion cannot be reconciled with any widely accepted system for the Eukaryotes. Molecular morphological studies were carried out on classical radiolarians, namely Acantharia (Decelle *et al.* 2012), Collodaria (Biard *et al.* 2015), Entactinaria (Nakamura *et al.* 2020), Nassellaria (Sandin *et al.* 2019), Phaeodaria (Nakamura *et al.* 2015), Spumellaria (Nakamura *et al.* 2020; Sandin *et al.* 2021) and Taxopodia (Not *et al.* 2007); thus, a considerable improved higher taxonomic system can be arranged (e.g., Matsuzaki *et al.* 2015). As radiolarian polycystines have a long geological record, dating back to the Cambrian, the higher taxonomic classification system should be arranged in order to integrate as much as possible the taxonomic systems of all Phanerozoic Polycystinea. For this reason, our catalogue employs superfamily ranks. Previous attempts to merge the Mesozoic and Paleozoic families into superfamily ranks were partly completed (Petrushevskaya 1981, 1984; O'Dogherty 1994; De Wever *et al.* 2001). An unexpected discovery of the molecular phylogeny studies was the presence of "Lineages" between taxonomic order and superfamily ranks in Acantharia, Nassellaria and Spumellaria; however, a "suborder" rank is not proposed in this paper as the common skeletal and/or cytological features at the "Lineage" level have not been identified yet.

2. Morpho- and phylogenetic distinctions between easily recognizable families

The benefit of Haeckel's taxonomy framework was to narrow down the options of plausible taxa; although, such mechanical procedure of classification was already abandoned. As the current family taxonomy is established on internal structures, it is difficult for new readers to understand why certain similar morpho-groups are separated and why completely different morpho-groups are classed together. Morphology-based classification can be prioritized when the molecular phylogenetic tree is supported by low values of PhyML bootstrap replications (10 000 BS) and small posterior probabilities (PP); e.g., family classification in Plagiacanthoidea, Nassellaria. In contrast, molecular phylogenetic clades are undeniable if the results are supported by 100% BS and >0.99 PP; obviously, starting from the principle that the identification of the specimen for molecular analyses was correct. In this case, the molecular phylogenetic results cannot be refuted and a radical change on the viewpoint of morphology-based taxonomy is customary. Typical cases are the clear separation between *Eucecryphalus* (Clade F) and *Cycladophora* (Clade H) at the Lineage level and solid combination of *Archipilium* and *Enneaphormis* (Clade X). If we only relied upon our morphological information, this result would have never been achieved. In our catalogue, we attempted to find the most appropriate solutions where and when possible. This catalogue might also induce to the reader into fatal error if the information given for the families are overlooked. Aside from this factor, critical taxa are compared as often as possible.

3. Major differences from previous family concepts

As declared in the introduction, the inclusion of genera into a specific family has strongly fluctuated through publications over the past half century. Our catalogue draws a line with those previous works as the taxonomy is complemented with molecular phylogenetic data. As much as possible, we explain the differences between our taxonomy and previous schemes.

4. Sources of evidence regarding the internal structure

The guiding principle of the taxonomy presented in the book authored by De Wever *et al.* (2001) is that the structure of the initial skeletal elements is the most important part during evolution and should be the foundation of the family level systematics. The impact of this publication has been successful, with more than five hundred citations over the twenty past years. Nevertheless, it has been the object of some criticisms because the taxonomy is lacking of sufficient evidences (Lazarus 2005). In most cases, only a few drawings were included in the list of genera and consequently, the reliability of these genera cannot be judged by its very nature. The senior author of this contribution (NS) examined in detail the taxonomy chapter of De Wever *et al.* (2001) and carefully evaluated the validity of families and superfamilies with many references and his own specimen's collection. The conclusion supports almost a large part of the taxonomic framework proposed in De Wever *et al.* (2001) and also raises a major issue with respect to the fact that De Wever *et al.*'s book compels readers to find objective evidences on their own.

Taking these problems into account, we have gathered numerous publications with photo illustrations at generic level when possible. The result is expressed in long comments and references in the remarks of every family, enabling to the reader with a solid background that can be used to evaluate objectively the taxonomy implemented in this revision paper.

5. Topics not discussed in this revision

The catalogue is a consensus work, but many key points are yet to be debated. We are well aware of several curious decisions for some genera. In fact, numerous genera were moved around families over the long process of revision of Cenozoic taxa. Uncertainty and unsolved issues were noted for tackling in the possible future.

6. The protoplasm and the presence of algal symbionts and parasites

Marine biologists interested in living Polycystinea frequently ask questions about the characteristics of protoplasm and further information on symbionts. These topics were primarily treated in the late 1830s to 1920s. The observations and descriptions in these classic papers may be precise, but they cannot be evaluated without photographic evidence. The firs images were published from 1950s onwards (e. g. Hollande & Enjumet 1953), but as of yet, nobody has been able to gather all sources of information with reliable photos. In this sense, as a much as possible, this information is included for the families. We have compiled such kind of information at generic level, summarizing sources of photos about living condition, fixed cell images, epi-fluorescent images with some dyeing like DAPI and PDMPO, sectioned protoplasm, etc. (Appendix 3).

SYSTEMATICS

Order SPUMELLARIA Ehrenberg, 1876

Phylogenetic molecular lineage I (Sandin *et al.* 2021).

Diagnosis. — No common morphological characters have been recognized yet.

Remarks

The lineage I includes the superfamilies Hexacromyoidea (including Clades A to C), Spongosphaeroidea (including Clade D), Lithocyclioidea (including Clade E1)and Spongodiscoidea (including Clades E2 and E3). This Lineage consists of Clades A, B, C, D and E. The group of Clades D and E is independent from other clades with 100% PhyML bootstrap values, with 10 000 replicates (BS) and >0.99 posterior probabilities (PP) in 18SrDNA. A group of Clades A, B and C is separable from the group of Clades D and E, but their clustering is not stable as of yet. *Hexacromyum* (originally *Hexacontium*) was clustered into both Clades A and B so that these two clades did not have to be grouped as a single superfamily in Hexacromyidae. *Hollandosphaera* was correctly grouped in a single Clade B and thus, Hollandosphaeridae was applicable to this Clade. Clade E exclusively includes *Spongosphaera* in order to assign it as Spongosphaeridae. Clade E1 includes *Didymocyrtis* and *Spongolivella* (originally *Cypassis*), Clade E2 includes *Spongocyclia* and *Schizodiscus*, and Clade E3 includes *Dictyocoryne*, *Spongodiscus*, *Spongaster* and *Tricranastrum* (originally *Myelastrum* and *Triastrum*). Almost all branches within Cluster E have a very low support in 18SrDNA; however, the Clade E fits well with the superfamily Spongodiscoidea. As Lithocyclioidea is considered an ancestor of *Didymocyrtis*, this superfamily is also included in Lineage I.

Superfamily Hexacromyoidea Haeckel, 1882 n. stat.

Hexacromyida Haeckel, 1882: 453 [as a tribe]; 1887: 170, 201 [as a subfamily].

Hexalonchata – Afanasieva *et al.* 2005: S272 [as an order]. — Afanasieva & Amon 2006: 109 [as an order].

Diagnosis. — Spherical Spumellaria with a tetrapetaloid microsphere or fine fibrous arisen from a center

Remarks

Hexacromyoidea consists of Hexacaryidae (including Clade A), Hexacromyidae (including Clade B) and Hollandosphaeridae (including Clade C). Hexacromyidae and Hollandosphaeridae roughly corresponds to Hexalonchidae *sensu* De Wever *et al.* (2001: 210, 212). Only a part of the Hexastylidae *sensu* De Wever *et al.* (2001) is equal to Hexacaryidae. Sandin *et al.* (2021) recognized three Clades A, B and C for genera belonging to the Hexacromyoidea, but the molecular differences among both Clades A and C are supported by small bootstrap values (BS) and posterior probabilities (PP). The independency of Clade B is supported by PhyML bootstrap values of 10 000 replicates (BS), >0.99 posterior probabilities (PP) and includes *Hollandosphaera*. *Hollandosphaera* may be separated from the other members of Hexalonchidae *sensu* De Wever *et al.* (2001), resulting in the family Hexacromyidae independent of Hexalonchidae. However, if we refer to Sandin *et al.* (2021), the independency between Hexacaryidae and Hexacromyidae is faced with another problem. Clades A and C includes *Hexarhizacontium* and *Hexacromyum* (originally *Hexacontium* in Sandin *et al.* 2021). Given the low BS and PP values, it is unhelpful to refer to the evaluation of the two-family scheme with Hexacaryidae and Hexacromyidae.

Afanasieva *et al.* (2005) proposed the order Hexalonchata based only in presence of six radial spines; however, that premise is inconsistent at rank level, not only within Radiolaria but also in Protista (see preceding discussion). These singles characters are probably related to convergent evolution leading to homeomorphic taxa.

Clade A (Sandin *et al.* 2021)

Family Hexacaryidae Haeckel, 1882 n. stat.

Hexacaryida Haeckel, 1882: 454 [as a tribe]; 1887: 170, 202 [as a subfamily]. — Schröder 1909: 9 [as a subfamily].

Haliphormida Haeckel, 1882: 428 [below tribe].

Hexacaryinae – Chediya 1959: 93.

Type genus. — *Hexacaryum* Haeckel, 1882: 454 (type species by subsequent monotypy: *Hexacaryum arborescens* Haeckel, 1887: 203).

Included genera. — *Cleveiplegma* Dumitrica, 2013a: 24. — *Haliphormis* Ehrenberg, 1846: 385 (= *Hexastylanthus* **n. syn.**, *Hexastylettus* **n. syn.**, *Hexastylissus* synonymized by Takahashi 1991: 71, *Hexastylurus* **n. syn.**). — *Hexacaryum* Haeckel, 1882: 454. — *Hexalonchetta* Haeckel, 1887: 182. — *Hexancistra* Haeckel, 1879: 705 (= *Hexancora* with the same type species). — *Hexapitys* Haeckel, 1882: 451.

Invalid name. — *Hexadendron*.

Nomina dubia. — *Hexadendrum*, *Hexastylarium*, *Hexastylidium*.

Diagnosis. — Six primary radial spines arise directly from a heteropolar or tetrapetaloid microsphere. They are generally distributed at right angles of each other. One spherical lattice shell, one octahedral shell with a polygonal frame, or a similar-shaped meshwork cover can be observed.
Protoplasm is illustrated for *Cleveiplegma*, *Hexapitys* and *Haliphormis*. The endoplasm is very small and fills the medullary shells and is also distributed around the medullary shell. In certain members, undeterminable transparent and brown granules surround the endoplasm. Algal symbionts are sometimes observed. When observed, algal symbionts are found at least inside the cortical shell (in the case of *Haliphormis*).

Stratigraphic occurrence. — Late Paleocene-Living.

Remarks

The available family-rank name "Haliphormida" and "Hexacaryida" were simultaneously published in Haeckel (1882). "Haliphormida" was established below the tribe, while "Hexacaryida" was established at the tribe rank, thus the valid family is "Hexacaryida." according to the ICZN (1999) Article 24.1. The internal skeletal structure was illustrated for *Cleveiplegma* (Dumitrica 2013a: pl. 1, figs 1-9) and *Hexalonchetta* (Anderson *et al.* 1986a: pl. 1, figs 3, 4). Protoplasm and algal symbionts were documented by epi-fluorescent DAPI dyeing methods in *Cleveiplegma* (Zhang *et al.* 2018: 14, fig.1), *Hexapitys* (Zhang *et al.* 2018: 11, fig. 17) and *Haliphormis* (Zhang *et al.* 2018: 11, fig. 18). The fine protoplasmic structure was illustrated in *Cleveiplegma* (Hollande & Enjumet 1960: pl. 47, fig. 5).

In the catalogue, the Hexacaryidae appear to be incorporated into different families. In poor preservation conditions, taxa with a single spherical cortical shell with six radial spines tend to be misidentified as *Hexalonchetta* (Hexacaryidae), *Haliphormis* (Hexacaryidae), six radial spine types of *Anomalosoma* (Hollandosphaeridae), six radial spine types of *Centrolonche* (Centrocubidae) and six radial spine types of *Stigmostylus* (Centrocubidae). It is essential to identify their internal structures in order to differentiate them. If the internal structure is lost, they will be related to *Haliphormis*.

Validity of genera

Hexancistra

As *Hexancistra* and *Hexancora* have the same objective type species, the older synonym is selected as the valid name.

Haliphormis

The oldest available name is *Haliphormis*. *Haliphormis* corresponds with the widely used concept of "*Hexastylus*" (a Mesozoic genus; see O'Dogherty *et al.* 2009a). The former was first synonymized with *Hexastylanthus*, *Hexastylettus* *Hexastylissus*, and *Hexastylurus*. The latter four genera have the following morphological characters: regular pores and smooth surface for *Hexastylanthus*, regular pores and spiny surface for *Hexastylettus*; irregular-shaped pores of different sizes for *Hexastylissus*; irregular-shaped pores of dissimilar in shape and spiny surface for *Hexastylurus* (Campbell 1954: D58). The lectotype of *Haliphormis* looks an empty space in the shell (Suzuki *et al.* 2009c: pl. 69, figs 1a-d) although the other specimen in the same microscopic slide has three concentric shells (Suzuki *et al.* 2009c: pl. 69, figs 2a-c). If these two specimens are conspecific each other, *Haliphormis* would not belong to the Hexacaryidae and would not be a senior synonym of *Hexastylanthus*, *Hexastylettus*, *Hexastylissus* and *Hexastylurus*. If we accept the topotypes, one of *Hexastylanthus*, *Hexastylettus*, *Hexastylissus* and *Hexastylurus* must be validated. This issue will put aside this time because real species without any internal structure are suspect for "*Hexastylus*".

Clade B (Sandin *et al.* 2021)

Family Hexacromyidae Haeckel, 1882 n. stat.

Hexacromyida Haeckel, 1882: 453 [as a tribe]; 1887: 170, 201 [as a subfamily]. — Schröder 1909: 9 [as a subfamily].

Hexalonchida Haeckel, 1882: 451 [*nomen dubium*, as a tribe]; 1887: 170, 179 [as a subfamily]. — Schröder 1909: 8 [as a subfamily].

Staurocontida Haeckel, 1882: 452 [*nomen dubium*, as a tribe]; 1887: 152, 163 [as a subfamily].

Hexacontida Haeckel, 1882: 452 [*nomen dubium*, as a tribe]; 1887: 170, 191 [as a subfamily]. — Schröder 1909: 9 [as a subfamily].

Staurocromyida Haeckel, 1882: 453 [*nomen dubium*, as a tribe]; 1887: 152, 166 [as a subfamily].

Hexadorida Haeckel, 1882: 455 [*nomen dubium*, as a tribe]; 1887: 170, 204 [as a subfamily]. — Schröder 1909: 9 [as a subfamily].

Cubosphaerida Haeckel, 1887: 55, 169-170 [as a family]. — Bütschli 1889: 1952 [as a family]. — *nec* Rüst 1892: 146. — Schröder 1909: 2 [as a family]. — Anderson 1983: 23.

Cubosphäriden [*sic*] – Haecker 1907: 118 [as a family].

Cubosphaeridae – Haecker 1908: 437. — Popofsky 1908: 209; 1912: 77, 84-87. — Enriques 1932: 982. — Clark & Campbell 1942: 31; 1945: 15. — Campbell & Clark 1944a: 14; 1944b: 5. — Deflandre 1953: 417. — Campbell 1954: D58. — Orlev 1959: 436. — Chediya 1959: 90. — Hollande & Enjumet 1960: 71-72. — Dieci 1964: 185. — Nakaseko & Sugano 1976: 122. — Tan & Su 1982: 142. — Tan 1998: 126. — Tan & Chen 1999: 146.

Hexalonchinae – Clark & Campbell 1942: 31 [*nomen dubium*]; 1945: 15. — Campbell 1954: D58. — Chediya 1959: 91. — Kozur & Mostler 1979: 20 (*sensu* emend.).

Hexacontinae – Campbell & Clark 1944a: 14 [*nomen dubium*]. — Campbell 1954: D60. — Chediya 1959: 92.

Hexadorinae – Campbell & Clark 1944b: 5 [*nomen dubium*]. — Chediya 1959: 94. — Petrushevskaya 1979: 107-108 (*sensu* emend.).

Staurocromyinae – Campbell 1954: D58 [*nomen dubium*]. — Chediya 1959: 88.

Staurocontiinae – Campbell 1954: D58 [*nomen dubium*].

Hexadoradinae – Campbell 1954: D60 [*nomen dubium*].

Cubosphaerinae – Campbell 1954: D58.

Stauracontinae [*sic*] – Chediya 1959: 87 (= Stauracontiinae) [*nomen dubium*].

Hexacromyinae – Campbell 1954: D60. — Chediya 1959: 93.

Hexadoridae – Dumitrica 1979: 21 [*nomen dubium*].

Naninninae Kozur & Mostler, 1982: 409.

Hexalonchidae – Dumitrica 1984: 94 [*nomen dubium*]; 1985: 186. — De Wever *et al.* 2001: 210, 212. — Afanasieva *et al.* 2005: S272-273. — Afanasieva & Amon 2006: 109.

Stauracontidae – Cachon & Cachon 1985: 279 [*nomen dubium*].

Type genus. — *Hexacromyum* Haeckel, 1882: 453 [type species by subsequent designation (Campbell 1954: D60): *Hexacromyum elegans* Haeckel, 1887: 201].

Included genera. — ? *Carpocanthum* Chen & Tan, 1989: 1. — *Hexacromyum* Haeckel, 1882: 453 (= *Cubosphaera* **n. syn.**, *Hexacontura* **n. syn.**). — *Hexalonchilla* Haeckel, 1887: 184 (= *Hexalonchusa* synonymized by Petrushevskaya 1975: 569; *Staurolonchantha* **n. syn.**). — *Nanina* Kozur & Mostler, 1982: 409 (= *Pentactinosphaera* with the same type species).

Nomina dubia. — *Cromyostaurus*, *Cubaxonium*, *Hexacontanna*, *Hexacontarium*, *Hexacontosa*, *Hexacontium*, *Hexadoras*, *Hexalonchara*, *Hexaloncharium*, *Hexalonche*, *Hexalonchidium*, *Spongiuspinus*, *Staurancistra*, *Stauracontarium*, *Stauracontellium*, *Stauracontidium*, *Stauracontium, Stauracontonium*, *Staurocromyum*, *Staurolonchella*, *Staurolonchissa*, *Staurolonchura*.

Diagnosis. — Bladed six primary radial spines or bladed six radial beams are directly arising from a tetrapetaloid microsphere or a heteropolar microsphere with tetrapetaloid apical structures. Two or three latticed spherical shells are present (except for *Nanina*).
Protoplasmic characters seem to be different between shallow and deep-water species. As for shallow water *Hexacromyum* and *Hexalonchilla*, the spherical endoplasm, reddish brown in color, fills the medullary shell and is outside of it. Capsular wall always situated within the cortical shell. A robust, straight, thick axoflagellum appears in *Hexacromyum* at least. Algal symbionts may be present or absent. Algal symbionts, if present, surround the endoplasm or are scattered within the cortical shell. No algal symbionts are outside of the cortical shell. As for the mesopelagic taxa of *Hexacromyum*, the endoplasm is a dark gray in color and fills the medullary shell. It is also found outside of it.
The Axopodial system is of centroaxoplastid-type: Axoplast is placed in the center of the endoplasm and is encrypted with a spherical nucleus. Bundles of axoneme penetrate through the one side of nucleus and form one thick bundle of axoneme in the endoplasmic reticulum zone of the intracapsular zone. This bundle probably forms a straight, thick and robust axoflagellum. A clear zone with radiated thin bundles of axoneme surrounds the nucleus. The axoplast is situated in the microsphere (the inner medullary shells) and the nucleus is placed in the outer medullary shell. A clear zone also appears inside the outer medullary shell. An endoplasmic reticulum occupies the space between the outer medullary shell and the cortical shell.

Stratigraphic occurrence. — Late Paleocene-Living.

Remarks

This family was originally called Hexalonchidae, but this family name is a *nomen dubium*. Yuasa *et al.* (2009) first proved that *Hexacromyum* (originally *Hexacontium*) is a member of Spumellaria. Several widely used taxon genus names such as *Hexacontium* and *Hexalonche* should be omitted in taxonomic works as they have been established on the basis of an un-illustrated type species. Internal skeletal structure, including growth line, was illustrated for *Hexacromyum* (Nishimura 1986: fig. 7.1; Sugiyama *et al.* 1992: pl. 14, figs 5, 6, 8; van de Paverd 1995: pl. 33, fig. 7; pl. 34, fig. 5), *Hexalonchilla* (Nishimura 1986: fig. 7.2; Suzuki 1998b: pl. 6, figs 2, 5-9) and *Nanina* (Nakaseko *et al.* 1982: pl. 1, figs 1-3; Sugiyama 1992a; pl. 1, fig. 1). A living image was given for *Hexacromyum* (Yuasa *et al.* 2009: fig. 1a; Suzuki & Not 2015: fig. 8.8.8; Matsuoka 2017: figs 7.1, 7.2, 8.1, 8.2) and *Hexalonchilla* (Suzuki & Not 2015: fig. 8.10.12). Protoplasm and algal symbionts were documented by epi-fluorescent observation via DAPI dyeing or other dyeing methods in *Hexacromyum* (Ogane *et al.* 2010: figs 1.9-1.10, 2.9-2.10; Zhang *et al.* 2018: 11, figs 14, 15; p. 14, fig. 10; pl. 17, fig. 9) and *Hexalonchilla* (Zhang *et al.* 2018: 11, fig. 16). Protoplasm was also illustrated for fixed specimens of *Hexacromyum* (Aita *et al.* 2009: pl. 9, figs 1, 2; Krabberød *et al.* 2011: figs 1.G-1.L). Fine protoplasmic structure was illustrated in *Hexacromyum* (Hollande & Enjumet 1960: pl. 33, fig. 4; pl. 35, fig. 4). *Hexacromyum* can be infected by Marine Alveolata of Group II (Ikenoue *et al.* 2016), but real images of these symbionts have not been captured as of yet.

Classic *Hexalonche* is largely transferred to *Hexalonchilla*. It is also mixed with *Hexalonchetta* (Hexacaryidae), *Hexancistra* (Hexacaryidae), *Hexarhizacontium* (Rhizosphaeridae), the six-radial spine-form of *Centrolonche* (Centrolonchidae), and the six-radial spine-form of *Stylosphaera* (Stylosphaeridae). They are carefully identified by an examination of their internal structure. Two shelled spherical radiolarians with six radial spines are generally classified into *Hexalonchilla*. However, types of bladed or non-bladed radial beams, types of bladed or non-bladed radial spines, and types of spherical and tetrapetaloid microspheres are still overlooked. For instance, the supporting image of *Hexalonchilla* in the catalogue has non-bladed radial beams, non-bladed radial spines and a tetrapetaloid microsphere, whereas the type-illustration for the representative genus shows non-bladed radial beams, bladed radial beam and a spherical microsphere.

Classic *Hexacontium* is largely transferred to *Hexacromyum*. It is also mixed with the six-radial spine-form of *Axoprunum* (Axoprunidae), the six-radial spine-form of *Haliomma* (Haliommidae) and *Hexacontella* (Haliommidae). Like in the case of *Hexalonchilla*, they were carefully identified by an examination of their internal structure. The morphological status of the radial spines, the radial beams and the microsphere were also poorly discriminated. Some three shelled morphospecies with six radial spines, likewise, have many radial beams between the outer double medullary shell and the cortical shell. Furthermore, some morphospecies, recovered from plankton samples, developed many fragile concentric shells between the outer double medullary shell and the cortical shell, which sometime is missing due to dissolution.

Validity of genera

Hexacromyum

Hexacromyum itself was used as a valid genus in Petrushevskaya (1975: 569). The usage of this genus in our paper is corresponded to the widely accustomed usage of *Hexacontium*. The definition of *Hexacromyum* mentioned the four concentric shells (Campbell 1954: D60) but the "4th" shell of the neotype is additionally formed following the secondary growth mode of Ogane *et al.* (2009c) (See the supporting image for *Cubosphaera* in the Atlas part). *Cubosphaera* has "five or more concentric shells" (Campbell 1954: D58) and *Hexacontura* has three concentric shells with irregular pores of dissimilar sizes (Campbell 1954: D60). The subsequent "4th" or "5th" concentric shell illustrated in the type species of *Cubosphaera* is also the shell formed following the secondary growth mode of Ogane *et al.* (2009c). Pore size and shape continuously changed from regular pores with similar size, so this difference is related to species or within species variations, if we refer to the numerous photos in publications. Aita *et al.* (2009) observed *Hexacromyum elegans* in the plankton slide from the *H.M.S. Challenger* Station 271 which was examined by Haeckel himself. The type material for this species is from a "Central Pacific, Station, surface" (Haeckel 1887: 201). The valid name is the oldest synonym among them (1882 for *Hexacromyum*; 1887 for both *Cubosphaera* and *Hexacontura*). However, one concern is the taxonomic status of *Haliphormis*. The specimen corresponding to the type-illustration of *Haliphormis hexacanhtus* in the Ehrenberg collection have a single cortical shell, whereas other specimens in the same collection have three concentric shell (see support image for *Haliphormis* in the Atlas). If these specimens are conspecific, *Haliphormis* would not belong to the Hexacaryidae, and hence it would not be a senior synonym of *Hexastylanthus*, *Hexastylettus*, *Hexastylissus* and *Hexastylurus*. This means that *Haliphormis* is the oldest synonym among *Hexacromyum*, although the genus name *Haliphormis* has not been used for recent 50 years so the valid genus remains unchanged as *Hexacromyum*.

Hexalonchilla

Hexalonchilla partly corresponds to *Hexalonche* based on both concentric shells but is limited for those that have a heteropolar microsphere with un-bladed six radial beams. *Hexalonchusa* is characterized by irregular pores of dissimilar sizes and the spiny surface of the cortical shell (Campbell 1954: D60) but these differences are related to infra- or intra-specific variations. The spiny surface is also induced by the preservation effect. *Staurolonchantha* was considered to have four equidistant main radial spines (Campbell 1954: D56) but the lectotype has a typical structure with six radial spines (Suzuki *et al.* 2009c: pl. 36, figs 2a-d). The lectotype of "*Haliomma hexagonum*" has an unclear innermost shell but has presumably three concentric shells. All these four "genera" were initially established with a subgenus rank in the same publication (Haeckel 1887: 170 for *Hexalonchilla*, 186 for *Hexalonchusa* and 158 for *Staurolonchantha*). In consideration of uncertainty for the type specimen of *Staurolonchantha*, the genus which is published first is selected as the valid name.

Nanina

Regarding the proposal of *Nanina* by Kozur & Mostler (1982), the genus name was established as follows. The new taxon status for *Nanina* was first published as a tentative genus name: *Pentactinosphaera* Nakaseko *et al.* (1982) with the mention of "*We assigned it to Pentactinosphaera hokurikuensis (Nakaseko) as a tentative name*" (Nakaseko *et al.* 1982: 423). The available description for *Pentactinosphaera* was formally described by Nakaseko *et al.* (1983) with the same type species for *Nanina* by Kozur & Mostler (1982) published in December 1982. Under the description of *Nanina*, Kozur & Mostler (1982) cited Nakaseko *et al.* (1982) with the comment: "*described the internal structure of this genus for the first time*", but they never cited the *nomen nudum* name "*Pentactinosphaera*" in the synonym list included in the English abstract or within the figure explanation of Nakaseko *et al.* (1982). At this time, the Code (ICZN 1964) included on page 93 a "code of ethics" which stated that : "*A zoologist should not establish himself a new taxon if he has reason to believe that another zoologist has already recognized the same taxon* [...] *He should communicate with the other zoologists* [...] *consider himself free to establish the new taxon only if the other zoologists* [...] *fail to do so in a reasonable period (not less than a year).*" As Kozur & Mostler (1982) recognized Nakaseko *et al.* (1982) as the first describer of the internal structure on page 409, there is no doubt they knew that Nakaseko would prepare a new taxonomic paper for "*Nanina*". Despite the prescribed code of ethics, Kozur & Mostler (1982) established a new taxon without communicating with Nakaseko (Kozur, personal comm.; Nishimura, personal comm. to NS) and after a very short waiting period (less than a year). The problem is not to identify the first discoverer; instead, the problem lies in understanding why Kozur & Mostler (1982) did not respect the "code of ethics" which could have avoided future trouble regarding the author priority of the taxon, even though this is not a scientific requirement.

Clade C (Sandin *et al.* 2021)

Family Hollandosphaeridae Deflandre, 1973

Hollandosphaeridae Deflandre, 1973: 1151. — Cachon & Cachon 1985: 288.

Coscinommida Haeckel, 1887: 208 [*nomen dubium*, as a subfamily]. — Wisniowski 1889: 684 [as a subfamily]. — Schröder 1909: 16 [as a subfamily].

Coscinomminae – Campbell & Clark 1944a: 15 [*nomen dubium*]. — Clark & Campbell 1945: 16. — Chediya 1959: 94.

Heliasteridae Hollande & Enjumet, 1960: 68, 86, 91 [unavailable name] (= Hollandosphaeridae). — Anderson 1983: 50.

Type genus. — *Hollandosphaera* Deflandre, 1973: 1150 [type species by monotypy; ICZN 1999: art. 67.8: *Heliaster hexagonium* Hollande & Enjumet, 1960: 92].

Included genera. — *Anomalosoma* Loeblich & Tappan, 1961: 223. — *Hollandosphaera* Deflandre, 1973: 1150. — *Tetrapetalon* Hollande & Enjumet, 1960: 92.

Nomina dubia. — *Coscinomma*, *Coscinommarium*, *Coscinommidium*, *Coscinommonium*.

Junior homonyms. — *Heterosoma* Hollande & Enjumet, 1960 (= *Anomalosoma*) *nec* Schaum, 1845; *Heliaster* Hollande & Enjumet, 1960 (= *Hollandosphaera*) *nec* Gray, 1840.

Diagnosis. — One spherical shell with a honeycomb structure and fine internal spicules originating in a center. Architecture of fine internal spicules are variable among genera. Many by-spines or more than eight fine radial spines are present. Neither robust radial beams or spines are present.
As for *Hollandosphaera*, a reddish endoplasm occupies a large portion inside the cortical shell. Hundreds of algal symbionts are scattered along important pseudopodia which radiate throughout the shell. A straight robust axoflagellum appears. *Tetrapetalon* also possesses algal symbionts. In the axopodial system of periaxoplastid-type: the axoplast is located outside of the nucleus and is attached on a side of the nucleus. Axonemes cross the nucleus through nucleus membrane tunnels and form a thick bundle of axonemes in the intracapsular zone. This thick bundle forms an axoflagellum. The axoplast either encloses the Median Bar (MB) or a relevant structure of the initial spicular system. Conversely, it may be attached on MB or a relevant structure. The nucleus is situated inside the central structure or encloses it. Bundles of axonemes extend to the opposite side of MB or a relevant structure.

Stratigraphic occurrence. — Holocene-Living.

Remarks

A precise determination of Hollandosphaeridae relies on the internal structure, but the honeycomb structure of the spherical shell is useful in specifying possible Hollandosphaeridae-taxa. The shell is so fragile that reliable fossil records have not been reported yet. Classical representatives of *Cenosphaera* and *Acanthosphaera*, currently *Ethmosphaera* (Ethmosphaeridae) and *Rhaphidocapsa* (Actinommidae) in the catalogue, may be mixed with members of Hollandosphaeridae (see remarks for Actinommidae). Internal skeletal structure is illustrated for *Hollandosphaera* (van de Paverd 1995: pl. 20, fig. 1; Onodera *et al.* 2011: pl. 3, fig. 3). Living or protoplasmic image was published for *Hollandosphaera* (Probert *et al.* 2014: S1, Vil 217, S2, VER 1; Suzuki & Not 2015: fig. 8.8.9) and *Tetrapetalon* (Anderson *et al.* 1998: pl. 1, fig. 1). Fine protoplasmic structure is illustrated for *Hollandosphaera* (Hollande & Enjumet 1960: pl. 2, figs 5-8; pl. 6, fig. 11; pl. 7, fig. 6; pl. 39, figs 1-5; pl. 41, figs 1, 2) and *Tetrapetalon* (Hollande & Enjumet 1960: pl. 1, fig. 10; pl. 41, fig. 4; Anderson *et al.* 1998: pls 1, 2). Some genera may not have been formally described yet (e.g., Itaki *et al.* 2012: pl. 2, fig. 3). Algal symbionts of *Hollandosphaera* are identified as *Brandtodinium nutricula* by Probert *et al.* (2014).

Clade D (Sandin *et al.* 2021)

Superfamily Spongosphaeroidea Haeckel, 1862

Spongosphaerida Haeckel, 1862: 239, 452 [as a tribe]; 1882: 455 [as a subfamily].

Spongosphaeroidea – Suzuki & Not 2015: 196.

Diagnosis. — Spongy spherical cortical skeleton. Inner part was empty or consisted of a single or double medullary shell. A variable number of three-bladed radial spines, or radial beams, are observed.

Remarks

The Spongosphaeroidea corresponds to the Clade D of Lineage I (Sandin *et al.* 2021) and includes only the family Spongosphaeridae. Classically, this superfamily includes the Spongosphaeridae and Spongodrymidae; however, the Spongodrymidae was grouped in Clade I of Lineage III (Sandin *et al.* 2021) and represented by "*Plegmosphaerella*"-form of *Plegmosphaeromma* (specimen ID Vil210, Vil451 of Sandin *et al.* 2021). The Spongosphaeridae possess robust three-bladed primary radial beams/spines. In contrast, the Spongodrymidae have fibrous radial beams radiating from the microsphere. Both families have a common centroaxoplastid-type protoplasmic structure of the intracapsular zone, but their central structures are quite different. The Spongosphaeridae have double or single medullary shells (Kurihara & Matsuoka 2004) as a stable character, while the central part of the Spongodrymidae is variable: empty hollow, with a structureless mesh, a fine polyhedron microsphere and other infra-species variations (Hollande & Enjumet 1960; Swanberg *et al.* 1990).

Family Spongosphaeridae Haeckel, 1862

Spongosphaerida Haeckel, 1862: 239, 452 [as a tribe]; 1882: 455 [as a subfamily]. — Mivart 1878: 177 [as a subsection]. — Stöhr 1880: 119 [as a family].

Spongosphaeria – Dunikowski 1882: 187 [as a subfamily].

Spongosphaerinae – Mast 1910: 177. — Popofsky 1912: 93, 111. — Hollande & Enjumet 1960: 68, 97. — Anderson 1983: 51, 57. — Cachon & Cachon 1985: 287 [with wrong authors as Hollande & Enjumet].

Spongosphaera – Hertwig 1937: 22-25 [as a group].

Spongosphaeridae – Hollande & Enjumet 1960: 68, 95, 96. — Anderson 1983: 50, 57. — Cachon & Cachon 1985: 286. — van de Paverd 1995: 104 [with wrong authors as Hollande & Enjumet].

Type genus. — *Spongosphaera* Ehrenberg, 1847: 54 [type species by subsequent monotypy: *Spongosphaera polyacantha* Müller, 1856: 487].

Included genera. — *Diplospongus* Mast, 1910: 61. — *Spongodendron* Hollande & Enjumet, 1960: 99. — *Spongosphaera* Ehrenberg, 1847: 54 (= *Hexadoridium* **n. syn.**; *Spongosphaeromma* synonymized by Kozur & Mostler 1979: 10).

Nomen dubium. — *Spongioconcha*.

Diagnosis . — Thick spongy spherical cortical skeleton with a single or double medullary shell and a variable number of three-bladed radial spines.
Protoplasm is well observed in *Spongosphaera*. Endoplasm of brownish gray color, filling a spongy shell. Dark brownish red to reddish brown granular pigments surround the surface of the endoplasm. Axopodia radiate throughout the endoplasm. Algal symbionts are scattered on the endoplasm. Axopodial system of centroaxoplastid-type: the Axoplast is a very small fused point, located within the inner microsphere (inner double medullary shell). Nucleus is located inside the outer medullary shell or is found wrapping it. Significant bundles of axoneme are not present. Instead of bundles, axoneme radiate evenly throughout the intracapsular zone.

Stratigraphic occurrence. — early Middle Miocene-Living.

Remarks

The genus *Spongosphaera* is characterized by a double medullary shell and straight three-bladed radial spines. We place the genera *Diplospongus* and *Spongodendron* into Spongosphaeridae based on the presence of three-bladed radial spines, although both genera seem to have a single medullary shell. As *Spongosphaera streptacantha* is typically found in plankton samples from tropical to subtropical oceans, many observations were related as well as personally observed. *S. streptacantha* is the only Spumellaria whose images can be captured in the ocean with an autonomous visual plankton recorder (A-VPR) (Nakamura *et al.* 2017: fig. 2.C). Thus, its taxonomic stability and oceanographic response are important. The number of radial beams of this species is varies from six to twelve, its internal structure was also illustrated in detail (Kurihara & Matsuoka 2004). By referring to this case, other genera belonging to Spongosphaeridae presumably have significant variations. The fine protoplasmic structure was illustrated in *Diplospongus* (Hollande & Enjumet 1960: pl. 6, figs 4-9), *Spongodendron* (Hollande & Enjumet 1960: pl. 6, figs 1-3; pl. 7, fig. 5) and *Spongosphaera* (Hollande & Enjumet 1960: pl. 9, figs 8-10; pl. 22, figs 8, 9; pl. 23, figs 1, 2; pl. 24, fig. 2; pl. 26, fig. 4). An image of living forms was illustrated for *Spongosphaera* (Cachon *et al.* 1989: fig. 1; Matsuoka 2007: fig. 5.a; 2017: figs 6.1, 6.2; Matsuoka *et al.* 2017: appendix A). According to Cachon (1964), "*Spongosphaera*" is infected with *Hollandella myceloides*, but it is impossible to amend the taxonomic name for the host without having a more complete image. *Spongosphaera streptacantha* can exceptionally survive in high temperatures (> 30°C) in the Malacca Strait (Zhang *et al.* 2020) and is also regularly found in 17.1-19.4°C in the Japan Sea (Kurihara & Matsuoka 2010). This is the only one species with this very wide range of survival sea water temperature.

Validity of genera

Spongosphaera

Morphological variation of *Spongosphaera* was well illustrated in many previous studies (Kurihara & Matsuoka 2004; van de Paverd 1995: pl. 28, figs 2, 5-7). *Hexadoridium* is characterized by two concentric medullary lattice shells and a spongy octahedral shell (Campbell 1954: D60). As the specimen identifiable as *Hexadoridium streptacanthum* is regarded as *Spongosphaera polyacantha* form *streptacantha* by van de Paverd (1995: pl. 2, fig. 2), *Hexadorium* is a synonym of *Spongosphaera*. *Spongosphaeromma* is characterized by two medullary lattice shells surrounded by a cortical shell bearing many radial spines (Campbell 1954: D68). Nishimura & Yamauchi (1984: 33) seems to be the first paper to illustrate the type species *Spongosphaeromma* as "*Spongosphaera helioides*" and this morphological character fits with not only the definition of *Spongosphaeromma* but also the variation in *Spongosphaera*. *Spongosphaera* is the oldest available name among them.

Clade E1 (Sandin *et al.* 2021)

Superfamily Lithocyclioidea Ehrenberg, 1846

Lithocyclidina Ehrenberg, 1846: 385 [as a family].

Phacodiscaria Haeckel, 1887: 409 [as a section between family and suborder]. — Chediya 1959: 120 [as a group between superfamily and family]. — Anderson 1983: 24.

Coccodiscaea – Loeblich & Tappan 1961: 224 [as a superfamily]. — Kozur & Mostler 1972: 7 (*sensu* emend.) [as a superfamily].

Coccodiscilae – Loeblich & Tappan 1961: 224 [as a subsuperfamily].

Coccodiscoidea – Dumitrica 1979: 21.

Phacodiscariacea – Lipman 1979: 114 [as a superfamily].

Artiscacea [*sic*] – Kozur & Mostler 1979: 47 [*nomen dubium*, as a superfamily].

Lithocycliacea – Kozur & Mostler 1981: 52.

Diagnosis. — Central structure comprised of a flattened double medullary shell. The flattened double medullary shell consists of a spherical inner medullary shell (or inner microsphere) and a convex, lens-shaped outer medullary shell. The equatorial plane is defined by a crossing plane that is parallel to the flattened double medullary shell. The double medullary shell that lies at the center of the large latticed shell. Large empty space is present between the large latticed and double medullary shell. The surface of the large latticed shell is parallel to the equatorial plane. Radial beams between the double medullary shell and the cortical shell develop along the shortest distance between the two aforementioned shells. Main appendages or additional structures develop along the longest axis, or on the plane vertical to the shortest axis.

Remarks

The Lithocyclioidea include the Astracturidae, Lithocycliidae, Panartidae and Phacodiscidae. The Lithocyclioidea correspond to the family "Coccodiscidae" *sensu* De Wever *et al.* (2001: 121). To keep consistency in the taxonomy of Polycystinea, this rank has been raised to the superfamily level. Three families Astracturidae, Lithocycliidae and Phacodiscidae are distinguished by their difference in exterior structure of the outermost latticed shell. The higher taxonomic position of this family is based on the molecular phylogeny of Panartidae.

Family Astracturidae Haeckel, 1882

Astracturida Haeckel, 1882: 458 [as a tribe]; 1887: 458, 469 [as a subfamily].

Astracturinae – Campbell 1954: D82. — Chediya 1959: 130. — Petrushevskaya 1979: 113 (*sensu* emend.). — Amon 2000: 49.

Astracturidae – Kozur & Mostler 1972: 46-48.

Type genus. — *Astractura* Haeckel, 1882: 458 [type species by subsequent designation (Campbell 1954: D82): *Astractura ordinata* Haeckel, 1887: 476] = junior subjective synonym of *Astromma* Ehrenberg, 1846: 385 [type species by subsequent monotypy: *Astromma aristotelis* Ehrenberg, 1847: 55].

Included genera. — *Astromma* Ehrenberg, 1846: 385 (= *Astractinium* with the same type species; *Astractura* **n. syn.**, *Astracturium* **n. syn.**, *Astrococcura* **n. syn.**, *Staurococcura* **n. syn.**). — *Amphactura* Haeckel 1882: 468 (= ? *Dicoccura* **n. syn.**, ? *Diplactinium* **n. syn.**). — *Hymeniastrum* Ehrenberg, 1846: 385 (= *Hymenastrella* with the same type species; *Hymenactura* **n. syn.**, *Hymenacturium* **n. syn.**, *Trigonactinium* **n. syn.**; *Hymenactinium*, *Pentactura*, *Trigonacturium* synonymized by Kozur & Mostler 1972: 46).

Invalid names. — *Amphiactura, Astrococcus.*

Nomen dubium. — *Diplacturium.*

Diagnosis. — Roughly flat shell with a large convex lens-shaped latticed shell. A three-dimensional grid-like architecture formed by the arms is observed; frequently evolving from two to four arms, rarely more. Radial beams arise from the outer medullary shell and radiate towards both sides of the equatorial plane. These beams are connected to the large latticed shell. A bladed, solid and robust spine penetrates through the central axis of each arm in some members but is never seen connected to the medullary shell. No structure extends to both sides of the equatorial plane.

Stratigraphic occurrence. — Late Middle Eocene-Early Oligocene.

Remarks

A series of publications by Riedel and Sanfilippo (e.g., Sanfilippo *et al.* 1985) grouped several genera of both Lithocycliidae and Astracturidae into the single genus *Lithocyclia*. These were apparently miscategorized with several genera of different stratigraphic ranges. Thus, we are separating more genera than they did for the goal of future discussion. Internal skeletal structure was illustrated for *Astromma* (Pisias & Moore 1978: pl. 5, figs 1, 2).

Validity of genera

Astromma

As "*Astromma entomocora*" was wrongly assigned as type species of *Astromma* by Campbell (1954: D74), this genus was once applied for *Didymocyrtis* (Petrushevskaya & Kozlova 1972: 522; Petrushevskaya 1975: 578). Once we disassembled *Astromma* (= *Astracturium* in original) and *Hymeniastrum* from the synonymy of *Lithocyclia* by Riedel & Sanfilippo (1971: 522), the so-called 50-year rule (ICZN 1999: Article 23.9 "Reversal of precedence") is not an applicable case for both these genera. *Astractura* and *Astracturium* have the same type species and are characterized by four crossed chambered arms, no patagium and a simple medullar shell (Campbell 1954: D82-83). *Astrococcura* and *Astrococcus* have the same type species and can be considered as having a double medullary shell (Campbell 1954: D83). *Staurococcura* is characterized by the presence of a patagium and double medullary shells (Campbell 1954: D84). The lectotype of *Astromma* found in the Ehrenberg collection (Ogane *et al.* 2009b: pl. 71, figs 1a-c) possess a double medullary shell and the different development of the patagium continues from a non-patagium form to a fully-grown form, and, thus, these genera listed here cannot be differentiated at a species level. *Astromma* is the oldest available name among them (1846 for *Astromma*; 1882 for *Astractura*; 1887 for *Astractinium*, *Astracturium*; 1896 for *Astrococcura* and *Staurococcura*; 1954 for *Astrococcus*).

Amphactura

The same type species was designated for both *Amphactura* and *Amphiactura*. The distinction of *Diplactinium* is suspect because no real specimens assignable to this genus were found during a long time. We simply keep it as valid for a future examination. *Diplactinium* is characterized by a single medullary shell, no patagium and the presence of a distal spine whereas *Amphactura* is characterized by the former and double medullary shell with a patagium (Campbell 1954: D82-83). *Dicoccura* is defined by the lack of a patagium and the presence of a double medullary shell (Campbell 1954: D83). The synonymy among *Amphactura*, *Diplactinium* and *Dicoccura* is problematic. The lectotype of *Amphactura* has a high possibility to a broken specimen of *Astromma*. A different medullary shell is not confirmed for *Diplactinium* so we have it questionably synonymized with *Amphactura*. The exactly same morphotypes, excepted for the occurrence of a distal spine on the arms, are commonly found in the same samples so this indicator is not used at genus-level. Like *Astromma*, the patagium has different growth stages in the same species. The valid name is automatically *Amphactura* because this genus was the oldest available name among them.

Hymeniastrum

Hymeniastrum was used as a valid genus within 50 years (Tan 1998: 224; Tan & Chen 1999: 221). *Hymenactura* and *Hymenacturium* have the same type species and are characterized by a patagium, blunt and truncated arms, but no terminal spines (Campbell 1954: D83). *Hymenactinium* has a patagium and a terminal spine on the distal end of each arm (Campbell 1954: D83); *Trigonactinium* is characterized by a patagium and arms with a distal radial spine (Campbell 1954: D84), and *Trigonacturium* by arms distally blunt, or truncated, not with a terminal spine (Campbell 1954: D84). The Nomarski imaging of *Hymeniastrum pythagorae* for the supporting image of *Hymenastrella* in the Atlas displays the axial rod which is relevant to the terminal spine inside an arm. As other genera of this family, the patagium as well as the terminal spine on the arm are not characteristic at genus level. The lectotype of *Pentactura* (Ogane *et al.* 2009b: pl. 69, figs 1a-c) confirms the simple drawing of Ehrenberg (1876: pl. 30, fig. 1) with more than five arms. The arrangement of the arms is not such as a cross unlike *Astromma* so this genus is close to *Hymeniastrum*. The oldest available names among this group is *Hymenastrella* (1846 for *Hymeniastrum*, 1882 for *Hymenactura* and *Pentactura*; 1887 for *Hymenastrella*, *Hymenacturium*, *Hymenactinium*, *Trigonactinium* and *Trigonacturium*).

Family Lithocycliidae Ehrenberg, 1846

Lithocyclidina Ehrenberg, 1846: 385 [as a family]; 1847: 54 [as a family]; 1876: 156. — Schomburgk 1847: 124, 126 [as a family].

Coccodiscida Haeckel, 1862: 240, 485 [as a tribe]; 1882: 458 [as a subfamily]; 1887: 409, 455-458 [as a family]. — Zittel 1876-1880: 124 [rank unknown]. — Mivart 1878: 176 [as subsection]. — Bütschli 1889: 1959 [as a family]. — *nec* Rüst 1892: 166 [as a family]. — Anderson 1983: 24 [as a family].

Lithocyclida – Haeckel 1882: 458 [as a tribe]; 1887: 458, 459 [as a subfamily].

Staurocyclida Haeckel, 1882: 458 [as a tribe].

Trochodiscida Haeckel, 1887: 411, 412 [*nomen dubium*, as a subfamily]. — Schröder 1909: 39 [as a subfamily].

Heliosestrida Haeckel, 1887: 421, 427 [as a subfamily]. — Schröder 1909: 41 [as a subfamily].

Coccodiscidae – Poche 1913: 209. — Campbell & Clark 1944b: 14. — Campbell 1954: D82. — Chediya 1959: 128. — Riedel 1967b: 294; 1971: 653-654. — Riedel & Sanfilippo 1971: 1588; 1977: 865. — Kozur & Mostler 1972: 45. — Petrushevskaya & Kozlova 1972: 522. — Nakaseko *et al.* 1975: 169. — Nakaseko & Sugano 1976: 125. — Dumitrica 1979: 21-22; 1984: 96. — Sanfilippo & Riedel 1980: 1009 (*sensu* emend.). — Anderson 1983: 38-39. — Sanfilippo *et al.* 1985: 653. — Blueford 1988: 248. — Takahashi 1991: 79. — van de Paverd 1995: 137. — Boltovskoy 1998: 31. — Anderson *et al.* 2002: 1002. — De Wever *et al.* 2001: 121. — Afanasieva *et al.* 2005: S288. — Afanasieva & Amon 2006: 131. — Chen *et al.* 2017: 137-138.

Lithocyclinae – Campbell & Clark 1944b: 14. — Chediya, 1959: 128.

Heliosestrinae – Campbell & Clark 1944b: 14. — Clark & Campbell 1945: 20. — Campbell 1954: D78. — Chediya 1959: 125.

Trochodiscinae – Campbell 1954: D77 [*nomen dubium*]. — Chediya 1959: 122.

Coccodiscinae – Campbell 1954: D82. — Kozur & Mostler 1972: 45-46. — Petrushevskaya & Kozlova 1972: 523. — Sanfilippo & Riedel 1980: 1009. — Dumitrica 1984: 97. — Sanfilippo *et al.* 1985: 653. — De Wever *et al.* 2001: 121. — Afanasieva *et al.* 2005: S288. — Afanasieva & Amon 2006: 131.

Lithocycliidae – Petrushevskaya 1986: 128. — Kozlova 1999: 83.

Type genus. — *Lithocyclia* Ehrenberg, 1846: 385 [type species by subsequent monotypy: *Astromma aristotelis* Ehrenberg, 1847: 55].

Included genera. — *Cromyatractus* Haeckel, 1887: 334 (= *Cromyatractium* with the same type species; *Caryatractus* **n. syn.**). — *Heliosestrum* Haeckel, 1882: 457 (= *Heliosestantha* with the same type species; *Astrosestrum* synonymized by Kozur & Mostler 1972: 19; *Astrosestantha* **n. syn.**, *Astrophacura* **n. syn.**). — *Heliostylus* Haeckel, 1882: 457 (= *Astrostylus* synonymized by Kozur & Mostler 1972: 19; *Stylodiscus* synonymized by Sanfilippo & Riedel 1973: 522, *Stylentodiscus* **n. syn.**). — *Lithocyclia* Ehrenberg, 1846: 385 (= *Astrocyclia* synonymized by Riedel & Sanfilippo 1970: 522; *Coccodiscus* synonymized by Kozur & Mostler 1972: 46). — *Phacostaurus* Haeckel, 1882: 457 (= *Phacostaurium* with the same type species; *Astrostaurus* synonymized with Kozur & Mostler 1972: 19; *Crucidiscus* **n. syn.**, *Heliostaurus* **n. syn.**, *Sethostaurium* **n. syn.**, *Sethostaurus* **n. syn.**, *Staurentodiscus* **n. syn.**). — *Phacotriactis* Sutton, 1896: 61. — *Sethostylus* Haeckel 1882: 457 (= *Sethostylium* with the same type species; *Amphicyclia* synonymized by Petrushevskaya & Kozlova 1972: 522; *Phacostylus* **n. syn.**, *Phacostylium* **n. syn.**). — *Staurocyclia* Haeckel, 1882: 458 (= *Coccostaurus* synonymized by Campbell 1954: D82). — *Triactiscus* Haeckel, 1882: 457 (= *Trigonocyclia* **n. syn.**).

Nomina dubia. — *Coccocyclia*, *Echinactura*, *Heliosestomma*, *Pristodiscus*, *Stauractinium*, *Stauractura*, *Stauracturium*, *Staurexodiscus*, *Stylexodiscus*, *Theodiscoma*, *Theodiscura*, *Theodiscus*, *Trochodisculus*, *Trochodiscus*.

Junior homonym. — *Staurodiscus* Krasheninnikov, 1960 (= *Heliosestrum*) *nec* Haeckel, 1879.

Diagnosis. — Shell roughly flat, consisting of a large convex lens-shaped latticed shell. Radial beams arise from the outer medullary shell and radiate to both sides of the equatorial plane. They are connected to the large latticed shell. No three-dimensional grid-like arms are observed. One of the following exterior structures is present outside of the large latticed shell: - a wide ring made of a grid-like structure (e.g., *Cromyatractus*, *Lithocyclia*, *Staurocyclia*); - a solid flat circular edge surrounded by many solid arrowhead-like short spines (e.g., *Heliosestrum*); - and/or two to four solid spines distributed under two-fold, threefold or four-fold symmetries (e.g., *Cromyatractus*, *Heliostylus*, *Phacostaurus*, *Phacotriactis*, *Staurocyclia*, *Triactiscus*). Radial spines, if present, are not connected with the double medullary shell; or connected to the double medullary shell (e.g., *Amphicyclia*, *Cromyatractus* and *Heliostylus*). No significant structures develop on each of the two sides of the equatorial plane.

Stratigraphic occurrence. — Late Paleocene-Living.

Remarks

This family used to be named Coccodiscidae. However, the oldest senior synonym is Lithocycliidae Ehrenberg 1846, and not Coccodiscidae Haeckel 1862. Lithocycliidae was used as a valid family (see synonymy above); the valid family name must therefore be Lithocycliidae. The Lithocycliidae are distinguished from the Astracturidae due to presence of three-dimensional grid-like arms. Lithocycliidae are also distinguished from the Phacodiscidae in the absence of any exterior structure excepting a simple, circular solid edge. Differing from the distinguishing characteristics of the family Lithocycliidae; *Amphicyclia*, *Cromyatractus* and *Heliostylus* possess two polar primary radial beams connected by the polar radial spines and a spindle-shaped second inner shell which is connected to the innermost shell by a few radial beams. These three genera are to be separated from the Lithocycliidae. The drawings of *Astrostaurus*, *Crucidiscus* and *Staurocyclia* show a crisscrossing of four radial beams in the third shell, but these structures have not been observed in an actual specimen. *Heliodiscus* (Heliodiscidae) is sometimes confused with *Heliosestrum* due to the presence of equatorial radial spines, but the former genus has a characteristically different microsphere that is unusually located in the second inner shell. It should be noted that the Lithocycliidae is an extinct family whereas the Heliodiscidae is a living family. Moreover, overall images of *Heliosestrum* can be distinguished from *Heliodiscus* by the observed lateral profile of the cortical and pore patterns (Suyari & Yamasaki 1987: pl. 3, fig. 15; 1988: pl. 3, fig. 14). Scanning electron images of *Heliosestrum* are also similar to those of *Lithocyclia,* but the latter tends to have an increased number of systematically arranged pores on the cortical shell and lattice margin (Suyari & Yamasaki 1988: pl. 8, fig. 14).

Validity of genera

Cromyatractus

Cromyatractus and *Cromyatractum* have the same type species. *Cromyatractus* has two medullary shells and two cortical shells whereas *Caryatractus* is marked by three or more elliptical lattice shells (Campbell 1954: D70). As displayed by the supporting images for *Cromyatractus* and *Cromyatractum*, the number of shells is different in ontogenetic stages and/or following preservation. All these available genera are established in the same publication (Haeckel 1887: 334 for *Cromyatractus*, 335 for *Cromyatractum* and 336 for *Caryatractus*), the valid genus is objectively decided to be *Cromyatractus* because the remaining two available names are established as subgenera of *Cromyatractus* under Article 24.1 of ICZN (1999).

Heliosestrum
The combination of *Astrosestrum* and *Astrosestantha*, and that of *Heliosestrum* and *Heliosestantha* have respectively the same type species. The differences among the genera we synonymize here are the number of radial spines on the margin of the shell, the state of development of a solid equatorial girdle, a spiny or smooth cortical shell (Campbell 1954: D78 for *Astrosestrum* and *Heliosestrum* and D82 for *Astrophacura*). These characteristics were regarded as intraspecific variations in numerous papers. *Astrosestrum* and *Heliosestrum* are the oldest available name published in 1882. Hollis (1997: 41) acted as a first reviser to validate *Heliosestrum*.

Phacostaurus
The combination of *Phacostaurus* and *Phacostaurium*, of *Crucidiscus* and *Staurentodiscus*, and of *Sethostaurus* and *Sethostaurium* is based respectively on the same type species. *Phacostaurus* is characterized by a simple margin (Campbell 1954: D79), *Astrostaurus* by a solid equatorial girdle or a corona of tiny by-spines (Campbell 1954: D80), *Crucidiscus* by internal centripetal rods (Campbell 1954: D79), *Sethostaurus* by a simple medullary shell and a simple margin (Campbell 1954: D81), and *Heliostaurus* by a solid equatorial girdle (Campbell 1954: D81). As other genera in the Lithocycliidae, the state of development of the solid equatorial ring and the tiny by-spines are intraspecies variations. However, the presence of internal centripetal rods may be different among genera. Four oldest available names were simultaneously published in Haeckel (1882: 457 for *Phacostaurus*, *Astrostaurus*, *Sethostaurus* and *Heliostaurus*). As there are no fundamental differences among them, we selected *Phacostaurus* which is well illustrated in Haeckel (1887).

Sethostylus
The combined *Phacostylus* and *Phacostylium*, and the combined *Sethostylus* and *Sethostylium* have the same type species, respectively. *Amphicyclia* is characterized by two solid spines, no chambered arms, and double medually shells (Campbell 1954: D82); *Phacostylus* by a margin of the disc with two opposite radial spines and a double medullary shell (Campbell 1954: D78, 80); *Sethostylus* by a disc with a simple margin, two opposite radial spines and a simple medullary shell (Campbell 1954: D78, 81). A thick cortical shell such as in *Sethostylus* prevents any observation of the innermost shell. As far as we read the distinguishing morphological characteristics written in Campbell (1954), nothing appears different among these three genera except for the connection between a radial spine and the outer medullary shell. *Amphicyclia*, *Phacostylus* and *Sethostylus* were established in the same publication (Haeckel 1882: 485, 457, in ascending order). Nobody had used *Amphicyclia* except Kozur & Mostler 1972 in a wrong way; however, *Sethostylus* has been used by Petrushevskaya & Kozlova (1972: 522) and even they considered *Phacostylus* a junior synonym of *Sethostylus*. In such case *Sethostylus* has priority over *Amphicyclia*.

Triactiscus
The illustrations of the type species of *Triactiscus* and *Trigonocyclia* show obviously different internal structures but no specimens supporting the illustration of *Trigonocyclia* were found. *Triactiscus* is an available name older than *Trigonocyclia*.

Family PANARTIDAE Haeckel, 1887

Panartida Haeckel, 1887: 288, 375 [as a family]. — Bütschli 1889: 1957 [as a family]. — *nec* Rüst 1892: 161. — Schröder 1909: 3 [as a family]. — Anderson 1983: 23.

Artiscida Haeckel, 1882: 462 [*nomen dubium*, as a subfamily]; 1887: 288, 354 [as a family]. — Bütschli 1889: 1956 [as a family]; Schröder 1909: 3 [as a family]. — Anderson 1983: 23.

Cyphinida Haeckel, 1882: 462 [*nomen dubium*, as a subfamily]; 1887: 288, 359-360 [as a family]. — Bütschli 1889: 1956 [as a family]. — *nec* Rüst 1892: 160. — Schröder 1909: 3 [as a family]. — Anderson 1983: 23.

Zygartida Haeckel, 1882: 462 [*nomen dubium*, as a family]; 1884: 29 [as a family]; 1887: 288, 391-392 [as a family]. — Bütschli 1889: 1958 [as a family]. — Schröder 1909: 3 [as a family]. — Anderson 1983: 23.

Artisoida – Haeckel 1887: 288 [*nomen dubium*, as a family].

Druppulida Haeckel, 1887: 288, 306 [*nomen dubium*, as a family]. — Bütschli 1889: 1955 [as a family]. — Schröder 1909: 3 [as a family]. — Anderson 1983: 23 [as a family].

Zygocampida Haeckel, 1887: 392 [*nomen dubium*, as a subfamily].

Desmocampida Haeckel, 1887: 392 [*nomen dubium*, as a subfamily].

Phacopylida Dreyer, 1889: 28 [*nomen dubium*, as a subfamily].

Druppuliden – Haecker 1907: 119 [*nomen dubium*].

Druppulidae – Popofsky 1908: 219 [*nomen dubium*]; 1912: 114; Clark & Campbell 1942: 32; 1945: 19. — Campbell & Clark 1944a: 18. — Frizzell & Middour 1951: 20. — Campbell 1954: D69. — Orlev 1959: 440. — Chediya 1959: 108. — Nakaseko & Sugano 1976: 122. — Tan & Su 1982: 149. — Blueford 1988: 248. — Chen & Tan 1996: 151. — Tan 1998: 189. — Tan & Chen 1999: 195. — Chen *et al.* 2017: 134.

Cyphinidae – Popofsky 1908: 220-221 [*nomen dubium*]. — Chediya 1959: 116. — Tan & Tchang 1976: 237. — Tan & Su 1982: 150. — Chen & Tan 1996: 151. — Tan 1998: 198. — Tan & Chen 1999: 201. — Chen *et al.* 2017: 137.

Panartidae – Popofsky 1908: 221; 1912: 121. — Campbell, 1954: D75. — Chediya 1959: 118. — Tan & Tchang 1976: 238. — Tan 1998: 200.

Pipettarida Schröder, 1909: 37 [as a subfamily].

Artiscidae – Poche 1913: 209 [*nomen dubium*]. — Deflandre 1953: 421 (*sensu* emend.). — Campbell 1954: D74. — Chediya 1959: 115. — Petrushevskaya 1975: 577. — Dumitrica 1979: 22. — Petrushevskaya 1979: 114-115.

Zygartidae – Campbell & Clark 1944a: 23 [*nomen dubium*]. — Campbell 1954: D76. — Chediya 1959: 119. — Chen & Tan 1996: 151.

Zygartinae – Campbell 1954: D76 [*nomen dubium*].

Desmocampinae – Campbell 1954: D76. — Chediya 1959: 119 [*nomen dubium*].

Cyphantidae Campbell, 1954: D74 [junior homonym].

Zygocampinae – Chediya 1959: 120 [*nomen dubium*].

Cyphantellidae – Loeblich & Tappan 1961: 223 [junior homonym].

Artiscinae – Riedel 1967b: 294 (*sensu* emend.) [*nomen dubium*]; 1971: 652. — Riedel & Sanfilippo 1971: 1587. — Petrushevskaya & Kozlova 1972: 521. — Nakaseko *et al.* 1975: 169. — Riedel & Sanfilippo 1977: 863. — Sakai 1980: 705. — Sanfilippo & Riedel 1980: 1009. — Anderson 1983: 37-38. — Dumitrica 1984: 97. — Sanfilippo *et al.* 1985: 655. — Takahashi 1991: 79. — De Wever *et al.* 2001: 123. — Afanasieva *et al.* 2005: S288. — Afanasieva & Amon 2006: 131.

Artistidae [*sic*] – Nakaseko & Sugano 1976: 122 [*nomen dubium*] (= Artiscidae).

Type genus. — *Panartus* Haeckel, 1887: 376 [type species by subsequent designation (Campbell 1954: D76): *Panartus tetrathalamus* Haeckel, 1887: 378] = junior subjective synonym of *Didymocyrtis* Haeckel, 1862: 445 [type species by absolute tautonomy: *Haliomma didymocyrtis* Haeckel, 1861a: 816].

Included genera. — *Cannartus* Haeckel, 1882: 462 (= *Cannartidissa*, *Cannartiscus*, *Pipetta*, *Pipettaria*, *Pipettella* synonymized by Riedel 1971: 652; *Druppula* **n. syn.**, *Druppuletta* **n. syn.**). — *Diartus* Sanfilippo & Riedel, 1980: 1010. — *Didymocyrtis* Haeckel, 1862: 445 (= *Artidium* **n. syn.**, *Cyphinura* **n. syn.**, *Cyphocolpus* **n. syn.**, *Desmartus* **n. syn.**, *Ommatocampula* **n. syn.**, *Panaromium* **n. syn.**, *Panartus, Panartella* synonymized by Sanfilippo & Riedel 1980: 1010*, Panartidium* **n. syn.**, *Panartissa* **n. syn.**, *Panartura* **n. syn.**, *Peripanartium* **n. syn.**, *Peripanartula* **n. syn.**, *Peripanartus* **n. syn.**, *Peripanicula* **n. syn.**). — *Spongolivella* Dumitrica, 2021: 2.

Invalid name. — *Artocarpium*.

Nomina dubia. — *Artiscium*, *Artiscus*, *Cannartidella*, *Cannartidium*, *Caryodruppula*, *Cladospyris*, *Cromyocarpus*, *Cromyodruppa*, *Cromyodruppium*, *Cypassis*, *Cyphantella*, *Cyphantissa*, *Cyphinidium*, *Cyphinidoma*, *Cyphinidura*, *Cyphinoma*, *Cyphinus*, *Cyphonium*, *Desmocampe*, *Didymospyris*, *Diplellipsis*, *Druppocarpetta*, *Druppocarpissa*, *Druppocarpus*, *Haeckelocyphanta*, *Ommatacantha*, *Ommatartus*, *Ommatocorona*, *Ommatocyrtis*, *Ommatospyris*, *Panarelium*, *Panarium*, *Panartoma*, *Panicidium*, *Panicium*, *Peripanarium*, *Peripanicea*, *Peripanicium*, *Phacopyle*, *Prunocarpetta*, *Prunocarpilla*, *Prunocarpus*, *Prunulissa*, *Spongoliva*, *Spongolivetta*, *Spongolivina*, *Stylartella*, *Stylartura*, *Stylartus*, *Zygartus*, *Zygocampe*.

Nomen nudum. — *Ommatocoryne*.

Junior homonyms. — *Cyphanta* Haeckel, 1887 *nec* Walker, 1865 (= *Cyphantella*).

Diagnosis. — Lithocyclioidea with twin oval balloon-shaped latticed shells. The equatorial plane of the flattened double medullary shell is vertical to the longest axis of the fully-grown shell. Balloon-shaped latticed shells, nearly all equal in size, are disposed along the equatorial plane. Radial beams emanating from the flattened double medullary shell extend across the equatorial plane to connect with the latticed shell.
A reddish endoplasm occupies the inner part of shell and a yellowish red endoplasm encases them within the outermost shell. Algal symbionts are scattered inside and outside of the outermost shell. Nucleus is located inside the medullary shell. A long, robust axoflagellum extends from the longest axis of the fully-grown shell. The axoflagellum is perpendicular to the equatorial plane of the flattened double medullary shell.

Stratigraphic occurrence. — Early Oligocene-Living.

Remarks

This family is easily distinguishable from any other of the spumellarian families by the virtue of its morphology closely resembling that of a drum. This family was once called either as "Artiscinae" or "Artiscinidae", but this familiar name is unacceptable as it is based on an unillustrated type species. The genus *Panartus* and the family name Panartidae were used in several Chinese radiolarian monographs (e.g., Tan & Tchang 1976; Tan 1998) and there is no longer logical reason to retain the family name "Artiscinae" or "Artiscinidae." Considering the genus *Actinomma* was significantly separated from the family Panartidae by molecular phylogeny analyses (Krabberød *et al.* 2011; Sandin *et al.* 2021). The Panartidae is presumed to be quite different from the Lithocycliidae (Riedel & Sanfilippo 1981: fig. 12-6). The morphological changes of Panartidae genera were continually traced over the early Miocene at a morphospecies level (Riedel & Sanfilippo 1971: pls 1C, 2C; Sanfilippo & Riedel 1980: text-fig. 1; Sanfilippo *et al.* 1985: 656). Their morphological changes were analyzed with quantitative methods (Sachs & Hasson 1979; Kellogg 1980) and using more sophisticated mathematical methods (Yoshino *et al.* 2019). The Panartidae are polycystines of particular importance to high resolution age determination so the criteria for identifying at specific level should be standardized (Sakai 1980; Sanfilippo *et al.* 1985). However, the Panartidae have been carefully identified in mid-latitudes samples due to there being several undescribed species in the mid-latitudes of the North Pacific (e.g., "*Cannartus* lineage" and "*Ommatartus* lineage" in Sakai 1980), of the Southern Ocean (e.g., Lazarus 1992) and of the North Atlantic (Nishimura A. 1987). This suggests that the evolutionary history of *Cannartus*, *Diartus* and *Didymocyrtis* shown in Sanfilippo & Riedel (1980) never included other panartid species.

Many biological studies were carried out on living *Didymocyrtis* as they are commonly collected in plankton sampling. The relationship between their cytological structures was examined in detail (Sugiyama & Anderson 1998a). Illustration of living forms were given for *Didymocyrtis* (Matsuoka 1993b: pl. 3, figs 5, 6; 2017: figs 9.1, 9.2; Sugiyama & Anderson 1998a; text-figs 1-7, Takahashi *et al.* 2003: figs 3, 4; Suzuki & Aita 2011: fig. 4K; Probert *et al.* 2014: S1, SES 19; Suzuki & Not 2015: fig. 8.4.1, 8.8.5; Matsuoka *et al.* 2017: appendix A) and its internal skeletal structure was illustrated (Anderson *et al.* 1986a: pl. 1, figs 3, 4; Sugiyama *et al.* 1992: pl. 4, fig. 7; Matsuoka 2009: fig. 3.20-3.24). Algal symbionts were documented by epi-fluorescent observation with DAPI dyeing for *Didymocyrtis* (Zhang *et al.* 2018: 11, fig. 8). Algal symbionts of *Didymocyrtis* were identified as *Brandtodinium nutricula* by Probert *et al.* (2014).

Validity of genera

Cannartus

In addition to the synonymy published by Riedel (1971: 652), *Druppula* and *Druppuletta* are synonymized with *Cannartus* because the young form of *Cannartus* lacks the polar tubes as shown by the supporting images for these two genera. *Cannartus* was established in 1882 and all the other available genera listed here were published in 1887.

Didymocyrtis

All type species listed in the genera synonymy fall in the species conception of the *Didymocyrtis*-lineages of Sanfilippo *et al.* (1985: 656-660). *Didymocyrtis*, the oldest available name was published in 1862. All the other available names were published in 1882 and later.

Family Phacodiscidae Haeckel, 1882

Phacodiscida Haeckel, 1882: 456 [as a subfamily]; 1887: 409, 419-421 [as a family]. — Bütschli 1889: 1958 [as a family]. — *nec* Rüst 1892: 165 [as a family]. — Schröder 1909: 3 [as a family]. — Anderson 1983: 24 [as a family].

Phacodisciden – Haecker 1907: 123.

Phacodiscidae – Haecker 1908: 444. — Popofsky 1912: 126. — Clark & Campbell 1942: 38; 1945: 20. — Campbell & Clark 1944b: 14. — Campbell 1954: D78. — Orlev 1959: 443. — Chediya 1959: 124. — Riedel 1967b: 294; 1971: 653. — Nigrini 1974: 1065. — Nakaseko *et al.* 1975: 169. — Nakaseko & Sugano 1976: 125. — Tan & Tchang 1976: 241. — Riedel & Sanfilippo 1977: 864. — Dumitrica 1979: 21. — Kozur & Mostler 1979: 35 (*sensu* emend.). — Tan & Su 1982: 151. — Anderson 1983: 38. — Takahashi 1991: 89. — Chen & Tan 1996: 151. — Hollis 1997: 40. — Boltovskoy 1998: 31. — Tan 1998: 203. — Tan & Chen 1999: 204. — Anderson *et al.* 2002: 1002.

Phacodiscinae – Campbell 1954: D78. — Petrushevskaya & Kozlova 1972: 522. — Dumitrica 1984: 96-97.

Type genus. — *Phacodiscus* Haeckel, 1882: 457 [type species by subsequent designation (Campbell 1954: D78): *Phacodiscus rotula* Haeckel, 1887: 424].

Included genera. — *Periphaena* Ehrenberg, 1874: 246 (= *Astrophacomma*, *Heliodiscomma* synonymized by Sanfilippo & Riedel 1973: 522; *Perizona* synonymized by Kozur & Mostler 1972: 19). — *Phacodiscus* Haeckel, 1882: 457 (= *Phacodiscinus* with the same type species; *Astrophacilla* **n. syn.**, *Paracenodiscus* **n. syn.**, *Phacodisculus* **n. syn.**, *Prunulum* **n. syn.**, *Prunuletta* **n. syn.**, *Sethodiscinus* **n. syn.**).

Invalid name. — *Coccymelium.*

Nomina dubia. — *Conophacodiscus*, *Pentadiscus*, *Triadiscus*.

Diagnosis. — Shell roughly flat, consists of a large convex lens-shaped latticed shell. Radial beams arise from the outer medullary shell and radiate to both sides of the equatorial plane. These beams are connected to the large latticed shell. Exterior structure outside of the large latticed shell absent or exclusively represented by a simple solid flat circular edge which is surrounded by distinctive solid arrowhead-like short spines. No structure extends to both sides of the equatorial plane.

Stratigraphic occurrence. — Early Eocene-Living.

Remarks

Phacodiscus shares a homeomorphous appearance to *Heliodiscus* representatives without spines. The latter genus is a living form and has a characteristic microsphere, always eccentrically placed in the second inner shell (outer double medullary shell). The Phacodiscidae are an extinct family, whereas Heliodiscidae is a common component of living plankton. *Periphaena* has a special distinguishable pore near its center on one side of the cortical shell, probably an exit for the axoflagellum (Sugiyama & Furutani 1992: pl. 16, fig. 6). The internal skeletal structure of *Periphaena* has been illustrated (Sugiyama & Furutani 1992: pl. 16, fig. 5).

Validity of genera

Phacodiscus

The same type species was designated for the following combinations of genera: *Phacodiscus* and *Phacodiscinus*; and *Prunulum*, *Prunuletta* and *Coccymelium*. Haeckel (1887) seems to propose new taxon name for differently oriented specimens in some cases. *Sethodiscinus* is considered to have a simple medullary shell (Campbell 1954: D78), but the innermost shell is known to be easily dissolved. *Phacodiscus* is validated due to the oldest available name among them. The type image for *Phacodiscus* is poor (Haeckel 1887: pl. 35, fig. 7) but it is unfortunately "*Phacodiscus*" can be precisely identified by using this poor image.

Superfamily Spongodiscoidea Haeckel, 1862 *sensu* Suzuki emend. herein

Spongodiscida Haeckel, 1862: 239, 452, 460 [as a tribe]; 1882: 461 [as a subfamily]; 1887: 409, 573-575 [as a family].

Euchitoniilae – Campbell 1954: D86 [as a subsuperfamily].

Spongodiscacea [*sic*] – Pessagno 1971a: 16, 19 [as a superfamily] (= Spongodiscoidea); 1972: 273, 296 [as a superfamily]; 1973: 50, 56 [as a superfamily]; 1976: 25 [as a superfamily]; 1977b: 930 [as a superfamily]. — Dumitrica 1984: 100 [as a superfamily]. — De Wever *et al.* 2001: 158.

Spongodiscilae – Pessagno 1971a: 19 [as a subsuperfamily]; 1972: 278 [as a subsuperfamily]; 1973: 50 [as a subsuperfamily]; 1976: 25 [as a subsuperfamily]; 1977b: 930 [as a subsuperfamily].

Spongodiscoidea – Petrushevskaya 1975: 573; Petrushevskaya 1979: 110-111; 1984: 132; Petrushevskaya 1986: 128. — Dumitrica 1979: 25. — Amon 2000: 33. — Bragin 2011: 757-758. — Suzuki *et al.* 2009d: 251.

Spongodiscata – Afanasieva *et al.* 2005: S288 [as an order, *pars*]. — Afanasieva & Amon 2006: 130-131.

Diagnosis. — Flat-shaped Polycystinea with or without, un-walled pylome (excluding *Ommatocampe*). Radial spines and radial beams emanating from the center to the periphery of disk are absent.

Remarks

The Spongodiscoidea include the Spongodiscidae (including Clade E2) Euchitoniidae (including Clade E3), Spongobrachiidae and. Panartidae and Spongosphaeridae should also be preferable grouped with these three families according to molecular results (100% PhyML bootstrap values with 10 000 replicates and >0.99 posterior probabilities), but we keep morphological (instead molecular) groups as a consensus. Spongodiscoidea in the sense of this catalogue comprise Clades E2 and E3 of Sandin *et al.* (2021). Not only are these subclades unstable, but representatives of the genus *Spongolivella* (originally *Cypassis*) were scattered in Clades E2 and E3.

Molecular phylogenetic studies (e.g., Ishitani *et al.* 2012; Sandin *et al.* 2021) clearly revealed that the so-called spongodiscids are divided into three groups at a superfamily level. One group includes *Dictyocoryne*, *Tricranastrum* (originally *Myelastrum*), *Spongaster* and *Spongodiscus*, classified in Spongodiscoidea; the second group, the Trematodiscoidea, includes *Flustrella*; and the third group is formed by *Schizodiscus* and *Spongobrachiopyle*, classified in Spongopyloidea. Flat-shaped Polycystinea show a high morphological convergence meaning that an unsophisticated recognition of such a structure as "spongy" or "concentric" leads to a completely false identification and contributes to confusion regarding Spongodiscoidea, Trematodiscoidea and Spongopyloidea. The principal differences among Euchitoniidae, Spongobrachiidae and Spongodiscidae are: 1) a central structure around the spinose microsphere; 2) an ultra-fine structure throughout the shell; and 3) an upcropping condition of the central structure on both polar sides. No simple difference between Spongodiscoidea and Trematodiscoidea is known. The Spongodiscoidea differs from Spongopyloidea by having a walled pylome tube emanating from the microsphere and a disk made of very short parts of discontinuous concentric structures. Trematodiscidae have a microsphere with decussate primary radial beams, exterior concentric hoops which never cover the inner hoops, and four or more straight radial beams originating from the center to the periphery of the disk. A simple way to differentiate the Spongodiscoidea from the Spongopyloidea lies in examining the wall-status of the pylome. The pylome was illustrated in *Dictyocoryne* (Euchitoniidae) (Matsuoka 1992c: pl. 2, figs 7, 8; 1993b: pl. 1, figs 1, 2; 1994: figs 3.B-3.D, 6.A-6.D), *Spongaster* (Spongodiscidae) (Matsuoka 1994: fig. 3.B-3.D) and the *Pseudocephalis*-form of an undescribed genus (Spongodiscidae) (Matsuoka 1994: figs 5.B-5.E).

Many described species cannot be placed into an appropriate genus as many genera of Spongodiscoidea remain undescribed. In particular, "*Spongotrochus glacialis*" which is quite different from any other flat-shaped polycystines (Petrushevskaya 1975: pl. 35, figs 1-6; Nakaseko & Nishimura 1982: pl. 29, figs 1-3; pl. 31, figs 2,3). Other undescribed genera remain in classically established Spongodiscoidea (Jouse 1977: pl. 137, fig. 7; pl. 141, fig. 16; Nakaseko & Nishimura 1982: pl. 32, figs 3; pl. 33, fig. 1; pl. 35, fig. 4).

Clade E2 (Sandin *et al.* 2021)

Family SPONGODISCIDAE Haeckel, 1862 *sensu* Suzuki emend. herein

Spongodiscida Haeckel, 1862: 239, 452, 460 [as a tribe]; Haeckel 1882: 461 [as a subfamily]; Haeckel 1887: 409, 573-575 [as a family]. — Stöhr 1880: 117 [as a family]. — Dunikowski 1882: 190 [as a subfamily]. — Bütschli 1889: 1964 [as a family]. — *nec* Rüst 1892: 172 [as a family]. — Schröder 1909: 3 [as a family]. — Anderson 1983: 24 [as a family].

Spongodiscidae – Pantanelli 1880: 49. — Popofsky 1908: 226; 1912: 143. — Clark & Campbell 1942: 47; 1945: 25 — Campbell & Clark 1944a: 27; 1944b: 18. — Frizzell & Middour 1951: 25-26. — Campbell 1954: D93. — Orlev 1959: 449-450. — Chediya 1959: 146. — Riedel 1967b: 295 (*sensu* emend.); Riedel 1971: 654. — Riedel & Sanfilippo 1971: 1588. — Petrushevskaya & Kozlova 1972: 528. — Sanfilippo & Riedel 1973: 523-524. — Nakaseko *et al.* 1975: 169. — Petrushevskaya 1975: 547. — Nakaseko & Sugano 1976: 125. — Tan & Tchang 1976: 255. — Riedel & Sanfilippo 1977: 866; 1977: 866. — Kozur & Mostler 1978: 156 (*sensu* emend.). — Dumitrica 1979: 25; 1984: 100; 1995: 26. — Petrushevskaya 1979: 111-112. — De Wever 1982a: 190. — Tan & Su 1982: 157. — Anderson 1983: 39. — Sanfilippo *et al.* 1985: 660. — Blueford 1988: 252. — Takahashi 1991: 83. — van de Paverd 1995: 148-149. — Chen & Tan 1996: 151. — Hollis 1997: 50. — Boltovskoy 1998: 31-32. — Cordey 1998: 92. — Kiessling 1999: 42. — Kozlova 1999: 93. — Tan & Chen 1999: 230. — Amon 2000: 33-34. — Anderson *et al.* 2002: 1002. — De Wever *et al.* 2001: 158, 160. — Afanasieva *et al.* 2005: S288. — Afanasieva & Amon 2006: 131. — Ogane *et al.* 2009a: 84. — Chen *et al.* 2017: 145.

Spongotrochida Haeckel, 1882: 461 [as a tribe]; Haeckel 1887: 575 [as a subfamily]. — Dunikowski 1882: 190 [as a tribe]. — Schröder 1909: 50 [as a subfamily].

Spongotrochinae – Clark & Campbell 1942: 48; Clark & Campbell 1945: 26. — Campbell & Clark 1944a: 27; 1944b: 18. — Campbell 1954: D94. — Chediya 1959: 147.

Spongodiscinae – Frizzell & Middour 1951: 26. — Campbell 1954: D93. — Tan & Tchang 1976: 255. — Kozur & Mostler 1978: 157 (*sensu* emend.). — Tan & Su 1982: 157. — Tan 1998: 236. — Tan & Chen 1999: 230.

Spongodiscudae [*sic*] – Tan 1998: 236 (= Spongodiscidae).

Spongolonchidae Afanasieva & Amon *in* Afanasieva, Amon, Agarkov & Boltovskoy, 2005: S281 [*nomen dubium*]. — Afanasieva & Amon 2006: 121.

TYPE GENUS. — *Spongodiscus* Ehrenberg, 1854b: 237 [type species by subsequent designation (Frizzell & Middour 1951: 26): *Spongodiscus resurgens* Ehrenberg, 1854b: 246].

INCLUDED GENERA. — *Spongaster* Ehrenberg, 1861b: 833 (= *Spongastrella* with the same type species; *Histiastrella* **n. syn.**). — *Spongodiscus* Ehrenberg, 1854b: 237 (= *Spongodisculus* with the same type species). — *Spongotrochus* Haeckel, 1861b: 844 (= *Spongotrochiscus* with the same type species).

NOMINA DUBIA. — *Pseudocephalis*, *Spongolonche*, *Stylotrochiscus*, *Stylotrochus*.

DIAGNOSIS . — Shell with a circular to rounded rectangle outline, complemented by a spinose microsphere and a dense, homogenous, concentric structure throughout the test. Large numbers of radial beams develop to join the adjacent concentric wall structure at very high to vertical angles. These radial beams barely penetrate through the concentric walls.

Endoplasm fills the entire spongy shell. Its color varies from green to red in *Spongaster* and dark brown to gray for *Spongodiscus* and *Spongotrochus*. A robust, long axoflagellum emerges out the non-walled pylome on the peripheral edge for *Spongaster*. This has not been confirmed for *Spongodiscus* and *Spongotrochus*. Dinoflagellate symbionts are found in *Spongaster tetras tetras* as well as cyanobacteria in *Spongaster tetras irregularis*. No algal symbionts have been determined in *Spongodiscus* and *Spongotrochus*. Pseudopodia radiate throughout the shell, and brown granules of an unknown origin are present in some bundles of pseudopodia in *Spongaster*. Isolated skeleton fragments are scattered in bundles of pseudopodia in *Spongotrochus*.

Stratigraphic occurrence. — Early Eocene-Living.

Remarks

Spongodiscus is often misinterpreted as *Spongocyclia* (Litheliidae). The former is distinguishable from the latter by its very distinctive and systematic concentric structure as well as its straight radial beams that penetrate through the concentric structure, the absence of a thick crust cover, a tunnel-like set of pores straightly disposed along the outermost concentric structure. Under a light microscope, the circular- outlined polycystines between the Spongodiscidae and Spongopylidae are commonly misidentified. The misidentification can be attributed to the overlooking of exact superficial shape and appendages. In the case of *Spongotrochus* (Spongodiscidae) and *Spongospira* (Spongopylidae), the former is flat with cover-like appendages (Yamauchi 1986: pl. 3, figs 15, 16) while the latter is "ringed" by a repeating pattern of thicker and thinner parts (Cheng & Yeh 1989: pl. 1, fig. 19). The importance of the disk's lateral profile will be discussed in the remarks regarding Trematodiscoidea.

The genus *Spongaster* is easily recognizable, regularly encountered in plankton samples from tropical to subtropical oceans and is relatively easy to maintain in culture. Consequently, this genus was used for various environmental control tests: growth, seasonality and opal productivity (Anderson *et al.* 1989a); trophic activity and primary productivity of symbiont (Anderson *et al.* 1989c); temperature, salinity and light influence on growth and survival (Anderson *et al.* 1989b); recognition of silicalemma in warping the siliceous skeleton (Anderson 1994: fig. 24); growth experiment (Anderson 1994: figs 25, 26); as well as analysis of the internal skeletal structure (Sugiyama *et al.* 1992: pl. 7, fig. 5). A living image was illustrated for *Spongaster* (Casey 1993: fig. 13.6; Matsuoka 1994: fig. 2B; 2007: fig. 4.D; 2017: figs 10.1, 10.2 Sugiyama & Anderson 1997a: pl.1, figs 1, 2; pl. 2, figs 1, 3; Takahashi *et al.* 2004: fig. 3; Suzuki & Aita 2011: fig. 4M; Suzuki & Not 2015: fig. 8.8.1; Matsuoka *et al.* 2017: appendix A), *Spongodiscus* (Suzuki & Not 2015: fig. 8.10.2), and *Spongotrochus* (Suzuki *et al.* 2013: fig. 7.3). Protoplasm and algal symbionts were documented by epi-fluorescent observation with DAPI dyeing in *Spongodiscus* (Zhang *et al.* 2018: 14, fig. 26, p. 16, figs 2-5), *Spongaster* (Suzuki *et al.* 2009b: figs 3M, 3N; Ogane *et al.* 2010: figs 1.3, 2.3; Zhang *et al.* 2018: 16, fig. 9). Several genera remain undescribed (e.g., Nakaseko & Nishimura 1982: pl. 43, fig. 1; Takahashi 1991: pl. 17, figs 12-16; van de Paverd 1995: pl. 41, fig. 1; Onodera *et al.* 2011: pl. 6, figs 3, 4).

Validity of genera

Spongaster

Histiastrella is marked by a quadrangular shell, a patagium, four undivided distally blunt arms (Campbell 1954: D87-88). The type species of *Histiastrella*, *Histiastrum quadrigatum*, is characterized by the presence of seven to nine dividers in each arm but this character is not used as a distinguishing feature at the genus-rank (Haeckel 1887: 544). Presence of patagium and arms distally blunt are considered as intraspecies variations.

Clade E3 (Sandin *et al.* 2021)

Family Euchitoniidae Stöhr, 1880 *sensu* Suzuki emend. herein

Euchitonida Stöhr, 1880: 86 [as a subfamily]. — Haeckel 1882: 460 [as a tribe]; Haeckel 1887: 484, 516 [as a subfamily]. — Wisniowski 1889: 685 [as a subfamily]. — Schröder 1909: 43 [as a subfamily].

Ommacampida Haeckel, 1887: 392 [as a subfamily].

Euchitoninae [*sic*] – Clark & Campbell 1942: 46 (= Euchitoniinae); Campbell & Clark 1944b: 17. — Chediya 1959: 136. — Tan & Tchang 1976: 246-248. — Tan 1998: 219. — Tan & Chen 1999: 217. — Amon 2000: 49.

Ommatocampinae Campbell, 1954: D76. — Chediya, 1959: 119.

Monaxoniinae Campbell, 1954: D76.

Euchitoniidae – Campbell 1954: D86. — Nakaseko & Sugano 1976: 125. — Kozur & Mostler 1978: 134-135 (*sensu* emend.). — Petrushevskaya 1979: 112-113 (*sensu* emend.). — Matsuzaki *et al.* 2015: 18-19.

Euchitoniinae – Campbell 1954: D86. — Kozur & Mostler 1978: 135-136. — Petrushevskaya 1979: 113 (*sensu* emend.).

Myelastrinae Riedel, 1971: 654. — Kozur & Mostler 1978: 153.

Chitonastrinae Kozur & Mostler, 1978: 136 [*nomen dubium*].

Myelastridae – Takahashi 1991: 87. — De Wever *et al.* 2001: 160-161. — Afanasieva *et al.* 2005: S284. — Afanasieva & Amon 2006: 127.

Euchitonidae [*sic*] – Amon 2000: 48-49 (= Euchitoniidae).

Type genus. — *Euchitonia* Ehrenberg, 1861b: 831 [type species by subsequent monotypy: *Euchitonia furcata* Ehrenberg, 1873a: 308] = junior subjective synonym of *Dictyocoryne* Ehrenberg, 1861b: 830 [type species by subsequent designation (Haeckel 1887: 591): *Dictyocoryne profunda* Ehrenberg, 1873a: 307].

Included genera. — *Amphicraspedum* Haeckel, 1882: 460 (= *Amphicraspedon* with the same type species; *Amphirrhopella* **n. syn.**). — *Dictyocoryne* Ehrenberg, 1861b: 830 (= *Dictyocorynula* with the same type species; *Dictyastrum* synonymized by Matsuzaki *et al.* 2015: 19, *Dictyastrella*, *Euchitonia*, ? *Hymenastromma*, *Rhopalodictya*, *Rhopalodictyum* synonymized by Ogane *et al.* 2009a: 89), *Styla* synonymized by Matsuzaki *et al.* 2015: 19; *Pteractis*. — *Hexinastrum* Haeckel, 1882: 461 (= *Hexalastromma* **n. syn.**, *Pentalastromma* **n. syn.**, *Pentinastrum* **n. syn.**). — *Ommatocampe* Haeckel, 1861b: 832 (= *Ommatocampium* with the same type species; *Amphymenium* synonymized by Petrushevskaya & Kozlova 1972: 527). — *Tessarastrum* Haeckel, 1887: 547 (= *Tessarastrella* with the same type species; *Hagiastromma* **n. syn.**, *Tessarostromma* **n. syn.**). — *Tricranastrum* Haeckel, 1879: 705 (= *Dicranaster* **n. syn.**, *Dicranastrum* **n. syn.**, *Myelastrella* **n. syn.**, *Myelastrum* **n. syn.**, *Spongomyelastrum* **n. syn.**, *Myelastromma* **n. syn.**, *Pentophiastromma* **n. syn.**, *Spongodi-*

cranastrum **n. syn.**, *Spongohagiastrum* **n. syn.**, *Spongopentophiastrum* **n. syn.**, *Spongostaurina* **n. syn.**, *Tetracranastrum* **n. syn.**, *Triastrum*, **n. syn.**). — *Trigonastrum* Haeckel, 1887: 538 (= *Trigonastrella* with the same type species; *Rhopalastromma* synonymized by Kozur & Mostler 1978: 128; *Chitonastromma* synonymized by Kozur & Mostler 1978: 136; *Amphicraspedina* **n. syn.**, *Amphirrhopoma* **n. syn.**, *Dictyastromma* **n. syn.**, *Monaxonium* **n. syn.**, *Trigonastromma* **n. syn.**).

Invalid name. — *Tessarastromma*.

Nomina dubia. — *Amphirhopalum*, *Amphirrhopalium*, *Chitonastrella*, *Chitonastrum*, *Hexalastrum*, *Pentalastrella*, *Pentalastrum*, *Pentophiastrum*, *Rhopalastrella*, *Rhopalastrum*.

Junior homonyms. — *Spongostaurus* Swanberg, Anderson & Bennett, 1985 (= *Spongostaurina*) *nec* Haeckel, 1882; *Stylactis* Ehrenberg, 1873 (Ehrenberg 1873a = *Styla* Stechow, 1921) *nec* Allman, 1864.

Diagnosis. — Flat shaped Polycystinea with circular center and arms. The central part is a convex lens-shaped structure (named "margarita") which includes a spinose microsphere and two to three concentric convex lens-shaped crusts. The exterior structure of the margarita with a variable number of arms: two to four, rarely eight. Arm is constituted by a very highly dense concentric structure which resembles a spongy, a segmented structure with dividers, or superimposed cupolas. Patagium developed in some members but were differentiated from the border of the arm. Both polar sides of the margarita crop out or are occasionally seen covered with fine appendages.

The protoplasm can be divided in *Dictyocoryne* - and *Tricranastrum*-types. Typically, the spongy shell in *Dictyocoryne* is filled with a light brown endoplasm. A robust, long axoflagellum emerges from a non-walled pylome on one-side of the test. Pseudopodia radiate throughout the shell. The margarita portion is more transparent than the other skeletal parts. It should be noted that *Dictyocoryne truncata* (Ehrenberg) and *Dictyocoryne profunda* Ehrenberg exclusively possess cyanobacteria as symbionts, on the surface of the endoplasm. *Dictyocoryne muelleri* harbors algal symbionts outside the shell, as opposed to cyanobacteria. In *Tricranastrum*, the shell is occupied by a light brown endoplasm. A probable ectoplasmic membrane wraps around all skeletons including by-spines.

Stratigraphic occurrence. — early Middle Miocene-Living.

Remarks

The central part of the Euchitoniidae is named by the special word: "margarita" (Matsuoka 1992c: pl. 2, figs 1, 5; 1993b: pl. 1, figs 4, 5; Zheng 1994: pl. 40, figs 4-7, 9). This is confirmed in the *Amphicraspedina*-form of *Trigonastrum* (Takayanagi *et al.* 1979: pl. 1, figs 11, 12; Poluzzi 1982: pl. 20, figs 2, 3; Wang & Yang 1992: pl. 2, figs 26-29; Zheng 1994: pl. 40, figs 5, 9; van de Paverd 1995: pl. 51, fig. 3), the *Dictyastromma*-form of *Trigonastrum* (Poluzzi 1982: pl. 20, fig. 5), *Dictyocoryne* (Poluzzi 1982: pl.20, fig. 4), the *Euchitonia*-form of *Dictyocoryne* (Poluzzi 1982: pl. 20, fig. 8; Anderson & Bennett 1985: pl. 1, figs 1, 2, 3), *Tricranastrum* (Matsuoka 2017: figs 12.1, 12.3, 12.5-12.7), *Ommatocampe* (Poluzzi 1982: pl. 20, fig. 1) and the *Pteractis*-form of *Dictyocoryne* (Matsuoka 2017: figs 15.4-15.7; Zheng 1994: pl. 40, figs 4, 6, 7). The margarita is not covered by a patagium in the *Amphicraspedina*-form of *Trigonastrum* (Cheng & Yeh 1989: pl. 1, figs 7, 10), *Dictyocoryne* (Onodera *et al.* 2011: pl. 6, fig. 8), the *Pteractis*- and *Euchitonia*-forms of *Dictyocoryne* (Yamauchi 1986: pl. 4, figs 10, 12), *Trigonastrum* (Dumitrica 1973a: pl. 10, figs 1-4). Typically, *Dictyocoryne* tends to thicken in its central part (Cheng & Yeh 1989: pl. 2, fig. 12) whereas the *Pteractis*-form of *Dictyocoryne* remains very flat (Cheng & Yeh 1989: pl. 2, figs 8, 14). Internal skeletal structure was illustrated for the *Hymenastromma*-form of *Dictyocoryne* (Sugano, 1976: pl. 6, fig. 3), but *Hymenastromma* appears to be similar to the Phorticiidae.

Molecular studies sometimes noted trouble separating *Dictyocoryne* and *Euchitonia.* This issue has been already solved from the morphological classification's point of view (Ogane *et al.* 2009a; Matsuzaki *et al.* 2015). The genus name *Euchitonia* must not no longer be applied. The existence of *Amphicraspedum* and *Hexinastrum* has been considered doubtful because no specimens identified as such have been reported. These genera are kept as valid until future confirmation of their existence.

Dictyocoryne is one of the most examined and studied living radiolarians in ecological observations (Matsuoka 1992a, 1992c, 1993a, 1993b, 2017; Sugiyama & Anderson 1997a), ecological experimental studies (Matsuoka & Anderson 1992; Sugiyama & Anderson 1997a), cytological ultrafine structures, symbionts, symbiosis (Matsuoka 1992c), and cytomechanics (Anderson *et al.* 1987). Images of living forms were repeatedly illustrated for *Dictyocoryne* (Matsuoka 1992a: pls 1, 3; 1992c: pls 1, 3; 1992b, figs 1A, 1B, 2A, 2B; 1993a: pl. 2, figs 1, 2; 1993b: pl. 3, figs 1-4; 1994: fig. 2A; 2017: figs 13.1, 13.2; 14.1, 14.2; Sugiyama & Anderson 1997a: pl. 2, figs 2, 4; Matsuoka *et al.* 2001: pl. 1, fig. 1; Takahashi *et al.* 2004: figs 1, 2; Yuasa *et al.* 2005: fig. 1a; Ichinohe *et al.* 2019: fig. 2), the *Euchitonia*-form of *Dictyocoryne* (Matsuoka 1993b: pl. 4, figs 1, 2), *Tricranastrum* (Yuasa *et al.* 2005: figs 1b, 1c; Matsuoka 2007: fig. 12; 2017: figs 12.1, 12.2), the *Pteractis*-form of *Dictyocoryne* (Matsuoka 1992b: figs 2C, 2D; 1993a: fig. 2.4; 1993b: pl. 4, figs 3, 4; 1994: fig. 2D; 2017: figs 15.1, 15.2) and the *Spongostaurus*-form of *Tricranastrum* (Caron & Swanberg 1990: fig. 3.B). Protoplasm and algal symbionts were documented by epi-fluorescent observation with DAPI dyeing and other dyeing methods for *Dictyocoryne* (Ogane *et al.* 2010: figs 1.14-1.15; 2.14-2.15; Zhang *et al.* 2018: 11, figs 1, 6, 7, p. 14, figs 4, 5; p. 16, figs 2, 3), the *Euchitonia*-form of *Dictyocoryne* (Ogane *et al.* 2010: figs 1.13, 2.13), and *Tricranastrum* (Zhang *et al.* 2018: 16, fig. 4). An image fixed using dye method was published for *Tricranastrum* (Aita *et al.* 2009: pl. 27, fig. 1; pl. 29, fig. 1). A cytological ultrafine-structure was observed in *Tricranastrum* (Swanberg *et al.* 1985: pl. 2).

Algal symbionts of *Dictyocoryne elegans* were identified as *Gymnoxanthella radiolariae* by Yuasa *et al.* (2016), the same dinoflagellate species as those of *Acanthodesmia* (Acanthodesmiidae, Nassellaria) and *Dictyopodium* (originally *Pterocanium*, Lithochytrididae, Nassellaria).

Validity of genera

Amphicraspedum

Amphirrhopella is characterized by terminal spines but this character is induced by intraspecies or intraspecies variation.

Dictyocoryne

The combinations *Dictyocoryne* and *Dictyocorynula*, *Dictyastrum* and *Dictyastrella*, and *Rhopalodictyum* and *Rhopalodictya* have respectively the same type species. Since *Rhopalodictyum* has already been synonymized with *Dictyocoryne* (Ogane *et al.* 2009a: 89) and *Dictyastrum* also synonymized with *Dictyocoryne* (Matsuzaki *et al.* 2015: 19), *Rhopalodictya* and *Dictyastrella* are both automatically synonyms of *Dictyocoryne*. "*Styla*" is also synonymized with *Dictyocoryne* as the name of *Stylactis* by Matsuzaki *et al.* (2015:19). In this context, our paper newly synonymized *Hymenastromma* with *Dictyocoryne*. As shown in the supporting image of the Atlas for *Hymenastromma*, the central structure is different from *Dictyocoryne*. Both these genera may be independent from each other.

The oldest available names are listed as *Dictyocoryne*, *Dictyastrum*, *Euchitonia* and *Rhopalodictyum* from Ehrenberg (1861b). The formal publication and years of publication for these genera have been confused due to a *nomen nudum* in Ehrenberg (1861a) and the mismatch of volume number as "1860" and the published year for Ehrenberg (1861a; 1861b) (Lazarus & Suzuki 2009: 31). The names *Dictyocoryne* and *Rhopalodictyum* are commonly used in references but the condition of preservation and the completeness of the shell are better for the lectotype of *Dictyocoryne* than for *Rhopalodictyum*.

Hexinastrum

As far as we know, real specimens identifiable as *Hexinastrum*, *Hexalastromma*, *Pentalastromma* and *Pentinastrum* have never been so far illustrated. Here we simply put together these suspected genera. Six-armed genera might be conjoined specimens like in the Jurassic *Tritrabs worzeli* illustrated by Dumitrica (2013b: fig. 4.1). The oldest available names are *Hexinastrum* and *Pentinastrum* in Haeckel (1882: 450 for *Hexinastrum* and 460 for *Pentinastrum*). If their morphology results from a conjoined phenomenon, six-armed specimens like *Hexinastrum* are predicted to be found rather than star-like five-armed specimens like *Pentinastrum*.

Tricranastrum

Tricranastrum corresponds to the current usage of *Myelastrum*. The following genera have the same type species, respectively: *Myelastrum*, *Myelastrella* and *Spongomyelastrum*; *Dicranastrum*, *Dicranaster* and *Spongodicranastrum*; *Pentophiastromma* and *Spongopentophiastrum*. The ontogenetic changes at intraspecies or species level are well illustrated in Tan & Tchang (1976: 246-250). The authors seemed to consider these variations at a genus level but their illustrated morphological variations are obviously continuous among specimens. The number of arms at least is variable at intraspecific level because if it is used as a genus criterion, many genera would be "created" by monotypy. The oldest available name is *Tricranastrum* Haeckel (1879: 705). As this name was once used as valid in van de Paverd (1995: 175), it is unable to keep the name *Myelastrum*.

Tessarastrum

The difference between *Tessarastrum* and *Ommatocampe* is in the number of arms but two of the four arms of *Tessarastrum* are developed in secondary growth mode in the sense of Ogane *et al.* (2010) (the supporting image for *Tessarastrella* in the Atlas). *Hagiastromma* is characterized by a patagium and dissimilar longitudinal arms (Campbell 1954: D86) whereas *Tessarostromma* by a bilateral symmetry along the long axis, the presence of a patagium and dissimilar arms (Campbell 1954: D88 as *Tessarastromma*, the invalid name at present). The shorter arms illustrated in the type images of *Hagiastromma* and *Tessarostromma* are explained by a different ontogenetic growth in *Tessarastrum*. The patagium changes during ontogenetic growth in the Euchitoniidae. The bilateral symmetry change is related to intraspecies variation. All of these available genera were simultaneously published in Haeckel (1887: 543 for *Hagiastromma*; 547 for *Tessarastrum* and *Tessarastrella*; 548 for *Tessarostromma*). Of these, *Tessarastrum* is the only name established with a generic-rank.

Trigonastrum

This genus is different from *Dictyocoryne* due to the significant diversity of each arm. The illustrated type specimen of *Dictyastromma* shows a significant diversity but the probable same species of *Dictyastrum trispinosum* looks to be a *Dictyocoryne* (the supporting image for *Dictyastromma* in the Atlas). The stratigraphically important species "*Amphirhopalum ypsilon*" is classified into this genus, although this species itself is a *nomen dubium* due to an un-illustrated type. *Monaxonium* initially belong to the Panartidae (= Zygartidae originally) (Popofsky 1912: 125-126) and it was later moved to the Spongodiscidae *sensu* Riedel (1971: 653). The distinguishing features of the listed genera are the occurrence of terminal spines (Campbell 1954: D86 for *Amphicraspedina* and *Dictyastromma*) or spinules on arms (Campbell 1954: D89 for *Rhopalastromma*), the occurrence of a patagium (*Amphicraspedina*, *Rhopalastromma*; Campbell 1954: D86 for *Chitonastromma*, D88 for *Trigonastromma*), the occurrence of two to three forked arms (*Amphicraspedina*, *Chitonastromma*, *Trigonastromma*) or undivided arms (*Dictyastromma*). As repeatedly responsible of the validity of genera in Euchitoniidae, terminal spines and spinules on arms as well as patagium are intraspecies variations. The condition of forked arms is so variable that it is considered as an intraspecies or species variation. All available synonym genera except for *Monaxonium* were simultaneously published in Haeckel (1887: 523 for *Amphicraspedina* and *Amphirrhopoma*; 525 for *Dictyastromma*; 528 for *Rhopalastromma*; 537 for *Chitonastromma*; 538 for *Trigonastrum*; 539 for *Trigonastrella*, *Trigonastromma*). As the forked arms are one of the characters of this morphotype, *Trigonastrum* is selected as the valid name.

Clade indet.

Family Spongobrachiidae Haeckel, 1882
sensu Suzuki *emend.* herein

Spongobrachida Haeckel, 1882: 461 [as a tribe]; Haeckel 1887: 575 [as a subfamily]. — Schröder 1909: 50 [as a subfamily].

Spongobrachinae [*sic*] – Clark & Campbell 1942: 49 (= Spongobrachiinae); Clark & Campbell 1945: 26. — Campbell & Clark 1944a: 28; 1944b: 20. — Chediya 1959: 149.

Spongobrachiinae – Campbell 1954: D94. — Kozur & Mostler 1978: 140-142 (*sensu* emend.).

Spongobrachiidae – Kozur & Mostler 1978: 139-140 (*sensu* emend.).

Type genus. — *Spongobrachium* Haeckel, 1882: 461 [type species by subsequent designation (Campbell 1954: D94): *Spongodiscus ellipticus* Haeckel, 1861b: 844].

Included genera. — *Spongasteriscus* Haeckel, 1862: 474 (= *Spongasterisculus* with the same type species; *Dictyocorynium* **n. syn.**). — *Spongastromma* Haeckel, 1887: 598. — *Spongobrachium* Haeckel, 1882: 461.

Diagnosis. — Flat shaped Polycystinea with a circular center and a spongy disk with an irregular outline. Central part is a convex lens-shaped structure (margarita) which includes a spinose microsphere and four to five densely-concentric, convex lens-shaped crusts. The center of the margarita is thick. The periphery of the margarita is more transparent than its center. A spongy structure surrounds the margarita and its outline varies from elliptical to rounded rectangle. The peripheral ends of the corners tend to be thicker than the central part; other remaining parts tend to be thin. The thicker, spongy part resembles an arm whereas the thinner part more closely resembles a patagium. These parts are intimately connected without a distinguishable boundary. Both polar sides of the margarita extend outwards or in certain cases are covered with fine appendages.
The endoplasm is bright red in color whereas the central part is discolored appearing as transparent or white. The peripheral region of the shell does not appear in red. A robust, long axoflagellum extends from the pylome and is located on the shortest line of the shell. No color is recognized along the central part to the exit of the pylome. The pylome is not walled.

Stratigraphic occurrence. — early Middle Miocene-Living.

Remarks

Spongobrachiidae was first recognized as an independent Clade E1 when *Dictyocoryne* and *Spongaster* were placed into another independent Clade E3 in a molecular phylogenetic study (Sandin *et al.* 2021). As explained in the remarks regarding Spongodiscoidea, an appropriate family needed to be applied to Clade E. Originally, the *Dictyocorynium*-form of *Spongasteriscus* was informally known as "strange *Dictyocoryne*" or was wrongly identified as "*Dictyocoryne perforatum* (Popofsky)" (see figs 8.8.3, 8.8.4 in Suzuki & Not 2015). This illustrated specimen is actually conspecific with specimens coded as Vil449 and Mge17-17 by Sandin *et al.* (2021). These specimens coded as Vil449 and Mge17-17 are the Clade E3 specimens. To maintain consistency between morphological and molecular phylogenetic classification, the genus *Dictyocorynium*-form of *Spongasteriscus* should be re-validated as a genus having an ambiguous disk with many concentric fine ambiguous hoops and spongy triangular-like external triangular parts. The importance of the disk's lateral profile was largely ignored in the taxonomic works of classic Spongodiscoidea (see remarks in Trematodiscoidea); however, it was an important character to define and differentiate this family. A detailed skeletal image in scanning electron microscopy (SEM) has been captured for the *Dictyocorynium*-form of *Spongasteriscus* (Matsuoka 2009: fig. 3.30). Fine protoplasmic structure is illustrated in *Spongasteriscus* (Hollande & Enjumet 1960: pl. 23, fig. 3), but protoplasmic structures particular to the Spongobrachiidae, or differences from Euchitoniidae, are unknown due to there being no section image of the protoplasm of Euchitoniidae.

Validity of genera

Spongasteriscus

This genus has been separated from the Euchitoniidae and Spongodiscidae in consideration of the molecular phylogeny observations published by Sandin *et al.* (2021). Until the molecular phylogenetic differences were pointed out, they have been identified as other genera of the Euchitoniidae, Spongodiscidae and other spongy discoidal groups. For instance, probable *Spongasteriscus* specimens might have been mixed with true *Spongaster* representatives in a previous study (Riedel & Sanfilippo 1978a: pl. 2). In consideration of the wide variation in the development of the arms and their number, the four-armed *Spongasteriscus* is the oldest synonym of the three-armed *Dictyocorynium*.

Phylogenetic Molecular Lineage II (Sandin *et al.* 2021)

Diagnosis. — Same as Cladococcoidea.

Remarks

The coverage of Lineage II is the same as that of Cladococcoidea.

Superfamily Cladococcoidea Haeckel, 1862 n. stat.

Cladococcida Haeckel, 1862: 238, 364 [as a family].

Heteracanthidea – Bertolini 1937: 1269-1270 [as an order, junior homonym].

Liosphaericae – Campbell 1954: D48 [as a superfamily]. — Nakaseko 1957: 23 [as a superfamily]. — Dieci 1964: 184 [as a superfamily].

Cenodiscicae – Campbell 1954: D76 [*nomen dubium*, as a superfamily] . — Nakaseko 1957: 23 [as a superfamily].

Cenodiscilae – Campbell 1954: D76 [*nomen dubium*, as a subsuperfamily].

Etmosphaeracea – Loeblich & Tappan 1961: 221 [as a superfamily].

Liosphaeracea – Pessagno & Blome 1980: 229. — Blome 1984: 350. — Pessagno *et al.* 1984: 22 (*sensu* emend.). — Cheng 1986: 173.

Arachnosphaerilae – Dumitrica 1984: 98 [as a subsuperfamily].

Liosphaeroidea – Matsuzaki *et al.* 2015: 12.

Diagnosis. — One large spherical latticed cortical shell with no internal skeletal structure.

Remarks

The Cladococcoidea consist of Ethmosphaeridae (including Clade F1) and Cladococcidae (including Clade F2), grouped in a major group, the Clade F1: *Heliosphaera* and *Liosphaera* in Ethmosphaeridae; and the Clade F2: *Arachnospongus*, *Diplosphaera* (originally *Astrosphaera*) and *Cladococcus* in Cladococcidae (Sandin *et al.* 2021). As this superfamily is primarily marked by a hollow large cortical shell, the Mesozoic Xiphostylidae Haeckel 1882 may likewise belong to the Cladococcoidea.

Clade F1 (Sandin *et al.* 2021)

Family Ethmosphaeridae Haeckel, 1862

Ethmosphaerida Haeckel, 1862: 238, 346 [as a family]; Haeckel 1882: 448 [as a tribe]; Haeckel 1887: 61 (*sensu* emend.) [as a subfamily]. — Mivart 1878: 179 [as a subsection]. — Dunikowski 1882: 184 [as a tribe]. — Wisniowski 1889: 682. — Schröder 1909: 5 [as a subfamily].

Monosphaerida Haeckel, 1862: 230 [*nomen nudum*, above Cladococcida]. — Stöhr 1880: 85. — Dreyer 1913: 5 [as a family].

Heliosphaerida Haeckel, 1862: 238, 348 [as a tribe]; Haeckel 1882: 450 [as a tribe].

Ethmosphaeriden – Haeckel 1865: 366 [as a family].

Etmosphaeridae – Claus 1876: 159. — Loeblich & Tappan 1961: 221. — Kozur & Mostler 1979: 23 (*sensu* emend.). — Dumitrica 1984: 95. — Takahashi 1991: 61. — Tan 1998: 95 [as a subfamily].

Monosphaeridae – Zittel 1876-1880: 119 [*nomen nudum*].

Triosphaeria Haeckel, 1882: 452 [*nomen nudum*, as a subfamily].

Monosphaeria – Haeckel 1882: 448 [*nomen nudum*, as a subfamily]. — Dunikowski 1882: 184.

Liosphaerida Haeckel, 1887: 59 [as a family] (not 1882: 449). — Wisniowski 1889: 682 [as a family]. — Rüst 1892: 133. — Bütschli 1889: 1948 [as a family]. — Cayeux 1894: 204 [as a family]. — Hill & Jukes-Browne 1895: 605. — Schröder 1909: 5 [as a family]. — Anderson 1983: 23 [as a family].

Cenodiscida Haeckel, 1887: 409-411 [*nomen nudum*, as a family]. — Bütschli 1889: 1958 [as a family]. — *nec* Rüst 1892: 161 [as a family]. — Schröder 1909: 3 [as a family]. — Anderson 1983: 24 [as a family].

Zonodiscida Haeckel, 1887: 411 [*nomen nudum*, as a subfamily. — Schröder 1909: 39 [as a subfamily].

Larcarida Haeckel, 1887: 604, 605-606 [*nomen nudum*, as a family]. — Bütschli 1889: 1965 [as a family]. — Schröder 1909: 4 [as a family]. — Anderson 1983: 24 [as a family].

Cenolarcida Haeckel, 1887: 606 [*nomen nudum*, as a subfamily]. — Schröder 1909: 52 [as a subfamily].

Coccolarcida Haeckel, 1887: 606, 610 [*nomen nudum*, as a subfamily]. — Schröder 1909: 52 [as a subfamily].

Liosphaeriden – Haecker 1907: 118 [as a family]. — Orlev 1959: 430.

Liosphaeridae – Popofsky 1908: 206; Popofsky 1912: 82. — Enriques 1932: 982. — Clark & Campbell 1942: 19; 1945: 5. — Campbell & Clark 1944a: 8. — Frizzell & Middour 1951: 9. — Campbell 1954: D48. — Chediya 1959: 68. — Orlev 1959: 430. — Hollande & Enjumet 1960: 70. — Dieci 1964: 184. — Nakaseko & Sugano 1976: 119. — Tan & Tchang 1976: 225. — Tan & Su 1982: 136. — Blueford 1988: 247. — Chen & Tan 1996: 150. — Tan 1998: 95. — Chen *et al.* 2017: 81 (*sensu* emend.).

Larcaridae – Popofsky 1908: 229 [*nomen nudum*]. — Enriques 1932: 985. — Clark & Campbell 1942: 50; 1945: 27. — Chediya 1959: 151.

Monosphaerinae – Mast 1910: 155. — Popofsky 1912: 95.

Larcariidae – Poche 1913: 209 [*nomen dubium*]. — Kozur & Mostler 1979: 45.

Cenodiscidae – Poche 1913: 209 [*nomen dubium*]. — Campbell 1954: D77. — Orlev 1959: 441. — Chediya 1959: 120. — Nakaseko & Sugano 1976: 125. — Amon 2000: 40.

Liosphaerinae – Clark & Campbell 1942: 19. — Frizzell & Middour 1951: 9. — Campbell 1954: D48.

Ethmosphaerinae – Clark & Campbell 1942: 19. — Campbell & Clark 1944a: 8. — Clark & Campbell 1945: 6. — Campbell 1954: D48. — Chediya 1959: 68. — Loeblich & Tappan 1961: 222. — Dieci 1964: 64. — Kozur & Mostler 1979: 25.

Coccolarcinae – Clark & Campbell 1942: 50 [*nomen dubium*]; Clark & Campbell 1945: 28. — Campbell 1954: D95. — Chediya 1959: 152.

Heliosphaerinae – Campbell 1954: D62. — Tan & Tchang 1976: 230.

Cenodiscinae – Campbell 1954: D77 [*nomen dubium*].

Zonodiscinae – Chediya 1959: 12 [*nomen dubium*].

Cenolarcinae – Chediya 1959: 151 [*nomen dubium*].

Macrosphaeridae Hollande & Enjumet, 1960: 48, 69, 114, 120 [*nomen nudum*]. — Cachon & Cachon 1972c: 297. — Petrushevskaya 1975: 571. — Anderson 1983: 51, 66. — Cachon & Cachon 1985: 286 [as a superfamily]. — Suzuki & Sugiyama 2001: 138.

Cyrtidosphaeridae Cachon & Cachon, 1972c: 293; Cachon & Cachon 1985: 288.

Ethmosphaerini – Kozur & Mostler 1979: 25 [as a tribe].

Cenodiscini – Kozur & Mostler 1979: 26 [*nomen nudum*].

Cyrtidosphaerid-type – Anderson 1983: 169.

Liosphaeracea – Göke 1984: 38 [as a subfamily].

Type genus. — *Ethmosphaera* Haeckel, 1861a: 802 [type species by monotypy: *Ethmosphaera siphonophora* Haeckel, 1861a: 802].

Included genera. — *Cyrtidosphaera* Haeckel, 1861a: 803. — *Ethmosphaera* Haeckel, 1861a: 802 (= *Ethmosphaerella* with the same type species; *Monosphaera* **n. syn.**). — *Haplosphaera* Hollande & Enjumet, 1960: 114. — *Heliosphaera* Haeckel, 1861a: 803 (= *Heliosphaerella* with the same type species). — *Liosphaera* Haeckel, 1887: 76 (= *Melitomma* with the same type species; *Craspedomma* **n. syn.**).

Nomina dubia. — *Briorradiolites*, *Cenodiscus*, *Cenolarcus*, *Coccolarcus*, *Ethmosphaeromma*, *Heliosphaeromma, Larcarium*, *Phormosphaera*, *Rhodosphaera*, *Rhodosphaerella*, *Rhodosphaeromma*, *Zonodiscus*.

Diagnosis. — Cladococcoidea without any other ornaments such as radial spines, excepting by-spines. Endoplasm is variable from transparent (*Haplosphaera*) to milky-white (*Cyrtidosphaera*) Size of the endoplasm is different in very large (*Cyrtidosphaera*) or very small forms (*Haplosphaera* and *Heliosphaera*).

Stratigraphic occurrence. — Late Oligocene-Living.

Remarks

This family used to be called Liosphaeridae, but the oldest senior synonym is Ethmosphaeridae. Since both Liosphaeridae and Ethmosphaeridae were used valid names, the correct valid name is Ethmosphaeridae. The Ethmosphaeridae are distinguishable from the Cladococcidae by virtue of their radial spines and other ornaments. *Cenosphaera* has long been characterized as the genus having a single latticed cortical shell without any internal structure, but the usage of *Cenosphaera* was also problematic due to the following conditions: 1) The genus name was applied to spherical radiolarians whose internal structure might have been absent due to poor preservation. More specifically, very large numbers of *Cenosphaera* species were described from thin sections, increasing the problem of *nomina dubia* species in this genus; 2) It is practically necessary to separate in a "provisional group" such specimens as a tentative genus; 3) As explained in detail in the remarks of Haliommidae, the name-bearing type specimen of *Cenosphaera* has three concentric shells. Thus, it does not reconcile with the practical use of the representative genus; 4) Following the Code, the real *Cenosphaera* is a junior synonym of *Haliomma*; 5) The true genus having a single latticed cortical shell may or may not exist; 6) No appropriate genus has been proposed to inherit the widely accepted concept of *Cenosphaera*; and 7) We previously thought to use *Monosphaera* as a replacement name of the single-shelled "*Cenosphaera*" but this would have created another problem as to the *nomen dubium* status of the type species of *Monosphaera*. Considering these reasons, the definition of *Ethmosphaera* is expanded so as to include the widely accepted concept of *Cenosphaera* in the catalogue. In accordance with the Code, it was not possible to keep *Cenosphaera* as is (see details in the Remarks for Haliommidae). Classic *Cenosphaera*, classified as *Ethmosphaera* in this catalogue, may be misidentified as spherical radiolarians whose radial spines were broken off, *Nanina* (Hexacromyidae), *Hollandosphaera* (Hollandosphaeridae), *Cyrtidosphaera* (Ethmosphaeridae), *Haplosphaera* (Ethmosphaeridae), young forms of *Liosphaera* (Ethmosphaeridae), young forms of *Cromyosphaera* (Haliommidae), *Haliomma* (Haliommidae), *Haliommantha* (Haliommidae) and *Entapium* (Entapiidae) when the internal structure is lost. Moreover, it is impossible to differentiate these genera with scanning electron photos or with light microscopic photos under very shallow focus depths.

The genus member of Ethmosphaeridae is solely determined by the lack of a skeletal structure within the large cortical shell and has not been supported by any molecular phylogenetic data. It is fundamentally impossible to discard morphospecies with a retrograde development of internal structures from the "true" Ethmosphaeridae. A living image for *Cyrtidosphaera* was obtained (Kurihara *et al.* 2006: figs 4.1, 4.2; Suzuki & Not 2015: fig. 8.10.7). Protoplasm and algal symbionts were documented by epi-fluorescent observation with DAPI dyeing for *Cyrtidosphaera* (Zhang *et al.* 2018: 19, fig. 3). Fine protoplasmic structure was illustrated for "*Cenosphaera*" (Hollande & Enjumet 1960: pl. 1, figs 1-6; pl. 3, figs 1-5, 8-14; pl. 6, figs 1-4, 6; pl. 31, figs 1-7; pl. 32, figs 1, 2; Cachon & Cachon 1972b: fig. 1) and *Heliosphaera* (Hollande & Enjumet 1960: pl. 55, figs 4, 5), but there are concerns regarding whether they were correctly identified as the same genus due to the fact that the axoplast system is often quite different among their assigned species.

Validity of genera

Ethmosphaera

Genera with one cortical shell are synonymized herein. The oldest available name is selected.

Liosphaera

Craspedomma is characterized by irregular pores on both inner and outer cortical shells (Campbell 1954: D48). Irregularity of pores is an intraspecies or intraspecies difference in such kinds of cortical shells in any families.

Clade F2 (Sandin *et al.* 2021)

Family Cladococcidae Haeckel, 1862

Cladococcida Haeckel, 1862: 238, 364 [as a family]. — Mivart 1878: 177 [as a subdivision].

Arachnosphaerida Haeckel, 1862: 238, 354 [as a tribe]; Haeckel 1882: 454 [as a tribe]; Haeckel 1887: 208.

Cladococcidae – Pantanelli 1880: 46.

Diplosphaerida Stöhr, 1880: 86 [*nomen dubium*, as a family]. — Haeckel 1882: 451 [as a tribe]; Haeckel 1887: 208. — Schröder 1909: 16 [as a rank between subfamily and genus].

Lychnosphaerida Haeckel, 1882: 452 [as a tribe].

Astrosphaerida Haeckel, 1887: 55, 206 (not 1882: 449). — *nec* Wisniowski 1889: 684. — Bütschli 1889: 1952 [as a family]. — *nec* Rüst 1892: 133. — Cayeux 1894: 205. — *nec* Hill & Jukes-Browne 1895: 605-606. — Schröder 1909: 2 [as a family]. — Mast 1910: 155 [as a family]. — Anderson 1980: 3, 5, 19 [as a family]; Anderson 1981: 248, 351, 360, 368 [as a family]; Anderson 1983: 23 [as a family].

Caryommida Haeckel, 1887: 208, 265 [*nomen dubium*, as a subfamily]. — Schröder 1909: 17 [as a subfamily].

Astrosphaeridae – Haecker 1908: 435. — Popofsky 1908: 211; 1912: 93. — Poche 1913: 207. — Enriques 1932: 982. — Campbell & Clark 1944a: 15; 1944b: 11. — Clark & Campbell 1945: 16. — Deflandre 1953: 416. — Campbell 1954: D60. — Dogiel & Reshetnyak 1955: 32. — Chediya 1959: 94. — Orlev 1959: 437. — Hollande & Enjumet 1960: 72-73. — Mamedov 1973: 49. — Pessagno 1976: 42. — Tan & Tchang 1976: 228. — Bjørklund 1976: 119. — Dumitrica 1979: 20. — Tan & Su 1982: 146. — van de Paverd 1995: 77. — Chen & Tan 1996: 150. — Tan 1998: 146. — De Wever *et al.* 2001: 108. — Afanasieva *et al.* 2005, S275. — Afanasieva & Amon 2006: 111. — Matsuzaki *et al.* 2015: 13. — Chen *et al.* 2017: 106.

Arachnosphaerinae – Mast 1910: 173 (*sensu* emend.). — Popofsky 1912: 104. — Campbell 1954: D66. — Tan & Tchang 1976: 231. — Petrushevskaya 1979: 108.

Astrosphaerinae – Campbell 1954: D60. — Tan & Tchang 1976: 228.

Caryomminae – Chediya 1959: 100 [*nomen dubium*].

Arachnosphaeridae – Petrushevskaya 1979: 106. — Dumitrica 1984: 99.

Cladococcid type – Anderson 1983: 168.

Astrosphaerins [*sic*] – Casey 1993: 253.

TYPE GENUS. — *Cladococcus* Müller, 1856: 485 [type species by monotypy: *Cladococcus arborescens* Müller, 1856: 485].

INCLUDED GENERA. — *Arachnosphaera* Haeckel, 1861a: 804 (= *Arachnosphaerella* with the same type species). — *Arachnospongus* Mast, 1910: 56. — *Cladococcus* Müller, 1856: 485 (= *Cladococcalis* with the same type species; *Anomalacantha* **n. syn.**, *Cladococcodes* synonymized by Mast 1910; 158; *Cladococcurus* **n. syn.**, *Porococcus* **n. syn.**). — *Diplosphaera* Haeckel, 1861a: 804 (= *Diplosphaeromma* with the same type species; *Astrosphaera*, *Diplosphaerella*, *Leptosphaera*, *Leptosphaerella*, synonymized by Hollande & Enjumet 1960: 116; *Astrosphaerella* **n. syn.**, *Astrospongus, Drymosphaeromma* **n. syn.**, *Leptosphaeromma* **n. syn.**). — *Haeckeliella* Hollande & Enjumet, 1960: 119. — *Lychnosphaera* Haeckel, 1882: 452 (= *Rhizoplegmidium* **n. syn.**, *Rhizospongus* **n. syn.**, *Thalassoplegma* **n. syn.**).

NOMINA DUBIA. — *Acanthospongus*, *Arachnopegma*, *Arachnopila*, *Arachnosphaeromma*, *Astrosphaeromma*, *Caryomma*, *Cladococcinus*, *Drymosphaera, Drymosphaerella, Elaphococcus, Elaphococcinus*, *Elaphococculus, Hexacladus*, *Rhizoplegma*, *Rhizoplegmarium*, *Spongopila*.

JUNIOR HOMONYM. — *Heteracantha* Mast, 1910 (= *Anomalacantha*) *nec* Brullé, 1834.

DIAGNOSIS. — Cladococcoidea with radial spines and/or other ornaments. Endoplasm is distributed from the center to the outer side of the first spherical cortical shell. Tens to hundreds of brownish grains, but not algal symbionts, are found scattered around the endoplasm in some genera with innumerous pseudopodia radiate throughout. In the "*Elaphococcinus*"-form of *Cladococcus*, a large reddish to brown endoplasm and a surrounding milky-white endoplasm nearly fill the entirety of the shell's area; such that, the distal ends of ramified radial spines are exposed. Algal symbionts also appear to be present.
The axopodial system is that of anaxoplastid-type; no axoplast and no bundles of axoneme are present. The intracapsular zone includes the nucleus, a thin endoplasmic reticulum, an empty area with axoneme strands and a main endoplasmic reticulum from the center to the outer part. The presence of an empty zone between the nucleus and the main endoplasmic reticulum zone is a significant protoplasmic character. The nucleus, as well as the empty zone with axoneme strands, is always encrusted in the innermost latticed shell.

STRATIGRAPHIC OCCURRENCE. — Early Middle Miocene-Living.

REMARKS
Cladococcidae is the oldest senior synonym of Astrosphaeridae. Classical papers considered the family Astrosphaeridae as a junior synonym of Actinommidae Haeckel 1882, but this was obviously rejected by both morphological and molecular studies. *Cladococcus* and *Haeckeliella* are regularly found in Cenozoic sediments and rocks. *Arachnosphaera*, *Diplosphaera*, the "*Elaphococcus*" form of *Cladococcus* are often encountered in shallow surface plankton samples. Notwithstanding, all genera except "*Elaphococcus*" are not preserved, not even on surface sediments other than in exceptional cases. As the living Cladococcidae are large and have easily recognizable endoplasm, they are easily observed in seawater momentarily after plankton towing and at lower magnitudes of binocular microscopes. Owing to this facility, living specimens were analyzed in several papers. Living image were illustrated for *Arachnosphaera* (Anderson 1983: fig. 1.1.B?; Yuasa *et al.* 2009: fig. 1c; Suzuki & Aita 2011: fig. 4J), *Diplosphaera* (Suzuki & Sugiyama 2001: figs 2.2-2.4; Matsuoka 2007: fig. 2.e; 2017: figs 2.1, 2.2; Yuasa *et al.* 2009: fig. 1d; Suzuki & Aita 2011: fig. 4B-right) and the "*Elaphococculus*" form of *Cladococcus* (Suzuki & Not 2015: fig. 8.8.23; Matsuoka 2017: figs 3.1, 3.2). Protoplasm and algal symbionts were documented by epi-fluorescent observation with DAPI dyeing or other dyeing methods for *Arachnosphaera* (Ogane *et al.* 2014: pl. 1, figs 5-6), *Diplosphaera* (Suzuki & Not 2015: fig. 8.8.19; Zhang *et al.* 2018: 19, fig. 4), and *Cladococcus* (Zhang *et al.* 2018: 19, fig. 2). Fixed images with dyeing were published for *Arachnosphaera* (Aita *et al.* 2009: pl. 6, fig. 4; pl. 19, fig. 4; pl. 21, fig. 2; pl. 22, fig. 3), *Cladococcus* (Aita *et al.* 2009: pl. 8, 4), "*Elaphococculus*" of *Cladococcus* (Aita *et al.* 2009: pl. 26, fig. 1) and *Lychnosphaera* (Aita *et al.* 2009: pl. 7, fig. 1). Fine protoplasmic structures were illustrated for *Arachnosphaera* (Hollande & Enjumet 1960: pl. 9, figs 11, 12; pl. 11, figs 1-7; pl. 12, figs 2-5; pl. 22, fig. 6; pl. 29, figs 1, 2), *Diplosphaera* (Hollande & Enjumet 1960: pl. 12, fig. 6; pl. 23, fig. 2; pl. 26, fig. 2), *Cladococcus* (Hollande & Enjumet 1960: pl. 6, fig. 12; pl. 12, fig. 1; pl. 15, figs 4-6; pl. 26, fig. 1), *Haeckeliella* (Hollande & Enjumet 1960: pl. 15, figs 1-3) and *Lychnosphaera* (Hollande & Enjumet 1960: pl. 30, figs 1, 2). Internal skeletal structures were illustrated for *Arachnosphaera* (Cachon & Cachon 1972b: pl. 29, fig. b) and *Haeckeliella* (Takahashi 1991: pl. 10, fig. 2; van de Paverd 1995: pl. 23, fig. 3). Although it is impossible to amend the taxonomy for the host, parasites were recognized in *Cladococcus* as *Solenodinium* (Hollande & Enjumet 1955: fig. 8). The environmental RAD-III Clade of Not *et al.* (2007) collected from 200-400 m water depths in the tropical Pacific was specified as the Cladococcidae (originally Astrosphaeridae) by Li & Endo (2020).

VALIDITY OF GENERA
Diplosphaera
The combinations of *Astrosphaera* and *Astrosphaerella* and of *Leptosphaera* and *Leptosphaeromma* have the same type species, respectively. *Astrosphaera*-specimens were repeatedly named *Diplosphaera* (Hollande & Enjumet 1960: 116; Kozur & Mostler 1979: 12; Suzuki & Sugiyama 2001: 118). Observation of living representatives of *Diplosphaera hexagonalis* easily proves the distinguishing characteristics between *Astrospongus*, *Diplosphaerella*, *Drymosphaeromma*, *Leptosphaera* and *Leptosphaeromma* at intraspecies or species levels. The oldest available name is *Diplosphaera* among them.

Cladococcus
The translated description of *Anomalacantha* (originally *Heteracantha*) by Mast (1910: 37) from German follows. "*Monosphaerids with main and secondary spines. Three-sided main spines ramified or not, secondary spines always dichotomized. Shell always very thick with funnel-shaped pores.*" *Cladococcodes* is characterized by ramified branches on the radial spine, regular pores with similar sizes on the cortical shell (Campbell 1954:

D63); and *Cladococcurus* by ramified branches on the radial spine, irregular pores with dissimilar sizes on the cortical shell (Campbell 1954: D63). Regularity of pores and their sizes are not distinguishing features at generic level. Ramified and branched patterns of radial spines are too variable among specimens to be useful for determination of genus. As for the taxonomic value of funnel-shaped pores, we have never met such pores like that in *Anomalacantha* so far. The young *Cladococcus*-form often looks like the type species of *Porococcus*, and the latter genus is, thus, regarded as a young form. This genus may be also used as a collective group that is defined by an assemblage of species, or stages of organisms, that cannot be allocated with confidence to nominal genera (See the Glossary of ICZN 1999). If *Porococcus* is a collective group, this genus does not compete in priority with another genus-group (ICZN 1999: article 23.7.2); typification for this genus is not necessary (ICZN 1999: article 42.3.1) and a type species can be disregarded (ICZN 1999: article 67.14). The oldest available name is *Cladococcus* among synonyms.

Lychnosphaera
Lychnosphaera has an empty space just above the cortical shell. *Thalassoplegma* is also the case with a very narrow space. The oldest synonym is *Leptosphaera* (Haeckel 1887: 452).

Phylogenetic Molecular Lineage IV (Sandin *et al.* 2021)

Diagnosis. — A spherical small microsphere with distinctive "dividers" which are significant in walls of hoops (Trematodiscoidea), three or more distinctive, spherical concentric shells (Litheliidae and Haliommoidea), and to several repetitions of girdles or cupolas (Phorticioidea and Larcospiroidea). However, this criterion does not apply to Sponguridae, Spongopylidae and Cristallosphaeridae.

Remarks

Lineage IV is subdivided into two sub-lineages; a group with Clades J, K, L1 and L2 and another other group with Clade M. The undermentioned groups are supported by 100% PhyML bootstrap values with 10 000 replicates (BS) and >0.99 posterior probabilities (PP). The morphological characters mentioned above cannot exclude Lithocyclioidea (including Clade E1 of Lineage I) from Lineage IV as the members having the "dividers" described above is partially recognized in Lineage IV. In this sense, Stylosphaeridae may belong to Lineage IV. The Lineage IV is separated from other Lineages with 100% PhyML bootstrap values with 10 000 replicates (BS) and >0.99 posterior probabilities (PP) and consists of Trematodiscoidea (including Clades J1 and J2), Haliommoidea (including Clade K), Lithelioidea (including Clade L1), Spongopyloidea (including Clade L2), Phorticioidea (including Clades M1 and M2) and Larcospiroidea (including Clades M3 and M4). The combination of superfamilies with Clades are based on: *Flustrella* and *Stylodictya* for Clades J1 and J2; *Actinomma* for Clade K; *Lithelius* for Clade L1; *Calcaromma*, *Schizodiscus*, *Spongobrachiopyle* for Clade L2; *Tholomura* for Clade M1; *Tholospira* for Clade M2; *Pylodiscus* for Clade M3; and *Tetrapyle* for Clade M4.

Clade J1-J2 (Sandin *et al.* 2021)

Superfamily Trematodiscoidea Haeckel, 1862 *sensu* Suzuki emend. herein

Trematodiscida Haeckel, 1862: 240, 485, 491 [as a tribe]; 1882: 459 [as a tribe]; 1887: 484, 491 [as a subfamily].

Trematodiscea – Zittel 1876-1880: 124 [rank unknown].

Trematodiscacea – Kozur & Mostler 1978: 125-126 [as a superfamily]; 1990: 217-218 [as a superfamily].

Stylodictyoidea – Suzuki *in* Matsuzaki *et al.* 2015: 25.

Diagnosis. — Flat or convex lens shape with circular outline. Central structure consisting of many discontinuous rings connected by short radial beams or a microsphere with four decussated primary radial spines.

Remarks
This superfamily includes only the family Trematodiscidae. Homeomorphy between Spongodiscoidea and Trematodiscoidea was first detected by a molecular phylogenetic study (Ishitani *et al.* 2012). The group of *Schizodiscus*, *Spongobrachiopyle*, *Flustrella* and *Stylodictya* was analyzed by molecular studies and further subdivided into two subgroups, namely a subgroup of *Schizodiscus* and *Spongobrachiopyle* (originally *Spongopyle*) as Clade L2, and a subgroup of *Flustrella* and *Stylodictya* as Clade J (Sandin *et al.* 2021). The former group morphologically corresponds to the Spongopylidae and the latter to the Trematodiscidae. The general morphology of Spongopylidae closely resembles that of Spongodiscidae (Spongodiscoidea).

It is estimated that identifying the classical Spongodiscidae family, used to include the Spongodiscoidea and Trematodiscoidea is difficult. However, this is largely due to an insufficient observation of many taxonomical markers. In particular, the difference in the disk's lateral profiles is almost completely ignored. This complicates the taxonomic process. The structural difference between the "empty" space and "thin" structural parts must be carefully recognized upon dark to bright appearance of disc parts under a light microscope. An "empty" space can be bright irrespective of disk thickness. Meanwhile, a "thin" place may be bright based on its relationship to the disk thickness. It is sometimes presumptively concluded, to a fault, that differences in brightness may be caused by supplemental gowns on both faces of the disk. If this is observed, shallow depth focused photos are essential. Many previous papers repeatedly noticed the different lateral profiles of the classical Spongodiscidae (Müller 1859b: pl. 1, figs 8, 9; Haeckel 1862: pl. 27, figs 3, 5; pl. 28, figs 6, 9; 1887: pl. 42, figs 5, 6, 9, 10; Hertwig 1879: pl. 6, 7a, 7b, 8a; Jørgensen 1905: pl. 10, figs 39a, 40b, 41c; Riedel 1953: pl. 84, fig. 6; Kozlova 1960; Krasheninnikov 1960: 3, figs 5-7; Moksyakova 1961: pl. 1, fig. 11; 1972: pls 1-9; Kozlova & Gorbovetz 1966: pl. 14, figs 1-2; Petrushevskaya 1967: pl. 19, fig. 2; pl. 20, figs 2, 4; pl. 21, figs 3, 6; pl. 22, fig. 7; pl. 25, figs 3, 5; 1975: pl. 34, figs 1, 2; pl. 36, figs 3, 5; pl. 38, figs 1, 3, 7; pl. 39, figs 2; pl. 40, fig. 4, Barwicz-Piskorz 1978: pl. 5, figs 1-3; Zaynutdinov 1978: pl. 7, figs 1-3; pl. 12, fig. 7;

Petrushevskaya & Kozlova 1979: figs 431, 432, 434, 438, 441; Nakaseko & Nishimura 1982: pl. 29, fig. 1c; pl. 31, figs 2b, 3a; pl. 32, fig. 3; pl. 34, fig. 2a; pl. 37, fig. 1b; pl. 40, fig. 6b; pl. 41, fig. 2a; pl. 42, figs 1, 4; pl. 43, figs 1b, 2a; Poluzzi 1982: pl. 20, fig. 17; O'Connor 1997b: text-fig. 2; pl. 4, figs 4, 6; Ogane & Suzuki 2006: pl. 1, figs 6, 9; pl. 2, fig. 2; Onodera *et al.* 2011: pl. 6, fig. 6). The difference of lateral profile in classic Spongodiscidae is directly related to the fundamental rule of skeletal growth patterns and construction scheme of a biological design. Regardless of the repeated rediscovery of this profile difference, systematic examination regarding these differences have been under-appreciated and the majority of studies identify a spongy disk without radial spines as *Spongodiscus*, a spongy disk without radial spines as *Spongotrochus*, a spongy disk with a pylome as *Spongopyle*, a concentric disk without radial spines as *Porodiscus*, and/or a concentric disk with radial spines as *Stylodictya*. Everyone empirically knows that this simple scheme does not work for any real specimens. This is easily recognizable if we look at names such as *Spongodiscus* spp., Spongodiscidae gen. et sp. indet. and other ambiguous indications for classic Spongodiscidae. Nevertheless, the validity of described genera such as *Schizodiscus*, *Spongobrachiopyle, Spongospira* and *Staurospira* was rejected without any further careful anatomical considerations. It is noteworthy that some studies still strongly adhere to this flawed principle, despite the clear rejection of this treatment by the molecular phylogeny (Ishitani *et al.* 2012). To understand these groups, shallow focus photos like pl. 13, fig. 3a of Suzuki *et al.* (2009d) are essential. Otherwise, progress is stifled.

Family Trematodiscidae Haeckel, 1862 *sensu* Suzuki emend. herein

Trematodiscida Haeckel, 1862: 240, 485, 491 [as a tribe]; Haeckel 1882: 459 [as a tribe]; Haeckel 1887: 484, 491 [as a subfamily]. — Mivart 1878: 176. — Stöhr 1880: 107 [as a family]. — Schröder 1909: 42 [as a subfamily].

Discospirida Haeckel, 1862: 240, 485, 513 [as a tribe]. — Zittel 1876-1880: 124 [rank unknown]. — Mivart 1878: 176 [as a subsection]. — Stöhr 1880: 113 [as a family].

Porodiscida Haeckel, 1882: 459 [junior homonym, as a subfamily]; Haeckel 1887: 409, 481-485 [as a family]. — Wisniowski 1889: 685 [as a family]. — Bütschli 1889: 1961 [as a family]. — *nec* Rüst 1892: 166 [as a family]. — Anderson 1983: 24 [as a family].

Stylodictyida Haeckel, 1882: 459 [as a tribe]; Haeckel 1887: 484, 503 [as a subfamily]. — Schröder 1909: 42 [as a subfamily].

Stylocyclida Haeckel, 1887: 458, 461.

Spongophacida Haeckel, 1882: 461 [*nomen dubium*, as a tribe]. — Dunikowski 1882: 190 [as a tribe]. — Haeckel 1887: 575 [as a subfamily]. — Schröder 1909: 50 [as a subfamily].

Porodiscidae – Popofsky 1908: 222 [junior homonym]; 1912: 127. — Clark & Campbell 1942: 41; 1945: 23. — Campbell & Clark 1944a: 24; 1944b: 15. — Orlev 1959: 444. — Chediya 1959: 132. — Kozlova 1967: 1171-1173 (*sensu* emend.). — Petrushevskaya & Kozlova 1972: 524-525 (*sensu* emend by Kozlova). — Tan & Tchang 1976: 242. — Riedel & Sanfilippo 1977: 865. — Dumitrica 1979: 24-25; 1984: 102. — Tan & Su 1982: 152. — Anderson 1983: 39. — Blueford 1988: 250. — Chen & Tan 1996: 151. — Hollis 1997: 53. — Tan 1998: 209. — Tan & Chen 1999: 208. — Amon 2000: 41. — Chen *et al.* 2017: 138.

Trematodiscinae – Clark & Campbell 1942: 41; 1945: 23. — Campbell & Clark 1944a: 24; 1944b: 15. — Frizzell & Middour 1951: 23. — Chediya 1959: 133. — Kozur & Mostler 1978: 128. — Tan & Su 1982: 152. — Tan 1998: 209. — Tan & Chen 1999: 208.

Stylodictyinae – Clark & Campbell 1942: 42; Clark & Campbell 1945: 23. — Campbell & Clark 1944a: 25; 1944b: 16. — Campbell 1954: D92. — Chediya 1959: 134. — Tan & Tchang 1976: 242. — Kozur & Mostler 1978: 128. — Tan & Su 1982: 153. — Tan 1998: 210. — Tan & Chen 1999: 210. — Chen *et al.* 2017: 141.

Spongophacinae – Clark & Campbell 1942: 47 [*nomen dubium*]; Clark & Campbell 1945: 25. — Campbell & Clark 1944a: 27;— Campbell & Clark 1944b: 18. — Chediya 1959: 146.

Trematodiscidae – Frizzell & Middour 1951: 23. — Kozur & Mostler 1978: 127.

Stylocycliinae – Campbell 1954: D82.

Flustrellinae Campbell, 1954: D88-89.

Stylocyclinae [*sic*] – Chediya 1959: 129 (= Stylocycliinae). — Kozur & Mostler 1972: 46.

Amphibrachiinae Pessagno, 1971a: 20 [*nomen dubium*].

Stylodictyidae – Petrushevskaya 1975: 576.

Spongostaurinae Kozur & Mostler, 1978: 157-159 [*nomen dubium*].

Type genus. — *Trematodiscus* Haeckel, 1861b: 841 [type species by subsequent designation (Frizzell & Middour 1951: 24): *Trematodiscus orbiculatus* Haeckel, 1862: 492] = junior subjective synonym of *Flustrella* Ehrenberg, 1839: 90 [type species by monotypy: *Flustrella concentrica* Ehrenberg, 1839: 132].

Included genera. — *Flustrella* Ehrenberg, 1839: 90 (*nec* Gray, 1848) (= *Centrospira*, *Discospirella*, *Trematodiscus* synonymized by Kozur & Mostler 1978: 128; *Perichlamydium* synonymized by Ogane *et al.* 2009a: 86; *Perispirella* **n. syn.**, *Stylochlamyum* **n. syn.**). — *Staurospira* Haeckel, 1887: 507 (= *Staurodictyon* synonymized by Petrushevskaya & Kozlova 1972: 525; *Tholodiscus* **n. syn.**, *Xiphospira* **n. syn.**). — *Stylodictya* Ehrenberg, 1846: 385 (= *Stylodictyon* with the same type species; *Stylochlamydium* **n. syn.**, *Stylochlamys* **n. syn.**, *Stylospongia* **n. syn.**; *Stylocyclia* synonymized by Müller 1859b: 41; *Stylospira* synonymized by Haeckel 1887: 513). — *Tripodictya* Haeckel, 1882: 459 (= *Xiphodictyon* **n. syn.**).

Nomina dubia. — *Amphibrachium*, *Spongophacus*, *Spongostaurus* Haeckel, 1882 (*nec* Swanberg *et al.*, 1985), *Spongotripodiscus*, *Spongotripodium*, *Spongotripus*, *Stylodictula*, *Stylospongidium*.

Junior homonyms. — *Discospira* Haeckel, 1862 (= *Discospirella*) *nec* Mantell, 1850; *Perispira* Haeckel, 1882 (= *Perispirella*) *nec* Stein, 1859.

Nomen nudum. — *Polydiscus*.

Diagnosis. — A spherical microsphere with four decussated radial beams is surrounded by 2 to 20 concentric rings. The ring wall has a variable appearance, ranging from a distinct shape to a very ambiguous shadow. In uncertain identifications, walls are observed in the sectioned specimens. Four, eight, or more non-bladed primary radial beams may be observed.

The endoplasm fills the disc part but does not fill the peripheral gowns or one to three of the peripheral hoops. The central part endoplasm is different from the endoplasm found in the concentric hoops. In these last cases, the U-letter shaped or round bracket-shaped designs are visible on the disk of the concentric hoop parts. The protoplasm sometimes appears as a transparent yellowish-green color under a light microscope, or as a light, bright blue autofluorescent emission after DAPI dyeing under an epi-fluorescent microscope.
No algal symbionts were identified. Ectoplasmic membrane wrapping the skeletal part including the radial spines. In general, a single axoflagellum is observable in living forms but there is no pylome.

Stratigraphic occurrence. — Middle Paleocene-Living.

Remarks
Despite the efforts to resolve the synonymy problem between *Flustrella* and *Porodiscus* (Ogane *et al.* 2009a), this family was classically known as "Porodiscidae". The genus name *Porodiscus* was proposed for a diatom (Greville 1863), for Polycystinea (Haeckel 1882), and for fungi (Murrill 1903). The genus *Porodiscus* has been erroneously considered as a primary junior synonym of *Trematodiscus* (see discussion p. 84-85 in Ogane *et al.* 2009a), actually there was a long debate on the type species of *Porodiscus*. Frizzell (in Frizzell & Middour 1951: 24) designates *Trematodiscus orbiculatus* Haeckel, 1862 as the type species of *Porodiscus*; later on, *Flustrella concentrica* Ehrenberg, 1854 (Ehrenberg 1854c) was designated as the type species of *Porodiscus* (Campbell 1954: D89). However, these seem inappropriate as neither species was among those first subsequently assigned to the genus *Porodiscus*. Species first subsequently assigned to *Porodiscus* are: *Porodiscus communis* Rüst, 1885; *P. nuesslinii* Rüst, 1885; *P. simplex* Rüst, 1885. The first attempt to fix the type species of *Porodiscus* among those first species subsequently assigned to the genus is by De Wever *et al.* 2001: 158. The Mesozoic revision of genera (O'Dogherty *et al.* 2009a) revalidate such taxonomic act and considered *Porodiscus* as an available Mesozoic radiolarian name (but *dubium*), being *Porodiscus communis* Rüst, 1885 the type species.

Molecular phylogeny supports a close relationship between *Flustrella* and *Stylodictya*. Thus, Stylodictyidae is herein synonymized with Trematodiscidae. Two types of equatorial radial spines were identified as primary radial spines: One type is the spine that is directly connects to the radial beams, the other is the spine that is disconnected from the radial beams. The latter has no value at genus level taxonomy. Ogane *et al.* (2009a: 84) originally thought that the structure of margarita was different between *Flustrella* and *Stylodictya*, but *Flustrella* in the sense of Ogane *et al.* (2009a) was tightly connected to *Stylodictya stellata* and *Stylochlamydium venustum* in the molecular phylogenetic study and belongs to Clade J (Sandin *et al.* 2021). According to Ogane *et al.* (2009a: 86), differences in the internal structure between *Flustrella* and *Perichlamydium* are unknown. Considering, these results and newly obtained images in the catalogue, we hereby grouped them together into a single genus.

The taxonomic definition employed hitherto for classical Spongodiscidae could not distinguish Trematodiscidae from the Spongodiscidae in *sensu stricto* (e.g., De Wever *et al.* 2001: 158, 160). In particular, their internal structure cannot be identified with normal observation methods. Nonetheless, surface images under scanning electronic microscopes (SEM) provide a clear, perceivable difference between the Trematodiscidae and the Spongodiscidae. The central part observed in several genera of the Trematodiscidae crop out throughout their life. Hoops are generally added one by one, outside the external most hoop on the equatorial plane. The subsequent hoops never cover the previous ones, as such, sutures between hoops remain well visible. Furthermore, external hoops tend to be larger and thicker than inner hoops. Consequently, the center of the disk is thinner than the outer extremities. The observed change in thickness of this disk helps us understand the structure of the Trematodiscidae under a light microscope. These patterns are confirmed by SEM image of the surface in *Flustrella* (Dumitrica 1973a: pl. 8, figs 1-6; Petrushevskaya 1975: pl. 40, figs 1-4; Nakaseko & Nishimura 1982: pl. 44, figs 1-3; Poluzzi 1982: pl. 20, figs 10-12; Yamauchi 1986: pl. 4, fig. 8; Cheng & Yeh 1989: pl. 1, figs, 15: 18; van de Paverd 1995: pl. 52, fig. 1; Ogane & Suzuki 2006: pl. 1, figs 5-9; pl. 2, figs 1-5; Onodera *et al.* 2011: pl. 6, figs 1, 2), *Staurospira* (Suyari & Yamasaki 1988: pl. 3, fig. 9) and *Stylodictya* (Suyari & Yamasaki 1987: pl. 7, fig. 11). The Trematodiscidae includes morphotypes with "covers" on the faces of the disk. Both "*Spongophacus*"- and "*Perichlamydium*"- forms of *Flustrella* have two gowns which circumscribe the disk on both faces, though a peripheral slit zone is recognizable in lateral view (Nakaseko & Nishimura 1982: pl. 41, figs 2, 3; pl. 42, figs 1-4; Poluzzi 1982: pl. 21, figs 1-8; Takahashi 1991: pl. 20, fig. 5; van de Paverd 1995: pl. 51, fig. 1; Onodera *et al.* 2011: pl. 5, figs 15, 16). The degree of coverage of the gown is varies from the peripheral edge, to the entire area of the disk. The *Stylochlamydium*-form of *Stylodictya* also tends to become smooth on the surface, as well as a peripheral gown is observed (Onodera *et al.* 2011: pl. 5, figs 17, 18).

Th internal skeletal structure of *Stylodictya* was illustrated (Dumitrica 1989: pl. 15, fig. 11). The images of living specimens were identified for the "*Stylochlamydium*"-form of *Flustrella* (Suzuki & Not 2015: fig. 8.10.6) and *Stylodictya* (Suzuki & Not 2015: fig. 8.8.13; Matsuoka *et al.* 2017: appendix A). Protoplasm and algal symbionts were documented by epi-fluorescent observation with DAPI dyeing in the "*Spongophacus*"-form of *Flustrella* (Zhang *et al.* 2018: 13, fig. 20, p. 19, fig. 9), the "*Stylocyclia*"-form of *Stylodictya* (Zhang *et al.* 2018: 14, figs 6-8, p. 23, fig. 2). Samples fixed with dyeing were shown for *Stylocyclia* (Aita *et al.* 2009: pl. 3, fig. 4; pl. 24, fig. 1; pl. 26, fig. 4; pl. 27, fig. 3; pl. 28, fig. 6). Many undescribed genera still remain (e.g., Ogane & Suzuki 2006: pl. 2, figs 8-12).

Validity of genera
Flustrella
The combination of *Discospira* and *Discospirella*, and that of *Perispira* and *Perispirella* have respectively the same type species. *Trematodiscus* has already been practically synonymized by Campbell (1954: D89) with all concentric rings forms. *Centrospira* is defined by a spiral inner ring and outer concentric

rings (Campbell 1954: D89-90), *Discospirella* is characterized by spiral rings (Campbell 1954 as *Discospira*: D90), *Perispirella* is characterized by concentric inner rings and outer spiral ones (Campbell 1954 as *Perispira*: D90). Many illustrations of the Trematodiscidae display the development of a partial ring outside the complete ring (van de Paverd *et al.* 1995: pl. 52, figs 2, 3, 5, 7), but no photos of spiral development are known to indicate the formation of a ring like that of a spiral foraminifer. These spiral morphologies are intraspecific variations. *Perichlamydium* is marked by a smooth shell margin with a thin porous equatorial girdle (Campbell: D91-92) and *Stylochlamyum* is marked by a thin porous equatorial girdle and all rings concentric (Campbell: D92). Equatorial rings develop in later growth stages so that there is no difference at the genus level.

Staurospira
Tholodiscus is characterized by four zig-zag radial lines and the multi-annular outline of the disk (Petrushevskaya & Kozlova 1972: 525) and *Xiphospira* is defined by the presence of all partly or completely spiral rings and two opposite radial spines (Campbell 1954: D92). The structure of the disk divided by four zig-zag radial lines gives a "decussate" appearance. The zig-zag lines depend obviously on the growth irregularity of each ring part between two "zig-zag radial lines". The type species of *Xiphospira* surely shows two radial spines but the type-illustration is a broken specimen in which the other two radial spines are broken off. As the difference between *Staurospira* and *Stylodictya* is characterized by the number of solid radial beams or the relevant structure inside the disk (four for *Staurospira* and more than four for *Stylodictya*), these three genera (*Staurospira*, *Tholodiscus* and *Xiphospira*) have in common a decussate appearance indicating synonymic relationships. *Staurodictyon* should be synonymized with *Staurospira* due to the decussate disk structure. *Staurospira*, *Staurodictyon*, and *Xiphospira* were simultaneously published as subgenera in Haeckel (1887: 504 for *Xiphospira*, 506 for *Staurodictyon*, and 507 for *Staurospira*). *Staurospira* is validated herein due to a more complete illustration of the type species.

Stylodictya
The combined genera *Stylodictya* and *Stylodictyon*, and the combined genera *Stylochlamydium* and *Stylochlamys* have respectively the same type species. Sandin *et al.* (2021) placed "*Flustrella arachnea*" and *Stylodictya stellata* in the same molecular clade J2 and "*F. arachnea*" and *Perichlamydium venustum* in clade J1. The criteria at generic level in Sandin *et al.* (2021) follow those established by Ogane *et al.* (2009a) who clarified the difference between *Flustrella* and *Stylodictya* by examination of the Ehrenberg collection. "*Flustrella arachnea*" is conspecific with *Stylodictya arachnea* which is also the type species of *Stylocyclia*. The results obtained by Sandin *et al.* (2021) likely imply small differences among *Stylodictya*, *Stylocyclia* and *Stylochlamydium*. *Stylochlamydium* is described as "Like *Stylodictya* but with thin porous equatorial girdle" and "all concentric rings" (Campbell 1954: D92) but presence of equatorial girdle developed in later growth stage like the *Perichlamydium*-form of *Flustrella*. *Stylospongia* looks like a spongy surface but the type-illustration shows no large difference from *Stylodictya arachnea* in principal. The oldest available name is *Stylodictya*.

Tripodictya
This synonymy is tentative. We have never confirmed the occurrence of real specimens similar to *Xiphodictyon*. *Tripodictya* is the oldest available name among them.

Clade K (Sandin *et al.* 2021)

Superfamily Haliommoidea Ehrenberg, 1846

Haliommatina Ehrenberg, 1846: 385 [as a family]; 1847: 54 [as a family]; 1876: 156.

Sphaeropylidea – Lankester *et al.* 1909: 145 [as a suborder].

Haliommoidea – Petrushevskaya 1975: 568; 1979: 105. — Dumitrica 1979: 19.

Actinommacea [*sic*] – Kozur & Mostler 1979: 2-7 (= Actinommoidea) (*sensu* emend.) [as a superfamily]. — Dumitrica 1984: 95 [as a superfamily]. — De Wever *et al.* 2001: 107-108 (*sensu* emend.) [as a superfamily].

Actinommilae – Dumitrica 1984: 96 [as a subsuperfamily].

Actinommoidea – Petrushevskaya 1984: 130; 1986: 125-127. — Bragin 2007: 971; 2011: 742. — Matsuzaki *et al.* 2015: 6-7.

Actinommaceae [*sic*] – O'Dogherty 1994: 277 (= Actinommoidea) [as a superfamily].

Actinommoida – Amon 2000: 29 [as an order].

Actinommata – Afanasieva *et al.* 2005: S274 [as an order]. — Afanasieva & Amon 2006: 111 [as an order].

Diagnosis. — Double medullary shell and one or more spherical or flattened concentric shells with many radial beams.

Remarks
Some authors placed this taxonomic category at the order level but this placement is unacceptable with regard to rank consistency in Eukaryotes (Cavalier-Smith *et al.* 2018; Adl *et al.* 2019). "Actinommoidea" has been a very large group that has included all spherical Polycystinea having many radial spines in traced history (11 families in Kozur & Mostler 1979; 14 family groups in Dumitrica 1984; 7 family groups in Petrushevskaya 1984; 18 family groups in De Wever *et al.* 2001). In the catalogue, the Haliommoidea include the Actinommidae, Haliommidae and Heliodiscidae, but molecular phylogenetic information is only available for *Actinomma* (Sandin *et al.* 2021). Thus, it is uncertain whether or not the Heliodiscidae belong to the Haliommoidea considering the Heliodiscidae are marked by the presence of a microsphere that is eccentrically located in the second shell. As for the Cenozoic families of "Actinommoidea" *sensu* De Wever *et al.* (2001) are here excluded from the Haliommoidea. The exclusion encompasses the Cladococcidae (originally Astrosphaeridae),

Stylatractidae and Stylosphaeridae, Entapiidae, Phacodiscidae (originally Coccodiscinae), Panartidae (originally Artiscinae), Suttoniidae and Conocaryommidae. Additionally, Cladococcidae and Panartidae are separated from Haliommoidea due to the strong molecular phylogenetic information presented by Sandin *et al.* (2021). Several spherical genera have not been formally described yet, as their probable taxonomic position at family or superfamily level is still difficult to determine (e.g., Nishimura 1982: pl. 1, figs 12, 13).

Family Actinommidae Haeckel, 1862 *sensu* Suzuki emend. herein

Actinommatida Haeckel, 1862: 239, 412, 440 [as a tribe]. — Mivart 1878: 177 [as a subsection].

Cromyommida Haeckel, 1882: 453 [as a tribe]; Haeckel 1887: 208, 260 [as a subfamily]. — Schröder 1909: 17 [as a subfamily].

Caryosphaerida Haeckel, 1882: 454 [*nomen dubium*, as a tribe]; Haeckel 1887: 60, 71 [as a subfamily]. — Schröder 1909: 5 [as a subfamily].

Staurocaryida Haeckel, 1882: 454 [as a tribe]; Haeckel 1887: 152, 167 [as a subfamily].

Actinommida [*sic*] – Haeckel 1887: 208, 251 (= Actinomminae) [as a subfamily]. — Schröder 1909: 17 [as a subfamily].

Sphaeropylida Dreyer, 1889: 11-12 [as a family].

Heterosphaerinae Mast, 1910: 49 [*nomen dubium*, as a subfamily]. — Popofsky 1912: 93. — Campbell 1954: D62.

Sphaeropylidae – Poche 1913: 207.

Caryosphaerinae – Campbell 1954: D50 [*nomen dubium*]. — Chediya 1959: 72.

Actinommatinae [*sic*] – Campbell 1954: D64(= Actinomminae). — Pessagno 1976: 42.

Staurocaryinae – Campbell 1954: D58. — Chediya 1959: 89.

Cromyommatinae – Campbell 1954: D66.

Sphaeropyinae – Campbell 1954: D66. — Kozur & Mostler 1979: 13-14.

Stomatosphaerinae Campbell, 1954: D66. — Kozur & Mostler 1979: 44-45.

Actinommidae – Loeblich & Tappan 1961: 222. — Riedel 1967b: 294 (*sensu* emend.); Riedel 1971: 651. — Riedel & Sanfilippo 1971: 1587; 1977: 862. — Sanfilippo & Riedel 1973: 486; 1980: 1008-1009 (*sensu* emend.). — Nakaseko *et al.* 1975: 167, 169. — Nakaseko & Sugano 1976: 122. — Kozur & Mostler 1979: 7-10 (*sensu* emend.). — De Wever 1982b: 175. — Anderson 1983: 37. — Dumitrica 1984: 96; 1995: 22-23. — Sanfilippo & Riedel 1985: 586. — Sanfilippo *et al.* 1985: 651. — *nec* Gourmelon 1987: 35. — Blueford 1988: 247. — Takahashi 1991: 64. — Sashida & Igo 1992: 1306. — Kito & De Wever 1994: 125. — van de Paverd 1995: 118. — Sashida & Uematsu 1996: 48. — Hollis 1997: 32. — Boltovskoy 1998: 31. — Cordey 1998: 54. — Kozlova 1999: 67. — Amon 2000: 32. — Anderson *et al.* 2002: 1002. — De Wever *et al.* 2001: 119-121 (*sensu* emend.). — Suzuki & Gawlick 2003: 164. — Afanasieva *et al.* 2005: S274-275. — Afanasieva & Amon 2006: 111. — Bragin 2007: 971; 2011: 742. — Chen *et al.* 2017: 152. — *nec* Suzuki H. *et al.* 2020: 109.

Actinomminae – Campbell & Clark 1944a: 17. — Chediya 1959: 98. — Petrushevskaya & Kozlova 1972: 515 (*sensu* emend.). — Kozur & Mostler 1979: 10-11 (*sensu* emend.).

Type genus. — *Actinomma* Haeckel, 1861a: 815 [type species by subsequent designation (Campbell 1954: D64): *Haliomma trinacrium* Haeckel, 1861a: 815].

Included genera. — *Actinomma* Haeckel, 1861a: 815 (= *Actinommetta* with the same type species; *Haliommura* **n. syn.**, ? *Rhaphidococcus* **n. syn.**, *Riedelipyle* **n. syn.**; *Dreyerella* synonymized by Burridge *et al.* 2014: 51; *Drymyomma* synonymized by Matsuzaki *et al.* 2015: 7; *Cromyomma* synonymized by Bjørklund 1976: 114; *Echinommura*, *Heliosomura*, *Sphaeropyle* synonymized by Petrushevskaya 1975: 568). — *Cromyechinus* Haeckel, 1882: 453 (= *Cromyodrymus* synonymized by Kozur & Mostler 1979: 12). — *Rhaphidocapsa* Haeckel, 1887: 211. — ? *Sphaeractis* Brandt *in* Wetzel, 1936: 50. — ? *Staurocaryum* Haeckel, 1882: 454. — *Stomatosphaera* Dreyer, 1889: 26. — ? *Stuermeria* Deflandre, 1964: 2119.

Invalid name. — *Heterosphaerina*.

Nomina dubia. — *Acanthosphaera*, *Caryosphaera, Echinomma, Echinommetta, Haliommetta, Heterosphaera, Parastomatosphaera*, *Raphidodrymus, Rhaphidosphaera*, *Sethosphaera.*

Nomen nudum. — *Dermatosphaera*.

Nomen oblitum. — *Chilomma*.

Diagnosis. — Concentric spherical shells with many bladed radial beams. Three shells are present, one or two may also be observed in rare cases. The central structure consists of a double medullary shell. Both shells of the double medullary shell are latticed, of spherical shape, and are connected by many radial beams. Radial spines, if present, arise directly from these radial beams. Endoplasm fills the cortical shell in *Actinomma*.

Stratigraphic occurrence. — Middle Paleocene-Living.

Remarks

The presence of radial spines is not a determining factor in identifying members of the Actinommidae. The Actinommidae are different from the Haliommidae. The latter have non-bladed radial beams. Many junior synonyms of *Actinomma* were determined by finding intermediate forms between three-shelled and four-shelled forms with a countless number of "*Actinomma*" (Bjørklund 1976; Suzuki 2006; Burridge *et al.* 2014). *Cromyechinus* is validated in this catalogue, but several previous papers (Bjørklund 1976: 114; Petrushevskaya 1975: 568; Matsuzaki *et al.* 2015: 7) presented it as a junior synonym of *Actinomma*. The genus name *Acanthosphaera* was used for a single cortical shell with numerous bladed spines, but the name-bearing type specimen of *Acanthosphaera,* archived in the Ehrenberg collection, apparently displays some internal structure (Suzuki *et al.* 2009c: pl. 42, figs 1a-1c). For the classic *Acanthosphaera*, the only viable solution is to apply the term *Rhaphidocapsa*. However, classic representatives of *Acanthosphaera* may be mixed with *Actinomma* (Actinommidae), *Anomalosoma* (Hollandosphaeridae), *Tetrapetalon* (Hollandosphaeridae), a single shelled-form of *Diplosphaera* (young form) (Cladococcidae), *Heliosphaera* (Ethmosphaeridae), *Centro-*

lonche (Centrolonchidae), *Stigmostylus* (Centrolonchidae) or *Stylosphaera* (Stylosphaeridae) consisting of many radial spine-forms if their internal structure is missing, dissolved or unseen; such as in scanning electron microscopic photos. Several genera selected as members of this family (e.g., *Rhaphidocapsa*, *Sphaeractis*, *Staurocaryum*, *Stuermeria*) are still problematic. Unfortunately, this problem could not be resolved in this catalogue due to insufficient reports of these genera. Internal skeletal structure was illustrated for *Actinomma* (Nakaseko & Nishimura 1982: pl. 21, fig. 6; Suzuki 1998b: pl. 3, figs 6-8), *Riedelipyle*-form of *Actinomma* (Nakaseko & Nishimura 1982: pl. 25, fig. 1; Nishimura 2003; pl. 1, figs 6-9) and *Sphaeropyle*-form of *Actinomma* (Suzuki 1998b: pl. 3, figs 13, 14; 2006: figs 3.1-3.15, 4.1-4.10). Protoplasm is illustrated for *Actinomma* (Krabberød *et al.* 2011: figs 1.A-1.D). *Actinomma* can be infected with the Marine Alveolata Group I and II (Ikenoue *et al.* 2016). Some still remain as undescribed genera (e.g., Nakaseko & Nishimura 1982: pl. 6, fig. 2; Sugiyama *et al.* 1992: pl. 1, figs 7, 8).

Validity of genera

Actinomma

The combination of *Actinomma* and *Actinommetta* has the same type species. The morphological commonality among several available genera with *Actinomma* is repeatedly explained in several previous studies (Petrushevskaya & Kozlova 1972; Bjørklund 1976; Burridge *et al.* 2014; Matsuzaki *et al.* 2015).The lectotype of *Acanthosphaera* has probably three concentric shells like *Actinomma* (Suzuki *et al.* 2009c: pl. 42, figs 1a-1b) but it is regarded as a *nomen dubium* because the lectotype is insufficient to observe important distinguishing features such as the number of internal shells. The type species for *Haliommura* was subsequently designated as *Haliomma beroes* in the Atlas due to the invalid designation status by Campbell (1954: D62) and the lectotype of this type species (Suzuki *et al.* 2009c: pl. 36, figs 1a-c) fits exactly with the morphological character of *Actinomma*. *Riedelipyle* was established by Kozur & Mostler (1979: 14) with *Sphaeropyle kuekenthalii* as type species. They differ from the *Sphaeropyle*-form of *Actinomma* by the empty space in the cortical shell, but the *H.M.S. Challenger* Station 267, the next to the Station 268, the type locality, includes "*Riedelipyle*" as the "*Sphaeropyle*" specimen whose internal structure is lost (See supporting image of the Atlas for *Riedelipyle*). The oldest available name is *Actinomma* among them.

Cromyechinus

Cromyodrymus is characterized by branched radial spines and four concentric lattice shells (Campbell 1954: D66). The branched part in the type-illustration of *Cromyodrymus* is identical to the lateral spinule vertical to the radial spine. This kind of lateral spinules is a pre-development condition for a new cortical shell which is reported in the *Sphaeropyle*- and *Dreyeropyle*-forms of *Actinomma* (Suzuki 2006; Burridge *et al.* 2014).

Family Haliommidae Ehrenberg, 1846 *sensu* Suzuki emend. herein

Haliommatina Ehrenberg, 1846: 385 [as a family]; 1847: 54 [as a family]; Ehrenberg 1876: 156. — Schomburgk 1847: 124, 126 [as a family].

Haliommatida – Haeckel 1862: 239, 412, 423 [as a tribe]. — Mivart 1878: 177 [as a subdivision of the subsection Ommatida].

Carposphaerida Haeckel, 1882: 451 [*nomen dubium*, as a tribe]; 1887: 60, 85 [as a subfamily]. — Schröder 1909: 5 [as a subfamily].

Cromyosphaerida Haeckel, 1882: 453 [as a tribe]; 1887: 60, 84 [as a subfamily]. — Schröder 1909: 5 [as a subfamily].

Haliommida – Haeckel 1887: 208, 230 [as a subfamily]. — Schröder 1909: 16 [as a subfamily].

Carposphaerinae – Clark & Campbell 1942: 20 [*nomen dubium*]; 1945: 9. — Chediya 1959: 70.

Cromyosphaerinae – Campbell & Clark 1944a: 9. — Campbell 1954: D50. — Chediya 1959: 72.

Haliomminae – Campbell & Clark 1944a: 16; 1944b: 11. — Clark & Campbell 1945: 17. — Chediya 1959: 97.

Cenosphaeridae Deflandre, 1953: 420-421. — Hollande & Enjumet 1960: 68, 86. — Petrushevskaya 1975: 567. — Dumitrica 1979: 18. — Anderson 1983: 49.

Haliommidae – Petrushevskaya 1975: 568; 1979: 105-106. — Dumitrica 1979: 20.

Type genus. — *Haliomma* Ehrenberg, 1839: 128 [invalid subsequent designation (new subsequent designation in this revision): *Haliomma medusa* Ehrenberg, 1839: 130].

Included genera. — *Cromyosphaera* Haeckel, 1882: 453 (= *Cromyommetta* **n. syn.**; *Cromyommura* synonymized by Matsuzaki *et al.* 2015:7). — *Haliomma* Ehrenberg, 1839: 128 (= *Actinommilla* **n. syn.**, *Cenosphaera* **n. syn.**, *Circosphaera* **n. syn.**; *Thecosphaerella* synonymized by Petrushevskaya 1975: 568). — *Haliommantha* Haeckel, 1887: 230. — *Hexacontella* Haeckel, 1887: 194. — *Melittosphaera* Haeckel, 1882: 451 (= *Conoactinomma* **n. syn.**). — *Pseudostaurosphaera* Krasheninnikov, 1960: 276 (= *Pseudostauroloche* synonymized Kozlova 1999: 75).

Invalid name. — *Circulosphaera*.

Nomina dubia. — *Chaunosphaera*, *Prunosphaera*, *Thecosphaerantha*, *Thecosphaerina*, *Thecosphaeromma*.

Junior homonym. — *Porosphaera* Haeckel, 1887 (= *Chaunosphaera*) *nec* Steinman, 1878.

Diagnosis. — Two to three, rarely more than three, concentric spherical shells with many non-bladed radial beams. Central structure consists of a double medullary shell. Both shells of the double medullary shell are latticed, spherical in shape, and connected by many radial beams. Radial spines may be present or absent. Node-like or by-spine-like short spines are observable in some species. Endoplasm is illustrated in the *Cromyommetta*-form of *Cromyosphaera* and in *Haliomma*. Endoplasm is gray to light gray in color and fills the double medullary shell. It is also distributed around the medullary shell in younger forms and occupies a large portion of the cortical shell. The axopodial system is unknown. No algal symbionts were observed.

Stratigraphic occurrence. — Late Paleocene-Living.

Remarks

Differing from the Actinommidae, the Haliommidae are distinguished by the presence of non-bladed radial beams. This family may include a single-latticed, cortical shell member whose internal shells and radial beams have been lost or dissolved. *Pseudostaurosphaera* is tentatively included in this family as the similarity to the number of shells of *Melittosphaera* was taken into consideration. The taxonomic differences between *Haliomma*, *Haliommantha* and *Melittosphaera* require further study.

The catalogue finally synonymized *Cenosphaera* with *Haliomma* following anatomical observations and rules included in the Code. The type species of *Cenosphaera* (*Cenosphaera plutonis*) was illustrated without any information about its internal structure (Ehrenberg 1854c: pl. 35B-B.IV, fig. 20) . The genus was originally defined as a single shell genus (Ehrenberg 1854b: 237). However, the real type-specimen illustrated and archived in the Ehrenberg collection possessed three concentric shells (Suzuki *et al.* 2009c: pl. 30, figs 1a-1d). Under the principles of the Code, "*every name within the scope of the Code* [...] *is permanently attached to a name-bearing type*." (see the Principles in the Introduction). Conforming to this rule, *Cenosphaera* based on the name-bearing type is a genus with three concentric shells, thus *Haliomma* is the oldest senior synonym for the group of *Cenosphaera* under this sense. This solution avoids an important instability and confusion between one-shelled and three-shelled genera. Conversely, we expanded the definition of *Ethmosphaera* to include the previous one-shelled species in order to avoid further potential confusion. Here, *Hexacontella* is included into Haliommidae due to the presence of non-bladed radial beams directly connected with bladed six radial spines (Dumitrica's personal observation).

Haliomma poses certain problems to common morphology if referring to the type material for *Haliomma medusa* Ehrenberg, 1839 (type species of *Haliomma* in the Ehrenberg collection). The illustration (publishes in pl. 22, figs 34a, 34b of Ehrenberg 1854c) appears to show six radial beams inside the shell. This drawing corresponds to the type specimen found and examined in the Ehrenberg collection (Suzuki *et al.* 2009c: pl. 1, fig. 3d). However, this type material contains several specimens of the morphotype that look identical, if the differing number of radial beams are not considered (Suzuki *et al.* 2009c: pls 1-3). This suggests intraspecific variability of *H. medusa* based on the number of radial beams. In light of this infra-species variation, the definition of *Haliomma* is expanded in so far as to include the morphotypes with variable numbers of radial beams. These morphotypes are generally identified as *Thecosphaera* (with non-bladed radial beams in the original diagnosis), but the representative genus can no longer be used because the type species is a Mesozoic *nomen dubium* (*Thecosphaera unica* Rüst, 1885). Although there is some doubt regarding the shape of the radial beams in the lectotype of *H. medusa*, the presence of non-bladed radial beams is considered specific to *Haliomma*.

Internal skeletal structure was illustrated for *Cromyosphaera* (Nishimura 1992: pl. 1, fig. 11), *Haliomma* (Sugiyama *et al.* 1992: pl. 1, fig. 4; pl. 4, figs 1, 4; Suzuki 1998b: pl. 3, figs 4, 5; pl. 6, figs 3, 4) and *Melittosphaera* (Barwicz-Piskorz 1997: pl. 1, fig. 1; 1999: figs 2.B-2.G). Protoplasm and algal symbionts were documented with epi-fluorescent observation with DAPI dyeing in the *Cromyommetta*-form of *Cromyosphaera* (Zhang *et al.* 2018: 17, fig. 4) and *Haliomma* (Zhang *et al.* 2018: 17, figs 7, 8). Some undescribed genera probably belonging to the Haliommidae remain (Hollis 1997: pl. 3, fig. 6: Jackett & Baumgartner 2007: pl. 1, fig. 37; Jackett *et al.* 2008: pl. 3, fig. 1).

Validity of genera

Cromyosphaera

Cromyommetta is characterized by regular pores with same sizes on the cortical shell, four concentric lattice shells, and numerous radial spines (Campbell 1954: D66). The type species of *Cromyomma* was subsequently designated as *Cromyomma villosum* in the Atlas due to an invalid designation of the type species by Campbell (1954). The "numerous radial spines" in the definition correspond to spiny by-spines in the modern terminological sense. The occurrence of by-spines is not used as a genus criterion in the Haliommoidea. The oldest available name is *Cromyosphaera* among them.

Haliomma

The same type species is designated for *Cenosphaera* and *Circosphaera*. As explained in the remarks for the Ethmosphaeridae and Haliommidae, the lectotype of *Cenosphaera* has three concentric shells with many radial beams, differing from the widely applied concept of a single cortical shell with an empty space. This structure is exactly the same as the current concept of *Thecosphaera* and *Haliomma* in the Atlas. *Actinommilla* was newly established as a subgenus of *Actinomma* by Haeckel (1887: 254) and is marked by irregular pores with dissimilar sizes on the cortical shell and spines covering the entire surface of the cortical shell (Campbell 1954: D65-66). The "spines" is an interpretation of by-spines if the illustration of the type species of *Actinommilla* is referred. Differences in both pores and by-spines on the cortical shell are variable within or between species. *Haliomma* is the oldest available genus among them.

Melittosphaera

Melittosphaera is characterized by one medullary shell, one cortical shell whose pores within hexagonal frames are circular or hexagonal in shape and dissimilar in size, radial beams joining two shells, and no radial spines on the shell surface (Campbell 1954 as *Melitosphaera* [sic]: D48). *Conoactinomma* is defined by three concentric shells, conical protuberances ("tubercles") on the cortical shell, and by-spines on each tubercle (Gorbunov in Kozlova & Gorbovetz 1966: 104). The supporting image of *Conoactinomma* in the Atlas shows a "weak" shadow of the innermost double medullary shell but this type of shell is easily dissolved. In consideration of difference on the resistance on preservation effect, *Conoactinomma* is separated from *Haliomma*. As *Melittosphaera* looks to lose the innermost double medullary shell, this genus is also separated from *Haliomma* until an exact observation could be carried out for both these genera. Roughness of the cortical shell is different between *Melittosphaera* and *Conoactinomma* but this difference is not so significant. It is unnecessary to differentiate them at the genus level. *Melittosphaera* is an available name older than *Conoactinomma*.

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

Heliodiscida Haeckel, 1882: 457 [as a tribe]; 1887: 421, 444 [as a subfamily]. — Schröder 1909: 41 [as a subfamily].

Heliodiscinae – Clark & Campbell 1942: 38; 1945: 22. — Campbell 1954: D82. — Chediya 1959: 127. — Kozur & Mostler 1972: 21 (*sensu* emend.). — Dumitrica 1984: 97-98 (*sensu* emend.).

Sethodiscinidae Chediya, 1959: 124.

Heliodiscidae – Kozur & Mostler 1972: 18-21 (*sensu* emend.). — Petrushevskaya 1975: 576. — Dumitrica 1979: 22. — De Wever *et al.* 2001: 124-125. — Afanasieva *et al.* 2005: S275. — Afanasieva & Amon 2006: 112. — Vishnevskaya 2006: 137; Matsuzaki *et al.* 2015: 14.

Type genus. — *Heliodiscus* Haeckel, 1862: 436 [type species by subsequent designation (Strelkov & Lipman 1959: 444): *Haliomma phacodiscus* Haeckel, 1861a: 815].

Included genera. — *Actinommura* Haeckel, 1887: 255 (= ? *Excentrosphaerella* **n. syn.**). — *Excentrococcus* Dumitrica, 1978: 238. — *Excentrodiscus* Hollande & Enjumet, 1960: 125. — *Heliodiscus* Haeckel, 1862: 436 (= *Heliodiscilla* with the same type species; *Heliocladus* **n. syn.**, *Heliodiscetta* **n. syn.**, *Heliodrymus* **n. syn.**; *Heliodendrum*, *Heliosestilla* synonymized by Kozur & Mostler 1972: 19). — *Helioferrusa* Dumitrica, 2019: 52. — *Phaenicosphaera* Haeckel, 1887: 75 (= *Dreyeropyle* **n. syn.**).

Invalid name. — *Anthomma.*

Nomina dubia. — *Actinommantha*, *Astrophacetta*, *Astrophacus*, *Astrosestilla*, *Astrosestomma, Cerasosphaera*, *Distriactis, Heliodiscura*.

Diagnosis. — Flat to spherical shells with an eccentric microsphere, and a spherical to ellipsoid outer medullary shell. Protoplasm illustrated for *Heliodiscus*. The endoplasm is situated near the double medullary shell and occupies the cortical shell in fully-grown cells. Tens to hundreds of algal symbionts are always found inside the cortical shell. A transparent endoplasm is located in the medullary shell, and this in turn, is enclosed by a reddish endoplasmic cover except on its apical side. The detailed protoplasmic structure is known in *Excentrodiscus*. In *Excentrodiscus*, no axopodial system was identified. The nucleus occupies the outer double medullary shell and its lobate parts sometimes extrude through pores of the outer double medullary shell.

Stratigraphic occurrence. — Early Eocene-Living.

Remarks

The Heliodiscidae show some homeomorphy with the Lithocycliidae and Phacodiscidae. Differing from Heliodiscidae, the latter two families do not have an eccentric innermost microsphere. The innermost microsphere appears to be covered by the second outer shell, but the figure shown in van de Paverd (1995: pl. 38, fig. 6) indicates that the heteropolar microsphere extends outwards from the second outer shell. Internal skeletal structure was illustrated for *Actinommura* (Dumitrica 2019: figs 11.a, 11.b), *Excentrococcus* (Sugiyama & Furutani 1992: pl. 16, fig. 4; Sugiyama *et al.* 1992: pl. 7, figs 1, 2; Suzuki 1998b: pl. 7, figs 11-12?; Dumitrica 2019: figs 8.a, 8.c), *Excentrodiscus* (Dumitrica 2019: figs 9.d-9.g, 10.c), *Heliodiscus* (Sugiyama *et al.* 1992: pl. 5, figs 1-8; van de Paverd 1995: pl. 38, fig. 6), *Helioferrusa* (Dumitrica 2019: figs 9.b, 9.c) and *Phaenicosphaera* (Sugiyama & Furutani 1992: pl. 16, fig. 3). A living image was illustrated for *Heliodiscus* (Takahashi *et al.* 2003: figs 2, 3; Probert *et al.* 2014: S1, Vil 219). Protoplasm and algal symbionts were documented by epi-fluorescent observation with DAPI dyeing for *Heliodiscus* (Zhang *et al.* 2018: 9, fig. 11, p. 11, figs 12, 13, 23; p. 16, fig. 7). Fine protoplasmic structure was illustrated in *Excentrodiscus* (Hollande & Enjumet 1960: pl. 24, figs 4, 5). Algal symbionts of *Heliodiscus* were identified as *Brandtodinium nutricula* by Probert *et al.* (2014).

Validity of genera

Actinommura

Any specimen fitting with *Actinomma capillaceum*, the type species of *Actinommura*, possess a microsphere which is eccentrically located in the outer medullary shell (See the supporting image for *Actinommura* in the Atlas). This character is exactly the same in *Excentrosphaerella*, but the type-illustration for *A. capillaceum* (Haeckel 1887: pl. 29, fig. 6) is drawn with a perfect concentric symmetry to the microsphere. We suspect the quality of this illustration but it has no value to questionably synonymize *Excentrosphaerella* with *Actinommura*. *Actinommura* is an available name older than *Excentrosphaerella*.

Heliodiscus

The combinations of the following genera have respectively same type species: *Heliodiscus* and *Heliodiscilla*, *Heliocladus* and *Heliodrymus*, and *Heliodendrum* and *Heliosestilla*. The specimens identifiable to *Heliodiscus* and *Heliodendrum* (the supporting images for both these genera in the Atlas) have eccentric microspheres, indicating they are members of the Heliodiscidae.

Heliocladus is defined by a smooth surface and no spines on the cortical shell, ten to 20 branched equatorial radial spines and a simple medullary shell (Campbell 1954: D82). *Heliodendrum* differs from *Heliocladus* by simple or branched robust spines on the cortical shell surface (Campbell 1954: D82). We have never met forked equal radial spines like in the type species of *Heliocladus* but the variability in the shape of the equatorial radial rings is commonly observed in the same samples. The development status of robust spines on the cortical shell surface also varies from absent to very robust like the supporting image for *Heliodendrum* in the Atlas in the same samples. These differences between *Heliocladus* and *Heliodendrum* are insufficient for a difference at generic level. The innermost shell of *Heliodiscus* specimens is easily lost by dissolution so as not to be applied as genus criteria.

Phaenicosphaera

Phaenicosphaera is defined by round, irregular but dissimilar pores on the spherical cortical shell and one medullary shell

(Campbell 1954: D48). The translated definition of *Dreyeropyle* in Kozur & Mostler (1979: 14) from German is *"two concentric spherical lattice shells with numerous short main spines. In the area of the large pylome bordered by spines, there are very large pores which are considerably larger than the remaining pores."* The type-illustrations were based from the sketches included in classic papers (Haeckel 1887 for *Phaenicosphaera*; Dreyer 1889 for *Dreyeropyle*). However, the drawings of the type species of *Phaenicosphaera* and *Dreyeropyle* do not show the eccentric microsphere; but it was probably overlooked because the existence of any eccentric microsphere had never been recognized until Hollande & Enjumet (1960) who erected *Excentrodiscus* on the basis of the presence of this structure. The most representative real specimens of *Carposphaera nodosa* for the type species of *Phaenicosphaera* and of *Sphaeropyle heteropora* for type species of *Dreyeropyle* (supporting image of this genus in the Atlas) possess eccentric microspheres in the periphery of the outer medullary shell and more flattened spherical cortical shells. Any specimens which have very large pores like the specimen type illustrated of *Dreyeropyle* have never been found and reported so far. This highly presumes of the occurrence of exaggerated drawings. The real specimens show no significant differences which could correspond to different genus criteria. *Phaenicosphaera* is an available name older than *Dreyeropyle*.

Superfamily Lithelioidea Haeckel, 1862 *sensu* Matsuzaki *et al.* (2015)

Lithelida Haeckel, 1862: 240, 515-519 [as both family and tribe]; 1882: 464 [as a family]; 1884: 29 [as a family]; 1887: 604, 688-691 [as a family].

Litheliacea [*sic*] – Loeblich & Tappan 1961: 226 (= Lithelioidea) [as a superfamily]. — Dumitrica 1984: 101 [as a superfamily].

Ommatodiscilae – Loeblich & Tappan 1961: 225 [as a subsuperfamily].

Sponguracea [*sic*] – Loeblich & Tappan 1961: 223 (= Spongurоidea). — Kozur & Mostler 1981: 37-38 (*sensu* emend.). — De Wever *et al.* 2001: 162.

Spongodruppilae – Pessagno 1973: 50, 75 [*nomen dubium*, as a subsuperfamily]; 1977c: 73; 1977b: 932-933 [as a subsuperfamily].

Lithelioidea – Petrushevskaya 1975: 571-572; 1979: 109; 1986: 130. — Dumitrica 1979: 24. — Matsuzaki *et al.* 2015: 37.

Oviformata [*pars*] Afanasieva & Amon *in* Afanasieva, Amon, Agarkov & Boltovskoy, 2005: S280-281 [as an order of Class Stauraxonaria] (= Spongolonchidae + Staurodruppidae + Gomberellidae + Archaeospongoprunidae + Phaseliformidae). — Afanasieva & Amon 2006: 121 [as an order].

Pyramidata [*pars*] Afanasieva & Amon *in* Afanasieva, Amon, Agarkov & Boltovskoy, 2005: S282 [as an order of Class Stauraxonaria] (= Tormentidae + Ruzhencevispongidae + Pyramispongiidae + Cavaspongiidae). — Afanasieva & Amon 2006: 122-123 [as an order].

Spongurata [*pars*] – Afanasieva *et al.* 2005: S287 [as an order of Class Stauraxonaria] (= Sponguridae + Litheliidae). — Afanasieva & Amon 2006: 130 [as an order].

Sponguroidea – Matsuzaki *et al.* 2015: 24.

Diagnosis. — The central part contains a tiny spherical microsphere and is characterized by distinctive concentric structures, or walls, which are densely and systematically spaced. Many straight radial beams, if present, evenly radiate from the central part and perforate the concentric structure. Shell shape is spherical, oval, elliptical, cylindrical or flat.

Remarks

This superfamily includes Conocaryommidae (although questionably), Litheliidae (Clade L1), Phaseliformidae, Pyramispongiidae and Sponguridae. A molecular phylogenetic analysis indicates a significantly long interval between *Lithelius* and *Ommatogramma* (originally *Spongocore* in Ishitani *et al.* 2012) by Ishitani *et al.* (2012) but it is likely to be close each other in other spumellarians (Sandin *et al.* 2021). The superfamily "Sponguroidea" *sensu* De Wever *et al.* (2001: 162) consists of seven families, and include the Litheliidae. We use Lithelioidea as the valid superfamily because the detailed internal structure of Sponguridae is not well documented yet. Spherical to ellipsoid Lithelioidea were sometimes confounded with Larcospiroidea and Phorticioidea of similar shape under light microscopy. As Lithelioidea lacks the girdle structure, the lithelioid central part does not appear to have a cornered (square) outline under a light microscope. By referring to the diagnosis of Lithelioidea, several Mesozoic families (Gomberellidae Kozur & Mostler 1981; Oertlispongidae Kozur & Mostler in Dumitrica *et al.* 1980; Pyramispongiidae Kozur & Mostler 1978; Spongotortilispinidae Kozur & Mostler in Moix *et al.* 2007) could potentially be classed into this superfamily.

Afanasieva *et al.* (2005) established two orders, namely "Oviformata" and "Spongurata". The combination of both these orders approximately corresponds to the Sponguroidea *sensu* De Wever *et al.* (2001), and thus an order-level classification is inappropriate with regard to consistency in the higher taxonomy of Eukaryotes (Cavalier-Smith *et al.* 2018; Adl *et al.* 2019).

Clade indet.

? Family Conocaryommidae Lipman, 1969

Conocaryomminae Lipman, 1969: 481.

Conocaryommidae – Empson-Morin 1981: 260. — Amon 2000: 29. — De Wever *et al.* 2001: 126-127 (*sensu* emend.). — Afanasieva *et al.* 2005: S277-278. — Afanasieva & Amon 2006: 116.

Type genus. — *Conocaryomma* Lipman, 1969: 184 [type species by original designation: *Conocaryomma aralensis* Lipman, 1969: 186].

Included Genus. — *Conocaryomma* Lipman, 1969:184 (= ? *Conocromyomma* **n. syn.**).

Diagnosis. — Conocaryommidae are characterized by a spherical cortical latticed shell with many tubercles and a central spherical part. The central part consists of three to five tight spherical concentric shells. A large space is present between the cortical shell and the innermost spherical part.

Stratigraphic occurrence. — Early Eocene-Late Eocene.

Remarks

According to one of us (PD), *Conocaryomma* differs from *Praeconocaryomma* Pessagno 1976 due to the presence of a phorticiid-type-type central structure. However, no support photos have been published. *Conocaryomma tuberculata* (Lipman, 1949) illustrated in text-fig. 7 of Lipman (1949) is different from *Praeconocaryomma* (Schmidt-Effing 1980: fig. 5). The latter possesses a central spherical part with a double medullary shell and a relatively larger third spherical shell. The exact same structure to *Praeconocaryomma* was drawn in the type series of the type species for *Conocaryomma* by Lipman (1969: pl. 1, fig. 4; pl. 2, fig. 1) but this drawing is imprecise according to the personal observation (PD).

Validity of genera

Conocaryomma

The internal structure is characteristics in *Conocromyomma* but is unable to be really evaluated due to the lack of illustrations of real specimens except the type specimen. We simply synonymize *Conocromyomma* with *Conocaryomma* in a future study.

Clade L1 (Sandin *et al.* 2021)

Family Litheliidae Haeckel, 1862 *sensu* Suzuki, emend. herein

Lithelida Haeckel, 1862: 240, 515-519 [as both family and tribe]; 1882: 464 [as a family]; 1884: 29 [as a family]; 1887: 604, 688-691 [as a family]. — Zittel 1876-1880: 124 [as a group]. — Mivart 1878: 176 [as a subsection]. — Bütschli 1889: 1968 [as a family]. — *nec* Rüst 1892: 175 [as a family]. — Schröder 1909: 4 [as a family]. — Anderson 1983: [as a family].

Spongocyclida Haeckel, 1862: 239, 452, 469 [as a tribe]. — Stöhr 1880: 119 [as a family].

Ommatodiscida Stöhr, 1880: 115 [as a family]. — Haeckel 1887: 484, 500 [as a subfamily]. — Dreyer 1889: 29 [as a subfamily]. — Schröder 1909: 42 [as a subfamily]. — Chen *et al.* 2017: 140 [as a subfamily].

Spireuma Haeckel, 1882: 464 [*nomen dubium*, as a subfamily].

Spiremida – Haeckel 1887: 691 [*nomen dubium*, as subfamily]. — Schröder 1909: 57 [as a subfamily].

Lithelidae [*sic*] – Popofsky 1908: 230 (= Litheliidae); 1912: 151. — Chediya 1959: 159. — Tan & Tchang 1976: 263. — Tan & Su 1982: 161. — Tochilina 1985: 101-102. — Chen & Tan 1996: 152. — Tan 1998: 274-275. — Kozlova 1999: 102. — Tan & Chen 1999: 260-261.

Litheliidae – Poche 1913: 210. — Campbell 1954: D99. — Riedel 1967b: 295; 1971: 655. — Nakaseko *et al.* 1975: 171. — Petrushevskaya 1975: 572; 1979: 109-110. — Nakaseko & Sugano 1976: 126. — Anderson 1983: 39. — Dumitrica 1984: 101. — Takahashi 1991: 91. — Hollis 1997: 44. — Boltovskoy 1998: 32. — Anderson *et al.* 2002: 1003. — De Wever *et al.* 2001: 164. — Afanasieva *et al.* 2005: S288. — Afanasieva & Amon 2006: 130. — Suzuki *et al.* 2009d: 248. — Chen *et al.* 2017: 157-158.

Ommatodiscinae – Campbell & Clark 1944a: 25; Frizzell & Middour 1951: 24. — Campbell 1954: D92. — Chediya 1959: 133.

Litheliinae – Campbell 1954: D99. — Tan & Tchang 1976: 263.

Spireminae [*sic*] – Chediya 1959: 159 (= Spirematidae) [*nomen dubium*]. — Tan 1998: 275. — Tan & Chen 1999: 261.

Spongocycliidae – Kozur & Mostler 1978: 132-133.

Ommatodiscidae – Kozur & Mostler 1978: 134.

Type genus. — *Lithelius* Haeckel, 1861b: 843 [type species by monotypy: *Lithelius haeckelspiralis* Haeckel, 1861b: 843, *nomen novum* Matsuzaki & Suzuki in Matsuzaki *et al.*, 2015].

Included genera. — *Lithelius* Haeckel, 1861b: 843 (= *Lithospira* with the same type species; ? *Azerbaidjanicus* **n. syn.**). — *Middourium* Kozlova, 1999: 101 (= *Monobrachium* **n. syn.**). — *Spiremaria* Kozlova, 1960: 315 (= *Spiromultitunica* **n. syn.**). — *Spongocyclia* Haeckel, 1862: 469 (= ? *Lithocarpium* **n. syn.**, *Ommatodiscinus* **n. syn.**, *Ommatodiscus* **n. syn.**, *Ommatodisculus* **n. syn.**).

Invalid name. — *Spirema.*

Nomina dubia. — *Spiremarium*, *Spiremidium*, *Spireuma*, *Spongodruppium*.

Diagnosis. — Densely concentric or densely coiled shells, of spherical, ellipsoidal, disk-like and/or flattened lenticular shape, are found around a spherical microsphere. Straight robust radial beams emanate from the microsphere or are adjacent to the innermost shells. Pylome, when present, is found without robust walls. The protoplasm is documented for *Lithelius*. An opaque reddish-brown endoplasm occupies the shell. Hence, the endoplasm is invisible in living specimens. Pseudopodia are found radiating throughout the shell. Isolated skeletal fragments are found scattered in bundles of pseudopodia. Strongly cohesive pseudopodia appear to be immobile. A gelatinous matter is also present. No algal symbionts were observed.

Stratigraphic occurrence. — Early Paleocene-Living.

Remarks

The typical structure of the Litheliidae shows an extremely organized distribution of concentric inner walls, straight radial beams and openings on the walls (*Spiremaria*: Chen 1974: pl. 1, fig. 8; 1975: pl. 9, figs 4, 5; Weaver 1976: pl. 7, fig. 1). This framework produces very straight holes from the surface to the center of the shell (see also Lazarus *et al.* 2005: pl. 11, fig. 19). This characteristic is important in distinguishing the Litheliidae from other similar genera of different families such as *Tholospira* (Larcospiridae). This structure is also well observed in *Lithelius* (Petrushevskaya 1975: pl. 32, figs 1-3).

The Litheliidae can be distinguished from the four-cornered Spongodiscidae (e.g., *Spongaster*) by the presence of concentric-type spongy structures on their corners. They are distinguished from the Euchitoniidae by the presence arms and the three distinctive innermost concentric shells called "margarita". The Litheliidae can also be distinguished from the Spongopylidae in having the walled pylome that penetrates though the internal structure to the center and the lack of straight robust radial beams. The non-walled pylome is illustrated by Chen (1974: pl. 2, figs 1, 2). The Trematodiscidae are easily distinguishable from the Litheliidae by their particular decussated central part. The *Spireuma*-form of *Lithelius* exceptionally lacks the straight robust radial beams, making their differentiation from *Larcopyle*-, or the *Stomatodiscus*-form of *Tholospira* (Larcospiridae) extremely difficult. The former is only distinguishable from the latter by absence of the box- or corner shaped central structure observable under a light microscope. *Spongocyclia* is also sometimes confused with *Flustrella* (Trematodiscidae), *Spongodiscus* (Spongodiscidae) and *Spongopylidium* (Prunopylidae), but it differs from the latter three genera by its tight, very systematic, concentric structure with robust straight radial beams originating from the central part. The difference between *Spiremaria* and *Middourium* can be found by observing additional incomplete concentric walls or a spongy structure, on one or both pole sides. The aforementioned may be conspecific with each other.

Internal skeletal structures were illustrated for *Spiremaria* with thin-section images (Popova 1991: pl. 2, figs 1, 2; 1993: pl. 9, figs 1a-2b; Tochilina 1985: pl. 3, fig. 3) and broken specimens (Chen 1974: pl. 1, fig. 4; Weaver 1975: fig. 2.4; 1976: pl. 7, fig. 1; Sugiyama *et al.* 1992: pl. 7, fig. 7), for the *Spirema*-form of *Lithelius* (Popova 1991: pl. 2, fig. 6; Tochilina 1985: pl. 2, figs 1, 2) and for the *Ommatodiscus*-form of *Spongocyclia* (O'Connor 1999: fig. 6M; Ogane & Suzuki 2006: pl. 2, fig. 7). This structure was also documented for *Middourium* (Tochilina 1985: pl. 2, figs 6, 9; Barwicz-Piskorz 1999: figs 2.J-2.L, 3.A-3.B; Jackett & Baumgartner 2007: pl. 1, fig. 35), the *Spireuma*-form of *Lithelius* (Barwicz-Piskorz 1999: figs 2.B-2.D; Nishimura 2001: pl. 2, fig. 16) and *Spongocyclia* (Li *et al.* 2018: figs 7.3, 7.4). Images of living specimens were obtained for *Lithelius* (Suzuki *et al.* 2013: figs 7.2, 7.4-7.6). Algal symbionts and protoplasm were documented using epi-fluorescent DAPI dyeing techniques and other dyeing methods for *Lithelius* (Ogane *et al.* 2014: pl. 1, figs 1-2). Undescribed genera still remain (Dumitrica 1973b: pl. 5, figs 4-6; Hollis 1997: pl. 10, fig. 9).

Validity of genera

Lithelius

The current concept of *Lithelius* is helpless to understand differences in the genera of the Litheliidae. This genus is characterized by its spherical to subspherical shape. No pylome in general is presented; but if the skeleton develops a "pylome-structure", that always opens towards the outermost hard cortical shell ("crust" in the terminology of Ogane & Suzuki 2006). In other words, it never penetrates through any other internal structure. The drawing of the type species for *Azerbaidjanicus* appears to indicate a convex-lens shape but in the original description Mamedov (1973: 61) clearly wrote about "a regularly spherical form" and, thus, *Azerbaidjanicus* is synonymized with *Lithelius*. The oldest available name is *Lithelius*.

Middourium

Both *Middourium* and *Monobrachium* were simultaneously established by Kozlova (1999: 101 for *Middourium* and 102 for *Monobrachium*). The translated description of *Middourium* from Russian follows. "*Sponguridae with a regular elliptical shell slightly truncated near polar areas; 10 or more lattice internal shells distributed in tight spirals separated by intervals no larger than 7-10 µm. Conical pylomes at each area. Shell sometimes enveloped by a thin porous plate.*" That of *Monobrachium* follows. "*Sponguridae with a shell elongated along a single axis composed of a sub-spherical or plainly ellipsoidal part and a single large appendage of also ellipsoidal shape. The thickly spongious tissue of the internal ellipsoidal part seems to form concentrical of closed ellipsoidal envelopes which are very closely distributed. Pylome-shaped aperture may be located at both pole of the shell, or a single one, and the whole shell may be enveloped by a finely porous envelope*." The major difference written in the original description is the presence of a single large appendage only in *Monobrachium*. Hetero-coverage on one pole of the ellipsoidal shell commonly occurs during ontogeny so this difference does not correspond to a genus level. Both these genera have also a conical pylome at each pole. Presence of the pylome may be recognized with tiny spinules around the pylome. Some confusion may occur when there is a single appendage at one polar end, so that *Middourium* is selected as valid name. The taxonomic position of *Middourium* at the family level needs to be reexamined because the support image of this genus in the Atlas has a walled pylome.

Spiremaria

Spiremaria is characterized by a highly dense concentric structure and an ellipsoidal to ovoidal shape. Almost all outer concentric shells cover throughout the shell. The original definition of *Spiromultitunica* specifies an ellipsoidal shape and a dense convolution (Tochilina & Popova *in* Tochilina 1985: 105). As referred to a thin sectioned specimen of *Spiromultitunica* (Popova 1993: pl. 9, fig. 2), this genus has the same internal structure and shape as *Spiremaria*. Kozlova (1960: 315) does not comment the occurrence of a pylome in *Spiremaria* whereas Tochilina & Popova (*in* Tochilina 1985) described a pylome at one pole. However, this "pylome-structure" opens on the outermost hard cortical shell ("crust" in the terminology of Ogane & Suzuki 2006) and it never penetrates through any other internal structure. Such ambiguous pylome is insufficient to clearly establish a division into two genera, and thus *Spiromultitunica* is synonymized with *Spiremaria*. Although the independency of *Spiremaria* from *Lithelius* needs a phylogenetic study of the Litheliidae, typical *Lithelius* always lack pylome or pylome-like structures on the crust.

Spongocyclia

Spongocyclia is distinguished from any other genera in the Litheliidae by a convex-lens discoidal shape. The independency of *Spongocyclia* from *Spongodiscus* has long been in debate among authors of this paper. The view perpendicular to the equatorial plane of the disk-shaped shell is clearly different from that of the typical *Spongodiscus* as shown in the lower photo of the supporting image for *Spongocyclia* in the Atlas. This photo shows obvious concentric structures but no-spongy structure. *Ommatodiscus* has the same type species as *Ommatodisculus*. Campbell (1954: D92) indicated an elliptical disc with two pylomes for *Ommatodiscus* and a circular disk with two pylomes for *Ommatodiscinus*, but one opening only is recognizable on the type-illustrations of both these genera. The translated definition of *Lithocarpium* by Stöhr (1880: 97) from German mentioned "*an elliptical shell with a tubular peristome, and a* *circular opening with a corona of small teeth*", and this explanation was insufficient to specify this genus. Worse, Campbell (1954: D119) wrongly classified *Lithocarpium* into the Nassellaria with a complete mismatched illustration of the nassellarian *Carpocanium* species on fig. 59.5. As any taxonomic act must be based on name-bearing specimens under ICZN (1999), the type-illustration prioritized the description. The type-illustration is surely different with a circular disk for *Ommatodiscinus* and an elliptical disk for *Ommatodiscus*, but this difference is too small to separate them independently. *Lithocarpium* looks to have a densely spiral concentric structure and a lobate shell according to Petrushevskaya (1975: 572). These three genera have one opening on one side but this opening does not form a true pylome (See the supporting image for *Ommatodiscus* in the Atlas). Such "pylome-structure" always opens on the outermost hard cortical shell ("crust" in the terminology of Ogane & Suzuki 2006) and it never penetrates inside the skeleton. In consideration of this character, no obvious differences can be found among *Spongocyclia*, *Ommatodiscus*, *Ommatodiscinus* and *Lithocarpium*. The oldest available name is *Spongocyclia* among them.

Family Phaseliformidae Pessagno, 1972

Phaseliformidae Pessagno, 1972: 273; 1976: 26. — Dumitrica 1995: 26-27. — Hollis 1997: 48. — De Wever *et al.* 2001: 165. — Afanasieva *et al.* 2005: S281 [in Order Oviformata]. — Afanasieva & Amon 2006: 121.

Type genus. — *Phaseliforma* Pessagno, 1972: 274 [type species by original designation: *Phaseliforma carinata* Pessagno, 1972: 274, pl. 22, fig. 1].

Included genus (Cenozoic only). — *Phaseliforma* Pessagno, 1972: 274.

Diagnosis. — According to De Wever *et al.* (2001: 165), the family Phaseliformidae is characterized by "*test subellipsoidal, thicker at anterior end than at posterior end. Internal meshwork more or less concentric*".

Stratigraphic occurrence. — Early Hauterivian-Early Paleocene.

Remarks

The practical internal structure of Phaseliformidae has not been illustrated as of yet. Thus, their taxonomic position tentatively follows that of De Wever *et al.* (2001: 165). As for *Phaseliforma*, they appear to belong to the Spongodiscidae, Spongobrachiidae, Spongopylidae or Litheliidae due to the observed presence of spongy structures. However, the molecular phylogenetic study indicates that a spongy structure, in and of itself, should not be a determining factor in defining a single group.

Family Pyramispongiidae Kozur & Mostler, 1978 *sensu* O'Dogherty (1994)

Pyramispongiidae Kozur & Mostler, 1978: 168. — O'Dogherty 1994: 304. — De Wever *et al.* 2001: 165-166 (*sensu* emend.). — Afanasieva *et al.* 2005: S283 [in Order Pyramidata]. — Afanasieva & Amon 2006: 124.

Type genus. — *Pyramispongia* Pessagno, 1973: 78 [type species by original designation: *Pyramispongia magnifica* Pessagno, 1973: 80].

Included genus (Cenozoic only). — *Pyramispongia* Pessagno, 1973: 78 (= *Nodotetraedra* synonymized by Baumgartner *et al.* 1995: 464).

Diagnosis. — According to O'Dogherty (1994: 304), the family includes tetrahedral spumellarians with very spongy meshwork, having only a tetrahedral cortical shell.

Stratigraphic occurrence. — Late Tithonian-Late Paleocene.

Remarks

The Pyramispongiidae were once placed in the superfamily Sponguroidea by De Wever *et al.* (2001: 166). The exact taxonomic position of the family Pyramispongiidae needs to be reexamined in the future as the paratype of *Pyramispongia magnifica* Pessagno, 1973, the type species of the representative genus (Pessagno 1973: pl. 20, fig. 1), possesses an obvious rigid cortical shell with an empty space between the rigid cortical shell and the outer spongy shell. The family Intermediellidae Lahm, 1984 was questionably synonymized with the Pyramispongiidae in De Wever *et al.* (2001). Later the "Intermediellidae" were transferred to the family Tritrabidae Baumgartner, 1980 as a subfamily (Dumitrica *et al.* 2013: 353-354). To exclude the Intermediellidae, we follow the definition of O'Dogherty *et al.* (2009b: 304).

Family Sponguridae Haeckel, 1862

Spongurida Haeckel, 1862: 239, 447-452 [as a family]; 1887: 288, 339-341 [as a family]. — Zittel 1876-1880: 124 [as a group]. — Stöhr 1880: 86 [as an order]. — Bütschli 1889: 1956 [as a family]. — *nec* Rüst 1892: 158. — *nec* Cayeux 1894: 206. — Schröder 1909: 3 [as a family]. — Anderson 1983: 23.

Sponguridae – Claus 1876: 160. — Popofsky 1912: 115. — Clark & Campbell 1942: 36; 1945: 20. — Campbell & Clark 1944a: 21; 1944b: 13. — Frizzell & Middour 1951: 22. — Campbell 1954: D73. — Orlev 1959: 441. — Chediya 1959: 112. — Pessagno 1973: 56; 1977b: 931. — Petrushevskaya 1975: 576-577 (*sensu* emend.); 1979: 114 (*sensu* emend.). — Nakaseko & Sugano 1976: 122. — Dumitrica 1979: 26; 1984: 100. — Kozur & Mostler 1981: 38-39 (*sensu* emend.). — De Wever 1982b: 181. — Tan & Su 1982: 150. — *nec* Noble 1994: 27-28. — Dumitrica 1995: 26. — Chen & Tan 1996: 151. — Hollis 1997: 46. — Cordey 1998: 75. — Tan 1998: 196. — Kozlova 1999: 101. — Tan & Chen 1999: 201. — Amon 2000: 51. — De Wever *et al.* 2001: 166. — Afanasieva *et al.* 2005: S287-288 [in Order Spongurata]. — Afanasieva & Amon 2006: 130. — Bragin 2007: 999. — Chen *et al.* 2017: 136.

Spongida [*sic*] – Mivart 1878: 176 [as a subsection].

Spongellipsida Haeckel, 1887: 341 [*nomen dubium*, as a subfamily].

Spongodruppida Haeckel, 1887: 341, 348 [*nomen dubium*, as a subfamily].

Spongellipsinae – Clark & Campbell 1942: 36 [*nomen dubium*]; 1945: 20. — Campbell & Clark 1944a: 21; 1944b: 13. — Chediya 1959: 112.

Spongodruppinae – Campbell & Clark 1944a: 22 [*nomen dubium*]. — Campbell 1954: D74. — Chediya 1959: 114.

Spongurinae – Frizzell & Middour 1951: 22. — Campbell 1954: D73. — Pessagno 1973: 57.

Type genus. — *Spongurus* Haeckel, 1861b: 844 [type species by monotypy: *Spongurus cylindricus* Haeckel, 1861b: 845].

Included Genus. — *Ommatogramma* Ehrenberg 1861b: 832 (= *Spongurus* **n. syn.**, *Spongocorisca* synonymized by Petrushevskaya & Kozlova 1972: 528; ? *Spongurantha* **n. syn.**, *Spongurella* **n. syn.**).

Nomina dubia. — *Spongellipsarium*, *Spongellipsidium*, *Spongellipsis*, *Spongocore*, *Spongocorina*, *Spongodruppa*, *Spongodruppula*, *Spongolena*, *Sponguromma*, *Stypolarcus*.

Diagnosis. — Shell is cylindrical to ellipsoidal in shape without bi-polar radial spines. Test filled with a structureless spongious tissue with a microsphere. Pylome may exist. No radial beams penetrating though the spongious meshwork were recognized.

The gray endoplasm is embedded in the spongy shell. No endoplasm is present outside of the shell. The protoplasm, emitting in an auto-fluorescent red with DAPI dyeing, occupies the spongy shell, with the exception of both inflated ends of the shell. Granular organisms of an unknown origin are distributed throughout the internal periphery of the spongy shell. Gelatinous matter covers the whole area around the shell to include a part of the spines.

Stratigraphic occurrence. — Late Campanian-Living.

Remarks

Many genera (*Amphicarydiscus*, *Ommatogramma*, *Spongocore*, *Spongocorisca*) were once synonymized with *Ommatogramma* (Petrushevskaya & Kozlova 1972: 528; Suzuki *et al.* 2009d: 247; Matsuzaki *et al.* 2015; 24), but the synonymy of *Ommatogramma* has been updated herein. As noted in Matsuzaki *et al.* (2015: 24), *Spongocore* cannot be used as a valid genus name due the absence of an illustrated type species. The genus *Ommathymenium* is often confused with *Ommatogramma* as a result of the ambiguous type drawings of these genera. Specimens classifiable into *Ommathymenium* have a phorticiid-type internal structure and consequently both genera must be separated at family or higher level. It is noted that Bragina (2003: 249) established a new species "*Spongurus cylindricus*" from the Cenomanian of Sakhalin, Far East, but it is a primary junior homonym of "*Spongurus cylindricus*" from the seawater in Messina, Haeckel (1861b: 845).

Living images (Suzuki & Not 2015: figs 8.8.15, 8.10.1) of protoplasm and algal symbionts by epi-fluorescent observation with DAPI dyeing (Zhang *et al.* 2018: 14, figs 27, 28) were documented.

Validity of genera

Ommatogramma

Spongurus has the same type species as *Spongurella*. Previous studies classified *Ommatogramma* into the Euchitonidae (Campbell 1954: D86), but its lectotype (Suzuki *et al.* 2009c: pl. 63, figs 4a-c) obviously does not fit with the classical definition of the Euchitonidae that are defined as "*flat disc-shaped shell* [...] *concentric rings* [...]" written in Campbell (1954: D86). The four available genera synonymized here are defined by the followings characters: two opposite similar arms with distal terminal spines and a complete lattice-mantle for *Ommatogramma* (Campbell 1954: D88); spongy shell without polar spines or lattice-mantle, tiny spinules throughout test, homogenous spongy framework everywhere for *Spongurus* (Campbell 1954: D74); absence of tiny spinules throughout surface as a subgenus of *Spongurus* for *Spongurantha* (Campbell 1954: D74); and solid shell with lattice-mantle but without terminal spines, shell distinctly three-joined for *Spongocorisca* (Campbell 154: D74 as *Spongocorissa* [*sic*]). The development of a lattice-mantle, tiny spinules through the test and terminal spines from two opposite ends of the test is variable within a species or among species. *Spongocorisca* is distinguished from the other genera by its three-jointed appearance but the type specimens of *Ommatogramma* and *Spongurus* also show a similar appearance. The name *Spongurus* has been widely used as a valid genus name but *Ommatogramma* was selected as the valid genus by Petrushevskaya & Kozlova (1972: 528). In addition, *Ommatogramma* is dated on 13 December 1860 and *Spongurus* is dated on 20 December 1860.

Clade L2 Sandin *et al.* (2021)

Superfamily Spongopyloidea Dreyer, 1889 n. stat. *sensu* Suzuki emend. herein

Spongopylida Dreyer, 1889: 42 [as a subfamily].

Diagnosis. — Test flat-disk shaped, ovoidal and spherical. Funnel-like pylome, aperture (large opening) or relevant structure is present. Very thick cortical shell develops in spherical to ovoid pattern. Flat-disc type, shows a concave central part, a peripheral inflation, and a circular depression zone between the central and peripheral zone. A margarita defined by Ogane & Suzuki (2006) is positioned in the center (Spongopylidae) or somewhere (Cristallosphaeridae). The outer around the margarita looks spongy, formed by highly dense concentric structure; however, it does not form a perfect concentrically wall (like occurs in Trematodiscidae). Endemic form might be reported in *Calcaromma* due to the loss of all siliceous skeletal parts except the margarita. The presence of a thick axoflagellum might be linked to a funnel-like pylome.

Remarks

This superfamily includes, Spongopylidae, Cristallosphaeridae and ? Prunopylidae. This superfamily corresponds to Clade L2 of Sandin *et al.* (2021) based on molecular data obtained for *Schizodiscus* and *Spongobrachiopyle* (=*Spongopyle* in Sandin *et al.*, 2021; Spongopylidae) and *Calcaromma* (Cristallosphaeridae). The family Prunopylidae is questionably assigned in this superfamily considering the presence of a Spongopylidae-like pylome, an aperture and a very thick outermost cortical shell, similar to that observed in *Enalomelon*. The diagnosis of the superfamily is based only on Spongopylidae and Cristallosphaeridae only, because little is known about the internal structure of the genera assigned in Prunopylidae.

Family Spongopylidae Dreyer, 1889 *sensu* Suzuki emend. herein

Spongopylida Dreyer, 1889: 42 [as a subfamily].

Spongopylinae – Campbell 1954: D94.

Spongopylidae – Kozur & Mostler 1978: 159.

Type genus. — *Spongopyle* Dreyer, 1889: 42 [type species by subsequent designation (Campbell 1954: D94): *Spongopyle setosa* Dreyer, 1889: 43].

Included genera. — *Schizodiscus* Dogiel *in* Dogiel & Reshetnyak, 1952: 8. — *Spongobrachiopyle* Kozur & Mostler, 1978: 160. — *Spongopyle* Dreyer, 1889: 42 (= *Spongopylarium* with the same type species). — *Spongospira* Stöhr, 1880: 120.

Nomen dubium. — *Spiropyle*.

Diagnosis. — The central part consists of a pit-like small microsphere directly connected to a tunnel-like pylome. The shell has a flat to simple, convex-lens shape (e. g. *Spongopyle* and *Spongobrachiopyle*). Another type is characterized by the lateral profile of the disk showing: 1) a simple convex-lens shape; or 2) an inflated convex-lens shape in the center, thinner zone or a groove outside the central part, as well as a thick peripheral spongy zone (*Schizodiscus*). A single, walled tunnel-like pylome is extended from, or near, the microsphere. The general spongy structure shows many discontinuous rings having very short radial beams or other fine columnar beams connected between adjacent discontinuous rings. These discontinuous rings and radial beams resemble a "structureless" sponge. This "structureless sponge" is highly dense near the central part and becomes looser away from the center
Protoplasm was reported for *Schizodiscus*, *Spongobrachiopyle* and *Spongospira*, but these characters will be described in the remarks as there are concerns about whether or not they truly belong to the same family. No algal symbionts were found.

Stratigraphic occurrence. — Late Eocene-Living.

Remarks

The independency of the Spongopylidae from the Spongodiscidae was recognized by molecular phylogenic studies (Ishitani *et al.* 2012). After updating the taxonomic name of Ishitani *et al.* (2012), *Schizodiscus* was transferred to Trematodiscidae (originally Stylodictyidae in Matsuzaki *et al.* 2015: 25). New molecular phylogenetic analysis on more genera and species resulted in the grouping of *Schizodiscus* and *Spongobrachiopyle* (originally *Spongopyle*) into a cluster (Cluster L) independent from the Trematodiscidae (Cluster J). Subsequently, we divided the "Stylodictyidae" of Matsuzaki *et al.* (2015) into two families: Spongopylidae and Trematodiscidae here.

A typical image of the walled tunnel-like pylome is given in pl. 39, fig. 3b of Nakaseko & Nishimura 1982. Under good conditions, the walled-pylome is distinctive under a light microscope (Kruglikova 1969: fig. 4.29). In identifying the genera of this family, the important points are: (a) the actual density of the "spongious part" with regard to the "thickness effect" under a light microscope, (b) the presence of primary radial beams, (c) the "wall type" of the pylome, and (d) the zonal structure of the disk from the center to the peripheral zone in relation with the "thickness effect". The radial spines disconnected from radial beams should be ignored at the genus level. The key differences between the Spongopylidae and the Trematodiscidae are that: (a) the pylome space is directly connected to the microsphere, (b) a porous but discrete wall surrounds the pylome, and (c) the area outside of the microsphere is structure-less, of non-hoop type so it might appear as fine bubbles in certain cases. Typical Spongopylidae have a structureless spongious disk so that *Spongospira* may not belong to this family. Many genera are in open nomenclature due to the difficulty of recognition about the detailed "spongy" and central structures. Many genera remain undescribed (e.g., Ogane & Suzuki 2006: pl. 1, figs 3-4).

The internal skeletal structure of *Spongobrachiopyle* was illustrated (Nakaseko & Nishimura 1982: pl. 39, figs 1-3; pl. 40, figs 5, 6). Illustration of living forms was documented for *Spongobrachiopyle* (Suzuki & Not 2015: fig. 8.10.10) and *Schizodiscus* (Suzuki & Not 2015: fig. 8.10.3). Protoplasm was analyzed with epi-fluorescent DAPI dyeing techniques in *Schizodiscus* (Zhang *et al.* 2018: 14, fig. 16), *Spongobrachiopyle* (Zhang *et al.* 2018: 19, fig. 10) and *Spongospira* (Zhang *et al.* 2018: 13, fig. 19). Following epi-fluorescent DAPI dyeing analyses, the protoplasm of aforementioned genera are defined below.

Validity of genera

Schizodiscus
The endoplasm is white in the center, opaque red in major thinner disk parts, with white zones in the thicker peripheral disk parts and reddish granule zones on the periphery of the disk. The DAPI autofluorescent red endoplasm is distributed in a U-letter shape. Most of these peripherical parts overlap in the disk's thin opaque red zone. This difference is marked in this genus.

Spongobrachiopyle
The dark grey endoplasm fills the inner shell. The protoplasm emits an autofluorescent-whitish light blue with DAPI in the spongy shell and does not include the peripheral area beneath the gown. A thick, strong axoflagellum is affixed to the walled pylome and extends outward. Pseudopodia radiate throughout the shell. This difference is marked in this genus.

Spongospira
The protoplasm fills the center, the area around the pylome from the center to the periphery, and the thick peripheral area. This difference is marked in this genus.

Family Cristallosphaeridae Popofsky, 1912

Cristallosphaeridae Popofsky, 1912: 155 — Campbell 1954: D44 [in Collodaria] — Chediya 1959: 67 [in Collodaria].

Type genus. — *Cristallosphaera* Popofsky, 1912: 155 [type species by monotypy: *Cristallosphaera cristalloides* Popofsky, 1912: 155] = junior subjective synonym of *Calcaromma* Thomson, 1877: 99 [type species by monotypy: *Calcaromma calcarea* Thomson, 1877: fig. 51 and its associated explanation].

INCLUDED GENERA. — *Calcaromma* Thomson, 1877: fig. 51 and its associated explanation (page number is variable in editions of the book) (= *Cristallosphaera* **n. syn.**). — *Enalomelon* Sugiyama, 1992b: 195.

DIAGNOSIS. — The protoplasm or outermost shell (if existent) is spherical. Very small, convex lens-shaped spongodiscid siliceous skeleton lies in in the center of the endoplasm or is located somewhere within a large spongy siliceous meshwork. Algal symbionts are found surrounding the endoplasm. In *Calcaromma*, several star-like materials characterized by an optical anisotropy are scattered in the extracapsular zone of the ectoplasm. These star-like materials are dissolved by acid.

REMARKS

Calcaromma is believed to lack siliceous skeletons and was subsequently considered as belonging to Collodaria (Haeckel 1862; Popofsky 1913; Campbell 1954; Chediya 1959). Hollande & Enjumet (1960) carefully examined cytological and skeletal characters of *Calcaromma* (originally *Cristallosphaera*), and discovered a very small, encrypted, convex lens-shaped spongodiscid siliceous skeleton with a cytological structure similar to that of the flat-shaped spongy skeleton of spumellarians (Hollande & Enjumet 1960: pl. 15, fig. 10). They concluded that this genus belongs to the classical Spongodiscidae. The presence of the siliceous convex lens-shaped skeleton and the taxonomic position was confirmed by molecular phylogenetic analysis (Sandin *et al.* 2021). According to Sugiyama (1992b), *Enalomelon* is a member of some flat-shaped spongy spumellarian family due to the presence of a very small convex lens-shaped spongodiscid siliceous skeleton within the outermost spherical shell as well as the development of a spongy meshwork. The internal skeletal structure of *Enalomelon* is illustrated (Chen 1974: pl. 1, figs 3-6; 1975: pl. 10, figs 1-3; Sugiyama 1992b: pl. 11, figs 1-5). Images of living specimens (Suzuki & Not 2015: fig. 8.8.7; Matsuoka *et al.* 2017: appendix A), of the fine cytological structure (Hollande & Enjumet 1960: pl. 15, fig. 10; pl. 35, figs 1-3) and of algal symbionts (Zhang *et al.* 2018: 11, fig. 2) were published for *Calcaromma*.

VALIDITY OF GENERA

The type specimen of *Cristallosphaera* is a shrinking *Calcaromma* specimen in the fixative medium. *Calcaromma* is an older available name than *Cristallosphaera*.

Clade indet.

Family PRUNOPYLIDAE Poche, 1913

Prunopylidae Poche, 1913: 207-209.

Prunopyle [*sic*] – Tochilina 1985: 96 (= Prunopylidae).

TYPE GENUS. — *Prunopyle* Dreyer, 1889: 18 [type species by subsequent designation (Campbell 1954: D72): *Prunopyle pyriformis* Dreyer, 1889: 18].

INCLUDED GENERA. — *Prunopyle* Dreyer, 1889: 18. — *Spongopylidium* Dreyer, 1889: 46.

NOMINA DUBIA. — *Ovulopyle*, *Spirotunica*.

DIAGNOSIS. — One robust, thick-walled oval to oblong shell with a large opening. Internal structure invisible or ambiguous with a thick-walled shell. Taxa without internal structure are also included.

STRATIGRAPHIC OCCURRENCE. — Late Eocene-Living.

REMARKS

This family is an artificial group for the members that are defined above. Anatomical study should be carried out for the taxa of this group by sectioned specimens. The position of this family into the superfamily is also tentative.

Superfamily PHORTICIOIDEA Haeckel, 1882 n. stat.

Phorticida Haeckel, 1882: 464 [as a subfamily]; 1887: 604, 708 [as a family].

Larnacillilae – De Wever *et al.* 2001: 153 [as a subsuperfamily].

Larnacillioidea [*sic*] – Afanasieva *et al.* 2005: S287 (= Larnacilloidea). — Afanasieva & Amon 2006: 129.

DIAGNOSIS. — Spumellarians with a heteropolar and ring-shaped (or ringed-ribbon shaped). Microsphere having two pairs of opposite gates growing in younger, or all stages, by formation of systems of three successively larges elliptical latticed girdles, which are disposed in three mutually perpendicular planes.

REMARKS

The superfamily name “Larnacillilae” is herein replaced by Phorticioidea. The type genus of the former is a *nomen dubium* as the type species is unillustrated. The Phorticioidea consist of the Amphitholidae (Clade M1), Circodiscidae, Cryptolarnaciidae (Clade M2), Histiastridae and Phorticiidae. The Phorticioidea genera with girdles (e.g., *Phorticium*, *Qiuripylolena*, *Sphaerolarnacillium*) are differentiated from the Larcospiroidea genera with girdles (e.g., *Pylospira*, *Tholospira*, *Sphaeropylolena*, *Pylozonium*, *Tetrapyle*). Identifying Phorticioidea members is quite difficult as they appear to change appearance in different orientations, even when observing the same specimen (Tan & Chen 1990: pls 1, 2; Itaki 2009: pl. 10, figs 1-5, 10, 12, 13; Ogane & Suzuki 2009: figs 2-4; *et al.* 2013: figs 3, 4). By using three-dimension resin models, the different orientations at different growth stages were illustrated by Zhang & Suzuki (2017: 8, fig. 3). To understand the organization of the skeleton is essential to gather: the absolute and relative geometrical cartesian coordinates, their mathematical expression, and the difference between anatomical recognition and visual perception under light microscopy (Zhang & Suzuki 2017: 5-8, 9-13). A failure to understand these points will surely lead to a series of fruitless debates. Phorticioidea are only distinguishable from Larcospiroidea in the absence of an S1a-girdle in the sense of Zhang & Suzuki (2017). The appearance of the triangle itself has no value in determining taxonomy. Instead of an S1a-girdle, a G1a girdle is directly attached to the microsphere (S1a) (see fig. 5.5 in Zhang & Suzuki 2017). This structure can be observed in several cases under a light microscope with the Plan or S-Plan level objective lens, and with a correction ring to adjust the optical spherical abbreviation (Zhang & Suzuki 2017: 4). The view from the overlapped orientation of the microsphere (S1a) and S1a-girdle in the Phorticioidea resembles the central part of Larcospiroidea (compare figs 5.2 with fig. 5.5 in Zhang & Suzuki 2017). In this view, the central part appears spherical in Phorticioidea.

Clade M1 (Sandin *et al.* 2021)

Family Amphitholidae Haeckel, 1887 n. stat. *sensu* De Wever *et al.* (2001)

Amphitholida Haeckel, 1887: 663 [as a subfamily].

Archidiscaria Haeckel, 1887: 484 [*nomen dubium*, as a section between subfamily and family].

Archidiscida Haeckel, 1887: 484-485 [*nomen dubium*, as a subfamily]. — Schröder 1909: 42. — Chen *et al.* 2017: 138 [as a subfamily].

Tholonida Haeckel, 1887: 604, 660-663 [*nomen dubium*, as a family]. — Bütschli 1889: 1967 [as a family]. — *nec* Rüst 1892: 141. — Schröder 1909: 4 [as a family]. — Anderson 1983: 24 [as a family].

Staurotholida Haeckel, 1887: 663, 670 [*nomen dubium*, as a subfamily].

Cubotholida Haeckel, 1887: 663, 677 [as a subfamily].

Tholoniidae – Poche 1913: 210 [*nomen dubium*]. — Campbell 1954: D98. — Riedel 1967b: 295; 1971: 655. — Nakaseko *et al.* 1975: 171. — Nakaseko & Sugano 1976: 126. — Riedel & Sanfilippo 1977: 867. — Petrushevskaya 1979: 110. — Anderson 1983: 39. — Dumitrica 1984: 101. — Takahashi 1991: 89. — Chen & Tan 1996: 152. — Boltovskoy 1998: 32. — Tan 1998: 270-271. — Anderson *et al.* 2002: 1003. — De Wever *et al.* 2001: 157-158. — Afanasieva *et al.* 2005: S287. — Afanasieva & Amon 2006: 130. — Matsuzaki *et al.* 2015: 35-36.

Archidiscinae – Campbell 1954: D88 [*nomen dubium*]. — Chediya 1959: 132.

Amphitholinae – Campbell 1954: D98. — Chediya 1959: 156.

Staurotholinae – Campbell 1954: D98 [*nomen dubium*]. — Chediya 1959: 157.

Tholoniinae – Campbell 1954: D98 [*nomen dubium*]. — Dumitrica 1989: 234, 237.

Tholonidae [*sic*] – Chediya 1959: 156 [*nomen dubium*] (= Tholoniidae). — Tan & Su 1982: 160. — Tan & Chen 1999: 257. — Chen *et al.* 2017: 156.

Cubotholinae – Chediya 1959: 157.

Type genus. — *Amphitholus* Haeckel, 1887: 666 [type species by subsequent designation (Campbell 1954: D98): *Amphitholus artiscus* Haeckel, 1887: 666] = junior subjective synonym of *Tholomura* Haeckel, 1887: 672 [type species by monotypy: *Tholoma metallasson* Haeckel, 1887: 672].

Included genera. — *Tholomura* Haeckel, 1887: 672 (= *Amphitholonium*, *Cubotholonium*, *Staurotholoma* synonymized by Matsuzaki *et al.* 2015: 36; *Amphitholissa* **n. syn.**, *Amphitholura* **n. syn.**, *Amphitholus* **n. syn.**, *Cubotholissa* **n. syn.**, *Cubotholus* **n. syn.**, *Staurotholura* **n. syn.**, *Tholartella* **n. syn.**, *Tholartus* **n. syn.**, *Tholocubitus* **n. syn.**, *Tholodes* **n. syn.**, *Tholocubulus* **n. syn.**, *Tholocubus* **n. syn.**, *Tholoma* **n. syn.**, *Tholomantha* **n. syn.**, *Tholonilla* synonymized by Zhang & Suzuki 2017: 59).

Invalid name. — *Tholothauma*.

Nomina dubia. — *Archidiscus*, *Axodiscus*, *Circoniscus*, *Cubotholura*, *Dioniscus*, *Hexoniscus*, *Pentoniscus*, *Staurotholissa*, *Staurotholodes*, *Staurotholonium*, *Staurotholus*, *Tetroniscus*, *Tholartissa*, *Tholonetta*, *Tholonium*, *Tholostaurantha*, *Tholostauroma*, *Tholostaurus*, *Trioniscus*.

Diagnosis. — Phorticioidea with gates of the girdles closed by pillars in earlier ontogenetic stages, which become completely closed with growing. In latest ontogenetic stages, the cupolas becoming opposite latticed domes successively disposed on each of the three cartesian axes. Protoplasm occupies the inner space of the cortical shell. No algal symbionts are detected. A gelatinous sheath wraps the entirety of shell, including the lower part of the radial spines.

Stratigraphic occurrence. — Holocene-Living.

Remarks

The reason of the synonymy with *Tholomura* was explained in detail by Matsuzaki *et al.* (2015). This family was called Tholoniidae but its type genus is a *nomen dubium*. We selected the family name Amphitholidae due to the illustration of the *Amphitholonium* type species displaying a clearer internal structure than that of *Cubotholonium*. The internal skeletal structure for *Tholomura* has been already illustrated (Dumitrica 1989: pl. 15, figs 7-10; Sugiyama *et al.* 1992: pl. 11, fig. 6-9). Protoplasm and algal symbionts were documented by epi-fluorescent techniques using DAPI methods (Zhang *et al.* 2018: 14, fig. 30, p. 17, fig. 12).

Validity of genera

Tholomura

The morphological terminology followed both an anatomical terminology (Zhang & Suzuki 2017: tables 1-4, figs 3-5) and a morphology under a transmitted microscope (Zhang & Suzuki 2017: fig. 2).

It is helpful to understand the validity of the genera using the knowledge of the formation of the shell in *Tholomura*. The ideal *Tholomura* has the following structures: the "central combination" of S1a (= microsphere) and S1a-girdle in the center, the six cupolas with the settings of two opposite cupolas aligned along the three perpendicular axes outside of the "central combination". The word "cupola" is also called "dome-shaped test", and is defined as a large vaulted dome (Zhang & Suzuki 2017: table 1). These six cupolas form the 2nd pseudo-concentric shell. The term pseudo-concentric shell is defined for an easy recognition of the concentric patterns for *Tholomura* in transmitted light microscopy and the 2nd pseudo-concentric shell corresponds to the anatomical term "S2-girdles". The three sets of two opposite cupolas in the case of S2-girdels are anatomically called "G1 of S2-girdle", "G2 of S2-girdle" and "G3 of S2-girdle from the inner one to the outer one within the S2-girdle. Outside of the 2nd pseudo-concentric shell (=S2-girdle), the next three sets of two opposite cupolas are developed as the 3rd pseudo-concentric shell (=S3-girdle). The Tholoniidae *sensu* Campbell (1954: D94) are subdivided into three subfamilies based on the development patterns of cupolas: A set of two opposite cupolas are aligned along three perpendicular axes in the "Tholoniinae", along to two perpendicular axes in the "Staurotholoninae", and along a single axis in the "Amphitholinae". They correspond to the presence of G3, G2 and G1 of a certain girdle, respectively. This means that the different ontogenetic stages of the same pseudo-concentric shell were separated at the subfamily level. The subfamily in the sense of Campbell (1954) was systematically divided into genera with "how many cupolas pile up?" and the existence of a medullary shell. The former reflects the number of pseudo-concentric shells and the latter is related with preservation conditions. Genera in the sense of Campbell (1954) are subdivided into subgenera with the occurrence of radial spines or thorns. Radial spines may or may not be different at species level.

The Atlas illustrated 14 available genera after exclusion of *nomina dubia*, junior objective synonyms and invalid names. In consideration of the definition of Campbell (1954), of the type-illustrations cited from Haeckel (1887) and our supporting image, these 14 available genera can be arranged as follows: 1) Three pseudo-concentric shells: *Amphitholura*, *Tholartus* (presumably) and *Tholodes* (presumably)(G1 mode); *Cubotholus*, *Staurotholura*, *Tholocubitus* (probably), *Tholonilla* (probably) (G2 mode); and 2) Four pseudo-concentric shells: *Amphitholonium*, *Amphitholus* (presumably) and *Staurotholoma* (G1 mode); *Tholoma* (presumably), *Tholocubus* (probably) and *Tholomura* (probably) (G2 mode); and *Cubotholonium* (G3 mode). Genera "probably" assigned here are based on supporting images of this Atlas and those "presumably" assigned here are classified on the basis of a probable existence of more internal shells from other specimens. These genera were compared under the same mode and the same number of pseudo-concentric shells and there are no significant differences within these groups. As the difference between G1, G2 and G3 is related with different ontogenetic modes under the same number of pseudo-concentric shells, this is not a criterion for genus. There are no differences among different numbers of pseudo-concentric shells so that all these 14 available genera are included in the same genus. In respect to the first formal discussion by Matsuzaki *et al.* (2015), *Tholomura* is validated among these genera that were simultaneous published in Haeckel (1887).

Family CIRCODISCIDAE Dumitrica, 1989 n. stat.

Circodiscinae Dumitrica, 1989: 237-238. — De Wever *et al.* 2001: 156. — Afanasieva *et al.* 2005: S287. — Afanasieva & Amon 2006: 130. — Zhang & Suzuki 2017: 54.

TYPE GENUS. — *Circodiscus* Kozlova *in* Petrushevskaya & Kozlova, 1972: 526 [type species by monotypy: *Trematodiscus microporus* Stöhr, 1880: 108].

INCLUDED GENERA. — *Annulatospira* Clark & Campbell, 1945: 26. — *Circodiscullus* Dumitrica, 2020: 30. — *Circodiscus* Kozlova in Petrushevskaya & Kozlova, 1972: 526 (= *Plectodiscus* synonymized by Petrushevskaya 1975: 575). — *Sanfiriedelus* Dumitrica, 2020: 18. — *Stylotrochellus* Dumitrica, 2020: 33.

DIAGNOSIS. — Phorticioidea with a discoid shell having as medullary shell the first or first two systems of girdles and the outer shell formed of rings, spirals or more or less spongy meshwork.

STRATIGRAPHIC OCCURRENCE. — Middle Paleocene-Living.

REMARKS

This family is raised herein from the subfamily Circodiscinae (originally included in the family "Larnacillidae") in consideration of rank consistency. Internal skeletal structure is illustrated for *Circodiscus* (Dumitrica 1989: pl. 9, figs 7-10; pl. 14, figs 7, 8).

Family CRYPTOLARNACIIDAE Dumitrica, 1989 n. stat.

Cryptolarnaciinae Dumitrica, 1989: 241-242. — De Wever *et al.* 2001: 156. — Afanasieva *et al.* 2005: S287. — Afanasieva & Amon 2006: 130.

TYPE GENUS. — *Cryptolarnacium* Dumitrica, 1989: 246 [type species by monotypy: *Cryptolarnacium hexastylus* Dumitrica, 1989: 246].

INCLUDED GENERA. — *Coccolarnacium* Dumitrica, 1989: 242. — *Cryptolarnacium* Dumitrica, 1989: 246. — *Globolarnacium* Dumitrica, 2020: 13. — *Phacolarnacium* Dumitrica, 2020: 7. — *Pylolarnacium* Dumitrica, 2020: 16.

NOMEN DUBIUM. — *Staurosphaerantha*.

DIAGNOSIS. — The shell of the phorticiid-type structure is completely hidden within a cortical shell, that strikingly resembles the cortical shell of some co-occurring spumellarians. However, in Cryptolarnaciidae this layout is separated by an empty space or a loose spongy framework.

STRATIGRAPHIC OCCURRENCE. — Late Paleocene-Late Eocene.

REMARKS

This group is raised herein from the subfamily Cryptolarnaciinae (originally included in family Larnacillidae) to the family level in order to maintain rank consistency. Internal skeletal structure for *Coccolarnacium* (Dumitrica 1989: pl. 10, figs 1-4; pl. 14, figs 2-4, 9) and *Cryptolarnacium* (Dumitrica 1989: pl. 10, figs 5, 6, 10; pl. 14, figs 5, 6) was illustrated. This family member is found in plankton samples from the Pacific Ocean, South China Sea and Eastern Indian Ocean (e.g., Onodera *et al.* 2011: pl. 4, fig. 13).

Family HISTIASTRIDAE Dumitrica, 1989 n. stat.

Histiastrinae Dumitrica, 1989: 238, 241. — De Wever *et al.* 2001: 157. — Afanasieva *et al.* 2005: S287. — Afanasieva & Amon 2006: 130.

?Prunobrachidae [*sic*] Pessagno, 1975: 1014 (= Prunobrachiidae). — Vishnevskaya 2011: 372; 2015: 12.

TYPE GENUS. — *Histiastrum* Ehrenberg, 1846: 385 [type species by subsequent designation (Haeckel 1887: 544): *Histiastrum quaternarium* Ehrenberg, 1874: 237].

INCLUDED GENERA. — *Amphicraspedula* Haeckel, 1887: 523 (= *Amphicarydiscus* **n. syn.**, *Prunobrachium* **n. syn.**). — *Histiastrum* Ehrenberg, 1846: 385 (= *Histiastromma* with the same type species). — *Ommathymenium* Haeckel, 1887: 520. — *Stephanastrum* Ehrenberg, 1846: 385 (= *Stephanastromma* with the same type species; *Hagiastrella* **n. syn.**; *Stauralastromma* synonymized by Petrushevskaya & Kozlova 1972: 527; *Stephanastrella* synonymized by Kozur & Mostler 1978: 136).

Nomina dubia. — *Stauralastrella*, *Stauralastrum*.

Diagnosis. — This family is characterized by a spongy shell or chambered cylindrical shell, or in certain cases, a flat shell with two or four arms originating from a phorticiid-type medullary shell.

Stratigraphic occurrence. — Late Campanian-Living.

Remarks

Herein, this group is raised from the subfamily Histiastrinae (originally included in family Larnacillidae) to the family level in order to maintain rank consistency. Internal skeletal structure for both *Histiastrum* (Dumitrica 1989: pl. 10, fig. 9) and *Ommathymenium* (Dumitrica 1989: pl. 10, figs.10-15) was documented. The morphological variation of the *Prunobrachium*-form of *Amphicraspedula* was repeatedly examined (Zagorodnyuk 1975: 50; Blueford & Amon 1993: pl. 1, figs 8-10; pl. 2, figs 1-9; pl. 3, figs 1-5, 7; Suzuki *et al.* 2009d: pl. 5, figs 11-16, 18; pl. 6, figs 1-8; Vishnevskaya 2015: pl. 2), but no clear solution was proposed for *Ommatogramma*, *Amphicarydiscus*- and *Prunobrachium* (Sponguridae) due to their strong similarity in external shape (Zaynutdinov 1978: pl. 1, fig. 5, 6; pl. 2, figs 2, 6; Vishnevskaya 2011: figs 1a-1d). The genus *Ommathymenium* has generally been misidentified with *Ommatogramma* (Sponguridae) but the internal structure is evidently quite different (see supporting image for *Ommathymenium*).

Validity of genera

Amphicraspedula

Specimens identifiable as the type species of *Amphicraspedula* (the supporting image of *Amphicraspedula* in the Atlas) have the identical internal structure of the type species of *Amphicarydiscus* (Lipman 1972: pl. 10, figs 1, 2) and *Prunobrachium* (Kozlova & Gorbovetz 1966: pl. 1, figs 5, 6). Differing from *Amphicraspedula*, the type species of *Amphicarydiscus* lacks robust radial spines whereas the type species of *Prunobrachium* shows a cylindrical appearance. These differences are, however, interpreted as intraspecies variations. The oldest available name is *Amphicraspedula* among them.

Stephanastrum

Stephanastrum has the same type species as *Stephanastromma*. *Stauralastromma* is characterized by spiny arms and no patagium (Campbell 1954: D88), but these differences are related to intraspecies and intraspecies variations or preservation effect. *Hagiastrella* is defined by similar longitudinal arms with patagium (Campbell 1954: D86), the length symmetry of the arms is different among species but not genera. *Stephanastrum* is characterized by a patagium with four large interbrachial openings (patagial girdle) (Campbell 1954: D88), but a difference in the patagium is not considered as a generic difference.

Family Phorticiidae Haeckel, 1882 *sensu* Dumitrica (1989)

Phorticida Haeckel, 1882: 464 [as a subfamily]; 1887: 604, 708 [as a family]. — *nec* Rüst 1892: 175 [as a family]. — Schröder 1909: 4, 62 [as a family]. — Anderson 1983: 25 [as a family].

Larnacida Haeckel, 1887: 604, 614-616 [*nomen nudum*, as a family]. — Bütschli 1889: 1965-1966 [as a family]. — Schröder 1909: 4 [as a family]. — Anderson 1983: 24 [as a family].

Larnacillida – Haeckel 1887: 616, 617 [as a subfamily].

Larnacalpida Haeckel, 1887: 616, 619 [as a subfamily].

Larnacidae [*sic*] – Popofsky 1908: 229-230 [*nomen nudum*] (= Larnacillidae). — Campbell & Clark 1944a: 30. — Chediya 1959: 152. — Tan & Tchang 1976: 258. — Tan 1998: 249. — Tan & Chen 1999: 240.

Phorticidae [*sic*] – Popofsky 1912: 153-154 (= Phorticiidae). — Campbell & Clark 1944a: 31. — Campbell 1954: D100. — Chediya 1959: 161. — Tan & Tchang 1976: 266. — Chen & Tan 1996: 152. — Chen *et al.* 2017: 163.

Phorticiidae – Poche 1913: 210.

Larnacillidae – Poche 1913: 210. — Frizzell & Middour 1951: 27. — Campbell 1954: D96. — Nakaseko & Sugano 1976: 126. — Kozur & Mostler 1979: 47. — Dumitrica 1989: 233; 1995: 25. — Takahashi 1991: 88. — De Wever *et al.* 2001: 153, 156. — Afanasieva *et al.* 2005: S287. — Afanasieva & Amon 2006: 129-130.

Larnacalpinae [*sic*] – Campbell & Clark 1944a: 30 (= Larnacalpidinae). — Frizzell & Middour 1951: 27. — Chediya 1959: 153.

Larnacillinae – Campbell 1954: D96. — Chediya 1959: 153. — Dumitrica 1989: 233-234. — De Wever *et al.* 2001: 156. — Afanasieva *et al.* 2005: S287. — Afanasieva & Amon 2006: 130.

Larnacalpidinae – Campbell 1954: D96.

Type genus. — *Phorticium* Haeckel, 1882: 464 [type species by subsequent designation (Campbell 1954: D100): *Phorticium pylonium* Haeckel, 1887: 709].

Included genera. — *Larnacilla* Haeckel, 1887: 617 (= *Larnacalpis* **n. syn.**). — *Phorticium* Haeckel, 1882: 464 (= *Phortopyle* with the same type species). — *Qiuripylolena* Zhang & Suzuki, 2017: 52. — *Sphaerolarnacillium* Zhang & Suzuki, 2017: 47.

Nomina dubia. — *Amphibrachella*, *Amphibrachidium*, *Amphibrachoma*, *Amphibrachura*, *Druppulissa*, *Larnacospongus*, *Larnacidium*, *Larnacoma*, *Larnacostupa*, *Phortolarcus*.

Diagnosis. — The skeleton consists of several systems of phorticiid-type structures. Protoplasm was only reported for *Sphaeropylolena*. A red endoplasm occupies the inner part of the shell, which is enclosed by a reddish-brown endoplasm. The outermost part of the skeleton outcrops from the endoplasm. Pseudopodia radiate throughout the endoplasm and an axoflagellum is sometimes observable. Isolated skeleton fragments are scattered throughout the endoplasm in bundles of pseudopodia. The pseudopodia seem to be immobile and are strongly cohesive. No algal symbionts are observed.

Stratigraphic occurrence. — late Middle Eocene-Living.

Remarks

This family was previously called Larnacillidae. However, Phorticiidae is the oldest senior synonym of Larnacillidae. Phorticiidae has been employed as family name in several Chinese monographs (see synonymy), hence the unfeasible use of Larnacillidae as a valid name. Internal skeletal structures for *Larnacilla* (Dumitrica 1989: pl. 11, figs 1-7), *Qiuripylolena* (Sugiyama *et al.* 1992: pl. 10, figs 1-5), *Phorticium* (Sugiyama *et al.* 1992: pl. 10, figs 8, 9; van de Paverd 1995: pl. 58, fig. 2) and *Sphaerolarnacillium* (Nakaseko & Nishimura 1982: pl. 27, fig. 5; Sugiyama *et al.* 1992: pl. 11, figs 2-8) were illustrated. Illustrations of living specimens and protoplasm images were published for *Sphaeropylolena* (Krabberød *et al.*, 2011: figs 1.N; Suzuki N. *et al.* 2013: figs 3.1-3.9, 4.1-4.9, 7.1; Matsuoka *et al.* 2017: appendix A).

Validity of genera

Larnacilla

Difference between *Larnacilla* and *Larnacalpis* is a single medullary shell in the former and a double medullary shell in the latter (Campbell 1954: D96). This difference is considered to be caused by preservation effects. As both these genera were simultaneously published, the available genus in the earlier page *Larnacilla* is validated herein (Haeckel 1887: 617 for *Larnacilla* and 620 for *Larnacalpis*).

Superfamily Larcospiroidea Haeckel, 1887 n. stat. *sensu* Dumitrica (1989)

Larcospirida Haeckel, 1887: 691, 695 [as a subfamily].

Pyloniacea [*sic*] – Dumitrica 1989: 228-229 [*nomen dubium*] (= Pylonioidea) (*sensu* emend.) [as a superfamily]. — De Wever *et al.* 2001: 127-128 [as a superfamily].

Pyloniaceae [*sic*] – O'Dogherty 1994: 306 [*nomen dubium*] (= Pylonioidea) [as a superfamily].

Pyloniilae – De Wever *et al.* 2001: 148 [*nomen dubium*, as a subsuperfamily].

Pylonioidea – Afanasieva *et al.* 2005: S286 [*nomen dubium*]. — Afanasieva & Amon 2006: 129. — Matsuzaki *et al.* 2015: 29. — Zhang & Suzuki 2017: 8-9.

Diagnosis. — A Spumellaria with a *Tetrapyle*-mode of growth and a first system consisting of a microsphere, a simple or forked antapical sagittal cap, and two lateral caps developed between the apical part of the microsphere and the top of the sagittal cap.

Remarks

Since the well-known name "pyloniids" is not any longer applicable to this group on account of its *nomen dubium* status, Larcospiroidea, a superfamily name, is used herein. The Larcospiroidea consist of the Dipylissidae, Larcospiridae, Palaeotetrapylidae, Pylodiscidae (Clade M3) and Zonariidae (Clade M4). As explained in the remarks for Phorticioidea, the presence of S1a-girdle in the sense of Zhang & Suzuki (2017) is the key distinguishing trait of the Larcospiroidea (see figs 5.1-5.4 in Zhang & Suzuki 2017). Differing from the G1 of Phorticioidea, the G1 of the Larcospiroidea is conjoined by both the microsphere (S1a) and the S1a-girlde. The appearance of the overlapped orientation of the microsphere (S1a) and S1a-girdle appears the same in Phorticioidea and Larcospiroidea (compare figs 5.2 with fig. 5.5 in Zhang & Suzuki 2017). Differing from its spherical outline in the Phorticioidea, the central part of the Larcospiroidea is elliptical, with two transparent apertures and an S1a-girdle shadow is present (the middle figure in fig. 5.2 in Zhang & Suzuki 2017).

Family Dipylissidae Dumitrica, 1988 n. stat.

Dipylissinae Dumitrica, 1988: 188-190; 1989: 261. — De Wever *et al.* 2001: 151. — Afanasieva *et al.* 2005: S286. — Afanasieva & Amon 2006: 129.

Type genus. — *Dipylissa* Dumitrica, 1988: 190 [type species by monotypy: *Dipylissa bensoni* Dumitrica, 1988: 190].

Included genus. — *Dipylissa* Dumitrica, 1988: 190.

Diagnosis. — A Larcospiroidea with systems of two single-capped latticed girdles that are arranged face to face along the polar axis and rotated at 90° of each another. The first system includes a microsphere and a wide apically-opened antapical cap.

Stratigraphic occurrence. — late Late Miocene-Holocene.

Remarks

As the hierarchical consistency in the family level is improved to concord with the ranking of other spumellarian, this subfamily is raised to the family level. The internal skeletal structure of *Dipylissa* was illustrated (Dumitrica 1988: pl. 6, figs 1-15; 1989: pl. 12, figs 18-24). Undescribed *Dipylissa* morphospecies are found in plankton samples (study in progress).

Family Larcospiridae Haeckel, 1887 n. stat.

Larcospirida Haeckel, 1887: 691, 695 [as a subfamily]. — Schröder 1909: 57 [as a subfamily].

Soreumida Haeckel, 1882: 464 [*nomen dubium*, as a subfamily]; 1887: 604, 712 [as a family]. — Schröder 1909: 4, 62 [as a family]. — Anderson 1983: 25 [as a family].

Streblacanthida Haeckel, 1887: 704 [as a subfamily]. — Schröder 1909: 60 [as a subfamily].

Streblopylida Haeckel, 1887: 704 [as a subfamily]. — Schröder 1909: 60 [as a subfamily].

Larcopylida Dreyer, 1889: 48 [as a family].

Soreumatidae – Poche 1913: 210 [*nomen dubium*]. — Campbell 1954: D100. — Blueford 1988: 254.

Larcopylidae – Poche 1913: 210. — Chen & Tan 1996: 152. — Tan 1998: 247. — Tan & Chen 1999: 239. — Chen *et al.* 2017: 149.

Soreumidae [*sic*] – Clark & Campbell 1942: 51 [*nomen dubium*] (= Soreumatidae); 1945: 28. — Chediya 1959: 161. — Tan & Tchang 1976: 267.

Larcopylinae – Campbell 1954: D96.

Larcospirinae – Campbell 1954: D100. — Chediya 1959: 159. — Tan & Tchang 1976: 264. — Tan 1998: 280. — Tan & Chen 1999: 265.

Streblopylinae – Campbell 1954: D100.

Tholospira [*sic*] – Tochilina 1985: 98 (= Tholospiridae).

Type genus. — *Larcospira* Haeckel, 1887: 695 [type species by subsequent designation (Campbell 1954: D100): *Larcospira quadrangula* Haeckel, 1887: 696].

Included genera. — *Larcospira* Haeckel, 1887: 695 (= *Larcospirema* with the same type species). — *Pylospira* Haeckel, 1887: 697 (= *Pylospirema* with the same type species). — *Streblacantha* Haeckel, 1887: 706 (= *Spironetta* **n. syn.**, *Spironium* **n. syn.**, *Streblopyle* **n. syn.**). — *Tholospira* Haeckel, 1887: 699 (= *Tholospirema* with the same type species; *Larcopyle* synonymized by Tochilina 1985: 99; *Stomatodiscus* **n. syn.**; *Tholospironium* synonymized by Popofsky 1912: 152).

Nomina dubia. — *Drymospira*, *Larcospironium*, *Pylospironium*, *Soreuma*, *Soreumidium*, *Soreumium*, *Sorolarcidium*, *Sorolarcium*, *Sorolarcus*, *Spironilla*.

Diagnosis. — A Spirally growing skeleton with a medullary shell of Zonariidae type (*Tetrapyle*) consisting of a microsphere, an antapical sagittal arch and two lateral symmetrical arches originating from the apical part of the microsphere and the top of the sagittal arch. Protoplasm is observed in the *Larcopyle*-form of *Tholospira* and *Larcospira*. Protoplasm fills the shell except but not the outermost peripheral region. Algal symbionts in *Larcopyle*-form of *Tholospira* are scattered inside the cortical shell.

Stratigraphic occurrence. — late Middle Eocene-Living.

Remarks

The internal skeletal structure for *Larcopyle*-form of *Tholospira* was already documented (Dumitrica 1989: pl. 15, figs 2, 3; Yamauchi 1986: pl. 1, fig. 18) and *Larcospira* (Sugiyama *et al.* 1992: pl. 9, fig. 1-5). A "pylome" was detected in the *Larcopyle*- and *Stomatodiscus*-forms of *Tholospira*, but it consists of a simple aperture without discrete margins (Barwicz-Piskorz 1999: figs 3.H-3J). There is often misidentification of the "*Spireuma*" form of *Lithelius* (Litheliidae) and *Tholospira* (Larcospiridae) due to their similar spiral appearance, but the Litheliidae are fundamentally different from the Larcospiridae as the former bear a spherical microsphere and do not have S1a-girdle, G1 and G2, girdle structures. Protoplasm and algal symbionts were documented in the *Larcopyle*-form of *Tholospira* (Zhang *et al.* 2018: 14, fig.11, p. 19, fig. 7) and *Larcospira* (Zhang *et al.* 2018: 11, fig. 20) using DAPI dyeing epi-fluorescent techniques.

Validity of genera

Streblacantha

Spironium has the same type species as *Spironetta*. The spiral appearance of *Spironium* has already been proved as an "artificial torsional" appearance of *Larcospira* by computer simulation (Ogane & Suzuki 2009: figs 3 and 4), but this doubtless geometric principle did not apply to the Atlas in time. This is the reason why *Spironium* is synonymized with *Streblacantha*. The supporting image of *Streblopyle* for the Atlas is conspecific with that of *Pylospira*, but this also failed to be fixed in the Atlas due to time limitation.

Tholospira

Identification of "larcopylids" and "lithelids" has been discussed from the anatomical point of views (Tochilina 1985: 95-101), practical usages (Lazarus *et al.* 2005 97-106; Suzuki *et al.* 2009d: 248-251; Matsuzaki *et al.* 2015: 29) and intraspecies variations and evolution (Tochilina & Vasilenko 2018a: fig. 6, pls 10-13). Lazarus *et al.* (2005) artificially put any larcopylids and lithelids into a single genus *Larcopyle* and Suzuki *et al.* (2009d) as the single genus *Lithelius*. These artificial treatments are not needed any longer because *Larcopyle* and *Lithelius* are completely different in their molecular phylogenetic positions (Ishitani *et al.* 2012; Sandin *et al.* 2021) as well as their evolutionary changes (Tochilina & Vasilenko 2018a). Our Atlas first visualized the detailed internal structure of *Tholospira* in Nomarski microscopy with the help of OKU Osamu, a professional of optical microscopy (supporting image for *Stomatodiscus* in the Atlas). These images are sufficient to recognize the same internal structures among *Larcopyle*, *Stomatodiscus*, *Tholospira* and *Tholospironium*. *Tholospira* was defined by simple spiral turns and *Tholospironium* by double spiral turns (Campbell 1954: D100), but the real specimen for *Tholospira* (the supporting image in the Atlas) looks to have double spiral turns and the topotypical specimen of *Tholospironium* from the *H.M.S. Challenger* Station 271 (Zhang & Suzuki 2017: figs 17.1, 17.2) looks as a simple spiral turn. Appearance of spiral turns depends on the orientation of the specimens. *Stomatodiscus* is defined by a disc shape with two openings (Campbell 1954: D92), but both sides of the shell are open in the young growing stages of them (Zhang & Suzuki 2017: figs 18.1-18.22). Zhang & Suzuki (2017) published the first paper to practically synonymize "*Stomatodiscus*" with *Tholospira* (*Larcopyle* in original). *Tholospira* is the oldest available name among them.

Clade indet.

Family Palaeotetrapylidae Dumitrica, 1989 n. stat.

Palaeotetrapylinae Dumitrica, 1988: 184-186; 1989: 258. — De Wever *et al.* 2001: 149. — Afanasieva *et al.* 2005: S286. — Afanasieva & Amon 2006: 129.

Type genus. — *Palaeotetrapyle* Dumitrica, 1988: 186 [type species by monotypy: *Palaeotetrapyle muelleri* Dumitrica, 1988: 186].

Included genus. — *Palaeotetrapyle* Dumitrica, 1988: 186.

Diagnosis. — A Larcospiroidea with sets of three elliptical girdles distributed in 3 successively perpendicular planes. The microsphere is heteropolar and consists of 12 pores, without an antapical sagittal beam but with 2 primary lateral beams.

Stratigraphic occurrence. — Early Paleocene.

Remarks

The internal skeletal structure was documented for *Palaeotetrapyle* (Dumitrica 1988: pl. 5, figs 1-17; 1989: pl. 12, figs 14, 16, 17). As quoted by Dumitrica (1988: 186), *Palaeotetrapyle* is distinguished from *Tetrapyle* by the lack of an antapical beam and the former's Paleocene stratigraphic range.

Clade M3 (Sandin *et al.* 2021)

Family Pylodiscidae Haeckel, 1887
sensu Dumitrica (1989)

Pylodiscida Haeckel, 1887: 409, 561-563 [as a family]. — Bütschli 1889: 1963 [as a family]. — Schröder 1909: 3 [as a family]. — Anderson 1983: [as a family].

Triopylida Haeckel, 1887:563 [*nomen dubium*, as a subfamily].

Hexapylida Haeckel, 1887: 563, 567 [*nomen dubium*, as a subfamily].

Discopylida Haeckel, 1887: 563, 571 [as a subfamily]. — Dreyer 1889: 38 [as a subfamily].

Pylodiscidae – Popofsky 1908: 225; Popofsky 1912: 142-143. — Clark & Campbell 1945: 24. — Campbell 1954: D92. — Chediya 1959: 144. — Tan & Su 1982: 156. — Dumitrica 1984: 102. — Chen & Tan 1996: 151. — Tan 1998: 232. — Tan & Chen 1999: 226-227. — Chen *et al.* 2017: 143.

Discopylinae – Clark & Campbell 1945: 25. — Campbell 1954: D93. — Chediya 1959: 145.

Pylodiscinae – Campbell 1954: D92. — Dumitrica 1989: 261. — De Wever *et al.* 2001: 152-153. — Afanasieva *et al.* 2005: S286. — Afanasieva & Amon 2006: 129.

Triopylinae – Campbell 1954: D92 [*nomen dubium*]. — Chediya 1959: 144.

Hexapylinae – Chediya 1959: 145 [*nomen dubium*].

Type genus. — *Pylodiscus* Haeckel, 1887: 570 [type species by subsequent designation (Campbell 1954: D92): *Pylodiscus triangularis* Haeckel, 1887: 570].

Included genera. — *Pylodiscus* Haeckel, 1887: 570 (= *Pylolena* synonymized by Zhang & Suzuki 2017: 25; *Discopyle* **n. syn.**, *Discozonium* **n. syn.**, *Triodiscus* **n. syn.**, *Triolena* **n. syn.**, ? *Trilobatum* **n. syn.**). — *Sphaeropylolena* Zhang & Suzuki, 2017: 38.

Nomina dubia. — *Hexapyle*, *Triopyle*.

Diagnosis. — Larcospiroidea with a three-ray first system (medullary shell) derived from the bifurcation of the antapical *Tetrapyle*-type sagittal arch. The following systems repeat the aforementioned or change the growth mode.
The protoplasm is well documented in *Sphaeropylolena*. The endoplasm fills the shell but not its outer part. An ectoplasmic membrane wraps the entirety of the skeleton, including the spines. No algal symbionts were detected.

Stratigraphic occurrence. — Late Miocene-Living.

Remarks

Recognition of the pylodiscid-type triangular center is key differentiating this family from the Larcospiridae. In the Pylodiscidae, the triangular center forms an isosceles triangle (De Wever *et al.* 2001: 153, fig. 90.2). The isosceles triangle is determined by the presence of three gates (the apertures formed by the lateral views of three girdles) and the surface view of other three girdles (that have an arm-like appearance). Some genera in the Larcospiridae (e.g., the *Larcopyle*-form of *Tholospira*) also show an isosceles triangle center in some illustrations (Zhang & Suzuki 2017: 12, figs 5.4). The noticeable visible difference between the Pylodiscidae and Larcospiridae is the position of the microsphere (S1a). The microsphere is always located on the base line of the isosceles triangle in the Pylodiscidae whereas it is always situated in the center of the isosceles triangle in the Larcospiridae. The internal skeletal structure of *Pylodiscus* (Dumitrica 1989: pl. 15, figs 1, 4-6; Takahashi 1991: pl. 23, fig. 7) and *Sphaeropylolena* (van de Paverd 1995: pl. 59, fig. 2) was illustrated. Protoplasm and algal symbionts have been already documented by epi-fluorescent observation with DAPI dyeing in *Sphaeropylolena* (Zhang *et al.* 2018: 17, fig. 11). In certain cases, *Sphaeropylolena* was found to be infected with the Marine Alveolata Group I (Ikenoue *et al.* 2016).

Validity of genera

Pylodiscus

The same morphological terminology used for the Amphitholidae is also applicable for the Pylodiscidae with a few modifications. The G1-mode girdle turns vertically to the equatorial plane (the Fr-plane in Zhang & Suzuki 2017: fig. 4), the G2-mode girdle turns sideways to the Fr-plane so as to connect the adjacent G1-mode girdles, and the G3-mode girdle developed in a parallel to the Fr-plane in order to cover the gate formed by the G2-mode girdle. The Pylodiscidae *sensu* Campbell (1954) are divided into the Triopylinae (*Triodiscus* and *Triolena* as available name) with two pseudo-concentric shells, the Pylodiscinae with three pseudo-concentric shells (*Pylodiscus* and *Pylolena*), and the Discopylinae (*Discopyle* and *Discozonium*) with four pseudo-concentric shells (Campbell 1954: D92-93). Each subfamily is subdivided into three geometric genera by the G1-mode form (*Pylolena*, *Triolena*), the G2-mode form (*Triodiscus*, *Discozonium*), and the G3-mode form (*Pylodiscus*, *Discopyle*). The visualized ontogenetic growth of *Pylodiscus* indicates that all these six genera are named for different ontogenetic modes (Zhang & Suzuki 2017: fig. 15). *Trilobatum* is defined by a triparted-lobular central chamber and solid radial spines on the shell margin (Campbell 1954: D92). This triparted-lobular central chamber looks similar to the G1-mode with the two pseudo-concentric shells but exact anatomical studies have not been carried out for this genus. All the available genera except *Trilobatum* were simultaneously published in Haeckel (1887). In respect to Zhang & Suzuki (2017), *Pylolena* is validated among them.

Clade M4 (Sandin *et al.* 2021)

Family Zonariidae Haeckel, 1887
sensu Dumitrica (1989)

Zonarida Haeckel, 1887: 604, 682-684 [as a family]. — Bütschli 1889: 1968 [as a family]. — Schröder 1909: 4 [as a family]. — Anderson 1983: 24 [as a family].

Pylonida Haeckel, 1882: 463 [as a family, *nomen dubium*]; 1884: 29 [as a family]; 1887: 604, 628-632 [as a family]. — Bütschli 1889: 1966 [as a family]. — *nec* Rüst 1892: 174. — Schröder 1909: 4 [as a family]. — Anderson 1983: 24 [as a family].

Streblemida [*sic*] Haeckel, 1887: 604 [*nomen nudum*] (= Streblonida) [as a family].

Streblonida Haeckel, 1887: 702-704 [*nomen dubium*, as a family]. — Bütschli 1889: 1969 [as a family]. — Schröder 1909: 4 [as a family]. — Anderson 1983: 25 [as a family].

Zonartidae [*sic*] – Popofsky 1912: 124 (= Zonariidae).

Pylonidae [*sic*] – Popofsky 1912: 145-146 [*nomen dubium*] (= Pyloniidae). — Chediya 1959: 154. — Tan & Tchang 1976: 259. — Tan & Su 1982: 159. — van de Paverd 1995: 184. — Chen & Tan 1996: 152. — Tan 1998: 249-252. — Tan & Chen 1999: 241-243.

Monozoniinae Campbell, 1954: D96 [*nomen dubium*].

Zonariidae – Poche 1913: 210. — Campbell 1954: D98.

Pyloniidae – Poche 1913: 210 [*nomen dubium*]. — Campbell 1954: D96. — Riedel 1967b: 295; 1971: 655. — Nakaseko *et al.* 1975: 171. — Nakaseko & Sugano 1976: 126. — Riedel & Sanfilippo 1977: 867. — Dumitrica 1979: 24; 1984: 101; Dumitrica 1989: 253, 258. — Petrushevskaya 1979: 110. — Kozur & Mostler 1979: 45-46. — Anderson 1983: 39. — Takahashi 1991: 90. — Hollis 1997: 43. — Boltovskoy 1998: 32. — Anderson *et al.* 2002: 1002-1003. — De Wever *et al.* 2001: 148. — Afanasieva *et al.* 2005: S286. — Afanasieva & Amon 2006: 129. — Chen *et al.* 2017: 150.

Strebloniidae – Poche 1913: 210 [*nomen dubium*]. — Campbell 1954: D100. — Tan & Su 1982: 163. — Chen & Tan 1996: 152. — Tan 1998: 283. — Tan & Chen 1999: 267. — Chen *et al.* 2017: 162.

Pyloniinae – Campbell 1954: D96 [*nomen dubium*]. — De Wever *et al.* 2001: 150-151. — Afanasieva *et al.* 2005: S286. — Afanasieva & Amon 2006: 129.

Tetrapyloniinae Campbell, 1954: D97 [*nomen dubium*].

Strebloniinae – Campbell 1954: D100 [*nomen dubium*].

Zonaridae [*sic*] – Chediya 1959: 158 (= Zonariidae).

Streblonidae [*sic*] – Chediya 1959: 160 [*nomen dubium*] (= Strebloniidae).

Type genus. — *Zonarium* Haeckel, 1887: 684 [type species by subsequent designation (Campbell 1954: D98): *Zonarium octangulum* Haeckel, 1887: 685] = junior subjective synonym of *Tetrapyle* Müller, 1859a: 154 [type species by monotypy: *Tetrapyle octacantha* Müller, 1859b: 33].

Included genera. — *Larcidium* Haeckel, 1887: 611. — *Pylozonium* Haeckel, 1887: 659. — *Tetrapyle* Müller, 1859a: 154 (= *Tetrapylura* with the same type species; *Echinosphaera*, *Trizonium*, *Trizonaris*, synonymized by Matsuzaki *et al.* 2015: 34; ? *Amphiaspis* **n. syn.**, *Amphipylura* **n. syn.**, *Dizonitis* **n. syn.**, *Larnacantha* **n. syn.**, *Octopylura* **n. syn.**, *Pylonura* **n. syn.**, *Schizomma*, *Tetrapylissa* synonymized by Itaki 2009: 47, *Zonarium* **n. syn.**, *Zonidium* **n. syn.**, *Zoniscus* **n. syn.**).

Nomina dubia. — *Amphipylissa*, *Amphipyle*, *Amphipylonium*, *Dizonaris*, *Dizonium*, *Monozonaris*, *Monozonitis*, *Monozonium*, *Octopylissa*, *Octopyle*, *Pylonissa*, *Pylonium*, *Spongophorticium*, *Spongophortis*, *Streblonia*, *Stypophorticium*, *Tetrapylonium*, *Trizonitis*.

Invalid name. — *Stylophorticium*.

Nomen nudum. — *Caryolithis*.

Diagnosis. — Larcospiroidea with systems of three elliptical girdles in 3 successive, perpendicular planes. First system (medullary shell) consists of a heteropolar microsphere with 12 pores, an antapical sagittal ring and two lateral arches. The following system repeats the first system previously described several times.

A Protoplasm is documented for *Tetrapyle*. The endoplasm occupies the shell and occasionally the external most girdle, depending on its growth stage. The central part of the endoplasm tends to be reddish in color and is surrounded by a light brown endoplasm. The nucleus is located inside the second pseudo-concentric shell in the sense of Suzuki & Zhang (2016). Several dozens of algal symbionts surround the endoplasm. Hundreds of pseudopodia radiate from the entire protoplasm. One axoflagellum, rarely two, extend on the side of the external most girdle's polar region. Gelatinous material covers all skeletons.

Stratigraphic occurrence. — late Late Miocene-Living.

Remarks

The family name "Pyloniidae" has been widely used, but it is impossible to retain this common family name as the "Pyloniidae" is based on an unillustrated type species. The oldest available name, "Zonarida", was automatically selected as a valid family name. *Tetrapyle* is often confused with *Phorticium* (Phorticiidae) in practical work regardless of their fundamental differences at the superfamily level. According to Zhang & Suzuki (2017: 42), *Phorticium* tends to possess numerous pillar beams between the pseudo-concentric shells. Otherwise, the presence or absence of the S1a-girdle is the only way to differentiate these two genera. Internal skeletal structure was illustrated for *Tetrapyle* (Dumitrica 1989: pl. 15, figs 12, 13; Sugiyama *et al.* 1992: pl. 11, figs 1-4). Algal symbionts of *Tetrapyle* were identified as *Brandtodinium nutricula* (Probert *et al.* 2014). Living and protoplasmic images were captured for *Tetrapyle* (Matsuoka *et al.* 2001: pl. 1, fig. 2; Suzuki & Aita 2011: fig. 4Q; Probert *et al.* 2014: S1, Vil 231; Suzuki & Not 2015: fig. 8.8.25; Matsuoka *et al.* 2017: appendix A; Zhang & Suzuki 2017: figs 7.1-7.8). Fine protoplasmic structure for *Tetrapyle* was illustrated (Hollande & Enjumet 1960: pl. 24, fig. 3).

Validity of genera

Tetrapyle

These synonymized genera with *Tetrapyle* are considered to be erected for different ontogenetic growth stages and different appearances differently oriented as such as the Amphitholidae and Pylodiscidae (Ogane & Suzuki 2009: fig. 3; Zhang & Suzuki 2017: fig. 3). The morphological terminology follows Zhang & Suzuki (2017) as briefly explained in the "Validity of genera" for the Amphitholidae. First it is necessary to determine the number of pseudo-concentric shells referred to the type-illustration in Haeckel (1887), the size of the specimens and supporting images for these available names. *Amphiaspis* looks to have two pseudo-concentric shells. *Schizomma* looks similar to *Amphiapis*; but the shell size is twice in *Schizomma* than in *Amphiaspis*, having three pseudo-concentric shells. The genera with three pseudo-concentric shells are *Amphipylura*, *Larnacantha*, *Octopylura*, *Pylonura*, *Tetrapyle*, *Tetrapylissa*, *Trizonaris*, *Zonarium*, *Zonidium* and *Zoniscus*. The type-illustration of *Dizonites* is very ambiguous but it presumably possess three pseudo-concentric shell in consideration of its size. *Echinosphaera* is the largest among the synonymized genera here but it is difficult to specify the number of its pseudo-concentric shells. According to Zhang & Suzuki

(2017: fig. 3), the morphotype with three pseudo-concentric shells has nine possibilities by the outermost girdle (G1, G2 or G3) and the anatomical orientation under the absolute Cartesian coordinates (Lt-, Pl- and Sg-views). From the Lt-view, the opening (gate) encircled by the first girdle (S1a-girdle) directly attached on the microsphere (S1a) is visible; from the Pl-view, the microsphere and the first girdle look to be overlapped; and from the Sg-view, the body of the first girdle (girdle itself) is visible. Referred to Zhang & Suzuki (2017), *Amphiaspis* is the Lt-view of the two pseudo-concentric shells with G3-girdle and *Zonarium* is the Sg-view of the four concentric shells with the G2-girdle. The remaining genera have three pseudo-concentric shells but the different view under the absolute Cartesian coordinates. *Amphipylura*, *Trizonium*, *Octopylura* and *Tetrapylissa* are the Pl-views. The former two genera have an incomplete G2-girdle whereas the latter two genera develop the complete G2-girdle. *Pylonura*, *Larnacantha*, *Zoniscus* and *Zonidium* (Haeckel 1887: pl. 50, fig. 12) have also the Pl-view. The first one has an incomplete G3-girdle and the remaining three genera have the complete G3-girdle. *Tetrapyle*, *Dizonitis* and *Schizomma* are the Sg-view. The first two genera have the complete G1-girdle and the last genus has an incomplete G2-girdle. In consideration of the specimen's orientations and their growth stages, the type-illustrations of these genera are derived from several limited species within the same genus. The oldest available name among them is *Tetrapyle*. *Amphiaspis* is possible to be regarded as a collective name for the Zonariidae for practical usage.

Phylogenetic Molecular Lineage indet.

Remarks

In contrast to the clear results for the subdivision of Lineages in Sandin *et al.* (2021), it was nearly impossible to clearly define the morphological "commonalities" in each Lineage. This is due to the fact that the superfamilies and families categorized here cannot be classified into known Lineages.

Superfamily Pseudoaulophacoidea Riedel, 1967 *sensu* De Wever *et al.* (2001)

Pseudoaulophacidae Riedel, 1967a: 148; 1967b: 295; 1971: 654-655.

Pseudoaulophacilae – Pessagno 1971a: 19 [as a subsuperfamily]; 1972: 273, 296 [as a subsuperfamily]; 1973: 50, 56 [as a subsuperfamily]; 1976: 26 [as a subsuperfamily]; 1977b: 930-931 [as a subsuperfamily]. — Blome 1984: 349, 352 [as a subsuperfamily].

Patulibracchiilae – De Wever *et al.* 2001: 138-139 (*sensu* emend.) [as a subsuperfamily].

Lobatiradiata [*pars*] Afanasieva & Amon *in* Afanasieva, Amon, Agarkov & Boltovskoy, 2005: S283 [as an order of Class Stauraxonaria]. — Afanasieva & Amon 2006: 125.

Diagnosis. — Pseudoaulophacoidea characterized by a flat, lenticular, disc-shaped shell or by 3 primary arms or spines originating in the prismatic microsphere.

Remarks

The known families in this superfamily are the Patulibracchiidae, Pseudoaulophacidae and Suttoniidae, from the Mesozoic to the Cenozoic as well as the Angulobracchiidae Baumgartner 1980 and Tritrabidae Baumgartner 1980 in the Mesozoic (Dumitrica *et al.* 2013). Afanasieva *et al.* (2005) established a new order, Lobatiradiata, for the flat-shaped polycystines with three or more arms. These include the Angulobracchiidae, Patulibracchiidae, Hexaporobrachiidae, Hagiastridae, Suttoniidae and Myelastridae. However, a strong homeomorphy among them was repeatedly observed since 1980s.

Family Patulibracchiidae Pessagno, 1971 *sensu* De Wever *et al.* (2001)

Patulibracchiinae Pessagno, 1971a: 22; 1976: 29. — Feary & Hill 1978: 366. — Baumgartner 1980: 300. — De Wever 1982b: 243. — Yang 1993: 38. — Cordey 1998: 86.

Patulibrachiinae [*sic*] – *nec* Ormiston & Lane 1976: 168-169 (= Patulibracchiinae).

Patulibracchiidae – Baumgartner 1980: 297, 300 (*sensu* emend.). — De Wever 1982b: 241-242. — Sanfilippo & Riedel 1985: 592-593. — Carter *et al.* 1988: 39. — Yang 1993: 38. — Dumitrica 1995: 26. — Hollis 1997: 49. — De Wever *et al.* 2001: 142-143 (*sensu* emend.). — Afanasieva *et al.* 2005: S284. — Afanasieva & Amon 2006: 126. — Bragin 2007: 1001; 2011: 760.

Patulibracchidae [*sic*] – Dumitrica 1984: 100-101 (= Patulibracchiidae).

Patulibracchinae [*sic*] – Blome 1984: 354 (= Patulibracchiinae).

Patulibrachiidae [*sic*] – Cordey 1998: 86 (= Patulibracchiidae).

Type genus. — *Patulibracchium* Pessagno, 1971a: 26 [type species by objective designation: *Patulibracchium davisi* Pessagno, 1971a: 30]

Included genera (Cenozoic only). — *Cryptomanicula* Dumitrica, 2019: 48. — ? *Heterosestrum* Clark & Campbell, 1945: 21 (= *Hexacyclia* synonymized by Petrushevskaya & Kozlova 1979: 103). — *Trimanicula* Dumitrica, 1991: 46.

Diagnosis. — Skeleton consists of a three-armed shell with an eccentric heptagonal microsphere. The arms unequal with 3-4 canals and one arm having a bracchiopyle.

Stratigraphic occurrence. — Early Paleocene-Early Pliocene.

Remarks

The internal skeletal structure for *Cryptomanicula* (Dumitrica 2019: figs 3.f, 3.h, 5.a-5.e, 7.e-7.e) and *Trimanicula* was already documented (Dumitrica 1991: pl. 8, figs 9-11; pl. 9, figs 1-13; Dumitrica 2019: figs 7.a, 7.b, 7.f). *Cryptomanicula* closely resembles *Homunculodiscus* (Suttoniidae). The former genus can be distinguished by the presence of three rods emanating from the central structure, whereas the central part of the latter genus resembles a snowman and consists of two to three large "snowballs" of different sizes or a treefoil chamber without three rods around this central structure.

Heterosestrum is commonly found in the Middle to Upper Eocene and is commonly used as a zonal marker species in the high-latitude northern hemisphere (Dzinoridze *et al.* 1976; Petrushevskaya & Kozlova 1979; Kozlova 1999; Popova *et al.* 2002; Suzuki *et al.* 2009d). The exact taxonomic position of this genus is uncertain due to the poor knowledge of its internal structure. This genus is well documented with many illustrations that include the equatorial and lateral views (Petrushevskaya & Kozlova 1979: figs 441-449, 451-457). According to Gorbunov (1979: pl. 13, figs 1a-1g), this genus may belong to the Heliodiscidae (based on observations of *Heterosestrum tschujenko*, which shows an eccentrically placed microsphere). However, *H. tschujenkio* illustrated in Dzinoridze *et al.* (1976: pl. 24, figs 1-4) resembles a Circodiscidae while *Heterosestrum rotundum* in Hull (1996: pl. 1, figs 10, 11) resembles Amphitholidae (originally Tholoniidae). The lateral view of this genus is similar to Phorticiidae (originally Larnacillidae in Dzinoridze *et al.* 1976: pl. 24, fig. 5; Popova *et al.* 2002: figs 10.I, 12.O). Suzuki *et al.* (2009d: pl. 3, fig. 12) interpreted *Heterosestrum rotundum* as a Lithocycliidae (originally Phacodiscidae).

Validity of genera

Heterosestrum

The whole appearance of *Heterosestrum* is nearly the same as that of *Hexacyclia*, although their internal structures have been so far poorly illustrated. Both these genera are synonymized here until the difference of their internal structures are clear. *Heterosestrum* is an available name older than *Hexacyclia*.

Family Pseudoaulophacidae Riedel, 1967 *sensu* De Wever *et al.* (2001)

Pseudoaulophacidae Riedel, 1967a: 148; 1967b: 295; 1971: 654-655. — Pessagno 1972: 296-297 (*sensu* emend.); 1977b: 932. — Nakaseko *et al.* 1975: 169. — Nakaseko & Sugano 1976: 126. — Foreman 1978: 744. — Kozur & Mostler 1978: 155. — Dumitrica 1979: 25; 1997: 212-214. — Schaaf 1984: 49. — Sanfilippo & Riedel 1985: 593-594. — Carter *et al.* 1988: 43. — O'Dogherty 1994: 315. — Dumitrica 1995: 26. — Kiessling 1999: 39. — Amon 2000: 45. — De Wever *et al.* 2001: 143-144. — Afanasieva *et al.* 2005: S286. — Afanasieva & Amon 2006: 128.

Pentapyloniinae Dumitrica *in* De Wever, Dumitrica, Caulet, Nigrini & Caridroit, 2001: 146. — Afanasieva *et al.* 2005: S286. — Afanasieva & Amon 2006: 128.

Pseudoaulophacinae – De Wever *et al.* 2001: 144, 146 (*sensu* emend.). — Afanasieva *et al.* 2005: S286. — Afanasieva & Amon 2006: 128.

Type genus. — *Pseudoaulophacus* Pessagno, 1963: 200 [type species by objective designation: *Pseudoaulophacus floresensis* Pessagno, 1963: 200].

Included genera (Cenozoic only). — *Pentapylonium* Dumitrica, 1991: 37.

Diagnosis. — Spongy discoidal spumellarians with surface completely or partially covered by a meshwork of equilateral triangular frames. The microsphere is shaped like triangular prism with 3 primary rays originating from its lateral edges.

Stratigraphic occurrence. — early Early Miocene-Early Pliocene.

Remarks

The internal skeletal structure of *Pentapylonium* was already illustrated (Dumitrica 1991: pl. 5, figs 1-9; pl. 6, figs 1-9; pl. 7, figs 1-7). As reporting of *Pentapylonium implicatum* is limited to the upwelling regions off Peru, Oman and Somali (Nigrini & Caulet 1992), this family can rarely be observed in other regions. The overall appearance of *Sphaeropylolena* (Pylodiscidae) is similar to that of *Pentapylonium*, but the former fundamentally differs from the latter by the presence of a pylodiscid center (Zhang & Suzuki 2017: 38).

Family Suttoniidae Schaaf, 1976 *sensu* Dumitrica (2019)

Suttonidae [*sic*] Schaaf, 1976: 790 (= Suttoniidae) [in Nassellaria]. — Dumitrica 1983b: 41 (*sensu* emend.) [in Spumellaria].

Suttoniidae – De Wever *et al.* 2001: 125-126 [in Spumellaria]. — Afanasieva *et al.* 2005: S284 [in Order Lobatiradiata]. — Afanasieva & Amon 2006: 126. — Dumitrica 2019: 40-41 (*sensu* emend.)

Type genus. — *Suttonium* Schaaf, 1976: 790 [type species by monotypy: *Suttonium praedicator* Schaaf, 1976: 790].

Included genera (Cenozoic only). — *Homunculodiscus* Dumitrica, 2019: 41. — *Parasuttonium* Dumitrica, 2019: 47. — *Suttonium* Schaaf, 1976: 790.

Diagnosis. — Bilaterally symmetrical spumellarians with initial skeleton consisting of an eccentric microsphere with or without primary rays and a crescent shaped deuteroconcha. Skeleton thin made usually of two parallel lattice plates interconnected by short bars. Rays, when present, surrounded by a cortical shell forming three arms in the most evolved members (Dumitrica 2019: 40).

Stratigraphic occurrence. — Early Paleocene-Holocene.

Remarks

The internal skeletal structure of *Homunculodiscus* was already documented (Dumitrica 2019: figs 1.a-1.g, 2.a-2.h, 3a.-3.d, 4.a-4.d), *Parasuttonium* (Dumitrica 2019: figs 6.a, 6.b) and *Suttonium* (Dumitrica 2019: figs 6.c, 6.d). The taxonomic position of the Suttoniidae has been changed among Nassellaria, Spumellaria and Lobatiradiata. The history and the definition of the current taxonomic position was documented in Dumitrica (2019).

Superfamily Stylosphaeroidea Haeckel, 1887 *sensu* Dumitrica (1984)

Stylosphaerida Haeckel, 1887: 121 [as a family], 133 [as a subfamily].

Stylosphaerilae – Dumitrica 1984: 98 [as a sub-superfamily].

Diagnosis. — Spumellarian consists of one to three shells with bipolar, bladed spines. The innermost shell is pyriform shape.

Remarks

This superfamily consists of the Entapiidae, Stylatractidae, Stylosphaeridae, and Tubosphaeridae Suzuki, n. fam. However, both

Stylatractidae and Tubosphaeridae Suzuki, n. fam. were excluded from the diagnosis above. The appropriate superfamily distributions of the Tubosphaeridae Suzuki, n. fam. and Stylatractidae are uncertain because of the absence of a pear-shaped internal shell.

Family Entapiidae Dumitrica *in* De Wever, Dumitrica, Caulet, Nigrini & Caridroit, 2001

Entapiidae Dumitrica *in* De Wever, Dumitrica, Caulet, Nigrini & Caridroit, 2001: 118-119.

Entapiinae – Afanasieva *et al.* 2005: 273. — Afanasieva & Amon, 2006: 110.

Type genus. — *Entapium* Sanfilippo & Riedel, 1973: 491 [type species by original designation: *Entapium regulare* Sanfilippo & Riedel, 1973: 492]

Included Genus. — *Entapium* Sanfilippo & Riedel, 1973: 491.

Diagnosis. — Skeleton consists of two shells. The innermost shell has a pyriform shape and the outer shell is latticed and spherical. Three to six radial bladed beams penetrate the outer shell to form bladed radial spines. No fine radial beams were observed.

Stratigraphic occurrence. — Middle Paleocene-early Middle Eocene.

Remarks

The internal skeletal structure for *Entapium* was illustrated (Nakaseko & Nishimura 1982: pl. 22, fig. 6? ; Nishimura 2001; pl. 1, fig. 13; Sanfilippo & Riedel 1973: pls 23, 24). However, *Entapium* showed an outward migration of the medullary shell towards the cortical shell which ultimately tends to disappear. O'Connor (1999) coined the new genus name *Zealithapium* but this latter genus is not an Entapiidae. The numerous radial spines similar to those of Stylosphaeridae morphotypes were observed, but the characteristics of these radial spines are different between the two families.

Family Stylatractidae Schröder, 1909 n. stat. *sensu* Matsuzaki *et al.* (2015)

Stylatractida [*sic*] Schröder, 1909: 37 (= Stylatractidae) [as a subfamily].

Sphaerostylida Haeckel, 1882: 451 [*nomen dubium*, as a tribe]; 1887: 122, 133 [as a subfamily]. — Schröder 1909: 7 [as a subfamily].

Amphistylida Haeckel, 1882: 452 [*nomen dubium*, as a tribe]; 1887: 142 [as a subfamily].

Cromyostylida Haeckel, 1882: 453 [*nomen dubium*, as a tribe]; 1887: 146 [as a subfamily].

Caryostylida Haeckel, 1882: 454 [*nomen dubium*, as a tribe]; 1887: 148 [as a subfamily].

Ellipsida Haeckel, 1887: 289 [*nomen dubium*, as a family]. — Rüst 1892: 150 [as a family]. — Carter 1893: 227 [as a family]. — Wisniowski 1889: 684 [as a family]. — Anderson 1983: 23 [as a family].

Sphaerostylinae – Clark & Campbell 1942: 24 [*nomen dubium*]; 1945: 11. — Campbell & Clark 1944a: 10; 1944b: 4. — Chediya 1959: 80.

Amphistylinae – Clark & Campbell 1945: 13 [*nomen dubium*]. — Campbell 1954: D54. — Chediya 1959: 82.

Lithapinae Deflandre, 1953: 418 [as a new Nassellaria subfamily].

Cromyostylinae – Campbell 1954: D54 [*nomen dubium*].

Ellipsidiicae – Campbell 1954: D68 [*nomen dubium*, as a superfamily].

Ellipsidiidae – Campbell 1954: D68 [*nomen dubium*]. — Kozur & Mostler 1979: 38-39 (*sensu* emend.).

Caryostilinae – Chediya 1959: 82 [*nomen dubium*].

Stylatractidae – Nishimura 1990: 156 [as a new Nassellaria family].

Amphisphaeridae Suzuki *in* Matsuzaki, Suzuki & Nishi, 2015: 10 [*nomen dubium*].

Type genus. — *Stylatractus* Haeckel, 1887: 328 [type species by subsequent designation (Campbell 1954: D73): *Stylatractus neptunus* Haeckel 1887: 328] = junior subjective synonym of *Druppatractylis* Haeckel, 1887: 325 [type species by subsequent designation (Campbell 1954: D71): *Druppatractus ostracion* Haeckel, 1887: 326].

Included genera. — *Druppatractylis* Haeckel, 1887: 325 (= *Stylatractylis* **n. syn.**; *Lithatractara*, *Lithatractus* synonymized by Kozur & Mostler 1979: 40; *Stylatractara*, *Stylatractus* synonymized by Petrushevskaya 1975:570). — *Ellipsostylus* Haeckel, 1887: 299 (= *Ellipsostyletta* with the same type species; *Ellipsostylissa* **n. syn.**, *Sphaerostylomma* **n. syn.**). — *Lithapium* Haeckel, 1887: 303 (= *Xiphatractara*, *Xiphatractus* synonymized by Petrushevskaya 1975: 570; *Xiphatractium* **n. syn.**). — *Lithomespilus* Haeckel, 1882: 450. — *Stylatractona* Haeckel, 1887: 330 (= *Amphisphaerissa* synonymized by Petrushevskaya 1975: 570). — *Stylosphaerantha* Haeckel, 1887: 133 (= *Praestylosphaera* synonymized by O'Dogherty *et al.* 2009a: 283; ? *Xiphosphaerantha* **n. syn.**). — *Xiphatractylis* Haeckel, 1887: 332 (= *Cromydruppocarpus* **n. syn.**, *Heliosestarium* **n. syn.**, ? *Xiphosphaeromma* **n. syn.**). — *Xiphostylantha* Haeckel, 1887: 127 (= *Druppatractus*, *Druppatractara*, *Sphaerostylantha*, synonymized by Petrushevskaya 1975: 570). — *Xiphostylissa* Haeckel, 1887: 129 (= *Xiphostyletta* **n. syn.**).

Invalid names. — *Ellipsis, Spongostylidium.*

Nomina dubia. — *Amphisphaera, Amphisphaerantha, Amphisphaerella, Amphisphaeromma, Amphistylus, Axellipsis, Caryostylus, Cenellipsis, Cenellipsium, Cenellipsula, Cromyostauroloncho, Cromyostylus, Druppatractium, Echinocapsa, Ellipsidium, Ellipsoxiphetta, Sphaerostyletta, Sphaerostylissa, Spongolonchis, Spongostylium, Stylatractium, Stylocromyum, Xiphatractona, Xiphosphaerissa.*

Junior homonym. — *Spongolonche* Haeckel, 1882: 455 (= *Spongolonchis*) *nec* Haeckel, 1882: 461; *Sphaerostylus* Haeckel, 1882 *nec* Chaudoir, 1854.

Diagnosis. — The shell consists of one to three concentric shells with bi-polar spines (rarely one). The innermost shell, if present, contains a spherical microsphere with many radial beams. The second inner shell is also a spherical macrosphere and this shell is connected to the outermost shell by many radial beams. The outermost shell is a cortical shell, occasionally found with by-spines or a fragile coverage. Most radial beams are disconnected between the concentric shells. A dark gray endoplasm occupies the cortical shell in *Stylatractona*.

Remarks

Since the Cenozoic Genera Working Group (CGW) decided to exclude any genera based on unfigured type species, the genus *Amphisphaera* is regarded as a "*nomen dubium*." Its type species, *Amphisphaera neptunus* Haeckel, 1887, has been interpreted as a probable junior synonym of *Stylatractus neptunus* (Petrushevskaya 1975; Hollis 1997). However, CGW postponed this decision. Therefore, the name Amphisphaeridae by Matsuzaki *et al.* (2015) should also be regarded as "*nomen dubium*". The subfamily/family rank commonly used for this group has been "Lithapiinae", originally pertained to the Nassellaria by Deflandre (1953) and Nishimura (1990) respectively; however, many authors have overlooked the name Stylatractidae proposed earlier by Schröder (1909). Stylatractidae is easily distinguishable from both Stylosphaeridae and Entapiidae due to the presence of an innermost pyriform shell. The genera *Druppatractylis*, *Lithapium* and *Stylatractona* are maintained as valid for future discussions although their basic differences only depend upon the position of the spines. Internal skeletal structure was illustrated for *Stylatractona* in fossils (Nakaseko & Nishimura 1982: pl. 17, fig. 4; Sugiyama *et al.* 1992: pl. 3, fig. 8) and a living form (Suzuki & Not 2015: fig. 8.10.13).

Validity of genera

Druppatractylis

The combination of *Lithatractus* and *Lithatractara*, and that of *Stylatractus* and *Stylatractara* have respectively the same type species. As the definitions written for *Lithatractus* and *Stylatractus* are the same even in Campbell (1954: D72 for *Lithatractus* and D73 for *Stylatractus*), both these genera are mostly conspecific. *Stylatractylis* is marked by a thorny or papillate surface (Campbell 1954: D73) but the type-illustration does not match with this description. Based on the principle of the name-bearing specimen, the type species for these three genera has a common structure as written in the Atlas.

Ellipsostylus

Ellipsostyletta has the same type species as *Ellipsostylus*. Both *Ellipsostylus* and *Ellipsostylissa* have a single elliptical shell and two opposite dissimilar polar spines, but the former has a regular network whereas the latter has an irregular network (Campbell 1954: D68-69 for *Ellipsostylus* and D69 for *Ellipsostylissa*). The difference in the network is insufficient as a genus criterion. *Sphaerostylomma* is marked by two concentric lattice shells, irregular pores with dissimilar sizes and presence of by-spines or thorns on the cortical shell (Campbell 1954: D54). Any specimens identical to the type species of these three genera are very rare so it is not possible to examine their descriptions in detail and these genera are tentatively synonymized here. All these genera are simultaneously established by Haeckel (1887: 299 for *Ellipsostylus*, 299 for *Ellipsostyletta*, 301 for *Ellipsostylissa*, and 140 for *Sphaerostylomma*). As a real specimen identifiable of *Ellipsostylus psittacus*, the type species of *Ellipsostylus*, has been found in the topotypic material of the *H.M.S. Challenger* Station 265, this genus is selected as a valid genus among the other ones.

Lithapium

Xiphatractus has the same type species as *Xiphatractara*. Specimens with no internal structure whose characteristics fit with the type-illustration in Haeckel (1887: pl. 14, fig. 9) are always associate with specimens having three concentric shells in the topotypic material from the *H.M.S. Challenger* Station 266. Based on this observation, the definition of *Lithapium* has changed in the Atlas. As *Lithapium*, the lectotype of *Xiphatractium* also has three concentric shells (Ogane *et al.* 2009b: pl. 12, figs 3a-d). *Xiphatractus* has three concentric shells based on its type-illustration (Haeckel 1887: pl. 17, fig. 11). Distinguishing characters are an elliptical or pear-shaped cortical shell with a single spine on one pole for *Lithapium* (Campbell 1954: D69); a cortical shell with a smooth surface and a regular network, and two opposite dissimilar polar spines for *Xiphatractus* (Campbell 1954: D73); and a cortical shell with a thorny or papillate surface and an irregular network, and also two dissimilar spines for *Xiphatractium* (Campbell 1954: D73). As indicated by the type-illustration of *Lithapium* (Haeckel 1887: pl. 14, fig. 9), *Lithapium pyriforme* has two opposite dissimilar polar spines and this character can be confirmed with topotypic specimens from the *H.M.S. Challenger* samples (the supporting image for *Lithapium*). The lectotype of *Xiphatractium* does not match with the description by Campbell (1954: D73). Rather, pore arrangement and size patterns are the same in the type species of both *Xiphatractus* and *Xiphatractium*. Although the exact internal structure is not well known for *Xiphatractus* and *Xiphatractium*, it is unnecessary to keep these three genera valid. All genera were simultaneously described in Haeckel (1887: 303 for *Lithapium*, 332 for *Xiphatractus*, 331 for *Xiphatractara*, and 334 for *Xiphatractium*). *Lithapium* is validated among them because many representative specimens are found in the topotypic material.

Stylatractona

The concept of this genus corresponds to the current usage of *Amphisphaera*. The difference between *Stylatractona* and *Amphisphaerissa* at "genus" level is the presence of an irregular network in the former (Campbell 1954: D73) or in the presence of irregular pores with dissimilar sizes in the latter (Campbell 1954: D54). This difference cannot be recognized from type-illustrations (Haeckel 1887: pl. 17, fig. 2 for *Stylatractona* and pl. 17, fig. 5 for *Amphisphaerissa*). No other differences are observed in the type species of both these genera. These two genera were simultaneously established in Haeckel (1887: 330 for *Stylatractona* and 144 for *Amphisphaerissa*). *Stylatractona* is validated because of a better illustrated type specimen in Haeckel (1887: pl. 17, fig. 2). The differences between *Lithapium* and *Stylatractona* need a more precise study.

Stylosphaerantha

Xiphosphaerantha is questionably synonymized with *Stylosphaerantha* herein, in consideration of the same number of shells and the bladed polar spines. This synonymy needs to evaluate by trace of evolutionary continuity between the type species of *Stylosphaerantha* and that of *Xiphosphaerantha*.

Xiphatractylis

Differing from the other genera of the Stylatractidae, *Xiphatractylis* has several radial spines which are directly connected by radial beams and these radial spines tend to appear in the equatorial zone of the shell. *Xiphosphaera* was defined by a double medullary shell, two opposite dissimilar polar spines, a regular network, and a spiny or thorny surface (Campbell 1954: D73), but this definition does not match with the lectotype which has only two lattice shells (Ogane *et al.* 2009b: pl. 3, figs 6a, 6b). Any well-preserved specimens identifiable as *Heliosestarium cretaceum*, the type species of *Cromydruppocarpus*, are not so far formally illustrated, so the total number of shells cannot be confirmed. However, the taxa belonging to the Stylatractidae are rarely associated with robust radial spines in the equatorial zone of the shell. *Xiphosphaeromma* is defined by the presence of irregular pores with dissimilar sizes, a spiny or thorny surface, two similar polar spines and a single latticed shell (Campbell 1954: D54). The specimen most similar to the type image for *Xiphosphaeromma* was found from an upper Eocene Barbados sample (supporting image for *Xiphosphaeromma*). If this specimen is the true *Xiphosphaeromma vestum*, this genus has three concentric shells and robust radial spines which are not connected by radial beams. This internal structure is similar to that of some Actinommidae. Until the internal structures could be well described, *Xiphatractylis*, *Praestylosphaera*, *Heliosestarium* and *Xiphosphaerantha* are synonymized herein. The oldest available names are *Xiphatractylis* and *Xiphosphaeromma* which were simultaneously published by Haeckel (1887: 322 for *Xiphatractylis* and 126 for *Xiphosphaeromma*). As the real type specimen of *Xiphatractylis* is in the Ehrenberg collection, *Xiphatractylis* is selected as a valid name.

Xiphostylantha

Druppatractus hippocampus is the type species of three genera *Druppatractus*, *Druppatractara* and *Sphaerostylantha*. *Xiphostylantha* was defined by a single lattice shell, two dissimilar polar spines, regular pores with similar sizes, and no by-spines or thorns on the surface (Campbell 1954: D54). The shorter polar spine of *Xiphostylus phasianus*, the type species of *Xiphostylantha*, is so characteristic of the Stylatractidae that this species is a synonym of "*Stylosphaera coronata*" (the supporting image for *Xiphostylantha*). The lectotype of the latter species (Ogane *et al.* 2009b: pl. 12, figs 1a-d) has two shells so *Xiphostylantha* should be regarded as a genus with two shells. *Druppatractus* is defined by an elliptical shell, a simple medullary shell and two dissimilar polar spines (Campbell 1954: D71). The sphericity of the outer shell in both *Xiphostylantha* and *Druppatractus* is a little bit different but it is explained by a difference at the species level. These two genera were simultaneously published by Haeckel (1887: 127 for *Xiphostylantha* and 324 for *Druppatractus*). The first genus in Haeckel (1887) is validated.

Xiphostylissa

Following Campbell (1954: D54), *Xiphostylissa* and *Xiphostyletta* have a common structure with a single lattice shell and dissimilar polar spines. The difference is the absence of by-spines and thorns in *Xiphostylissa* and the presence of by-spines and thorns in *Xiphostyletta*. These characters, however, are helpless to precisely determine the real specimen referable to their type species, *Xiphostylus trogon* for *Xiphostylissa* (Haeckel 1887: pl. 14, fig. 12) and *Xiphostylus picus* for *Xiphostyletta* (Haeckel 1887: pl. 14, fig. 13). Based on the type-illustrations, *Xiphostylissa* lacks a prominent polar spine whereas *Xiphostyletta* has a prominent polar spine. The difference in its length can be explained by an intraspecies variation.

Stratigraphic occurrence. — Late Campanian-Holocene.

Family Stylosphaeridae Haeckel, 1887 *sensu* Dumitrica (1985)

Stylosphaerida Haeckel, 1887: 121 [as a family], 133 [as a subfamily]. — Rüst 1892: 141 [as a family]. — Anderson 1983: 23 [as a family].

Stylosphaeridae – Haecker 1908: 440. — Popofsky 1912: 83. — Clark & Campbell 1942: 24; 1945: 11. — Campbell & Clark 1944a: 10; 1944b: 4. — Frizzell & Middour 1951: 12. — Deflandre 1953: 417. — Campbell 1954: D53. — Chediya 1959: 78. — Orlev 1959: 433. — Zhamoida & Kozlova 1971: 79. — Tan & Su 1982: 141. — Dumitrica 1984: 98; 1985: 185. — Chen & Tan 1996: 150. — Tan 1998: 121. — Tan & Chen 1999: 144. — De Wever *et al.* 2001: 117. — Bragin 2007: 889. — Bragin 2011: 753. — Matsuzaki *et al.* 2015: 10. — Chen *et al.* 2017: 124. — Dumitrica & Hungerbühler 2017: 88.

Stylosphaerinae – Clark & Campbell 1942: 24; 1945: 11. — Campbell & Clark 1944b: 4. — Frizzell & Middour 1951: 13. — Campbell 1954: D53. — Kozur & Mostler 1979: 15; 1984: 118. — Afanasieva *et al.* 2005: S273. — Afanasieva & Amon 2006: 110. — Bragin 2007: 889. — Bragin 2011: 753.

Stylosphaerids – Sugiyama *et al.* 1992: 11.

Type genus. — *Stylosphaera* Ehrenberg, 1846: 385 [type species by monotypy: *Stylosphaera hispida* Ehrenberg, 1854b: 246]

Included genera. — *Druppatractona* Haeckel, 1887: 326. — *Lithatractona* Haeckel, 1887: 322. — *Spongatractus* Haeckel, 1887: 350 (= ? *Spongoprunum* **n. syn.**; *Spongoxiphus* synonymized by Sanfilippo & Riedel 1973: 519). — *Stylosphaera* Ehrenberg, 1846: 385 (= *Stylosphaerella* with the same type species; *Stylosphaerissa* **n. syn.**).

Nomina dubia. — *Lithatractium, Lithatractylis, Stylosphaeromma.*

Diagnosis. — The skeleton consists of one to three concentric shells and two prominent polar spines (that may be absent in older species). The skeleton may also consist of one to three concentric shells with a cluster of shorter polar spines instead of one prominent polar spine. A single or double internal shell is present, the innermost shell is always of ovoid or pyriform shape. The outermost shell is robust and latticed, or made by fine spongy layer. It is of spherical to ellipsoid shape and is connected to the inner shells by many radial spines. The polar spine is usually three-bladed (cylindrical in rare cases) and originates from the innermost shell. The polar spine that joins the sharp end of the pyriform inner shell tends to be shorter than the opposite polar spine. Intraspecific variability, reveals a spectrum of morphotypes differing by having numerous radial beams from the opposite side of the pyriform inner shell, which give rise to the radial spines. Additional radial secondary spines may sometimes be present on the external shell.

Stratigraphic occurrence. — Late Campanian-Living.

Remarks

The Stylosphaeridae are externally similar to the Axoprunidae and Stylatractidae by them having two prominent polar spines. The former family is distinguishable from the Axoprunidae in that the latter has cylindrical polar spines, and microbursa-type microspheres (see remarks for Heliosaturnaloidea). Stylosphaeridae is also different from the Stylatractidae due to its spherical innermost shell. The genera belonging to the Stylosphaeridae can be identified by the number of shells and the type of the polar spines (cylindrical or three-bladed). It is only possible to differentiate *Lithatractona* from *Stylatractona* (Stylatractidae) by an examination of the innermost shell. The number and length of radial spines are variable at species level. This is recognized in the late Eocene to early Middle Miocene *Stylosphaera radiosa* (Gorbunov 1979: pl. 2, figs 2a-2e; Nakaseko 1955: pl. 2, fig. 6; pl. 3, fig. 1; pl. 4, fig. 6; pl. 5, figs 1, 4; Suzuki *et al.* 2009d: pl. 1, figs 9, 10) and in the extant *Stylosphaera pyriformis* (Takahashi 1991: pl. 15, fig. 12-14; Itaki & Bjørklund 2007: pl. 6, figs 9-13; Nishimura 2015: pl. 11, figs 2-5, 7, 8; Chen *et al.* 2017: pl. 15, figs 18-21; pl. 28, figs 12-16; pl. 30, figs 8-10; pl. 35, figs 12-19). These observations were possible by the presence of co-occurring variable forms in a single sample. The number and length of radial spines are an important characteristic at genus level but need to be carefully examined. Internal structure for *Druppatractus* (Nakaseko & Nishimura 1982: pl. 20, fig. 2) and *Stylosphaera* (Nakaseko & Nishimura 1982: pl. 19, fig. 4; pl. 21, figs 1, 3; pl. 24, figs 1, 4; Nishimura 1982: pl. 2, figs 1-7; Sugiyama & Furutani 1992: pl. 15, figs 2, 6, 7) was well illustrated.

Validity of genera

Spongatractus

The synonymy between *Spongatractus* and *Spongoxiphus* was well established by Sanfilippo & Riedel (1973). Any real specimen identifiable as *Spongoprunum*, the type species of *Spongoprunum*, have not been so far illustrated. *Spongoprunum* is tentatively synonymized with *Spongatractus* due to the occurrence of their spongy elongate shells. *Spongatractus*, *Spongoprunum* and *Spongoxiphus* were simultaneously published in Haeckel (1887: 350 for *Spongatractus*, 347 for *Spongoprunum*, and 353 for *Spongoxiphus*). In respect to the first reviser rule, *Spongatractus* is selected as a valid genus between *Spongatractus* and *Spongoxiphus*.

Stylosphaera

Stylosphaerella has the same type species as *Stylosphaera*. *Stylosphaerissa* is defined by two concentric lattice shells, irregular pores with dissimilar sizes, no by-spines or thorns on the surface (Campbell 1954: D53). The specimen most similar to the illustration of *Stylosphaera nana* (Haeckel 1887: pl. 16, figs 12, 13) was found in an upper Paleocene to lower Eocene sample from the Pacific Ocean (supporting image of *Stylosphaerissa*). Based on this specimen, all morphological features, except the shape of the inner shell, do exactly match between them. The real sample has a pyriform inner shell and subsequently *Stylosphaerissa* is a synonym of *Stylosphaera*. The oldest available genus is *Stylosphaera*.

Family Tubosphaeridae Suzuki, n. fam.

urn:lsid:zoobank.org:act:A8584914-5C69-4F52-A4B5-B93D21B66EA3

Staurostylida Haeckel, 1882: 450 [*nomen dubium*, as a tribe].

Type genus. — *Tubosphaera* Popofsky, 1917: 268 [type species by monotypy: *Tubosphaera quadrispina* Popofsky, 1917: 268].

Included genera. — *Staurosphaerella* Haeckel, 1887: 154. — *Stauroxiphos* Haeckel, 1887: 163 (= *Staurolonchidium* **n. syn.**). — *Stylostaurus* Haeckel, 1882: 450. — *Tubosphaera* Popofsky, 1917: 268.

Nomina dubia. — *Staurosphaeromma*, *Staurostylus*.

Diagnosis. — Skeleton consists of four radial spines and one to three spherical shells.

Stratigraphic occurrence. — late Middle Eocene-Living.

Remarks

This new family is represented by some genera previously included in the "Staurostylidae". Because the type genus *Staurostylus* is a *nomen dubium* based on a poorly illustrated Mesozoic specimen, a new family name is required. There are some doubts regarding the phylogenetic relationships among the assigned genera, but no other appropriate family is yet available.

Validity of genera

Stauroxiphos

Real specimens with two shells and four decussate radial spines aligned on the equatorial plane are quite rare. *Staurolonchidium* is synonymized with *Stauroxiphos* for an easy identification until new information is provided in the future.

Incertae familiae spumellarians

Included genera. — *Peritiviator* Pessagno, 1976: 45. — *Tanochenia* Dumitrica, 2014b: 95. — *Tepka* Sanfilippo & Riedel *in* Sanfilippo *et al.,* 1973: 228.

Remarks

Hollis (1997: 43; pl. 4, fig. 16) regarded *Peritiviator* as a genus of Phorticiidae (originally Pyloniidae). However, the high contrast photo makes this impossible to confirm. *Tepka* was once considered as Nassellaria (Riedel & Sanfilippo 1977: 870) but nothing is known about the complete appearance of this genus, making this grouping impossible to confirm. *Tanochenia* seems to be an endemic form; its internal skeletal structure was already illustrated (Dumitrica 2014b: pl. 1, figs 1-4).

Orphaned spumellarian family ranks

Discida Haeckel, 1862: 239-240, 476-485 [invalid name, as a family]; 1882: 456 [as a family]; 1884: 29 [as a family]. — Claus 1876: 160 [as a family]. — Dunikowski 1882: 190 [as a family]. — Lankester 1885: 849 [as a family].

Polysphaerida Zittel, 1876-1880: 120 [invalid name, rank unknown]. — Stöhr 1880: 90 [as a family].

Dyssphaeriden [*sic*] Hertwig, 1879: 179-185 [invalid name] (= Dyosphaeriden) [as a family].

Disciden – Hertwig 1879: 185-196 [invalid name, as a family].

Discidae – Pantanelli 1880: 48 [invalid name].

Sphaerida Haeckel, 1882: 448 [invalid name, as a family]. — Dunikowski 1882: 184 [as a family].

Dyosphaerida Haeckel, 1882: 451 [invalid name, as a subfamily].

Polysphaeria Haeckel, 1882: 454 [invalid name, as a subfamily].

Pylocapsida Haeckel, 1882: 463 [*nomen nudum*, as a subfamily].

Pylophormida Haeckel, 1882: 463 [invalid name, as a subfamily].

Sphaeroida – Haeckel 1884: 28-29 [invalid name, as a family].

Diplozonaria Haeckel, 1887: 632, 640 [invalid name]. — Schröder 1909: 53 [as a subfamily]. — Tan & Chen 1990: 111-113 (*sensu* emend.); Tan & Chen 1999: 243 [as a subfamily]. — Tan 1998: 252 [as a subfamily]. — Chen *et al.* 2017: 151 [as a subfamily].

Haplozonaria Haeckel, 1887: 632 [invalid name, as a subfamily]. — Schröder 1909: 53 [as a subfamily]. — Tan & Chen 1990: 124-125; 1999: 257 [as a subfamily]. — Tan 1998: 270 [as a subfamily]. — Chen *et al.* 2017: 150 [as a subfamily].

Triplozonaria Haeckel, 1887: 632, 656 [invalid name, as a subfamily]. — Schröder 1909: 53 [as a subfamily]. — Tan & Chen *in* Tan 1998: 267 [as a subfamily]. — Tan & Chen 1999: 255 [as a subfamily].

Monostomida Dreyer, 1889: 12 [invalid name, as a subfamily].

Amphistomida Dreyer, 1889: 25 [invalid name, as a subfamily].

Sphaeroidea – Deflandre 1953: 415 (*sensu* emend.) [invalid name, as a superfamily].

Discoidea – Deflandre 1953: 416, 422 [invalid name, as a superfamily]. — Chediya 1959: 120 [as a superfamily].

Diplozonarinae – Chediya 1959: 154 [invalid name].

Haplozonarinae – Chediya 1959: 154 [invalid name].

Triplozonarinae – Chediya 1959: 155 [invalid name].

Remarks

Families with no assigned species that are identified as probable Spumellaria and *nomen nudum* without any taxonomic information are simply listed herein. This list does not include any higher rank than the family-rank (e.g., Discida).

Order ENTACTINARIA Kozur & Mostler, 1982

Molecular phylogenetic lineage III (Sandin *et al.* 2021)

Diagnosis. — One, to rarely two or three, spherical cortical shells, whose wall are made of a spongy layer or of a spherical shape consisting of a full coarse mesh. The central cubic structure is framed with sharp corners and contains a heteropolar microsphere; with MB and two A-rays on its top. Following an author's recommendation (PD), the Lineage III is regarded as a living Entactinaria. Nonetheless, it is noted that the true genus *Entactinia* have a MB and two sets of radial rays at both ends; however, it has never been observed in living Entactinaria (Nakamura *et al.* 2020: supplement).

Remarks

We include the Rhizosphaeroidea (Clade G: *Haliommilla*, *Rhizosphaera*), Centrocuboidea (Clade H: *Octodendron*; Clade I: *Plegmosphaeromma*), Centrolonchoidea, Heliosaturnaloidea and Thalassothamnoidea in the Entactinaria sensu Dumitrica, but the diagnosis for the Lineage III shown above does not include Centrolonchoidea, Heliosaturnaloidea and Thalassothamnoidea due to the lack of molecular support. The axopodial system was regarded as a determinant character applicable to superfamily or order level taxonomy (Hollande & Enjumet 1960; Cachon & Cachon 1985). However, molecular phylogenetic studies (Sandin *et al.* 2021) discarded this hypothesis.

Clade G (Sandin *et al.* 2021)

Superfamily Rhizosphaeroidea Haeckel, 1882 n. stat.

Rhizosphaerida Haeckel, 1882: 455 [as a tribe].

Anaxoplastidiés [*pars*] Hollande & Enjumet, 1960: 22-23, 30-31, 69, 112-113 (= Macrosphaeridae + Centrocubidae). — Cachon & Cachon 1972c: 297-300.

Périaxoplastidiés [*pars*] Hollande & Enjumet, 1960: 20-22, 25-30, 48, 68, 85 (= Cenosphaeridae + Stigmophaeridae + Excentroconchidae + Heliasteridae). — Cachon & Cachon 1972c: 293-297.

Cryptoaxoplastidés Cachon & Cachon, 1972c: 303-305.

Periaxoplastidies [*pars*] Anderson, 1983: 49.

Cryptoaxoplastida Cachon & Cachon, 1985: 286 [as an order].

Periaxoplastida [*pars*] – Cachon & Cachon 1985: 288.

Cryptoaxoplastidiata – Cachon *et al.* 1989: 341.

Periaxoplastidiata [*pars*] – Cachon *et al.* 1989: 341.

Capsulata Afanasieva & Amon *in* Afanasieva, Amon, Agarkov & Boltovskoy, 2005: S278 [as an order of Class Spumellaria] (= Centrocubidae + Quinquecapsulariidae + Rhizosphaeridae). — Afanasieva & Amon 2006: 116 [as an order].

Diagnosis. — Spherical entactinarians with a cortical and a single or double medullary shell. First medullary shell ovoid, or spherical, with spicule ectopically placed in its wall. Spicule with a median bar, two apical spines and four basal spines. All spines well developed, radially prolonged to the cortical shell, or short, prolonged only to the second medullary shell, or even shorter.

Remarks

This superfamily was established in order to separate the Rhizosphaeridae from the Centrocuboidea at superfamily level. The central structure is more similar to that of the Heliosaturnaloidea, rather than that of the Centrocuboidea and Centrolonchoidea, when accounting for the presence of a "microbursa-like" central structure (Dumitrica *et al.* 2010: 285). Afanasieva *et al.* (2005) proposed an Order "Capsulata" to include the families Centrocubidae, Quinquecapsulariidae and Rhizosphaeridae. Unfortunately, their rank concept is unacceptable when considering higher rank consistency in Eukaryotes compiled by Adl *et al.* (2019).

Family Rhizosphaeridae Haeckel, 1882 *sensu* Dumitrica (2017b)

Rhizosphaerida Haeckel, 1882: 455 [as a tribe]. — Dunikowski 1882: 188 [as a tribe]. — Haeckel 1887: 209 [as a tribe]. — Schröder 1909: 18 [as a tribe].

Elatommida Haeckel, 1887: 208 [*nomen dubium*, as a tribe]. — Schröder 1909: 16 [as a rank between subfamily and genus].

Actinosphaerinae Mast, 1910: 40. — Popofsky 1912: 93, 101.

Rhizosphaeridae – Hollande & Enjumet 1960: 69, 95, 106. — Petrushevskaya 1975: 571. — Anderson 1983: 51. — Dumitrica 1984: 99. — Cachon & Cachon 1985: 287 [in Order Centroaxoplastida]. — De Wever *et al.* 2001: 201-202 [in Entactinaria]. — Afanasieva *et al.* 2005: S278 [in Order Capsulata]. — Afanasieva & Amon 2006: 117. — Dumitrica 2017b: 471-473 (*sensu* emend.) [in Order Entactinaria].

Rhizosphaerinae – Petrushevskaya 1979: 107; Petrushevskaya 1986: 127. — Dumitrica 2017b: 478.

Type genus. — *Rhizosphaera* Haeckel, 1861b: 840[type species by subsequent designation (Campbell 1954: D68): *Rhizosphaera leptomita* Haeckel, 1861b: 840].

Included genera (Cenozoic genera only). — *Haliommilla* Haeckel, 1887: 226 (= *Actinosphaera* with the same type species; *Elatommura* synonymized by Dumitrica 2017b: 478). — *Heliosoma* Haeckel, 1882: 451 (= *Heliosomantha* with the same type species). — *Hexarhizacontium* Dumitrica, 2017b: 488. — *Rhizosphaera* Haeckel, 1861b: 840.

Nomina dubia. — *Elatomma*, *Elatommella*, *Pityomma*.

Junior homonym. — *Rhizospongia* Hertwig, 1932 *nec* d'Orbigny, 1852.

Diagnosis. — Shell with one (rarely two to three) spherical cortical shells and a medullary shell. The medullary shell contains a centrally-placed innermost microsphere that is covered by a sponge-like or latticed frame network. The innermost microsphere does not form a discrete shell. Instead, MB, two A-rays (apical rays) and four B-rays (basal rays) are identified on the microsphere. The A-rays are equals or unequals in appearance and are commonly not connected. The B-rays are interconnected by several arches to form part of the outer sponge-like, or latticed, coarse frame network. The network, outside of the innermost microsphere, tends to develop further on the opposite side of the MB rather than on the MB side of the microsphere. The spherical cortical shell is latticed or sponge-like. Regarding the axopodial system of centroaxoplastid-type: the axoplast is located in the center of the shell and the nucleus wraps the axoplast. Bundles of axoneme from the axoplast penetrate through the fine tunnels that are surrounded by the nucleus membrane. The endoplasm is a gray to yellowish orange color and occupies a large portion inside the cortical shell. The axopodia is flexible (*Haliomma capillacea*, *Rhizosphaera trigonacantha*) or robust and straight (*Rhizosphaera arcadophora*). Algal symbionts are absent in *H. capillacea* and *R. trigonacantha* but are scattered throughout the endoplasm in *R. arcadophora*.

Stratigraphic occurrence. — Early Paleocene-Living.

Remarks

The internal skeletal structure of *Haliommilla* has been well documented (Cachon & Cachon 1972b; pl. 11, fig. a; Takahashi 1991: pl. 9, fig. 2; van de Paverd 1995: pl. 14, figs 1, 2, 3; Suzuki *et al.* 2009a: figs 1.3, 1.6; Dumitrica 2017b: pl. 3, figs 3-6; pl. 4, figs 1-7), *Hexarhizacontium* (Dumitrica 2017b: pl. 9, figs 1-6), and *Rhizosphaera* (Dumitrica 1973a: pl. 7, fig. 4; 2017b: pl. 4, figs 8, 9; pl. 5, figs 1-4; pl. 6, figs 1-3; pl. 7, figs 1-12; pl. 8, figs 1-14; Nakaseko & Nishimura 1982: pl. 9, figs 2, 3; Sugiyama & Furutani 1992: pl. 15, figs 8-10?).

Major living members of *Rhizosphaera* in the modern taxonomy are *Rhizosphaera banzare* (Riedel, 1958) (= so-called *Actinomma antarctica* Haeckel, 1887, an unillustrated species), *Rhizosphaera mediana* (Nigrini, 1967) and *Rhizosphaera aracadophora* (Haeckel, 1887). These species were referred by Nigrini (1967: 26) to the genus in order to expand the definition of *Actinomma* to include a medullary meshwork. This idea was eventually discarded by both anatomical (Dumitrica 2017b) and molecular phylogenic studies (Sandin *et al.* 2021). It is generally difficult to identify living cells with protoplasm as their important skeletal characteristics are hidden within the protoplasm, but this is not the case for *Haliommilla* and *Rhizosphaera*. Abundant *Haliommilla* and *Rhizosphaera* specimens are easily collected in plankton samplings and the relationships between the protoplasm and the skeleton has been easily observed. Protoplasmic structures of *Haliomma* and *Rhizosphaera* were already illustrated in the 1870s for *Haliommilla* (Hertwig 1879: pl. 4, figs 1, 3). The fatal symbiosis (Hertwig 1932: pls 3-5), axopodial system (Hollande & Enjumet 1954: fig. c; 1960: pl. 5, figs 1-8), and ultrafine protoplasmic structure (Cachon & Cachon 1972b; Anderson 1984: fig. 8) were studied. Images of living specimens and protoplasm were captured for *Haliommilla* (Suzuki *et al.* 2009a: figs 1.1, 1.4, 1.8; Matsuoka 2017: figs 5.1, 5.2) and *Rhizosphaera* (Anderson 1984: fig. 8; 1994: fig.4; Suzuki 2005: pl. 1, figs 1-8; Matsuoka 2017: fig. 4.2; Matsuoka *et al.* 2017: appendix A). Fine protoplasmic structure was also illustrated in *Haliommilla* (Hollande & Enjumet 1960: pl. 5, figs 4, 6; pl. 20, fig. 1; pl. 34, fig. 2; pl. 52, figs 1, 2) and *Rhizosphaera* (Hollande & Enjumet 1960: pl. 5, figs 1-3, 5, 7, 8; pl. 24, fig. 1; pl. 34, fig. 1; pl. 49, figs 1-4; pl. 50, figs 1-5; pl. 51, figs 1-3; pl. 59, fig. 1). Protoplasm and algal symbionts were documented by epi-fluorescent observation with DAPI dyeing in *Haliommilla* (Suzuki *et al.* 2009b: figs 3K, 3L; Zhang *et al.* 2018: 17, fig. 3) and *Rhizosphaera* (Ogane *et al.* 2009c: fig. 3A-3D; 2010: figs 1.1-1.2, 2.1-2.2; 2014; pl. 1, figs 3-4; Zhang *et al.* 2018: 11, fig. 28). *Haliommilla* is infected by the syndinean dinoflagellate genus *Euduboscquella* (Suzuki *et al.* 2009b; Bachvaroff *et al.* 2012). According to Cachon (1964), "*Actinosphaera*" is infected by *Hollandella piriformis*, but it is impossible to amend the taxonomic name of the host without a complete image.

Validity of genera

Haliommilla

Actinosphaera has the same type species as *Haliommilla*. It is noted that the description of the internal structure in *Haliom-*

milla and *Elatommura* by Campbell (1954: D62) is already outdated. *Haliommilla* is marked by radial spines covering whole surface (Campbell 1954: D62) whereas *Elatommura* is by an outer shell covered by branched radial spines (Campbell 1954: D62). This difference is not necessary to use for genus classification. These two genera were simultaneously published in Haeckel (1887: 236 for *Haliommilla* and 242 for *Elatommura*). As the real *Haliomma capillaceum* specimen examined by Haeckel himself, the type species of *Haliommilla*, was found in the Enrst-Haeckel Haus, Jena, Germany (Sakai *et al.* 2009: pl. 23, fig. 4a), *Haliommilla* is selected as a valid genus.

Superfamily Centrocuboidea Hollande & Enjumet, 1960 *sensu* Dumitrica (2001)

Centrocubidae Hollande & Enjumet, 1960: 48, 51, 69, 120-121.

Centrocubacea [*sic*] – Dumitrica 2001: 193 (= Centrocuboidea).

Diagnosis. — The central structure is very small: a simple frame made of short bars with several sharp corners. The external skeleton is outside the central structure. It is spherical, made of a normal latticed shell, a spongy layered shell, and is full of coarse polygonal meshes.

Remarks

The Centrocuboidea consist of the Centrocubidae (Clade H), Excentroconchidae (Clade I), Quinquecapsulariidae and Spongodrymidae (Clade I) in the Cenozoic. The presence of sharp corners on the edges of the central structure is helpful in differentiating Centrocuboidea from other superfamilies such as the Rhizosphaeroidea.

Clade H (Sandin *et al.* 2021)

Family Centrocubidae Hollande & Enjumet, 1960 *sensu* De Wever *et al.* (2001)

Centrocubidae Hollande & Enjumet, 1960: 48, 51, 69, 120-121. — Petrushevskaya 1975: 571. — Anderson 1983: 52. — Dumitrica 1983a: 224 [in Spumellaria]; 1984: 95. — Cachon & Cachon 1985: 286 [in Order Cryptoaxoplastida]. — Kiessling 1999: 44 [in Entactinaria]. — De Wever *et al.* 2001: 197, 200 [in Entactinaria]. — Afanasieva *et al.* 2005: S278 [in Order Capsulata]. — Afanasieva & Amon 2006: 116.

Centrocubinae – Petrushevskaya 1979: 108. — Kozur & Mostler 1979:15.

Type genus. — *Centrocubus* Haeckel, 1887: 277 [type species by subsequent designation (Campbell 1954: D66): *Centrocubus cladostylus* Haeckel, 1887: 278].

Included genera (Cenozoic only). — *Centrocubus* Haeckel, 1887: 277. — *Octodendron* Haeckel, 1887: 279 (=*Octodendridium* with the same type species; *Heterospongus* **n. syn.**).

Nomen dubium. — *Octodendronium*.

Diagnosis. — The central structure is constructed of a cubic frame and eight rays emerging from the cubic frame. The external part outside the cubic frame consists of a spherical shell made of homogenous layers of coarse polygonal meshes, or a spherical shell made of coarse polygonal meshes. Eight or more radial bladed spines are present. Eight radial spines directly arise from the eight internal rays while the remaining radial spines appear at some points of the shell and are made of coarse polygonal meshes.
The protoplasm is observed in *Centrocubus*. The endoplasm occupies the central part and appears as a dark brown sphere surrounded by a brownish grey ectoplasm. The ectoplasm is distributed in the inner half of the meshed shell. In regard to the axopodial system of an anaxoplastid-type; no axoplast and no bundles of axonemes are observed. The central structure is attached to the nucleus which is located at the center of the intracapsular zone. Instead of bundles of axoneme, the axoneme densely radiates throughout the endoplasm. No algal symbionts were detected.

Stratigraphic occurrence. — early Middle Miocene-Living.

Remarks

It is nearly impossible to differentiate *Centrocubus* from *Spongodendron* and *Spongosphaera* (Spongosphaeridae) without an examination of its central structure. However, it may be possible to identify these species by an examination of both siliceous skeletal parts and protoplasmic characteristics. A fixed image with dyeing was published for *Centrocubus* (Aita *et al.* 2009: pl. 23, fig. 3). The living status of *Centrocubus* is plausible if the photo of "Ses55" specimen of Sandin *et al.* (2021) is compared to the pl. 23, fig. 3 of Aita *et al.* (2009). A specimen covered with protoplasm may appear different when observed. Living specimens of *Spongosphaera*, *Tetrasphaera* (? Spongodrymidae), *Cladococcus* and "*Elaphococcus*" (Cladococcidae) are well documented due to the fact that these genera are commonly found in warm shallow seawaters; such good documentation enables differentiation from *Centrocubus* easier. The endoplasm of *Lychnosphaera* (Cladococcidae) never covers the outer part of the skeleton. Consequently, it cannot be confused with *Centrocubus* even in living cells. However, the living status of *Spongodendron* has not been confirmed making difficult to compare them with living cells. The living specimen shown in De Wever *et al.* (1994: figs 13, 16) was identified as *Octodendron* but it is impossible to confirm this identification given the quality of the images. The fine protoplasmic structure was illustrated for *Centrocubus* (Hollande & Enjumet 1960: pl. 9, fig. 7; pl. 13, figs 1-8; pl. 26, fig. 3; pl. 60, fig. 1), and *Octodendron* (pl. 60, fig. 7).

The internal skeletal structure for *Centrocubus* was documented (Dumitrica 1983a: pl. 3, figs 1-3; van de Paverd 1995: pl. 27, figs 1, 2). The overall character of the specimen illustrated in van de Paverd (1995: pl. 26, fig. 2) is identical to *Octodendron*, but the central structure is probably the same as that of the Excentroconchidae. A new and undescribed genus probably belongs to this family (e.g., Aita *et al.* 2009: pl. 40, fig. 1; pl. 43, fig. 3). Old Centrocubidae genera such as the Triassic *Arcicubulus* (Dumitrica 1983a), the Jurassic *Solicubulus* (Dumitrica 1983a), and the Cretaceous *Marianasphaera* (Li & Sashida in Li *et al.* 2011) and *Pessagnulus* (Dumitrica 1983a) are also included in this family.

Validity of genera

Octodendron

Octodendridium has the same type species as *Octodendron*. Genera in the Centrocubidae are mainly classified by the construction of the microsphere, the number of rays from the microsphere, branched patterns of these rays, and relationship of rays with shells. *Heterospongus* is defined by branched eight main spines, cube-shaped microsphere, radial spines produced from corners (Campbell 1954: D68). *Octodendron* is defined by latticed cortical shell surrounded by spongy network which may bear small radial spines and no secondary radial spines (Campbell 1954: D68). Ridiculously, attention points are not overlapped each other between these definitions, it is unable to pinpoint the difference points from them. The definition of *Octodendron* is properly applicable for *Heterospongus*; on the other hand, that of *Heterospongus* is also properly applicable for *Octodendron*. This concludes the synonymy relationship even under the concept of Campbell (1954). As *Octodendridium* is simultaneously published as a subgenus of *Octodendron* with *Octodendron* in Haeckel (1887), *Octodendron* prioritized over *Octodendridium* as a valid name.

Clade I (Sandin *et al.* 2021)

Family Excentroconchidae Hollande & Enjumet, 1960 *sensu* Dumitrica (2014a)

Excentroconchidae Hollande & Enjumet, 1960: 68, 86. — Dumitrica 1979: 18; 1984: 94; 2001: 193-194 (*sensu* emend.); 2014a: 59-60 [in Entactinaria]. — Petrushevskaya 1979: 105. — Kozur & Mostler 1979: 33. — Anderson 1983: 50. — Cachon & Cachon 1985: 288 [in the Order Periaxoplastida].

Type genus. — *Excentroconcha* Mast, 1910: 64 [type species by subsequent designation (Campbell 1954: D67): *Excentroconcha minor* Mast, 1910: 64].

Included genera. — *Excentroconcha* Mast, 1910: 64. — *Gonosphaera* Jørgensen, 1905: 132. — *Lonchosphaera* Popofsky, 1908: 217 (= *Arachnostylus* synonymized by Dumitrica 1984: 94).

Diagnosis. — The central structure consists of an MB, two A-rays, four B-rays (rarely two), one to three AA-rays, and a central frame. The MB is also a part of the central frame. A-rays, B-rays and AA-rays are oriented towards upper, lateral (equatorial) and lower directions, respectively, from the central frame. A-rays emerge from both ends of MB. Four B-rays extend laterally from each corner of the central frame at the equatorial plane. The central frame is vertically subdivided into upper and lower hemispheres by the height level of the central frame where B-rays are joined. The upper hemisphere of the central frame is constructed by the MB and four to three downward rays. The lower hemisphere is variable but two sets of the four downward rays are joined near the opposite side of MB, respectively. The junction point is visible from a view parallel to MB. These two joint points are connected by a small arch at the antapical end of the central frame (named the antapical arch). The plane of the antapical arch is perpendicularly oriented to the length of MB. One to three AA-rays extend from the end of the antapical arch towards the opposite direction of the double A-rays. Some members develop an additional equatorial ring that is also connected by four B-rays and, or, other arches in the lower hemisphere of the central frame. One latticed, one spongy layered cortical shell, or a spherical structure made of coarse spongy meshwork is present. Short to long radial spines directly connected to the internal rays or beams are visible. The by-spine may be present or absent.
Regarding the axopodial system of periaxoplastid-type; the axoplast is located at the center of the protoplasm and a bundle of axonemes radiates from the center. The nucleus is independent of the axopodial system and has an arch shape. No axoflagellum was recognized. The central structure is attached to the capsular wall, placing it at the center of the skeleton. The arched nucleus is placed on the opposite side of the central structure.

Stratigraphic occurrence. — early Early Miocene-Living.

Remarks

This family is specified by reference to fig. 3 in Dumitrica (2014a). Some undescribed species remain. The internal skeletal structure for *Lonchosphaera* (Helmcke & Bach 1990: 75; Matsuoka 2009: fig. 3.12; Dumitrica 2014a: figs 3.a-3.h) was illustrated. The fine protoplasmic structure was illustrated for *Excentroconcha* (Hollande & Enjumet 1960: pl. 1, fig. 7; pl. 19, fig. 5; pl. 43, fig. 1) and *Lonchosphaera* (Hollande & Enjumet 1960: pl. 1, figs 8, 9).

Family Quinquecapsulariidae Dumitrica, 1995

Quinquecapsulariidae Dumitrica, 1995: 21. — De Wever *et al.* 2001: 200-201 [in Entactinaria]. — Afanasieva *et al.* 2005: S278 [in Order Capsulata]. — Afanasieva & Amon 2006: 117.

Quinquecapsulariidae O'Dogherty, 1994: 268 [*nomen nudum*].

Type genus. — *Quinquecapsularia* Pessagno, 1971b: 362 [type species by objective designation: *Quinquecapsularia spinosa* Pessagno, 1971b: 364].

Included genera (Cenozoic only). — *Joergensenium* Bjørklund, Dumitrica, Dolven & Swanberg, 2008: 460.

Diagnosis. — The central structure is very small with twin pentagonal frames located parallel to each other. Three to five connecting bars between these two pentagonal frames are present. This central structure comprises two acute corners and one straight beam is arising from each corner. A Cenozoic member of this family has three concentric shells: the innermost shell is the central structure, the second internal shell is a spherical outer medullary shell with a patterned, indented surface, and the outermost is large latticed cortical shell. The shape of the outer medullary shell is closely related by radial beams. The endoplasm completely surrounds the outer medullary shell.

Stratigraphic occurrence. — Late Miocene-Living.

Remarks

The family Quinquecapsulariidae was initially proposed for a Cretaceous spherical polycystine *Quinquecapsularia spinosa* Pessagno, 1972. *Joergensenium* is the only known Cenozoic genus. The oldest report of this family dates back to the Early Jurassic (*Empirea* Whalen & Carter in Carter *et al.* 1998). Bjørklund *et al.* (2008) insisted on *Joergensenium* being an endemic Norwegian genus but the *Joergensenium*-species was already identified everywhere in the Neogene. The Internal skeletal structure for *Joergensenium* was illustrated (Ikenoue *et al.* 2016; pl. 6). Based on molecular data, *Joergensenium* is infected with Marine Alveolata Groups I and II (Ikenoue *et al.* 2016).

Family Spongodrymidae Haeckel, 1887 **n. stat.**

Spongodrymida Haeckel, 1887:209 [as a tribe]. — Schröder 1909: 17 [as a tribe].

Tetrasphaeria Haeckel, 1882: 453 [as a subfamily, *nomen nudum*].

Plegmosphaerida Haeckel, 1882: 455 [*nomen dubium*, as a tribe]; 1887: 60, 86 [as a subfamily]. — Schröder 1909: 6 [as a subfamily].

Tetrasphaeridae – Enriques 1932: 987.

Plegmosphaerinae – Campbell & Clark 1944a: 10 [*nomen dubium*]. — Campbell 1954: D50. — Chediya 1959: 72. — Hollande & Enjumet 1960: 68, 102. — Tan & Tchang 1976: 225. — Petrushevskaya 1979: 109. — Cachon & Cachon 1985: 287. — Tan 1998: 101. — Tan & Chen 1999: 128.

Spongodryminae – Hollande & Enjumet 1960: 104. — Anderson 1983: 50-51, 57, 170. — Cachon & Cachon 1985: 287.

Type genus. — *Spongodrymus* Haeckel, 1882: 455 [type species by subsequent designation (Campbell 1954: D96): *Spongodrymus elaphococcus* Haeckel, 1887: 272].

Included genera. — *Plegmosphaeromma* Haeckel, 1887: 89. — *Spongodictyum* Haeckel, 1862: 459 (= *Spongodictyoma* with the same type species). — *Spongodrymus* Haeckel, 1882: 455. — ? *Tetrasphaera* Popofsky, 1912: 111. — ? *Tricorporisphaera* O'Connor, 1999: 4.

Invalid name. — *Spongodictyon.*

Nomina dubia. — *Dictyoplegma*, *Dictyosphagma*, *Dispongia*, *Plegmosphaera*, *Plegmosphaerantha*, *Plegmosphaerella*, *Plegmosphaerusa*, *Spongiommella*, *Spongothamnus, Styptosphaera*.

Junior homonym. — *Dictyosoma* Müller 1856 (= *Dictyoplegma*) *nec* Temminck & Schlegel, 1845.

Diagnosis. — Spherical spongy cortical shell with a variable number of medullary shells, a very delicately framed central structure and no robust three-bladed radial beams are present.
A brownish to reddish brown opaque endoplasm occupies almost all shells, excluding the peripheral parts of the skeleton. The capsular wall is well visible. An ectoplasmic membrane covers all skeletons including by-spines. No algal symbionts are observed. Axopodial system of centroaxoplastid-type: axoplast placed in the center of the intracapsular zone as a very small fused point and no significant bundles of axoneme. Instead of bundles, axoneme radiate evenly throughout the intracapsular zone. Nucleus is placed in the center of the intracapsular zone and enclosing the axoplast.

Stratigraphic occurrence. — Middle Pleistocene-Living.

Remarks

The number of medullary shells is varied among the genera belonging to Spongodrymidae and the central structure is unstable in several genera. *Spongodrymus* species at least have a single framed microsphere with fibrous radial beams radiating from the microsphere. Both *Spongodictyum* and *Tricorporisphaera* seem to possess latticed double medullary shells. *Tetrasphaera* has three concentric medullary shells and always co-occurs with *Plegmosphaeromma* in a same sample. *Tricorporisphaera* has mildly bladed radial beams arising from the medullary shell. In contrast, both *Spongodictyum* and *Tetrasphaera* have fibrous radial beams comparable to *Spongodrymus*. The family "Tetrasphaeria" was proposed by Haeckel (1882), prior to the establishment of the tribe "Spongodrymida" by Haeckel (1887) himself. The genus *Tetrasphaera* was first established by Popofsky (1912), and subsequently Haeckel's family "Tetrasphaeria" became *nomen nudum*.

The internal skeletal structure was illustrated for the "*Plegmosphaerusa*"-form of *Plegmosphaeromma* (Nakaseko & Nishimura 1982: pl. 10, fig. 1) and the "*Styptosphaera*"- form of *Plegmosphaeromma* (Suzuki 1998b: pl. 3, fig. 1). The fine protoplasmic structure was illustrated for the "*Plegmosphaerella*"- form of *Plegmosphaeromma* (Swanberg *et al.* 1990; pl. 3, figs 1-6), *Plegmosphaeromma* (Hollande & Enjumet 1960: pl. 7, figs 7-9; pl. 8, figs 1-9; pl. 10, figs 1-8; pl. 48, figs 1-5) and *Spongodrymus* (Hollande & Enjumet 1960: pl. 7, fig. 3). An image of living specimens was captured for the "*Plegmosphaerella*"- form of *Plegmosphaeromma* (Suzuki & Not 2015: fig. 8.8.) and protoplasm and algal symbionts were documented by epi-fluorescent observation with DAPI dyeing for the *Plegmosphaerusa* - form of *Plegmosphaeromma* (Zhang *et al.* 2018: 19, fig. 1). According to Cachon (1964), "*Plegmosphaera*" is infected with *Hollandella lobata*, but it is impossible to amend the taxonomic name for the host without its overall image.

Several papers for living radiolarian studies wrote about "*Spongodrymus* sp. (spp.)", but its identification is doubtful because "*Spongodrymus*" appears as nearly covered by full opaque endoplasm, similar in appearance to *Spongosphaeromma* and the *Elaphococcus*-form of *Cladococcus* (Cladococcidae). These papers never clarified the key points distinguishing between the above-mentioned genera.

Clade indet.

Superfamily Centrolonchoidea Campbell, 1954 n. stat.

Centrolonchinae Campbell, 1954: D60.

Hexastyloidea – Petrushevskaya 1975: 567 [*nomen dubium*]. — Dumitrica 1979: 15-16; 1984: 91.

Hexastylioidea – Petrushevskaya 1979: 104 [*nomen dubium*]; 1984: 128; 1986: 125.

Hexastylacea – Kozur & Mostler 1981: 5-12 [*nomen dubium*, as a superfamily]; 1982: 402 [as a superfamily in Entactinaria].

Hexastyliidae [*sic*] – Dumitrica 1984: 93-94 [*nomen dubium*] (= Hexastylidae).

Hexasilioidea [*sic*] – Amon 2000: 29 [*nomen dubium*] (= Hexastyloidea).

Diagnosis. — Same as the family.

Remarks

The reason why Centrolonchoidea is validated as opposed to Hexastyloidea is written in the remarks for Centrolonchidae.

Family Centrolonchidae Campbell, 1954 *sensu* Hollande & Enjumet (1960)

Centrolonchinae Campbell, 1954: D60. — Kozur & Mostler 1979: 29 (*sensu* emend.).

Hexastylida Haeckel, 1882: 450 [*nomen dubium*, as a tribe]; 1887: 170-171 [as a subfamily]. — Schröder 1909: 8 [as a subfamily].

Hexastylinae – Campbell 1954: D58 [*nomen dubium*]. — Chediya 1959: 90. — Dieci 1964: 185.

Stigmosphaeridae Hollande & Enjumet, 1960: 68, 86, 89 [*nomen dubium*]. — Anderson 1983: 49-50. — Cachon & Cachon 1985: 288 [in Order Periaxoplastida].

Hexastylidae – Petrushevskaya 1975: 567 [*nomen dubium*]; 1979: 104-105. — Dumitrica 1979: 16, 18. — Kozur & Mostler 1981: 12 (*sensu* emend.); 1982: 402-403 [in Entactinaria]. — Dumitrica 1995: 21. — Amon 2000: 29. — De Wever *et al.* 2001: 202-203 [in Entactinaria]. — Suzuki H. *et al.* 2002: 166, 167 [in Spumellaria]. — Afanasieva *et al.* 2005: S272 [in Entactinaria]. — Afanasieva & Amon 2006: 108. — Chen *et al.* 2017: 100.

Centrolonchidae – Kozur & Mostler 1979: 27-28 (*sensu* emend.).

Centrolonchini – Kozur & Mostler 1979: 29 (*sensu* emend.).

Stigmosphaerini – Kozur & Mostler 1979: 29 [*nomen dubium*, as a tribe]; 1981: 16 [a tribe].

Stigmosphaerinae – Kozur & Mostler 1981: 16 [*nomen dubium*]; Kozur & Mostler 1989: 192.

Type genus. — *Centrolonche* Popofsky, 1912: 89 [type species by monotypy: *Centrolonche hexalonche* Popofsky, 1912: 89].

Included genera. — *Centrolonche* Popofsky, 1912: 89. — *Stigmosphaerusa* Hollande & Enjumet, 1960: 90. — *Stigmostylus* Hollande & Enjumet, 1960: 90.

Nomina dubia. — *Centracontium*, *Stigmosphaera*.

Diagnosis. — One latticed cortical shell with a few fiber strings which are fused at a point in the center of the cortical shell. The fibers directly join the cortical shell or are attached at some point to other fibers. Radial spines, if present, are very thin and connected to each fiber. Short to long by-spines radiate throughout the pore frame of the cortical shell. Endoplasm of a tiny size is transparent and surrounds the fused point of the previously mentioned fibers. Probable algal symbionts surround the endoplasm inside the cortical shell. The axopodial system classified as periaxoplastid-type. The axoplast is located on one side of the nucleus; the thick bundle of axonemes penetrates through the nucleus to the opposite side of the axoplast and extends outside the capsular wall, becoming an axoflagellum. The fused point of the fibers is attached on the axoplast. Usually, the fused point is placed at the center of the cortical shell (e.g., *Stigmostylus*) or on the capsular wall (e.g., *Stigmosphaerusa*).

Stratigraphic occurrence. — late Late Miocene-Living.

Remarks

The taxonomic concept of the so-called Hexastylidae was historically based on *Hexastylus phaenaxonius* defined by Haeckel, 1887. This type of designation by Campbell (1954: D58) seems to violate the Article 69.3 of the Code. The validation of the type species of *Hexastylus* involves a complex issue. *Hexastylus* was first established in Haeckel (1882) without including any particular species. The first species belonging to *Hexastylus* is *Hexastylus primaevus* Rüst, 1885, a Mesozoic radiolarian of Hornfels from Csernye (Hungary) and black hornfels from Rigi (Italy). Under the current Code, the species by Rüst (1885) is the first and only nominal species included in *Hexastylus*, hence this species is the type species by subsequent monotypy (Article 69.3) regardless the coherence the Mesozoic species with Haeckel's description for *Hexastylus*. Campbell (1951: 528) thought the identification of *Hexastylus* by Rüst (1885) was a mistake, and Campbell (1954: D58) erroneously designated *H. phaenaxonius* as type species of *Hexastylus*. The species *H. primaevus* was illustrated by Rüst (1885) but this is a *nomen dubium* due to the fact that the distinguishing skeletal structure are invisible at the generic level. Hence, the "*nomen dubium*" status can only be fixed after Rüst's drawing because the name-bearing type specimen was destroyed during the Second World War (Steiger 1995). Unfortunately, reexamination of topotypical material is not possible because the outcrops in and around the type locality have been deeply buried at the present (Suzuki 1998a). As the concept of the Hexastylidae, based on *H. phaenaxonius*, concords with the Centrolonchidae and because "Centolonchinae" was once synonymized with the Hexastylidae (De Wever *et al.* 2001: 202-203), we replace the valid family name for these members by Centrolonchidae. The internal skeletal structure of *Stigmosphaerusa* was documented in Helmcke & Bach (1990: 104) and Takahashi (1991: pl. 9, fig. 1). The protoplasm for *Centrolonche* was illustrated (Zhang *et al.* 2018: 11, fig. 19). The fine protoplasmic structures were documented for *Centrolonche* (Hollande & Enjumet 1960: pl. 2, fig. 10), *Stigmosphaerusa* (Hollande & Enjumet 1960: pl. 1, fig. 11; pl. 43, fig. 2) and *Stigmostylus* (Hollande & Enjumet 1960: pl. 2, figs 1-4; pl. 31, fig. 8). Hollande & Enjumet (1960) detailed the homogeny of cellular microstructures between Ethmosphaeridae (originally "Macrosphaeridae") and Centrocubidae, and subsequently proposed the "Anaxoplastidies" as an informal group. Later, the Centrocubidae was included into another informal group: the "Cryptoaxoplasides" by Cachon & Cachon (1972c).

Superfamily Heliosaturnaloidea Kozur & Mostler, 1972 n. stat.

Heliosaturnalinae Kozur & Mostler, 1972: 27 [as a subfamily].

Saturnalicaea [*sic*] Kozur & Mostler, 1990: 182-187 [*nomen dubium*, as a superfamily of Spumellaria].

Saturnaliacea [*sic*] – Dumitrica *et al.* 2010: 285, 287 [as a superfamily of Entactinaria, *nomen dubium*] (= Saturnaloidea).

Saturnaloidea – Dumitrica & Zügel 2008: 59 [*nomen dubium*, in Entactinaria] .

Saturnalata [*pars*] – Afanasieva & Amon *in* Afanasieva *et al.* 2005: S279 [as an order of Class Spumellaria]. — Afanasieva & Amon 2006: 118 [as an order].

Diagnosis. — This superfamily includes the Axoprunidae and Saturnulidae Suzuki, n. fam. (not Saturnalidae) in the Cenozoic. Skeleton formed by a spherical shell or spongy spherical shell with a heteropolar microsphere and a ring directly connected to the shell by polar spines. The heteropolar microsphere resembles a sack-like formation and was named "microbursa" (Dumitrica *et al.* 2010: 285). Virtually, the microbursa is divided by polar beams (P) into an apical side (upper side) and an antapical side (lower hemisphere). The apical side of the microbursa is constructed by MB and consists of four polygonal pores (coded as LG when parallel to MB and as TG when vertical to MB) whose frames are assembled by four basal bars from MB. The antapical side displays a tetrapetaloid structure. P is oriented in an orthogonal direction to MB and is adjoined to the antapical side of the microsphere. The microbursa is covered by an outer spherical medullary shell or a spherically arranged coarse frame. Both spheres are connected with four apical bars from the apical side of the microbursa and other short bars from the antapical side. Outside these two spheres, a single ring of variable type (densely concentric convex lens-shaped shell, or cortical shell) is developed. However, no ornaments on polar beams are present for the Axoprunidae. Several connecting bars are visible between the ring and the inner structures in some members, but the only Ps are directly connected to the ring. Polar beams are never bladed.

Remarks

As *Saturnalis* is a *nomen dubium* without an illustrated type specimen, it is impossible to retain the name "Saturnaloidea." for the superfamily rank. The "Saturnaloidea" is subdivided into four families, namely the Saturnulidae Suzuki, n. fam. (synonym of "Saturnalidae Deflandre, 1953"), Heliosaturnalidae Kozur & Mostler, 1972, Hexasturnalidae Kozur & Mostler, 1983, and Axoprunidae Dumitrica, 1985 (Dumitrica & Zügel 2008; Dumitrica *et al.* 2010). Thus, the superfamily name must be replaced for the senior family name Heliosaturnalidae Kozur & Mostler, 1972. The concept of Heliosaturnaloidea has been subject of discussion among Mesozoic specialists (Dumitrica *et al.* 2010: 285, 287).

Family Axoprunidae Dumitrica, 1985

Axopruninae Dumitrica, 1985: 186. — De Wever *et al.* 2001: 209-210. — Afanasieva *et al.* 2005: S280. — Afanasieva & Amon 2006: 119.

Spongostylida Haeckel, 1882: 455 [*nomen dubium*, as a tribe]; 1887: 122, 148 [as a subfamily]. — Schröder 1909: 8 [as a subfamily].

Spongostylinae – Campbell & Clark 1944a: 12 [*nomen dubium*]. — Frizzell & Middour 1951: 15. — Campbell 1954: D54. — Chediya 1959: 83.

Dorydiscinae Campbell, 1954: D89 [*nomen dubium*].

Axoprunidae – Suzuki *et al.* 2009d: 241. — Dumitrica *et al.* 2010: 287.

Type genus. — *Axoprunum* Haeckel, 1887: 298 [type species by monotypy: *Axoprunum stauraxonium* Haeckel, 1887: 289].

Included genera. — *Axoprunum* Haeckel, 1887: 298 (= *Ellipsoxiphium* **n. syn.**, *Xiphosphaerella* **n. syn.**; *Stylacontarium* synonymized by Sugiyama *et al.* 1992: 16). — *Dorylonchella* Clark & Campbell, 1942: 22.

Nomina dubia. — *Dorylonchomma, Dorydiscus, Dorydruppa, Doryphacus, Doryprunum*.

Diagnosis. — Heliosaturnaloidea without equatorial ring, with two polar spines and a latticed cortical shell (Dumitrica *et al.* 2010: 287). A dark grey endoplasm fills the medullary shell and is additionally observed in its surrounding periphery.

Stratigraphic occurrence. — Early Paleocene-Living.

Remarks

Polycystinea with a spherical to oblong shell with bi-polar spines (also present in the Stylatractidae and Stylosphaeridae). The initial differentiation marker for Axoprunidae was based on the presence of inner non-bladed bi-polar spines. Instead, the precise identification of this family's representatives should be based on the presence of a microbursa. Skeletal structure, including growth line, was documented for *Axoprunum* (Dumitrica 1985: pl. 3, figs 19, 20; Nishimura 1986: fig. 7.3; Sugiyama & Furutani 1992: pl. 16, figs 9, 11; Sugiyama *et al.* 1992: pl. 12, fig. 4; Vasilenko 2019: pl. 1, fig. 6). A " living" image for the *Axoprunum* collected in the Mesopelagic zone (Suzuki & Not 2015: fig. 8.10.14) was documented. The last occurrence of "*Axoprunum*" *angelinum* (Campbell & Clark 1944a), as senior synonym of "*Stylatractus*" *universus* Hays 1970", is dated as 0.46 ± 0.04 Ma age in the Pacific (Matsuzaki *et al.* 2014; Kamikuri 2017), Atlantic (Morley & Shackleton 1978) and Southern Ocean (McIntyre & Kaczmarska 1996). Notwithstanding, no appropriate genus has been proposed for this species (e.g., Nakaseko & Nishimura 1982: pl. 12, figs 3, 4; Dumitrica 1985: pl. 3, figs 16-18; Sugiyama *et al.* 1992: pl. 13, fig. 3).

Validity of genera

Axoprunum

The central part of the type species for *Axoprunum* is missing in the type-illustration (Haeckel 1887: pl. 48, fig. 4), but all other characters, except the central part, are sufficient to specify this genus of the Cenozoic. The definition of *Axoprunum* in Campbell (1954: D68) is useless because his definition did not include the probable presence of internal shell(s), the presence of six radial beams whose pairs are perpendicular to each other, and the presence of two un-bladed similar opposite polar spines. These characters are fully or partly overlooked in the definition of the remaining genera in Campbell (1954: D54 for *Xiphosphaerella*, D60 for *Stylacontarium* and D69 for *Ellipsoxiphium*) so that they are useless to understand the differences between these genera. The internal structure is invisible in the type-illustrations for *Ellipsoxiphium* (Haeckel 1887: pl. 14, fig. 7) as well as *Xiphosphaerella* (Haeckel 1887: pl. 14, fig. 4), but the occurrence of a completely empty shell has not been clearly proved in these two genera. The definition of *Xiphosphaerella* includes the presence of a papillose to spiny or thorny surface, but this characteristic is not significant (supporting image for *Xiphosphaerella*). Until the exact internal structures of *Xiphosphaerella* and *Ellipsoxiphium* are documented, the four genera discussed here are regarded as synonyms. *Axoprunum*, *Ellipsoxiphium* and *Xiphosphaerella* were simultaneously published by Haeckel (1887: 124 for *Xiphosphaerella*, 296 for *Ellipsoxiphium* and 298 for *Axoprunum*). *Axoprunum* is validated because this is the only genus whose internal structure is illustrated in images of the type.

Family Saturnulidae Suzuki, n. fam.

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Saturnalinae Deflandre, 1953: 419-420 [*nomen dubium*]. — Riedel 1967b: 294. — Kozur & Mostler 1972: 30. — Petrushevskaya & Kozlova 1972: 521. — Foreman 1973b: 260. — Nakaseko *et al.* 1975: 169. — Nakaseko & Sugano 1976: 121. — Riedel & Sanfilippo 1977: 863. — Donofrio & Mostler 1978: 20-22. — De Wever *et al.* 1979: 79; 2001: 208-209. — Anderson 1983: 37. — De Wever 1984: 16 (*sensu* emend.). — Sanfilippo & Riedel 1985: 590-591. — Takahashi 1991: 78. — Carter 1993: 52. — Dumitrica 1995: 23. — Dumitrica *et al.* 1997: 18. — Afanasieva *et al.* 2005: S280. — Afanasieva & Amon 2006: 118-119. — Dumitrica & Zügel 2008: 66.

Saturnalidae – Kozur & Mostler 1972: 30 [*nomen dubium*] (*sensu* emend.); 1981: 53 [as a subfamily] (*sensu* emend.); 1983: 12 [in Spumellaria]; 1990: 213-214 [in Spumellaria]. — Dumitrica 1979: 26; 1984: 101. — Petrushevskaya 1979: 115-116; 1986: 128. — De Wever 1984: 13. — Carter 1993: 51. — O'Dogherty 1994: 248 [in Spumellaria]. — Dumitrica 1995: 23. — Hollis 1997: 41. — Cordey 1998: 91. — De Wever *et al.* 2001: 205. — Afanasieva *et al.* 2005: S279 [in Order Saturnalata]. — Afanasieva & Amon 2006: 118. — Bragin 2007: 991, 993 [in Spumellaria]; Bragin 2011: 758.

Saturnalideidae [*sic*] – Kozur & Mostler 1990: 206 [*nomen dubium*] (= Saturnalidae).

Type genus. — *Saturnulus* Haeckel, 1879: 705 [type species by monotypy: *Saturnulus planeta* Haeckel, 1879: 705].

Included genera (Cenozoic only). — *Saturnulus* Haeckel, 1879: 705 (= ? *Saturnalium* **n. syn.**). — *Spongosaturninus* Campbell & Clark, 1944b: 7.

Nomina dubia. — *Saturnalina*, *Saturnalis*, *Saturninus, Spongostylus*.

Diagnosis. — Heliosaturnaloidea with an equatorial ring and no polar spines. The ring's shape is circular to elliptical and elongated in the perpendicular direction to the polar rays. Polar rays flat to elliptical in cross section, or, most frequently, three or four-bladed. Shell spongy to latticed with two layers (Dumitrica *et al.* 2010: 287). A dark grey endoplasm fills the microsphere and is also present in the surrounding area.

Stratigraphic occurrence. — Early Toarcian-Early Paleocene.

Remarks

The name "Saturnalidae" and "*Saturnalis*" have been widely accepted by the majority of radiolarists. However, it was impossible to retain this name due to the absence of an illustrated type specimen for *Saturnalis*. The internal spicular system was illustrated for *Saturnulus* (Dumitrica 1985: pl. 3, figs 3, 7, 15; van de Paverd 1995: pl. 30, figs 1, 2, 5) and *Spongosaturninus* (Dumitrica 1985: pl. 3, fig. 11). A "living" image for *Saturnulus* was collected and documented from the Bathypelagic zone (Suzuki & Not 2015: fig. 8.10.16).

Validity of genera

Saturnulus

Real specimens identifiable as the type species of *Saturnalium* have not been found so far. We simply synonymized *Saturnulus* and *Saturnalium* due to the existence of a ring.

Phylogenetic Molecular Lineage indet.

Superfamily Thalassothamnoidea Haecker, 1906

Thalassothamnidae Haecker, 1906: 879; 1908: 394-400 [in Col-lodaria].

Thalassothamnacea – Kozur & Mostler 1982: 405 [as a superfamily of Entactinaria].

Diagnosis. — Same as the family Thalassothamnidae.

Remarks

See the remarks for Thalassothamnidae.

Family Thalassothamnidae Haecker, 1906

Thalassothamnidae Haecker, 1906: 879; 1908: 394-400. — Popofsky 1908: 203-205. — Lankester *et al.* 1909: 144. — Hollande & Enjumet 1953: 108 [in Collodaria]. — Campbell 1954: D46 [in Collodaria]. — Kozur & Mostler 1981: 5; 1982: 406 [in Entactinaria]. — Cachon & Cachon 1985: 284 [in Sphaerocollina]. — Petrushevskaya 1986: 122-123. — De Wever *et al.* 2001: 175, 177 [in Entactinaria].

Cytocladidae Schröder, 1908: 209.

Type genus. — *Thalassothamnus* Haecker, 1906: 888 [type species by subsequent designation (Campbell 1954: D46): *Thalassothamnus genista* Haecker, 1906: 881].

Included genera. — *Cytocladus* Schröder, 1908: 219. — *Thalassothamnus* Haecker, 1906: 888.

Diagnosis (contributed by Yasuhide Nakamura). — A radiolarian with a single large diverging spicule. The several radial spines of the diverging spicule merge together at several points.

Stratigraphic occurrence. — Holocene-Living.

Remarks (contributed by Yasuhide Nakamura)

The genus *Cytocladus* was classified into the family Thalassothamnidae Haecker 1906. It should be noted that *Cytocladus* is covered with a spherical extracapsular protoplasm and that its skeletal architecture is similar to the Sphaerozoidae and Thalassosphaeridae. These features suggest a close relationship to Collodaria (Cachon & Cachon 1985; Petrushevskaya 1984; Nakamura *et al.* 2020). Living specimens were illustrated and examined by Cachon & Cachon (1985: 284) and Nakamura *et al.* (2020: figs 2.D-2.F). The overall appearance of *Thalassothamnus* somewhat resembles that of the family Astracanthidae of Phaeodaria (Cercozoa, Rhizaria). However, this genus differs from the aforementioned phaeodarians in several ways: a) the cross-section of the radial spines is solid (not hollow), b) several divergent points occasionally exist, and, c) there is generally one central capsule (whereas, several central capsules can be found in Astracanthidae).

Order NASSELLARIA Ehrenberg, 1876

Phylogenetic Molecular Lineage I (Sandin *et al.* 2019)

Diagnosis. — Multi-segmented Nassellaria having a simple cephalis and discrete dividers between the subsequent segments below the thorax.

Remarks

Lineage I is the oldest clade in the entire Nassellaria order as the molecular clock indicates that it may date back to the Devonian (Sandin *et al.* 2019). Although only one genus *Eucyrtidium* was confirmed as a member of Lineage I, Amphipyndacoidea, Archaeodictyomitroidea and Eucyrtidioidea are likewise considered members of Lineage I. This inclusion is done because the huge number of studies devoted to them over the last century.

Superfamily Amphipyndacoidea Riedel, 1967

Amphipyndacidae Riedel, 1967a: 148; 1967b: 296; 1971: 657.

Amphipyndacaceae [*sic*] O'Dogherty, 1994: 98 (= Amphipyndacoidea)[as a superfamily].

Amphipyndacea [*sic*] – De Wever *et al.* 2001: 266 (= Amphipyndacoidea)[as a superfamily].

Amphipyndacioidea [*sic*] – Afanasieva *et al.* 2005: S302 (= Amphipyndacoidea). — Afanasieva & Amon 2006: 151.

Diagnosis. — Amphipyndacoidea are multisegmented Nassellaria whose cephalis is divided into two parts, a spherical cavity and flattened space, by a thick, horizontal divider. This divider is formed by horizontally or subhorizontally extended branches of A-rod. A-, D-, V-, Lr- and Ll-rods are observed.

Remarks

This superfamily consists of the Mesozoic Amphipyndacidae, Canoptidae Pessagno in Pessagno *et al.* (1979), Parvicingulidae Pessagno 1977c, Syringocapsidae Foreman 1973b, and Spongocapsulidae Pessagno 1977c (De Wever *et al.* 2001). Amphipyndacidae is the only known member appearing in the Cenozoic. Suzuki H. *et al.* (2002: 180) noted the similarity between the cephalic initial spicular system of the earliest Jurassic *Canoptum* and that of Amphipyndacidae. They subsequently concluded that Canoptidae is a junior synonym of the Amphipyndacidae. However, the photographic evidence of Suzuki H. *et al.* (2002: fig. 8K) was insufficient in evaluating the illustrated structure of the Canoptidae that was drawn and published in De Wever *et al.* (2001: fig. 177). The difference between De Wever *et al.* (2001) and Suzuki, Hisashi's opinion (Suzuki H. *et al.* 2002) is the rank of superfamily/family.

Family Amphipyndacidae Riedel, 1967

Amphipyndacidae Riedel, 1967a: 148; 1967b: 296; 1971: 657. — Petrushevskaya 1971b: 985 [as a subfamily]. — Petrushevskaya & Kozlova 1972: 545. — Nakaseko *et al.* 1975: 174. — Nakaseko & Sugano 1976: 131. — Riedel & Sanfilippo 1977: 877. — Dumitrica 1979: 32; 1995: 30. — Anderson 1983: 44. — Sanfilippo & Riedel 1985: 596. — Takemura 1986: 55. — O'Dogherty 1994: 138. — Hollis 1997: 66. — De Wever *et al.* 2001: 266, 268. — Suzuki H. *et al.* 2002: 180; 2004: 383. — Suzuki & Gawlick 2003: 191. — Afanasieva *et al.* 2005: S303. — Afanasieva & Amon 2006: 152-153.

Amphipyndacinae – Dumitrica 1995: 31.

Type genus. — *Amphipyndax* Foreman, 1966: 355 [type species by subsequent designation: *Amphipyndax enesseffi* Foreman, 1966: 356].

Included genus (Cenozoic only). — *Amphipternis* Foreman, 1973a: 430 (= *Amphiparvex* synonymized by O'Dogherty *et al.* 2009a: 327; *Protostichocapsa* synonymized by De Wever *et al.* 2001: 268).

Diagnosis. — A multisegmented Nassellaria whose post-cephalis segments are separated by distinct dividers. The apical part is robust and consists of a spherical cephalis, a narrowly necked tunnel with a thick separator in the lower part of the cephalic cavity. The robust proximal top part is fully or partially covered by a thick poreless wall. No rods from the initial spicular system extend outwards from the shell.

Stratigraphic occurrence. — Early Berriasian-early Middle Miocene.

Remarks

The initial spicular system of the Amphipyndacidae has been repeatedly discussed and documented (Foreman 1966: text-fig. 1-9; Empson-Morin 1982: text-fig. 2; Takemura 1986: 36-37; De Wever *et al.* 2001: fig. 176). According to Empson-Morin (1982), the cephalis and thorax correspond to the cephalic cavity of aforementioned papers.

Superfamily Archaeodictyomitroidea Pessagno, 1976

Archaeodictyomitridae Pessagno, 1976: 49; 1977a: 41 (*sensu* emend.); 1977b: 934.

Archaeodictyomitracea [*sic*] – Grill & Kozur 1986: 254 (= Archaeodictyomitroidea) [as a superfamily]. — O'Dogherty 1994: 69. — De Wever *et al.* 2001: 262.

Diagnosis. — A multisegmented Nassellaria with a simple cephalis with MB, A-, V-, D- and double L-rods. The shell is covered with continuously aligned longitudinal costae. One to two (or more) rows of pores; similar rows of relict pores, or platy longitudinal depression, are arranged between adjacent longitudinal costae.

Remarks

This superfamily consists of the Mesozoic Bagotidae Pessagno & Whalen 1982, Archaeodictyomitridae Pessagno 1976, Hsuidae Pessagno & Whalen 1982, and Unumidae Kozur 1984 (De Wever *et al.* 2001: 262-266). The Archaeodictyomitridae are the only known family in the Cenozoic. This type of multisegmented structure is shared with the Ruesticyrtiidae Kozur & Mostler 1979, Amphipyndacoidea and Eucyrtidioidea. Dissimilarly to the Archaeodictyomitroidea, the Ruesticyrtiidae have a more complex initial spicular system (De Wever *et al.* 2001: fig. 171).

Family Archaeodictyomitridae Pessagno, 1976

Archaeodictyomitridae Pessagno, 1976: 49; 1977a: 41 (*sensu* emend.); 1977b: 934. — Dumitrica 1979: 31; 1995: 29. — Blome 1984: 354. — Sanfilippo & Riedel 1985: 598. — Petrushevskaya 1986: 135. — Dumitrica *et al.* 1997: 37-38. — Hollis 1997: 68. — Hull 1997: 78. — Amon 2000: 70. — De Wever *et al.* 2001: 263. — Afanasieva *et al.* 2005: S302. — Afanasieva & Amon 2006: 151.

Archaeodictyomitrinae – Petrushevskaya 1981: 192-194.

Type genus. — *Archaeodictyomitra* Pessagno 1976: 49 [type species by original designation: *Archaeodictyomitra squinaboli* Pessagno 1976: 50].

Included genus (Cenozoic only). — *Dictyomitra* Zittel, 1876: 81 (= *Dictyomitroma* with the same type species; *Diplostrobus* synonymized by Petrushevskaya & Kozlova 1972: 550; *Zifondium* synonymized by Petrushevskaya 1981: 196).

Diagnosis. — A multisegmented Nassellaria whose shell is covered by continuously arranged longitudinal costae. One, rarely two, rows of pores are aligned along adjacent longitudinal costae. The pores are open or relict. In some members, relict pores are completely missing in platy grooves between adjacent longitudinal costae.

Stratigraphic occurrence. — Early Berriasian-late Middle Eocene.

Remarks

Illustrations of their cephalic initial spicular system were too rarely published (Pessagno 1976: pl. 14, fig. 5; Pessagno 1977a: pl. 6, 13: De Wever *et al.* 2001: fig. 173) to gain an adequate understanding of its organization.

Superfamily Eucyrtidioidea Ehrenberg, 1846 *sensu* Suzuki emend. herein

Eucyrtidina Ehrenberg, 1846: 385 [as a family]; 1847: 54 [as a family]; 1876: 156.

Stichocyrtoidea – Clark & Campbell 1942: 91 [*nomen dubium*, as a section above a family]; 1945: 49. — Campbell & Clark 1944a: 51; 1944b: 36 [as a section].

Stichoperilae – Loeblich & Tappan 1961: 229 [*nomen dubium*, as a subsuperfamily].

Eucyrtidioidea – Petrushevskaya 1971a: 166-169 (*sensu* emend.); 1971b: 985 (*sensu* emend.); 1975: 578; 1981: 165-167; 1986: 136. — Petrushevskaya & Kozlova 1972: 535. — Grill & Kozur 1986: 246 (*sensu* emend.). — Afanasieva *et al.* 2005: S297-298. — Afanasieva & Amon 2006: 146. — Matsuzaki *et al.* 2015: 56-57. — Suzuki *in* Sandin *et al.* 2019: 201 (*sensu* emend.).

Stichocyrtoidae – Cachon & Cachon 1985: 294 [*nomen dubium*].

Eucyrtidioida – Amon 2000: 62 [as an order].

Eucyrtidiacea [*sic*] – De Wever *et al.* 2001: 273 (= Eucyrtidioidea).

Diagnosis. — Multisegmented Nassellaria with a simple cephalis. Cephalic base clearly separated from the thorax by a basal ring of the cephalis. The subsequent segments are separated by significant dividers.

Remarks

The Cenozoic Eucyrtidioidea includes the Eucyrtidiidae, Lithostrobidae and Xitomitridae, but molecular data was only provided for *Eucyrtidium* by Sandin *et al.* (2019). The identified family members of the Eucyrtidioidea were different among authors. For instance, nine families were identified in Petrushevskaya (1981) compared to the eight families in De Wever *et al.* (2001). In order to respect consistency between the morphological classification and molecular phylogenic studies (Sandin *et al.* 2019), the Cenozoic families Theocotylidae, Theoperidae, Lophocyrtiidae and Bekomidae were herein excluded from the Eucyrtidioidea. Petrushevskaya (1981) included the Cenozoic families Lychnocaniidae, Sethoperidae, Artostrobiidae, Pterocorythidae and Carpocaniidae in the Eucyrtidioidea but all of them were also excluded in this catalogue. All previously mentioned families identified by De Wever *et al.* (2001) and Petrushevskaya (1981) that were herein excluded; differ from the Eucyrtidioidea on a variety of points. The main distinguishing features are the absence of significant dividers below the cephalo-thoracic area, a fewer number of segments (less than three or four), the possession of a more complex cephalic initial spicular system, and/or elongated robust feet generated by the A-, D- and double L-rods of the cephalis.

Family Eucyrtidiidae Ehrenberg, 1846 *sensu* Suzuki emend. herein

Eucyrtidina Ehrenberg, 1846: 385 [as a family]; 1847: 54 [as a family]; 1876: 156. — Schomburgk 1847: 124, 125 [as a family].

Stichocyrtida Haeckel, 1862: 238, 280, 312 [*nomen dubium*, as a tribe]; 1882: 438 [as a subfamily]; 1887: 1434 [a section between suborder and family]. — Zittel 1876-1880: 121 [rank unknown]. — Mivart 1878: 178 [as a subdivision of subsection Cyrtida]. — Stöhr 1880: 101 [as a family]. — Bütschli 1889: 1993 [as a suborder]. — Rüst 1892: 186 [as a suborder]. — Poche 1913: 221 [as super-superfamily]. — Popofsky 1913: 401 [as a section between suborder and family]. — Schröder 1914: 91, 132 [as a group between suborder and family]. — Chediya 1959: 225 [as a group between superfamily and family].

Artocapsida Haeckel, 1882: 438 [as a tribe].

Artophormida Haeckel, 1882: 438 [as a tribe].

Artophatnida Haeckel, 1882: 439 [*nomen dubium*, as a tribe].

Stichocorida Haeckel, 1882: 438 [as a tribe]; 1887: 1435, 1468 [as a subfamily]. — Wisniowski 1889: 690.

Stichophatnida Haeckel, 1882: 439 [as a tribe].

Stichoperida Haeckel, 1882: 439 [*nomen dubium*, as a tribe]; 1887: 1435, 1436, 1447 [as a subfamily].

Stichophormida Haeckel, 1882: 439 [as a tribe]; 1887: 1435, 1454 [as a subfamily].

Podocampida Haeckel, 1887: 1435, 1436 [*nomen dubium*, as a family]. — Bütschli 1889: 1993 [as a family]. — *nec* Rüst 1892: 186.

Stichophaenida Haeckel, 1887: 1435, 1454, 1463 [as a subfamily].

Lithocampida Haeckel, 1887: 1435, 1467-1468 [as a family]. — Wisniowski 1889: 689. — Bütschli 1889: 1994 [as a family]. — *nec* Rüst 1892: 187 [as a family].

Podocampidae – Popofsky 1908: 290 [*nomen dubium*]; 1913: 401. — Schröder 1914: 132. — Campbell & Clark 1944b: 36. — Chediya 1959: 225. — Tan & Tchang 1976: 290. — Tan & Su 1982: 179. — Chen & Tan 1996: 154. — Tan & Su 2003: 113, 206. — Chen *et al.* 2017: 219.

Lithocampidae – Haecker 1908: 460. — Popofsky 1908: 292; 1913: 406. — Schröder 1914: 133. — Clark & Campbell 1942: 91; 1945: 49. — Campbell & Clark 1944a: 51; 1944b: 38. — Chediya 1959: 230. — Chen & Tan 1996: 154. — Tan & Su 2003: 113, 216. — Chen *et al.* 2017: 222.

Stichocorinae [*sic*] – Clark & Campbell 1942: 91 (= Stichocorythinae); 1945: 49. — Campbell & Clark 1944a: 51; 1944b: 38. — Ichikawa 1950: 308-309. — Frizzell & Middour 1951: 32. — Chediya 1959: 230.

Stichophorminae [*sic*] – Campbell & Clark 1944b: 37 (= Stichophormidinae). — Clark & Campbell 1945: 38. — Chediya 1959: 228.

Stichocoridae [*sic*] – Frizzell & Middour 1951: 32 (= Stichocorythidae).

Stichoperinae – Campbell 1954: D136. — Chediya 1959: 227.

Artophormididae – Campbell 1954: D138.

Arthophormidinae – Campbell 1954: D138-139.

Stichocorythidae – Campbell 1954: D140. — Dieci 1964: 188.

Stichocorythinae – Campbell 1954: D140. — Dieci 1964: 188.

Lithocampinae – Orlev 1959: 458.

Stichoperidae – Loeblich & Tappan 1961: 229 [*nomen dubium*].

Eucyrtidiidae – Petrushevskaya 1971a: 169-171 (*sensu* emend.); 1971b: 985 (*sensu* emend.); 1975: 578; 1981: 200-202. — Petrushevskaya & Kozlova 1972: 545. — Dumitrica 1979: 30-31; 2017a: 47. — De Wever 1982b: 293. — Steiger 1992: 68-70. — Hollis 1997: 73-74. — Cordey 1998: 106. — Kozlova 1999: 152. — De Wever *et al.* 2001: 278, 280. — Afanasieva *et al.* 2005: S298. — Afanasieva & Amon 2006: 146. — Matsuzaki *et al.* 2015: 57.

Eucyrtidiinae – Petrushevskaya 1971a: 215 (*sensu* emend.); 1971b: 985 (*sensu* emend.); 1975: 580; 1981: 202. — Takahashi 1991: 114. — Afanasieva *et al.* 2005: S298. — Afanasieva & Amon 2006: 146-147.

Eucyrtididae [*sic*] – Amon 2000: 62-63 (= Eucyrtidiidae).

Eucyrtidinae [*sic*] – Amon 2000: 63 (= Eucyrtidiinae).

Type genus. — *Eucyrtidium* Ehrenberg, 1846: 385 [type species by subsequent designation (Frizzell & Middour 1951: 33): *Lithocampe acuminata* Ehrenberg, 1844a: 84].

Included genera. — *Artocapsa* Haeckel, 1882: 438 (=? *Acanthocyrtis* **n. syn.**). — *Cymaetron* Caulet, 1991: 536. — *Cyrtocapsella* Haeckel, 1887: 1512 (= *Syringium* synonymized by Riedel & Sanfilippo 1970: 530). — *Eucyrtidium* Ehrenberg, 1846: 385. — *Glomaria* Sanfilippo & Riedel, 1970: 455. — *Lithocampe* Ehrenberg, 1839: 128 (= *Lithocampula* with the same type species; *Ariadnella* **n. syn.**, *Cyrtopenta*, synonymized by Haeckel 1862: 316, *Lithomitrissa* **n. syn.**). — *Lithopera* Ehrenberg, 1846: 385. — *Stichocorys* Haeckel, 1882: 438 (= *Artophormis* **n. syn.**, *Cyrtharia* **n. syn.**, ? *Cyrtocapsoma* **n. syn.**, *Cyrtophormiscus* synonymized by Petrushevskaya & Kozlova 1972: 547; *Cyrtophormium* **n. syn.**, ? *Eusyringoma* **n. syn.**; *Cyrtophormis*, *Stichophaenoma*, synonymized by Petrushevskaya 1981: 213). — *Stichophatna* Haeckel, 1882: 439 (= *Stichophaenidium* with the same type species; *Cyrtolagena*, *Stichophormium* synonymized by Petrushevskaya 1981: 175; *Sticholagena* synonymized by Petrushevskaya 1975: 582; *Stichophormiscus* synonymized by Nishimura & Yamauchi 1984: 55). — *Stichopterygium* Haeckel, 1882: 439 (= *Artocyrtis* **n. syn.**, **n. syn.** *Conostrobus*, *Stichopodium* **n. syn.**; *Spirocyrtoma* synonymized by Petrushevskaya 1981: 205). — *Theocoronium* Haeckel, 1887: 1415 (= *Theocapsetta* **n. syn.**, *Theocapsomma* **n. syn.**). — *Tricolocamptra* Haeckel, 1887: 1413. — *Udan* Renz, 1976: 127.

Invalid names. — *Artophaena*, *Stichophaena*.

Nomina dubia. — *Artophatna*, *Diabolocampe*, *Podocampe*, *Pylosphaera*, *Spirocampe*, *Stichocyrtis*, *Stichopera*, *Stichoperina*.

Diagnosis. — Eucyrtidiidae with two to six segmented shell with an aperture. The segments are divided by distinctive inner-ring dividers. Feet are not observed. The cephalis is spherical to globular in shape, with a thick wall and relict or true fine pores. The wall of the cephalis is discernible in such a way that the collar suture between the cephalis and the thorax appears distinctive. Even if covered by silica, the cephalic boundary with the thorax remains recognizable under a light microscope. The cephalis is attached to the cephalic base by a base ring or to a thickened wall. The sutural pores are developed to separate the cephalis and thorax in some species or genera. The pores are randomly scattered or horizontally aligned. The cephalic initial spicular system is characterized by MB, A-, V-, D-, and double L-rods. When present the ax-rod has a dot-like shape. The double l-rod is absent, except in *Lithocampe*. The A-rod is embedded inside the cephalic wall or is freely oriented upright in the cephalic cavity. In some members, an indistinct tubular structure is visible near the end of the V-rod. Basal ring is directly connected with the A-rod side end of MB, V- and double L-rods to form four collar pores. A basal ring is bended along the line with the double L-rod such that double pores related to the LV-arch are raised towards the ventral side. The D- and double L-rods are visible on the thoracic and subsequent segmental wall in some members.
The size of the endoplasm is variable, but never occupies the complete shell. A very long pseudopodium (axial projection) extends from the aperture of the shell and is used as a tool to capture food. Algal symbionts are observed in some species of *Eucyrtidium*.

Stratigraphic occurrence. — Early Paleocene-Living.

Remarks

The cephalic initial spicular system have been illustrated for: *Cyrtocapsella* (Nishimura H. 1987: figs 6.A, 6.B; pl. 1, figs 2, 3 5; pl. 2, figs 1, 2; 1990: figs 4, figs 40.1, 40.2), *Stichophatna* (Sugiyama 1998: pl. 4, fig. 2b), *Eucyrtidium* (Cachon & Cachon 1972a: figs 4.a-4.c, fig. 5.a; Nishimura & Yamauchi 1984: pl. 39, figs 5, 11; Takemura & Nakaseko 1986: figs 5.4-5.5, 5.8-5.9; Nishimura 1990: fig. 41.2; Sugiyama *et al.* 1992: pl. 23, fig. 7?), *Lithocampe* (Sugiyama *et al.* 1992: pl. 22, figs 2-8), *Lithopera* (Nishimura & Yamauchi 1984: pl. 33, fig.6; Nishimura H. 1987: pl. 1, fig. 4) and *Stichocorys* (Takemura & Nakaseko 1986: figs 5.10-5.11; Nishimura H. 1987: pl. 1, fig.1; 1990: fig. 41. 4; O'Connor 1997a: pl. 9, figs 13-16; pl. 11, figs 4, 8). The basal ring with four collar pores is a common feature among the genera *Lithocampe* due to the lack of a double l-rod. Nishimura (1986) thought that the l-rods are covered through a thickening process of the cephalic wall; however, this is unlikely for most of the genera because the edge of the double arch between MB and L-rod occupies the place where that the l-rod occupies. The generic assignment is uncertain for *Cyrtocapsa osculum* O'Connor because the cephalic structure remains unknown (O'Connor 1997a: pl. 1, figs 15-17; pl. 2, figs 1, 2; pl. 8, figs 3-10), *Eucyrtidium inflatum* (Takemura & Nakaseko 1986: figs 5.6-5.7) and *Eucyrtidium calvertense* (Sugiyama *et al.* 1992: pl. 23, fig. 3), *Eucyrtidium ventricosum* O'Connor, 1999 (O'Connor 1999: pl. 3, figs 17-21b; pl. 6, figs 28-31). *Eucyrtidium inflatum* and *E. calvertense* have double l-rods that form very small double pores with the double Dl-arch as in *Lithocampe*.

Over the last century, the taxonomy of the Eucyrtidiidae has been problematic because few keys were available to determine the evolutionary lineages. This was partly due to the polyphyletic character denoted in many groups of the

Eucyrtidiidae (De Wever *et al.* 2001). Based on the consistency with molecular phylogeny, five Cenozoic genera (*Buryella*, *Calocyclas*, *Calocycloma* and *Phormocyrtis*) are excluded from the family. Instead, seven Cenozoic genera (*Stichophatna*, *Lithocampe*, *Stichopterygium*, *Theocoronium*, *Tricolocamptra* and *Udan*) are newly included as their cephalic similarity with *Eucyrtidium* was considered. Many genera of Eucyrtidiidae were historically included in "theoperids" but this name is inappropriate for a taxonomic position as the Eucyrtidiidae have no morphological characters in common with the genus *Theopera* (see also De Wever *et al.* 2001: 278).

The evolutionary hypotheses in some linages of Eucyrtidiidae were well documented (Sanfilippo & Riedel 1970; Sanfilippo *et al.* 1985: figs 16, 23). The "*Eucyrtidium*" spp. in the sense of Sanfilippo & Riedel (1970) is considered a direct ancestor of *Cyrtocapsella* and *Stichocorys*; *Lithopera* originated from *Stichocorys diploconus* in Sanfilippo & Riedel 1970, and *Glomaria* diverged from *Lithopera* (Riedel & Sanfilippo 1981: fig. 12.9). Little is known about the evolutionary phylogenies of other genera. The specific divergent process between *Eucyrtidium calvertense* and *Eucyrtidium matuyamai* was also noted. This was quantitively evaluated with high-resolution models as a typical gradual evolution phenomenon (Hays 1970; Kellogg 1976). Morphological changes in the *Lithocampe peregrina* (originally *Stichocorys peregrina*) lineage associated to different geographic areas were also quantitatively documented (Kamikuri 2012). The paleobiogeographic morphotypes of *Lithocampe* (originally *Stichocorys*, Casey *et al.* 1983) were well studied in time-series distribution changes in the North Pacific (Lombari 1985; Oseki & Suzuki 2009).

The protoplasm and living specimen images were illustrated for *Eucyrtidium* (Matsuoka 1993a: fig. 2:7; 2007: fig. 4a; 2017: figs 24, 25; Sugiyama & Anderson 1997b: pl. 1, figs 1, 2; Sashida & Kurihara 1999: figs 11.6, 11.9, 11.11; Sugiyama *et al.* 2008: figs 2-6; Suzuki & Aita 2011: fig. 5.P; Suzuki & Not 2015: figs 8.4.3, 8.11.18, 8.11.19; Matsuoka *et al.* 2017: Appendix B), *Lithopera* (Gowing 1989: figs 2.D-2.F; 1993: fig. 6.i; Zhang *et al.* 2018: 21, fig. 8.11) and *Stichopterygium* (Sashida & Uematsu 1994: fig. 3.1). Cytological ultrafine structure was also observed in *Eucyrtidium* (Sugiyama & Anderson 1997b: pls 2, 3). Growth lines of pore frame are well documented in *Cyrtocapsella* (Nishimura H. 1987: pl. 1, figs 5b, 5c; pl. 2; 1990: figs 4, 40), *Eucyrtidium* (Nishimura 1990: figs 41.2b), *Lithopera* (Nishimura H. 1987: pl. 1, fig. 4b) and *Lithocampe* (Nishimura H. 1987: pl. 1, fig. 1b; Nishimura 1990: figs 41.4b). Live silicification sites on the shell were localized for *Eucyrtidium* with an epi-fluorescence microscopy PDMPO dyeing method (Ogane *et al.* 2010: figs 1.11-1.12, 2.11-2.12, 3, 4.3).

Validity of genera

Artocapsa

Artocapsa is defined by a pointed, conical, terminal segment with a basal spine and an apical horn (Campbell 1954: D143) and *Acanthocyrtis* is defined by a solid apical horn, variable heights of segments, a spiny surface, and an open aperture (Campbell 1954: D140). As the remarkable characteristics for these genera are different in each other except for the presence of an apical horn and the distal terminal structure, it is impossible to discuss about their synonymy based on the definition. The topotypic specimen of *Eucyrtidium tricinctum* from the *H.M.S. Challenger* Station 225 is a little bit different from the description in Campbell (1954) by the similar height of the segments (supporting image for *Acanthocyrtis*). This difference is well explained by intra-species variations. The topotypic specimen has a thorny appearance but it is not significant compared to the type-illustration for *Artocapsa*. The genus *Artocapsa* has a closed final segment whereas *Acanthocyrtis* has a fenestrated aperture. This is insufficient to separate them at generic level. Both these genera were simultaneously published in Haeckel (1887: 437 for *Acanthocyrtis* and 438 for *Artocapsa*). As the species with a basal spine at the end of the final segment is rare in other genera, *Artocapsa* is selected as a valid name.

Stichophatna

The synonymy of *Cyrtolagena*, *Sticholagena*, *Stichophaenidium*, *Stichophatna*, *Stichophormium*, *Stichophormiscus* has been well established by previous studies (Petrushevskaya 1975; De Wever *et al.* 2001; Nishimura & Yamauchi 1984). *Cyrtolagena* published in Haeckel (1887: 1449) has been used a long time as the valid name but the oldest available name is *Stichophatna* published in Haeckel (1882: 439).

Lithocampe

Lithocampanula has the same type species as *Lithocampe*. Tochilina (1989a, 2008) erected two genera *Ariadnella* and *Cyrtopenta* associated with *Stichocorys* under the Lithocampidae in her sense. The translated diagnosis from the original Russian for *Cyrtopenta* follows. "*Fundamental part of the shell constituted by five segments relatively of same height, progressively enlarging from the first one to the fourth, but the fifth narrower. From two to five additional segments. Shell of conical shape. Pores distributed symmetrically*". The topotype of *Lithocampe radicula* (Suzuki *et al.* 2009c: pl. 12, figs 8a, 8b), type species of *Lithocampe*, exactly matches the definition of *Cyrtopenta*. It is noted that "*Stichocorys delmontensis*" and "*Stichocorys peregrina*" were placed in *Cyrtopenta* in Tochilina (1989a). This also means that both these species belong to *Lithocampe* but not to *Stichocorys*.

Ariadnella is defined by "*six to seven main segments and one to two additional ones with a nearly conical-cylindrical shape, and by a terminal tube with a mesh structure*" (translation from Tochilina 2008: 62-63). Tochilina (2008) commented that *Ariadnella* differs from *Lithocampe* and *Stichocorys* by its general shape and the much greater number of segments. When compared, *Lithocampe radicula* and *Lithocampe subligata*, respectively type species of *Lithocampe* and *Ariadnella*, the former has six segments and the latter eight segments. However, all other characters including the general shape are nearly identical. The difference pointed out by Tochilina (2008) is not applicable as genus criteria. Tochilina (1989a: 63) includes *Lithomitra infundibulum* as a member of this *Ariadnella*. As *L. infundibulum* is the type species of *Lithomitrissa*, Tochilina (2008) herself agrees with the synonymy relationship between *Ariadnella* and *Lithomitrissa*. The oldest available name is *Lithocampe* among them.

Stichocorys

The practical usage of *Stichocorys* was once extremely broaden by Sanfilippo & Riedel (1970) in order to include "*Stichocorys peregrina*" and "*Stichocorys delmontensis*." *Stichocorys* differs from *Lithocampe* by the fact that the proportions between the segments are less variable and that external constrictions are well-differentiated (translation from Petrushevskaya 1981: 212). *Stichocorys* in the sense of Sanfilippo & Riedel (1970) was mixed with *Lithocampe* under the modern sense. Tochilina (1989a: 56) revised the definition to separate *Lithocampe* (*Cyrtopenta* in original) from *Stichocorys* on the basis of "*a three-segmented conical shell, thin-walled fourth and fifth segments (when present), the third segment with a maximum width, and the occurrence of regular pores on the second and third segments differently from the irregular pores located on the fourth and fifth segments*" (translation from Tochilina 1989a by J. P. Caulet). Except pore patterns, these distinguishing points are well fit with our concept of *Stichocorys*.

The same type species is designated for *Cyrtophormis*, *Cyrtophormium* and *Cyrtophormiscus*. Referred to Campbell (1954), the main difference at family level in the sense of Campbell (1954: D139-143) is the number of radial apophyses around the test (four to nine or more radial apophyses for *Artophormis*, *Cyrtophormis*, *Stichophaenoma*; presence of radial apophyses for *Cyrtocapsoma* and *Eusyringoma*). Obviously, the state of development of the radial apophyses illustrated in the type specimens are intraspecies variations but cannot be a criterion for genus level. The next distinguishing character of lower value at the subfamily level in the sense of Campbell (1954) is the fenestrated basal end of the test (*Cyrtocapsoma* and *Stichophaenoma*), or the opened basal end (*Artophormis*, *Cyrtophormis* and *Eusyringoma*). The difference between "fenestrated" and "open" is easily recognizable in the type-illustrations, but such kind of variation is commonly encountered in each of the samples. If this difference is accepted for subfamily classification, tens or hundreds of subfamilies will be created with only a few samples. Due to these reason, the difference under the definition written is as follows: oval or spindle-shaped shell, radial ribs prolonged into feet for *Artophormis* (Campbell 1954: D139); oval or spindle-shaped shell, absence of lateral ribs, and six to five feet for *Cyrtophormis* (Campbell 1954: D139); pointed final segment with basal spines for *Stichophaenoma* (Campbell 1954: D140); long narrow appendage as the last segment and 4 or more segments for *Eusyringoma* (Campbell 1954: D140); and presence of apical horn and four or more ring-like strictures for *Cyrtocapsoma* (Campbell 1954: D143). The type-illustration for *Artophormis* shows very indistinguishable radial ribs, sufficient characteristic to be separated from *Cyrtophormis*. "Feet" for both *Artophormis* and *Cyrtophormis* depend on specimens but not even at species level nor genus level. There are no reasons to separate *Artophormis* and *Cyrtophormis*. As both these genera, the characteristic of a pointed final segment with basal spines can be included in a variation between "*Artophormis*/*Cyrtophormis*", thus *Stichophaenoma* is also a synonym of these two genera at genus level. The definition of *Eusyringoma* written in Campbell (1954) does not match the illustrated type specimen (Stöhr 1880: pl. 4, fig. 8). More clearly, the type specimen is exactly the same as that of *Stichocorys* in the sense of Tochilina (2008). The presence of an apical horn is noted only for *Cyrtocapsoma* among the genera discussed here, but the apical horn of the type specimen (Stöhr 1880: pl. 4, fig. 9) is so tiny as not to be differentiate in other genera. In conclusion all characteristics pointed by Campbell (1954) have no value for generic differences. Excluded these characteristics, the synonymy is simply evaluated following the similitude with *Stichocorys* in the sense of Tochilina (2008). It is a little bit unclear for *Stichophaenoma* but all other genera are fallen in her concept. *Artophormis* and *Stichocorys* were simultaneously published in Haeckel (1882: 438 for both genera). *Stichocorys* is the best valid genus for taxonomic stability.

Stichopterygium

The five genera listed here were used to be classified into the "Tricartinae" (Campbell 1954: D136 for *Stichopodium* and *Stichopterygium*) and "Stichocorythinae" (Campbell 1954: D140 for *Artocyrtis*, D141 for *Conostrobus*, and D142 for *Spirocyrtoma*) in the sense of Campbell (1954). They are synonymized herein with a significant apical horn, an open aperture, and four or more segments. The presence of a significant apical horn in *Stichopterygium* makes the difference with *Eucyrtidium* and *Lithocampe*. The following discussion is largely commented after Campbell (1954): All these five genera have "radial apophyses" but these structures are not recognizable in any type-illustrations; *Stichopodium* is characterized by three latticed basal feet but real specimens (supporting image for *Stichopodium*) are exactly similar with *Conostrobus* except for the basal feet (supporting image for *Conostrobus*). *Conostrobus* is defined by a conical shell with a straight axis and similar strictures between segments (Campbell 1954: D141) and these characters do exactly fit with the type species of *Stichopodium*. *Spirocyrtoma* is marked by an ovate to spindle-shaped shell and spirally disposed strictures (Campbell 1954: D142). The ovate to spindle appearance can be classed into intraspecies variations and spirally disposed strictures occur in any species of bizarre forms. As these characteristics are not considered as valuable at genus level, "*Spirocyrtoma*" can be classified into *Conostrobus* or *Spirocyrtoma*. *Artocyrtis* is characterized by joints of dissimilar lengths and a smooth surface, according to Campbell (1954: D140). Referred to the lectotype of *Artocyrtis* (Suzuki *et al.* 2009c: pl. 55, figs 5a-c), "joints of dissimilar length" is interpreted as a larger thorax (2nd segment). This larger thorax and a smooth surface are also characteristics in common with the type-illustration of *Stichopterygium*. Except for the larger thorax, *Artocyrtis* can be interpreted as a cylindrical form typical of *Conostrobus* and *Spirocyrtoma*.

This synonymy, however, should be re-examined by the shape of the evolutionary lineages. The first, latticed lateral ribs, or wings, is the only character in *Stichopterygium* (Campbell 1954: D136). As the type species of *Artocyrtis*, *Conostrobus*, *Stichopodium* and *Stichopterygium* are living species, as the occurrence of latticed lateral ribs or wings is impossible to be explained by intraspecific variations, this characteristic must be considered to be as differences at species or genus level. This point has not yet been evidenced. The second characteristic, the importance of the larger thorax, has not yet been evaluated. If this character is important, these five genera would be divided into two groups. For the lack of lattice lateral ribs or wings, *Artocyrtis* is the only genus which can be synonymized with *Stichopterygium*. The third characteristic (presence of a significant apical horn) is regarded as a major character to differentiate *Stichopterygium* from *Eucyrtidium* and *Lithocampe*. No papers prove it can be considered as a phylogenetic marker based on evolutionary phylogeny. For example, *Artocyrtis* is exactly similar to "*Cyrtopenta*" except for the apical horn as referred to the lectotypes of these two type species in Suzuki *et al.* (2009c: pl. 15, fig. 7b for *Cyrtopenta* and pl. 55, figs 5a-c for *Artocyrtis*). These three points must be evaluated in future studies.

Theocoronium

As *Theocoronium* was placed in the "Theocorythinae" (Campbell 1954: D134) while *Theocapsetta* and *Theocapsomma* were placed in the "Theocapsinae" (Campbell 1954: D136) *sensu* Campbell (1954), the difference at subfamily level is relied on whether the distal end of the last segment is open or fenestrated. As commonly discussed for the Eucyrtidiidae, this difference is within intra-or infra variations. According to Campbell (1954), these three genera have in common similar thoracic and abdominal pores. For Campbell (1954) *Theocoronium* is marked by a swollen ovate abdomen and a single apical horn, *Theocapsetta* has thorax and abdomen of nearly the same size, and *Theocapsomma* has a thorax much smaller than the abdomen. Referred to the lectotype of *Theocoronium* (Suzuki *et al.* 2009c: pl. 55, figs 11a, 11b) and type-illustrations in Haeckel (1887: pl. 66, fig. 6 for *Theocapsetta* and pl. 66, fig. 13 for *Theocapsomma*), all these three genera have a single apical horn. The shape of the abdomen is only noted for *Theocoronium* but the difference in the abdomen among the three type species is commonly observable as a difference in the ontogenetic growth. The characteristic difference between *Theocapsetta* and *Theocapsomma* is the size ratio between the thorax and the abdomen. As already commented, the difference of abdomen is a difference in the ontogenetic growth stages. These three genera were simultaneously published in Haeckel (1887: 1415 for *Theocoronium*, 1426 for *Theocapsetta* and 1428 for *Theocapsomma*). *Theocoronium* is validated among them because the real type specimen is found in the Ehrenberg collection.

Family LITHOSTROBIDAE Petrushevskaya, 1975

Lithostrobiidae [sic] Petrushevskaya, 1975: 582 (= Lithostrobidae).

TYPE GENUS. — *Lithostrobus* Bütschli, 1882: 529 [type species by subsequent designation (Campbell 1954: D141): *Eucyrtidium argus* Ehrenberg, 1874: 225].

INCLUDED GENUS. — *Lithostrobus* Bütschli, 1882: 529 (= *Cornustrobus* synonymized by Petrushevskaya 1981: 173; *Cyrtostrobus* synonymized by Petrushevskaya 1981: 171; *Eostichomitra* **n. syn.**).

DIAGNOSIS. — Lithostrobidae are multisegmented Nassellaria whose proximal part consists of a long apical horn, a poreless small cephalis, a latticed thorax, and a large thorax. The collar stricture between cephalis and thorax is unclear. The abdomen is distinctive from the cephalon-thoracic part by significant width differences. Subsequent segments below the abdomen are similar in height and are latticed with pores that are nearly equal in size. The exact structure of the cephalic spicular system is unknown. A-rod is upright in the cephalic cavity and is attached to the cephalic wall. A narrow tunnel typical to the A-rod extends to the stem of an apical horn. A basal ring-like structure is visible inside the bottom part of the cephalis.

STRATIGRAPHIC OCCURRENCE. — Early Turonian-late Late Miocene.

REMARKS

As *Lithostrobus* is the only member of the Lithostrobidae, the particular characteristics common to this family are partially understood. *Lithostrobus* was placed in the Stichocorythidae (originally Stichocoridae) (Campbell 1954), Stichocapsidae (Petrushevskaya 1981: 171-173), and Eucyrtidiidae (Hollis 1997: 79). However, these three families are now synonymized to Eucyrtidiidae (see synonym of Eucyrtidiidae). The cephalic structure of the type species lectotype of *Lithostrobus* (*Eucyrtidium argus*) was illustrated in Ogane *et al.* (2009b: pl. 48, figs 8d-8f). As described in the diagnosis, the presence of a basal ring-like structure is common in the Eucyrtidiidae. It should be noted that the segmentation patterns on the proximal part of the *Lithostrobus* are different from the Eucyrtidiidae.

VALIDITY OF GENERA

Lithostrobus

As the type specimen of *Lithostrobus* was found from the Ehrenberg collection (Ogane *et al.* 2009b: pl. 48, figs 8a-c), its drawing in Ehrenberg (1876: pl. 9, fig. 1) appeared to be partly wrong as for the first three segments. Referred to this lectotype and type-illustrations, the segmentation patterns and a non-bladed robust apical horn are common among *Lithostrobus*, *Cornustrobus* and *Cyrtostrobus* (Campbell 1954: D141). *Cornustrobus* is marked by the horn-shaped shell with similar segmentations and *Cyrtostrobus* is distinguished by a conical shell with a straight axis and dissimilar segmentations. The differences noted here are not so significant among them. *Eostichomitra* is defined by a conical multi-segmented shell, a small cephalis with an elongate apical horn, a simple initial spicule system in the cephalis, segments increasing in width and height, a smooth or slightly papillose surface and a large circular aperture on the distal end of the test. These characteristics are slightly different in the type species of *Lithostrobus*; but this difference can be explained by different stratigraphic ranges because *Eostichomitra* was initially found from the lower Turonian and the lectotype of *Lithostrobus* was found from the upper Eocene from Barbados. The robust long, un-bladed apical horn, the simple cephalis, the conical multi-segmented shell similar to *Eostichomitra* and *Lithostrobus* is limitedly recognized in multi-segmented Nassellaria from the Upper Cretaceous to the upper Eocene so that these two genera should be linked by a single phylogeny at generic level. The oldest available name is *Lithostrobus*.

Family Xitomitridae O'Dogherty, Goričan & Gawlick, 2017

Xitomitridae O'Dogherty, Goričan & Gawlick, 2017: 60.

Type genus. — *Xitomitra* O'Dogherty, Goričan & Gawlick, 2017: 62 [type species by objective designation: *Stichomitra*? *tairai* Aita 1987: 72].

Included genera (Cenozoic only). — *Dictyomitrella* Haeckel 1887: 1476 (= *Parvimitrella* **n. syn.**).

Diagnosis. — A multisegmented Nassellaria whose cephalis is both small and poreless. All of its segments, except for the cephalis, are covered with a latticed meshwork of uniform sized pores. The distal end of the test is open or nearly closed, without distal projections or appendages. The cephalic initial spicular system present at least a MB, A-, V-, D- and double L-rods. MB is rises obliquely to the A-rod side. Thus, the basal ring of the cephalis is also oriented obliquely. The A-rod extends upright in the cephalic cavity to attach itself to the cephalic wall or even penetrate the wall. An amphipyndacid-like divider is visible in the cephalis. The divider in the proximal upper-section is constructed by the MB, D- and double L-rods.

Stratigraphic occurrence. — Early Aalenian-late Middle Eocene.

Remarks

The Xitomitridae were related with the Canoptidae, Parvicingulidae and Xitidae (O'Dogherty *et al.* 2017). The cephalic structure of the type species of *Xitomitra* O'Dogherty *et al.* 2017 (the Middle-Late Jurassic *Stichomitra*? *tairai* Aita, 1987) is well recognized in its paratypes (Aita 1987: pl. 3, fig. 8a). Referring to this photo, "the divider" in the proximal top is constructed by MB, D- and double L-rods. This does not correspond to the characteristics of the divider in Amphipyndacoidea. The proximal top of the *Xitomitra tairai* consists of a cephalis and thorax. The divider in *Xitomitra* is poorly developed in comparison to the basal ring of the cephalis in the Eucyrtidiidae. Conversely, *Dictyomitrella*, and the Paleogene member of the Xitomitridae appear to have a well-developed cephalis basal ring such as in the Eucyrtidiidae; however, the MB of *Dictyomitrella* is obliquely oriented. The cephalic view of the type species (lectotype) of *Dictyomitrella* is also shown in pl. 22, figs 1e and 1f of Ogane *et al.* (2009b).

Phylogenetic Molecular Lineage II (Sandin *et al.* 2019)

Diagnosis. — Anatomically, one or two segments, but usually one segment, is observed. This is true for most cases except Lampromitridae and some members of the Artostrobiidae. If a subsequent shell develops, the final segmented part is not divided by an inner ring. This is unlike the Eucyrtidiidae. No common characteristics in the cephalic structure are recognized among the members. No feet are observed except in some members of the Acanthodesmioidea and Diacanthocapsidae.

Remarks

Lineage II includes the Plectopyramidoidea (originally Acropyramioidea), Carpocanioidea (originally Carpocaniidae), Artostrobioidea, and Acanthodesmioidea (originally Acanthodesmoidea in Sandin *et al.* 2019). Although the independency of the Lineage II from the other Lineages is supported with 100% PhyML bootstrap values with 10 000 replicates (BS) and >0.99 posterior probabilities (PP); the independency of superfamilies inside Lineage II is only supported for the Acanthodesmioidea with 100% PhyML bootstrap values with 10 000 replicates (BS) and >0.99 posterior probabilities (PP). The trees of the remaining three superfamilies have not been agreed upon within Lineage II. As for the Carpocaniidae and Artostrobiidae, both families have a common structure with very complex arches around the V-rods. Thus, it may not be necessary to separate them at the superfamily-level (see remarks for the Carpocanioidea, Carpocaniidae and Artostrobiidae). However, this possibility should be carefully examined in consideration of the Mesozoic members.

Superfamily Plectopyramidoidea Haecker, 1908 n. stat.

Plectopyramididae Haecker, 1908: 157.

Acropyramidoidea – Petrushevskaya 1981: 99-103 [*nomen dubium*]; 1986: 133-135. — Afanasieva *et al.* 2005: S293. — Afanasieva & Amon 2006: 140.

Acropyramidoida – Amon 2000: 57-58 [*nomen dubium*, as an order].

Diagnosis. — Two segments with no, to very weak, constriction between the cephalis and thorax. The cephalis is very small, while the thorax is very long, or very wide resembling a shallow-depth hat. Thoracic pores are systemically distributed throughout the segment.

Remarks

This superfamily consists of two Cenozoic families: the Lampromitridae (questionably included) and the Plectopyramididae. The inclusion of Lampromitridae in this superfamily is questionable (see remarks in Lampromitridae). It is not necessary to prioritize a questionably assigned family name for a valid superfamily name in order to use "Plectopyramidoidea" as a valid name. Sandin *et al.* (2019) commented the high 28S rDNA gene in deep ocean forms of "Plectopyramidoidea" (originally Acropyramidoidea). This contract the idea that the Lampromitridae are generally found in shallow water. The "molecular Plectopyramidoidea" may not include the Lampromitridae.

Family Plectopyramididae Haecker, 1908

Plectopyramididae Haecker, 1908: 157. — Petrushevskaya & Kozlova 1972: 550. — Dumitrica 1979: 34. — Hollis 1997: 71.

Acropyramida Haeckel, 1882: 428 [*nomen dubium*, below tribe].

Archiphormida Haeckel, 1882: 428 [*nomen dubium*, as a tribe]; 1887: 1133, 1158, 1159 [as a subfamily].

Haliphormida Haeckel, 1882: 428 [junior homonym, below tribe].

Archiphormididae – Campbell 1954: D118 [*nomen dubium*]. — Takahashi 1991: 136.

Archiphormidinae – Campbell 1954: D118 [*nomen dubium*].

Archiphorminae – Clark & Campbell 1942: 64 [*nomen dubium*]; 1945: 34. — Campbell & Clark 1944a: 39; 1944b: 21. — Chediya 1959: 192.

Plectopyramidinae – Petrushevskaya 1971a: 225-226 (*sensu* emend.); 1971b: 986 (*sensu* emend.). — Takahashi 1991: 113.

Acropyramididae – Petrushevskaya 1981: 155-157 [*nomen dubium*]; 1986: 135. — Kozlova 1999: 124-125. — De Wever *et al.* 2001: 245-246. — Afanasieva *et al.* 2005: S295. — Afanasieva & Amon 2006: 143.

Cornutellidae Takemura, 1986: 68. — Nishimura 1990: 150-151, 153 (*sensu* emend.).

Type genus. — *Plectopyramis* Haeckel, 1882: 432 [type species by subsequent designation (Campbell 1954: D128): *Plectopyramis magnifica* Haeckel, 1887: 1257] = junior subjective synonym of *Cinclopyramis* Haeckel, 1879: 705 [type species by monotypy: *Cinclopyramis murrayana* Haeckel, 1879: 705].

Included genera. — *Cinclopyramis* Haeckel, 1879: 705 (= *Cephalopyramis* **n. syn.**, *Plectopyramis* **n. syn.**, *Sestropyramis* **n. syn.**, *Spongopyramis* **n. syn.**: *Enneapleuris* synonymized by Suzuki *et al.* 2009d: 262, *Peripyramis* synonymized by Suzuki *et al.* 2009d: 262, *Sethopyramis* synonymized by Suzuki *et al.* 2009d: 262). — *Cladarachnium* Haeckel, 1882: 430. — *Cornutella* Ehrenberg, 1839: 128 (= *Cornutissa* with the same type species; *Orthocornutanna* **n. syn.**). — *Haliphormartidium* Campbell, 1951: 528. — *Litharachnium* Haeckel, 1861b: 835 (= *Litharachnidium* with the same type species). — *Polypleuris* Haeckel, 1887: 1260.

Invalid names. — *Ceratarachnium*, *Craspedilium*, *Sethodrepanum*.

Nomina dubia. — *Acropyramis*, *Actinopyramis*, *Archiphormis*, *Bathropyramis*, *Cladopyramis*, *Cornutanna*, *Cornutosa*, *Heterocornutanna*, *Hexapleuris*, *Litharachnoma*.

Junior homonyms. — *Cornutellium* Haeckel, 1887 (= *Cornutella*), *nec* Haeckel, 1882; *Haliphormis* Haeckel, 1887 (= *Haliphormartidium*) *nec* Ehrenberg, 1847.

Diagnosis. — Plectopyramididae consist of high-angled conical or very flat umbrella-like shaped shells. They appear as two segmented Nassellaria from an anatomical point of view but seem to be single segmented. The cephalic initial spicular system is highly degraded in some members. The proximal part above the cephalis is poreless and covered with a thick wall. The thoracic part is constructed of a gridwork pore frame. Pores are usually distributed in a longitudinal direction. If existent, four collar pores are visible in *Cinclopyramis* and *Cornutella*, and three collar pores are observed in *Polypleuris*. Endoplasm is small yet very long and thee cephalic part includes a proximal top. No pseudopodia or algal symbionts were observed.

Stratigraphic occurrence. — Late Anisian-Living.

Remarks

The protoplasm and living specimen images were illustrated for *Cornutella* (Gowing 1993: fig. 6j; Suzuki & Not 2015: fig. 8.10.19), *Litharachnium* (Zhang *et al.* 2018: 15, fig. 4.16, p. 21, fig. 8.9) and *Polypleuris* (Suzuki & Not 2015: fig. 8.10.21). Environmental molecular data indicate a deep-water normal environment for the Plectopyramididae (Sandin *et al.* 2019). The cephalic structure was observed and documented for *Cinclopyramis* (Nishimura & Yamauchi 1984: pl. 25, fig. 9b; Takemura & Yamauchi 1984: pl. 1, fig. 5; Nishimura 1990: figs 32.4b, 32.6b, 32.10b; Sugiyama 1998: pl. 5, fig. 10b), *Cornutella* (Nishimura & Yamauchi 1984: pl. 25, figs 5b, 7b; Takemura & Yamauchi 1984: pl. 1, figs 1-3; Nishimura 1990: fig. 32.9b; Sugiyama 1998: pl. 6, fig. 1b), *Litharachnium* (Cachon & Cachon 1972a: fig. 9) and *Polypleuris* (Nishimura 1990: figs 32.1b, 32.2b, 23.3c, 32.5c). The development stage of the cephalic initial spicular system is variable among the genera. MB, V- and double L-rods occasionally develop in *Cornutella* with infra-species variations (Nishimura 1990: fig. 32.8b). It was presumed that the initial spicule was embedded in the cephalic wall but this prediction was discarded after careful examination of thin-walled *Cornutella* specimens by Sugiyama (1998: 237). *Cinclopyramis* always has a cephalic initial spicular system consisting of MB, A-, D-, V-, double L-rods, and a cephalic basal ring. *Litharachnium* has both D- and double L-rods but the MB seems to be degraded. The apertural view of *Polypleuris* shows the presence of MB, D-, V-, double l-, and double L-rods, as well as a basal ring-like structure.

Validity of genera

Cinclopyramis

As pointed in Suzuki *et al.* (2009d: 262), *Cinclopyramis* was published by Haeckel (1879: 705) but not Haeckel (1887). *Cinclopyramis* includes the current usage of *Acropyramis* and *Bathropyramis* whose type species have not been illustrated. The genera synonymized in our paper are classified into two different subsuperfamilies in the sense of Campbell (1954): one is “Archipiliilae” defined by no joints and strictures on shells (Campbell 1954: D117) and the other one is “Sethopiliilae” whose shells are divided by transverse strictures into cephalis and thorax (Campbell 1954: D122). These differences do exactly reflect the absence of a cephalic cavity for the former group (Haeckel 1879: pl. 16, fig. 8 for *Cinclopyramis* ; Haeckel 1887: pl. 54, fig. 5 for *Peripyramis*). The latter is relevant to the presence of a cephalic cavity (Haeckel 1887: pl. 54, fig. 6 for *Enneapleuris*, pl. 54, fig. 2 for *Sethopyramis* and pl. 56, fig. 10 for *Spongopyramis*) and of a ball-like cephalis (Bury 1862: pl. 11, fig. 1 for *Plectopyramis*; Haeckel 1887: pl. 56, fig. 7 for *Cephalopyramis*; Ogane *et al.* 2009b: the lectotype shown in pl. 21, figs 6a-6d for *Sestropyramis*). However, there are no specimens without cephalic cavities in these groups so the differences at the Campbell’s (1954) subsuperfamily level are wrong. This can be also concluded at the family and subfamily levels in the sense of Campbell (1954). The former two genera belong to the “Archiphormidinae” of the “Archiphormididae” (Campbell 1954: D118) whereas the remaining six genera to the “Sethophormidinae” of the “Sethophormididae” (Campbell 1954: D124). These families are defined by exactly the same phrases: "radial apophyses 4 to 9 or more" for both "Archiphormidiae" and "Sethophormididae". These subfamilies are also expressed with the exactly same phrases: "basal shell mouth open" for both "Archiphormidinae" and "Sethophormidinae". Thus, even under the concept of Campbell (1954), all these genera belong to the same family and "subfamily." The distinguishing characters are a double meshwork in *Cinclopyramis* (Campbell 1954: D118), an outer mantle in *Peripyramis* (Campbell 1954: D119) and meshes closed by a spongy framework in *Spongopyramis* (Campbell 1954: D128). These characters are relied to ontogenetic growth differences formed by the secondary growth mode of Ogane *et al.* (2009c) in some limited species. In ignoring these secondary growth parts, *Cinclopyramis* and *Peripyramis* include a morphotype with a pyramidal shell with straight ribs and simple fenestration, and nine radial ribs in the thorax. This was cited from the definition for *Sethopyramis* in Campbell (1954: D127). This obviously indicates a synonymy relationship among *Cinclopyramis*, *Sethopyramis* and *Peripyramis*. *Enneaphormis* is marked by meshes fenestrated by secondary lattices and eight to nine radial beams (Campbell 1954: D127), but this can be synonymized with these three genera as discusses here. The type-illustration for *Spongopyramis* shows irregular framed pores, differing from any other genera listed here. *Spongopyramis*-like morphotypes seemed to be limited in range but this difference is not sufficient to be regarded as to constitute an independent genus from the others. *Plectopyramis*, *Cephalopyramis* and *Sestropyramis* are characterized by the presence of a ball-like cephalis but this character has not been used for genus differentiation. Instead, *Cephalospyris* is distinguished by nine radial ribs in the thorax (Campbell 1954: D127) and *Sestropyramis* by six radial ribs in the thorax (Campbell 1954: D127) as a subgenus of *Plectopyramis* (Campbell 1954: D128). The number of "radial ribs in the thorax" is not significant among their type-illustrations as to be relevant for genus differences. In conclusion, these three genera are synonyms. The specimens with ball-like cephalis are generally found in the Eocene but it is unclear whether this character is of genus or species level. The oldest available name is *Cinclopyramis*.

Cornutella

Cornutissa has the same type species as *Cornutella*. Semi-objective morphological studies of *Cornutella* by Reynolds (1978) are references to evaluate the validity of genera for the *Cornutella* group. *Cornutella* in the sense of Reynolds (1978) is subdivided into two genera (*Cornutanna* and *Cornutella*) by occurrence of an apical horn in Campbell (1954: D121) but this character is obviously an infraspecific variation. *Orthocornutanna* is marked by a straight shell axis (Campbell 1954: D121) but a curved specimen was found in the Messinian (by upper Miocene-upper upper Miocene; Cortese & Bjørklund 1999: figs 21.G, 21.I). These curved specimens including the topotype of *Cornutella clathrata* (Suzuki *et al.* 2009c: pl. 16, figs 4a, 4b) are not significant to separate *Orthocornutanna* from *Cornutella*. The oldest available name is *Cornutella*.

? Family LAMPROMITRIDAE Haeckel, 1882 *sensu* Suzuki emend. herein

Lampromitria Haeckel, 1882: 431 [below tribe].

Lampromitridae – Petrushevskaya & Kozlova 1972: 534 (*sensu* emend.). — Petrushevskaya 1975: 589; 1981: 103. — Kozlova 1999: 113. — Amon 2000: 59. — Afanasieva *et al.* 2005: S295. — Afanasieva & Amon 2006: 143.

Lampromitrinae – Petrushevskaya 1981: 103-104; 1986: 134. — Amon 2000: 59-60. — Afanasieva *et al.* 2005: 295. — Afanasieva & Amon 2006: 143.

TYPE GENUS. — *Lampromitra* Haeckel, 1882: 431 [type species by subsequent designation (Campbell 1954: D122): *Lampromitra coronata* Haeckel, 1887: 1214].

INCLUDED GENERA. — *Lamprodiscus* Ehrenberg, 1861b: 831. — *Lampromitra* Haeckel, 1882: 431 (= *Hexaphormis*, *Pentaphormis* synonymized by Petrushevskaya 1971a: 103).

INVALID NAME. — *Heptaphormis*.

DIAGNOSIS. — Lampromitridae consists of a shallow hat-like conical shape formed by the cephalis and thorax. The cephalis is, small, perforated and smoothly adjoined to the thorax. No feet and no apical horn are present. The thoracic pores are systematically distributed in both longitudinal and lateral directions. A velum or velum-like structure develops in some members. The cephalis consists of a initial spicular system with A-, V-, D-, double L- and Ax-rods. The MB is either short or pointed. Both, double l-rods and a basal ring are absent. Instead of a basal ring, double AL-, double AD-, and double VL-arches develop to form a suture between the cephalis and the thorax. These are almost completely merged, forming parts of the pore frames. Direct rods from D- and double L-rods extend downward and are merged with the thoracic wall at certain points to form significant rims. The endoplasm is too small to be visible around the cephalis. Single very long robust pseudopodium (axial projection) are absent.

STRATIGRAPHIC OCCURRENCE. — Early Pliocene-Living.

REMARKS

As subsequently explained, the cephalic structure of *Lamprodiscus* is completely different from that of *Lampromitra*, ergo the diagnosis shown above is based upon *Lampromitra*. The taxonomic relationship between the Lampromitridae and Plectopyramididae is highly questionable due to the lack of molecular support data. Furthermore, the overall appearance and ecology of the Lampromitridae are quite different from that of the Plectopyramididae. Petrushevskaya (1981: 102) placed the Lampromitridae in the Plectopyramidoidea (originally Acropyramidoidea). *Lampromitra* was later placed in the Pseudodictyophimidae Suzuki, n. fam. (originally Lophophaenidae) by De Wever *et al.* (2001: 226). *Lamprodiscus* was not treated in De Wever *et al.* (2001). We simply pursued the approach of Petrushevskaya (1981).

As mentioned, the cephalic structure is different between *Lamprodiscus* (Nishimura 1990: figs 19.2, 19.3; Sugiyama *et al.* 1992: pl. 16, fig. 2) and *Lampromitra* (Nishimura 1990: figs 19.1, 19.6). In *Lamprodiscus*, the cephalic initial spicular system consists of A-, D-, double L- and Ax-rods. The MB is pointed or very short. The V-rod may be present or absent. Both, double l-rods and basal rings are absent. Instead of a basal ring, a basal ring-like structure is present above MB or the relevant structure. The former structure is directly connected to the supplementary rods arising from the D- and double L-rods, forming the three collar-like pores of the MB. This basal ring-like structure is completely merged with the meshwork of the shell. LL-arch, or double VL-arches, develop and partially merge with a section of the cephalic meshwork. AL-arches are absent. The D- and double L-rods are subdivided at some points, or near their ends. D- and double L-rods extend downward and merge with the thoracic wall to form significant rims. The basal ring-like structure above MB is a structure unique to the Pseudodictyophimidae Suzuki, n. fam. As such, *Lamprodiscus* may belong to the Pseudodictyophimidae Suzuki, n. fam. *Lampromitra* is similar to the Theopiliidae as no basal ring is present; however, the cephalic structure is not well known, for this reason the assignation in this superfamily is queried.

The protoplasm was observed in *Lamprodiscus* (Suzuki & Not 2015: fig. 8.11.20; Zhang *et al.* 2018: 10, figs 2.9) and *Lampromitra* (Sashida & Kurihara 1999: fig. 12.13). One or two algal symbiont cells were observed several times near the cephalis in the shallow water representatives of *Lamprodiscus*.

Incertae familiae

INCLUDED GENUS. — *Zealithapium* O'Connor, 1999: 5.

STRATIGRAPHIC OCCURRENCE. — Early Eocene-early Late Miocene.

REMARKS

Zealithapium was initially included in the Spumellaria without a clear explanation. This may be due to the lack of a recognized cephalic spicular system in the illustration of pl. 2, fig. 11 from O'Connor (1999). The proximal end of *Zealithapium oamaru* test shown in O'Connor (1999: pl. 2, fig. 11) is equivalent to that of other *Zealithapium* species of Nishimura (1990: figs 33.2-33.8). Thus, the proximal end of *Zealithapium* consists of MB, A, double l- and double L-rods whose structures crop out as parts of the pore meshwork. Thickness and length of both double-l and double L-rods are similar. These rods extend downward to connect with a hexagonal ring. The attachment point of these rods is always at the mid-point of the bar on the hexagonal ring. Viewed from the hexagonal ring, the MB appears to be situated in the center. The degraded cephalic spicular system is similar to that of the Plectopyramididae but other characters are dissimilar. One evolutionary hypothesis suggest that *Zealithapium* evolved from a spherical species with pyriform microsphere to an umbrella-type form (Riedel & Sanfilippo 1981: 338). The forerunner belongs to *Entapium* (Entapiidae, Spumellaria), but its pear-shaped microsphere has no MB or MB-like structure.

Superfamily CARPOCANIOIDEA Haeckel, 1882 n. stat.

Carpocanida Haeckel, 1882: 427 [below a tribe].

DIAGNOSIS. — Consists of an oval to spindle shape shell with two to three (rarely four) segments. Cephalis small, tending to sink into the thorax.

REMARKS

As no appropriate superfamily name has been proposed for this family, the taxonomic rank of the Carpocaniidae sensu De Wever *et al.* (2001) is used here. However, some partial definitions of this superfamily used by De Wever *et al.* (2001), "cephalis simple", are excluded from its definition as the type genus of the Carpocaniidae is known to have a very complex, cephalic initial spicular system (see remarks for Carpocaniidae). The "Carpocaniidae" sensu both Petrushevskaya (1981: 225-226) and De Wever *et al.* (2001) used to be a member of the superfamily Eucyrtidioidea, but Matsuzaki *et al.* (2015: 66) excluded this family from the Eucyrtidioidea based on the different cephalic structures observed. This morphological decision was later confirmed by a molecular study (Sandin *et al.* 2019). The cephalic structure, similar to the Carpocaniidae and Artostrobiidae, is a complex arch and composed of supplementary rod-systems along the V-rod. As these families are poorly differentiated by molecular studies (99 PhyML bootstrap value 10 000 replicates, BS and 0.68 posterior probabilities), it may not be necessary to separate them at the superfamily level. This superfamily includes the Carpocaniidae and probably the Diacanthocapsidae in the Cenozoic.

Family CARPOCANIIDAE Haeckel, 1882 *sensu* Sugiyama (1998)

Carpocanida Haeckel, 1882: 427 [below a tribe].

Cyrtocalpida Haeckel, 1882: 427 [below tribe]; 1887: 1133 1178-1179 [as a family]. — Wisniowski 1889: 687. — Bütschli 1889: 1986 [as a family]. — *nec* Rüst 1892: 179 [as a family]. — *nec* Cayeux 1894: 207.

Cyrtocalpidae [*sic*] – Popofsky 1908: 273(= Cyrtocalpididae); 1913: 332. — Schröder 1914: 91. — Clark & Campbell 1942: 65; 1945: 35. — Campbell & Clark 1944a: 39; 1944b: 22. — Chediya 1959: 196. — Chen & Tan 1996: 153. — Tan & Chen 1999: 295. — Tan & Su 2003: 113, 125. — Chen *et al.* 2017: 179.

Cyrtocalpididae – Poche 1913: 220.

Cyrtocalpinae [*sic*] – Orlev 1959: 454 (= Cyrtocalpididae).

Carpocaniidae – Riedel 1967b: 296 (*sensu* emend.); 1971: 656-657. — Petrushevskaya 1971a: 238; 1971b: 988; 1975: 587-588; 1981: 255-256. — Riedel & Sanfilippo 1971: 1596; 1977: 875. — Petrushevskaya & Kozlova 1972: 535. — Nakaseko *et al.* 1975: 174. — Nakaseko & Sugano 1976: 130. — Dumitrica 1979: 35. — Tan & Su 1982: 175. — Anderson 1983: 42. — Sanfilippo *et al.* 1985: 690. — Nishimura 1990: 165 (*sensu* emend.). — Takahashi 1991: 130. — Chen & Tan 1996: 154. — Hollis 1997: 62. — Boltovskoy 1998: 33. — Sugiyama 1998: 234. — Kozlova 1999: 142-143. — Tan & Chen 1999: 319. — Anderson *et al.* 2002: 1018. — De Wever *et al.* 2001: 256. — Tan & Su 2003: 113, 165. — Afanasieva *et al.* 2005: S299. — Afanasieva & Amon 2006: 148. — Matsuzaki *et al.* 2015: 66.

Carpocaniinae – Petrushevskaya & Kozlova 1972: 535. — De Wever *et al.* 2001: 258.

Carpocannidae [*sic*] – Sanfilippo & Riedel 1973: 530 (= Carpocaniidae).

Carpocanidae [*sic*] – Amon 2000: 68 (= Carpocaniidae).

Type genus. — *Carpocanium* Ehrenberg, 1846: 385 [type species by subsequent monotypy: *Lithocampe solitaria* Ehrenberg, 1839: 130].

Included genera. — *Anthocyrturium* Haeckel, 1887: 1276. — *Artobotrys* Petrushevskaya 1971a: 237. — *Carpocanium* Ehrenberg, 1846: 385 (= *Carpocanidium* with the same type species; *Asecta* synonymized by Petrushevskaya 1971a: 240; *Cyrtocalpis* synonymized by Petrushevskaya 1971a: 239; *Cryptoprora* **n. syn.**, *Spongiocanium* **n. syn.**; *Sethamphora* synonymized by Petrushevskaya & Kozlova 1972: 535). — *Carpocanopsis* Riedel & Sanfilippo, 1971: 1596 (= *Cryptocarpium* **n. syn.**). — *Tripterocalpis* Haeckel, 1882: 427.

Nomina dubia. — *Carpocanistrum*, *Carpocanobium*, *Cystophormis*, *Dictyoprona*.

Diagnosis. — Carpocaniidae having two ovoidal segments. Little to no trace of a collar constriction between the very small cephalis and large thorax is observed. The initial cephalic structure is quite complex and consists of MB, A-, V-, D-, double l-, and double L-rods. The Ax-rod may be present or absent. The basal ring well-developed and isolated from the shell wall; it is directly connected to the MB, double L-, double l- and V-rods to form four collar pores. No Dl-arches development is observed. The double collar pores related to Ll-arch are larger than the double collar pores related to the LV-arch. The basal ring is bended along the double L-rods, and the double collar pores related to LV-arch is oriented upward at high angle. The A-, D- and double L-rods are directly connected to the shell wall, but the end of the V-rod is free, acting as a very small spine. From the basal ring several rods extend laterally and several other reach up the cephalic wall. The lateral rods are D-rods, double L-rods, double supplement rods emerging from the Ll-arch near the ends of the l-rod, and other supplementary rods. The upward-oriented rods are A-rod type, with double supplementary rods arising from the mid-point of Ll- and LV-arches. These rods originating from the basal ring either join the shell wall or branch further to eventually join the shell wall.
The endoplasm of variable size may be located in the upper half of the shell or present in the entire shell. Bundle of pseudopodia mainly extends downward from the shell aperture. No thick stick-like pseudopodium (axial projection) are observed. Algal symbionts are found in shallow water *Carpocanium* species around the distal end of the endoplasm.

Stratigraphic occurrence. — Early Eocene-Living.

Remarks

The structure of the cephalic initial spicular system of *Carpocanium* varies among different papers. However, there is consensus regarding the very complex structure embedded in the flattened cephalic part (Caulet 1974: pl. 8, figs 3-6; Nishimura 1990: figs 42, 43; Sugiyama *et al.* 1992: pl. 27, figs 7b, 9b; O'Connor 1997b: pl. 5, fig. 8; Sugiyama 1998: pl. 5, fig. 8b). Although almost all supplement rods and arches above the basal ring were omitted, a schematic structure is illustrated in Sandin *et al.* (2019: supplement 1). *Carpocanopsis* (O'Connor 1999: pl. 2, fig. 5, text-fig. 5) also has a very complex cephalic structure similar to *Carpocanium*. The cephalic structures in the remaining genera are unknown. "Living" and protoplasm images were illustrated for *Carpocanium* (Matsuoka 1993a: fig. 2.8; Suzuki & Not 2015: fig. 8.11.22; Zhang *et al.* 2018: 10, figs 2.1-2.3).

Validity of genera

Carpocanium

Carpocanidium has the same type species as *Carpocanium*. The three genera listed here (*Asecta*, *Cyrtocalpis* and *Sethamphora*) have already been synonymized with *Carpocanium* (Petrushevskaya 1971a; Petrushevskaya & Kozlova 1972). *Cryptoprora* was once classified in the "Theophormidinae of the Theophormididae" with a subsequent designation of the type species as "*C. fundicola*" in Campbell (1954: D132). However, the first species related to *Cryptoprora* is *Cryptoprora plutonis* in Ehrenberg (1854b). This species has never been illustrated before 2009 but the real specimen, as indicated by Ehrenberg himself, was specified in the Ehrenberg collection (Suzuki *et al.* 2009c: pl. 32, figs 8a-c), and the taxonomic availability of this genus was guaranteed. The lectotype is obviously identified as "*Carpocanium*" although this shell is filled with an internal bubble. *Spongiocanium* was defined as "*Carpocaniidae with spongy wall and V ray attached to cephalic wall. Shell ovate or subcylindrical. Cephalis without A spine. Thorax without peristome. Shell wall composed of inner lattice and outer spongy layers*" (Nishimura 1990: 169) and was individualized by a spongy shell wall. The type specimens have rough surfaces with nodes on pore frames, but no spongy structure defined by complex fibers or an irregular distribution of bubble-like structures. Its recognition is wrong so that *Spongiocanium* is a synonym of *Carpocanium*. The oldest available name is *Carpocanium* among those published by Ehrenberg (1846: 385). Some papers indicate a published year for *Cryptoprora* in 1846 but this is a volume number, not the published year (Lazarus & Suzuki 2009).

Carpocanopsis

Riedel & Sanfilippo (1971: 1596) erected *Carpocanopsis* to provide a category, distinct from the genus *Carpocanistrum*, for a group of carpocaniids with a heavy structure, with abdomen, and a lumber stricture that is internally pronounced. These points are actually different in the type specimens of *Carpocanium*. Specimens identifiable as *Carpocanopsis* are limitedly found from the lower Eocene to lower upper Miocene, differing from *Carpocanium*; but these two genera are artificially divided for biostratigraphic purposes. *Cryptocarpium* was erected by Sanfilippo & Riedel (1992: 6) with *Cryptoprora ornata* Ehrenberg as a three segmented pterocorythid. After this erection, the type specimen examined by Ehrenberg himself was located in the Ehrenberg collection (Ogane *et al.* 2009b: pl. 83, figs 5a-d). The specimen is poorly preserved but it is not regarded as a member of the pterocorythids and three segments correspond to the morphotype of *Carpocanopsis* but are not of pterocorythid-type. They are difficult to differentiate from each other. *Carpocanopsis* is an available name older than *Cryptocarpium*.

Family Diacanthocapsidae O'Dogherty, 1994

Diacanthocapsidae O'Dogherty, 1994: 216.

Diacanthocapsinae – De Wever *et al.* 2001: 256-258.

Type genus. — *Diacanthocapsa* Squinabol, 1903: 129 [type species by monotypy: *Diacanthocapsa euganea* Squinabol 1903: 133].

Included genus (Cenozoic only). — *Myllocercion* Foreman, 1968: 37 (= *Schadelfusslerus* synonymized by Hollis 1997: 62).

Diagnosis. — The family is oval to fusiform in shape. Two to four segments with a small simple cephalis that tends to be encased in the abdomen. The thorax is larger than the abdomen or develops three to four feet characteristics instead of a thorax.

Stratigraphic occurrence. — Early Campanian-early Middle Eocene.

Remarks

The Diacanthocapsidae are fundamentally different from the Carpocaniidae by the presence of a simple cephalis. We consider the Diacanthocapsidae a member of the Carpocanioidea due to the similarity of all their characteristics, except for the difference in cephalic initial spicular systems. This decision undoubtedly needs to be re-examined in the future.

Superfamily ARTOSTROBIOIDEA Riedel, 1967

Artostrobiidae Riedel, 1967a: 148; 1967b: 296; 1971: 657.

Artostrobiaceae [*sic*] – O'Dogherty 1994: 158 (= Artostrobioidea) [as a superfamily].

Artostrobioidea – Matsuzaki *et al.* 2015: 55.

Diagnosis. — The shell is tubular or with a highly angled, conical shape. They consist of two or three segments. Some members have a subsequent undulated thorax whose segmentations are not marked by inner-ring dividers.

Remarks

The higher taxonomic position of this superfamily is based on *Botryostrobus* (Artostrobiidae) and *Spirocyrtis* (Artostrobiidae). In Sandin *et al.* (2019), *Ectotoxon* (= misspelled *Extotoxon* originally, Stichopiliidae) was grouped with both previous mentioned genera, but this was owed to a misidentification based on supplemental photos. Thus, this superfamily consists of the Artostrobiidae Riedel 1967a and the Rhopalosyringiidae Empson-Morin 1981 in the Cenozoic. The Artostrobioidea are highly abundance in environmental sequences from deep waters (Sandin *et al.* 2019).

Family ARTOSTROBIIDAE Riedel, 1967 *sensu* Sugiyama (1998)

Artostrobiidae Riedel, 1967a: 148; 1967b: 296; 1971: 657. — Riedel & Sanfilippo 1971: 1599; 1977: 878. — Petrushevskaya & Kozlova 1972: 536. — Foreman 1973a: 431. — Nakaseko *et al.* 1975: 174. — Petrushevskaya 1975: 585. — Nakaseko & Sugano 1976: 131. — Nigrini 1977: 243. — Dumitrica 1979: 34. — Petrushevskaya 1981: 263-264. — Anderson 1983: 44. — Sanfilippo *et al.* 1985: 702. — Takemura 1986: 63-64. — Nishimura 1990: 158 (*sensu* emend.). — Takahashi 1991: 127. — Chen & Tan 1996: 154. — Hollis 1997: 57. — O'Connor 1997a: 69 (*sensu* emend.); O'Connor 2001: 4 (*sensu* emend.). — Boltovskoy 1998: 33. — Sugiyama 1998: 234. — Kozlova 1999: 134. — Tan & Chen 1999: 355. — Anderson *et al.* 2002: 1018. — O'Connor 2000: 198. — De Wever *et al.* 2001: 255-256. — Tan & Su 2003: 113, 226-227. — Afanasieva *et al.* 2005: S300. — Afanasieva & Amon 2006: 148-149. — Chen *et al.* 2017: 234.

Artostrobiinae – Petrushevskaya 1971a: 235-236; 1971b: 985-986. — Petrushevskaya & Kozlova 1972: 538.

Type genus. — *Artostrobium* Haeckel, 1887: 1482 [type species by subsequent designation (Campbell 1954: D140): *Lithocampe aurita* Ehrenberg, 1844a: 84] = junior subjective synonym of *Botryostrobus* Haeckel, 1887: 1475 [type species by subsequent designation (Campbell 1954: D141): *Lithostrobus botryocyrtis* Haeckel, 1887: 1475].

Included genera. — *Botryostrobus* Haeckel, 1887: 1475 (= *Artostrobium* synonymized by Caulet 1974: 236). — *Buryella* Foreman, 1973a: 433. — *Dictyoprora* Haeckel, 1887: 1305 (= *Streptodelus* with the same type species). — *Lithamphora* Popofsky, 1908: 294 (= *Phormostichoartus* synonymized Petrushevskaya 1981: 273; *Poroamphora* synonymized Petrushevskaya 1967: 129). — *Plannapus* O'Connor, 1997a: 69. — *Sertiseria* Sugiyama, 1994: 2. — *Siphocampe* Haeckel, 1882: 438 (= *Lithomitra*, *Lithomitrella*, synonymized by Nigrini 1977: 254; *Siphocampula* **n. syn.**, *Tricolocampium* **n. syn.**). — *Siphostichartus* Nigrini, 1977: 257. — *Spirocyrtis* Haeckel, 1882: 438 (= *Spirocyrtidium* with the same type species). — *Theocamptra* Haeckel, 1887: 1424. — *Tricolocapsa* Haeckel, 1882: 436 (= *Tricolocapsula* with the same type species; *Carpocanarium* **n. syn.**).

Invalid name. — *Tricolopera*.

Nomina dubia. — *Chlamidophora*, *Stylocapsa, Tricolocapsium*.

Junior homonym. — *Acanthocyrtis* Haeckel, 1887 (= *Phormostichoartus*) *nec* Haeckel, 1882.

Diagnosis. — Skeleton having three or more segments with a small cephalis. The dividers between the segments below the thorax are weak or not associated with discrete inner rings. A ventral tube is developed around the collar stricture or at the lower part of the cephalis. Pores are regularly distributed along lateral and/or longitudinal directions. Wings, or other relevant structures are absent. The cephalic initial spicular system consists of MB, A-, V-, D-, double L-, double l- and Ax-rods. The MB is oriented upwards, bundles of very long straight rods (Ax and "extra spines" in the sense of Sugiyama & Anderson 1997b: fig. 2) downwardly directed in some genera. A free A-rod is present in the cephalic cavity and extrudes the cephalic wall as a rod-like apical horn. A free V-rod is present in the center or attached to the bottom of a ventral tube. It may also be ramified near the distal end, attaching itself on the shell wall. Several arches sometimes originate from the V-rod to make a complex structure in the cephalis, but these arches are never visible through the tube. Basal ring with two, four or six collar pores is observed. A double collar pore related to the Ll-arch is always present. In the case of four collar pores being present, another double collar pore related to the VL-arch develops. In the case of six collar pores, the double pore related to the Dl-arch appears as a tiny pore. As the MB is obliquely oriented, the basal ring zigzags along the line of the double L-rod and along the line of the double l-rod. A double pore related with the VL-arch is oriented up to the V-rod side; the double pore enmeshed to the Ll-arch rises up to the D-rod side, and the double pore related to the Dl-arch bends down with the D-rod.
An endoplasm is observed and occupies variable places from the cephalis to the distal end of the shell. A bundle of thick pseudopodia extending from the aperture of the shell in *Spirocyrtis* is observed. However, this observation is not confirmed for *Botryostrobus* and *Tricolocapsa*. The nucleus is encrypted within the cephalic cavity in the case of *Spirocyrtis*. No algal symbionts are reported in living forms.

Stratigraphic occurrence. — Early Toarcian-Living.

Remarks

The Artostrobiidae were usually included in the Eucyrtidioidea (Petrushevskaya 1981; De Wever *et al.* 2001), but both the cytological and cephalic structures are fundamentally different when comparing *Spirocyrtis* and *Eucyrtidium* (Eucyrtidiidae). Thus, they cannot be grouped into the same superfamily (Sugiyama & Anderson 1997b; Sugiyama 1998). This is supported by molecular phylogeny (Sandin *et al.* 2019). With the exception of *Dictyoprora*, the cephalic initial spicular system has been well illustrated in all genera: *Botryostrobus* (Caulet 1974: pl. 10, fig. 1; Poluzzi 1982: pl. 28, fig. 16; Nishimura 1990: fig. 34.1, 34.6; Takahashi 1991: pl. 44, fig. 5; Sugiyama *et al.* 1992: pl. 28, figs 1-3), *Buryella* (O'Connor 2001: pls 3, 4), *Lithamphora* (Nishimura 1990: fig. 34.7, 34.9; O'Connor 1997b: pl. 5, fig. 4), *Plannapus* (O'Connor 1997a: pl. 6, figs 4, 5), *Sertiseria* (Sugiyama 1994: pl. 1, figs 1-3), *Siphocampe* (O'Connor 1997b: pl. 4, figs 11, 12; Sugiyama 1998: pl. 4, fig. 7; O'Connor 2000: pl. 3, figs 7, 8, 16-18), *Siphostichartus* (Sugiyama 1998: pl. 5, fig. 5), *Spirocyrtis* (Nishimura & Yamauchi 1984: pl. 40, fig. 11b; Nishimura 1990: fig. 34.12), *Theocamptra* (Nishimura 1990: fig. 35.4) and *Tricolocapsa* (Caulet 1974: pl. 7, figs 3, 4; Nishimura 1990: figs 35.6-35.9; Sugiyama 1998: pl. 5, fig. 6b). Sugiyama (1998) thought that the schematic illustrations by both Nishimura and O'Connor were imprecise.

The Artostrobiidae are distinguished from the Rhopalosyringiidae by the presence of a ventral tube, the absence of wings or another relevant structure, and by the shell's more regularly distributed pores.

The evolutionary history of the Artostrobiidae at the genus level follows the lineage from *Dictyoprora* to *Siphocampe*, *Lithamphora* (originally *Phormostichoartus*), *Siphostichartus*, *Botryostrobus* and *Spirocyrtis.* This order was established according to the stratigraphic range of species (Nigrini 1977: text-fig. 2; Caulet 1979: fig. 4). The evolution hypothesis of *Buryella* at the species level was illustrated by O'Connor (2001: text-fig. 5) but the relationship of the Cretaceous *Dictyoprora* to *Buryella* is unknown. No bundle of Ax-rod and extra spines is found in *Buryella*, *Dictyoprora*, *Plannapus*, *Sertiseria*, *Theocamptra* and *Tricolocapsa*. When specimens are treated, it may be difficult to identify them in the case of: a) three tiny spines on the cephalis (*Pterocyrtidium* and *Tricolocapsa*), b) a partially encrypted cephalis (*Plannapus* and *Carpocanium*), and c) an undulated outline on thorax and subsequent segments (*Botryostrobus* and *Siphocampe*). The genus *Tricolocapsa* has an artostrobid-type tube on the cephalis, differentiating it from *Pterocyrtidium*. The cephalis of *Carpocanium* is generally flattened and appears to have a very complex structure under light transmitted microscopy. Conversely, the cephalis of *Plannapus* appears to have a simple structure. The difference between *Botryostrobus* and *Siphocampe* has not been resolved as of yet because due to the existence of many intermediate forms between these genera in the Miocene. High variability in undulation of thorax and subsequent segments create classification problems at genus and species level (Boltovskoy & Vrba 1989).

Protoplasm and living condition were illustrated for *Botryostrobus* (Sashida & Kurihara 1999: fig. 11.12; Suzuki & Not 2015: fig. 8.11.12), *Spirocyrtis* (Matsuoka 1993b: pl. 5, figs 3, 4; 2007: fig. 4c; 2017: fig. 29; Sugiyama & Anderson 1997b: pl. 1, figs 7, 8; Ogane *et al.* 2009c: figs 3L-3N; Suzuki *et al.* 2009b: figs 2E, 2F; Matsuoka *et al.* 2017: Appendix B; Zhang *et al.* 2018: 15, figs 4.23) and *Tricolocapsa* (Suzuki & Not 2015: fig. 8.11.13). A cytological ultrafine structure was also documented in *Spirocyrtis* (Sugiyama & Anderson 1997b: pls 6, 7).

Validity of genera

Siphocampe

Lithomitra has the same type species as *Lithomitrella* so the latter is automatically synonymized with *Siphocampe*, following Nigrini (1977: 254). *Tricolocampium* was placed in the "Stichocorythinae" of the "Stichocorythidae" within the "subsuperfamily Triacartilae" *sensu* Campbell (1954: D141-142), and then this genus was characterized by a shell divided by many strictures into cephalis, thorax, abdomen, the presence of radial apophyses, an open aperture on the terminal end of the last segment, a hollow cylindrical cephalic tube, similar heights of segments (Campbell 1954: D136, 140-142). When referred to the real specimens identifiable as *Siphocampe tubulosa* (Haeckel 1887: pl. 79, fig. 13), type species of *Siphocampula*, the description by Campbell (1954) is not precise. This test looks to have many segments but it is due to the repetitions of surface ornaments identical to those of *Siphocampe* (See support images for *Siphocampe* and *Lithomitrella* in the Atlas). They are also no true dividers inside the test of *Siphocampula* as shown in the support image for *Lithomitra* in the Atlas. *Tricolocampium* was placed in the "Theocorythinae" of the "Theocorythidae" in the "subsuperfamily Theopiliilae" *sensu* Campbell (1954: D129, 132, 134). The taxa under these higher taxonomic ranks are characterized by a shell divided by two transverse strictures into cephalis, thorax and abdomen, no basal apophyses, and open aperture. *Tricolocampium* itself is defined by a cylindrical abdomen, no apical horn, and similar pore patterns on thorax and abdomen in Campbell (1954: D134). The description at higher ranks also matches with the type-illustration of *Siphocampe* (Haeckel 1887: pl. 79, fig. 10). Campbell (1954) documented similar pore patterns on thorax and abdomen, but this does not correspond to the type-illustration of *Tricolocampium*. Rather, the pore patterns on thorax and abdomen in the type species of *Tricolocampium* (Haeckel 1887: pl. 66, fig. 21) is similar to the type-illustration of *Siphocampe*. The remaining difference between these two genera is the occurrence, in the definition, of a tube on the cephalis. However, real specimens identifiable as *Tricolocampe cylindrica* have a tube extending laterally to the cephalis (the support image for *Tricolocampium* in the Atlas) and, thus, there is no reason to keep *Tricolocampium* as valid. The oldest available names are *Siphocampe* and *Lithomitra* which were published in the different papers of the same year (Haeckel 1882 for *Siphocampe* and Bütschli 1882 for *Lithomitra*). As the first reviser, Nigrini (1977: 254) has already validated *Siphocampe*.

Tricolocapsa

Tricolocapsula has the same type species as *Tricolocapsa*. *Tricolocapsa* is defined by the lack of an apical horn, no latticed septum between the thorax and the abdomen and a thorax as large as the abdomen or larger (Campbell 1954: D136). *Carpocanarium* is defined by a corona of six feet, no thoracic ribs and a hornless cephalis hidden within the thorax (Campbell 1954: D127). These descriptions, however, completely mismatch the type-illustrations of both *Tricolocapsa* (Haeckel 1887: pl. 66, fig. 1) and *Carpocanarium* (Stöhr 1880: pl. 3, fig. 8). First, identical specimens having a perfect third segment have not been so far found. Real specimens most similar to *Tricolocapsa theophrasti*, the type species of *Tricolocapsa*, always have a poreless corona with an open aperture instead of a perfect third segment, a very thin tiny horn which is probably lost in most specimens, and no latticed septum between the thorax and the poreless corona (the support image for *Tricolocapsa*). The illustration of *Carpocanium calycothes* in Stöhr (1880), the type species of *Carpocanarium*, has a perfect spherical cephalis above the thorax, unlike a "cephalis hidden within the thorax" as written in Campbell (1954: D127). The "corona with six feet" mentioned by Campbell (1954) is an obviously wrongly recognized broken peristome if we refer to the type-illustration. The real specimens identical to this species mostly confirm the illustrations of the type. Different characteristics observable in real specimens point out a very tiny apical horn, a tube in the cephalis-thoracic suture, a trace of a thoracic rib, and six undulations on the peristome of the corona instead of six feet. Based on support images for both *Tricolocapsa* and *Carpocanarium*, these two specimens obviously should belong to the same genus. *Tricolocapsa* is the oldest available name among them.

Family Rhopalosyringiidae Empson-Morin, 1981

Rhopalosyringiidae Empson-Morin, 1981: 264. — O'Dogherty 1994: 158. — Bak 1999: 156.

Lithocampaninae Petrushevskaya, 1981: 115-116 [*nomen dubium*]. — Afanasieva *et al.* 2005: S295. — Afanasieva & Amon 2006: 143.

Type genus. — *Rhopalosyringium* Campbell & Clark, 1944b: 30 [type species by monotypy: *Rhopalosyringium magnificum* Campbell & Clark, 1944b: 30].

Included genera (Cenozoic only). — *Artostrobus* Haeckel, 1887: 1481 (= *Artostrobulus* with the same type species). — *Botryometra* Petrushevskaya, 1975: 590. — *Ectonocorys* Foreman, 1968: 40. — *Pterocyrtidium* Bütschli, 1882: 531. — *Rhopalosyringium* Campbell & Clark, 1944b: 30 (= *Calompterium* **n. syn.**).

Nomen dubium. — *Lithocampana*.

Diagnosis. — The overall size of the Cenozoic representatives of the genus is small. Two (rarely three) segments are observed with or without a collar constriction. The cephalis is poreless or contains small relict pores. A single vertical apical horn emerges from a free A-rod in the cephalic cavity, an MB is obliquely oriented toward the A-rod side, and a V-rod is found oriented upward relative to the shell wall or ventral tube. The above-mentioned features are well visible under a light microscope. Double *ap*-arches (type of AL-arches) are also visible on the cephalic wall. The cephalic initial spicular system is composed of MB, A-, V-, D-, double L- and double l-rods. The Ax-rod is present or absent. In *Pterocorythium*, at least, the basal ring is separated from the shell wall and directly connected to the V-, double L- and double l-rods to form four collar pores. The basal ring bends along the line with the double L-rod. The orientation of the MB upwards to the A-rod side implies that the double pore of the VL-arch rises up to the V-rod side and the double pore of the Ll-arch also rises up to the D-rod side. The A-, D-, V- and double L-rods are directly connected to the shell wall. Several rods are laterally distributed around the basal ring and connected with the shell wall. Excepting A- and V-rods, no vertical rods are present. Lateral rods include the D-rods, the double L-rod and several sets of double supplement rods that emerge from the Ll-arch. These rods that are connected to the basal ring are not recognizable under a light microscope. A relatively robust double arch between the l-rod and the A-rod lateral end of MB (named MA-arch) is also present in some specimens. D- and double L-rods extend outwards from the thorax near the cephalis and become external spines in Cenozoic members.

Stratigraphic occurrence. — Early Bajocian-Living.

Remarks

The representatives of the genus *Artostrobus* in the Cenozoic have as common character the small size of their test. No molecular support data have been obtained for this family, but the presence of a ventral tube or a ventral tube-like structure is similar to both Carpocaniidae and Artostrobiidae. This family have a basal ring isolated from the shell wall, indicating some similarity with the Carpocaniidae. However, the overall appearance and the presence of apical horns suggest a larger similarity to the Artostrobiidae. As commented in the remarks for Lineage II, these three families may potentially be grouped into a single superfamily. *Artostrobus* was once placed in the Plectopyramididae (originally Acropyramididae in De Wever *et al.* 2001: 246); meanwhile *Botryometra* and *Rhopalosyringium* were both placed in the Cannobotrydidae (originally Cannobotryidae in De Wever *et al.* 2001: 244). *Ectonocorys* and *Pterocyrtidium* were not treated in De Wever *et al.* (2001). Originally, they were grouped by the latter on the basis of a common cephalic structure; however, the initial spicular system have not been examined in SEM analyses except for *Pterocyrtidium* (O'Connor 1999: pl. 4, figs 21a, 21b). Therefore, the details of the cephalic structure largely relied on the SEM photos of *Pterocyrtidium* (O'Connor 1999: pl. 4, figs 21a, 21b) with references to a drawing of *Artostrobus* (Petrushevskaya 1967: figs 56, 57; 1968: fig. 4; 1971a: figs 82.IX, 82.X, 82.XII) and *Botryometra* (Petrushevskaya 1971a: figs 79.I, 79.II).

Validity of genera

Rhopalosyringium

The synonymy between *Rhopalosyringium* and *Calompterium* is in debate among the authors of this paper. The cephalic structure of the Cenozoic *Rhopalosyringium* and the topotypic *Calompterium* specimens are quite similar externally. However, the potential topotype "*Calocyclas rachiphora* Clark & Campbell, 1945" from Laguna Seca Creek section of the Kreyenhagen Formation, south of Los Banos (Blueford & White 1984:67-68; pl. 2, fig. 4), lacks a rhopalosyringiid initial spicular system. The older synonym is *Rhopalosyringium*.

Superfamily Acanthodesmioidea Haeckel, 1862

Acanthodesmida Haeckel, 1862: 237, 265-266 [as both family and tribe]; 1882: 445 [as a tribe]; 1887: 970, 973 [as a subfamily of Coronida].

Spyridina Ehrenberg, 1846: 385 [*nomen nudum*, as a family]; 1847: 54 [as a family]; 1876: 156 [in Spumellaria]. — Schomburgk 1847: 124, 126 [as a family]. — Petrushevskaya 1981: 327-328 [as a suborder].

Spyrida – Haeckel 1882: 440 [*nomen nudum*, as a family]. — Lankester 1885: 850 [as a family]. — Petrushevskaya 1971a: 240-243 [as a suborder]; 1971b: 990 [as a suborder]. — Petrushevskaya & Kozlova 1972: 529. — Riedel & Sanfilippo 1977: 868 [as a suborder]. — Anderson 1983: 39-40 [as a suborder]. — Sanfilippo *et al.* 1985: 661.

Spyroidea – Haeckel 1884: 31 [*nomen nudum*, as a family]; 1887: 895 1015-1021 [as a suborder]. — Bütschli 1889: 1979 [as an order]. — Haecker 1908: 445 [as a rank between suborder and family]. — Calkins 1909: 41 [as an order]. — Lankester *et al.* 1909: 147 [as an order]. — Schröder 1914: 90, 141-142 [as a suborder]. — Dacque 1933: 42 [rank unknown]. — Clark & Campbell 1942: 53 [as a suborder]; 1945: 29. — Campbell & Clark 1944a: 33 [as a suborder]; 1944b: 21. — Deflandre 1953: 430-431 [as a superfamily]. — Chediya 1959: 176 [as a superfamily]. — Anderson 1983: 29. — Cachon & Cachon 1985: 293 [as a superfamily]. — Chen & Tan 1996: 152 [as a suborder]. — Tan & Su 2003: 86 [as a suborder]. — Chen *et al.* 2017: 167 [as a suborder].

Stephoidea Haeckel, 1887: 895, 931-937 [as a suborder]. — Bütschli 1889: 1976 [as an order]. — *nec* Rüst 1892: 176 [as an order]. — Lankester *et al.* 1909: 147 [as an order]. — Popofsky 1913: 283 [s a suborder]. — Schröder 1914: 72, 87 [as a suborder]. — Dacque 1933: 42 [rank unknown]. — Clark & Campbell 1945: 29 [as a suborder]. — Deflandre 1953: 429-430 [as a superfamily]. — Chediya 1959: 167 [as a superfamily]. — Anderson 1983: 29. — Cachon & Cachon 1985: 291 [as a superfamily]. — Chen & Tan 1996: 152 [as a suborder]. — Tan & Su 2003: 83 [as a suborder]. — Chen *et al.* 2017: 165 [as a suborder].

Stephoidae – Delage & Hérouard 1896: 219 [as a suborder].

Spyroidae – Delage & Hérouard 1896: 233 [as a suborder].

Stephoida – Calkins 1909: 41 [as an order].

Spyroideen – Popofsky 1913: 304 [as a suborder].

Stephaniicae [*sic*] – Campbell 1954: D105-106 (= Stephanioidea) [as a superfamily].

Acanthodesmiacea [*sic*] – Loeblich & Tappan 1961: 227 (= Acanthodesmioidea) [as a superfamily]. — De Wever *et al.* 2001: 227 [as a superfamily].

Acanthodesmoidea [*sic*] – Petrushevskaya 1986: 136, 138 (= Acanthodesmioidea).

Spyridiniformes – Amon 2000: 25-26.

Spyridinata – Afanasieva *et al.* 2005: S304 [as an order]. — Afanasieva & Amon 2006: 153 [as an order].

Diagnosis. — One sagittal ring (or D-shaped ring) including MB, A-rod, V-rod and AV-arch. D-, double L-, double l-rods tend to be well developed. The AV-arch is rarely absent. Many small appendages systematically extend from particular portions of these rods. Endoplasm of spherical shape with a thick capsular membrane, transparent in color. Gelatinous matter, if present, wraps the endoplasm, siliceous skeleton, and algal symbionts. Ectoplasm poorly recognized. Pseudopodia visible or invisible.

Remarks

The Acanthodesmioidea consists of the Acanthodesmiidae, Cephalospyrididae, Paradictyidae and Stephaniidae. Molecular data obtained by Sandin *et al.* (2019) cannot be used when considering the morphological classification of the family within the Acanthodesmioidea. However, it amounts to the second highest environmental sequence, relative to Plagiacanthoidea, which have the highest (Sandin *et al.* 2019). Moreover, sequences of Acanthodesmioidea are particularly abundant in the subtropical and tropical South China Sea (Wu *et al.* 2014).

The appearance of the Acanthodesmioidea species may drastically vary. The images of the same specimen under different orientations were provided in several papers (Goll & Bjørklund 1980: pls 2, 3; 1985: figs 6-9; Tan & Su 1981: pls 1-3; Itaki 2009: pl. 13, figs 1-20). Based on absolute and relative Cartesian coordinates, a precise orientation is the first step to identify this group. The next steps should be followed: 1) Like in pylonioids (Zhang & Suzuki 2017: fig. 4), the absolute Cartesian coordinates (Type 1) are used to define the anatomical orientation of the specimen while the relative Cartesian coordinates (Type 2) are use to describe the orientation of a real specimen in the Type 2 coordinate system. Under Euclidean geometry, the way to define Types 1 and 2 of Acanthodesmioidea is mathematically identical to that of pylonioids by Zhang & Suzuki (2017). To do that, some modifications in previous studies of the Acanthodesmioidea were taken into account (Goll 1968: text-fig. 3B; Goll & Bjørklund 1985: fig. 5B); 2) the origin (O-point) under Euclidian geometry is defined as the joint point of Ax-rod with MB or the V-rod side end of MB for both coordinates of Types 1 and 2; 3) As for Type 1 coordinate, the sagittal plane (Sg-plane) is defined as to roughly include MB, A- and V-rod as well as the sagittal axis (Sg-axis) which is defined in order to include MB; 4) once O-point, Sg-plane and Sg-axis are defined, the polar axis (Pl-axis) is defined in a direction perpendicular to the Sg-axis on Sg-plane and the lateral axis (Lt-axis). The lateral axis is defined by an axis that is in a direction perpendicular to both the Sg- and Pl-axes. The lateral plane (Lt-plane) is defined by the plane including the Pl- and Lt-axes. Additionally, the equatorial (Eq-plane) plane is defined by the plane including the Lt- and Sg-axes; 5) Regarding, Type 2 coordinates, the short and longest axes of the shell are coded as the shortest axis (Sh-axis) and longest axis (Lo-axis). The remaining axis is placed on the remaining direction as middle axis (Md-axis). The longest side plane (Lo-plane) includes the Lo- and Sh-axes; the shortest side plane (Sh-plane) is defined by the Sh- and Md-axes, and the remaining plane as a middle one (Md-plane, including Md- and Lo-axes). The intersection angles among three axes, or three planes, are not necessary to be equal to 90° between each other although all of them must include the O-point. The coordinate system proposed by Goll (1968) and Goll & Bjørklund (1985) cannot be used due to an inappropriate mathematical definition with no O-point and mixture of Types 1 and 2 coordinate systems; 6) the orientation of a specimen faced to observers is defined by the A-rod being in front of the observers. Under the Type 1 coordinate system, the A-rod side direction along Sg-axis is specified as "dorsal" because of presence of D- (dorsal) rod and its opposite direction as "ventral" because of presence of V- (ventral) rod. The right side along the Lt-axis is named "iustum" and left one "sinistram". The direction of the Ax-rod or of the relevant structure is defined as "inferior" while the opposite side is defined as "supra"; and 7) in the Type 2 coordinate system, the front-back is oriented in the Sh-axis, the right and left in the Lo-axis and the apex-base in the Md-axis.

A second key aspect in understanding the structure of the Acanthodesmioidea, are many common skeletal frames and pores termed by Petrushevskaya (1969: fig. 1; 1971a: fig. 10): 1) Small appendages are systemically coded: *c*-spinule on the D-rod; *t*-spinule on the l-rod; *p*- and *d*-spinules on L-rod of the MB side; *a*-, *m*- and *g*-spinules on A-rod from the MB side; *j*-spinule on the V-rod; and *f*-, *z*- and *q*-spinules on the AV-arch of the V-side (Petrushevskaya 1969: fig. 1); 2) Large "pores" along a sagittal ring are named "sagittal pores." A sagittal pore is always located on the Sg-plane under Type 1 coordinates; 3) Basal pores in the basal ring are coded as *J*-pores on the Dl-arch, *Ca*-pores on the Ll-arch and *Cerv*-pore found on the LV-arch (Petrushevskaya 1971a: fig. 10). These pores are aligned as *J-, Ca-* and *Cerv*-pores from the A- to V-rod sides (from the dorsal to the ventral sides).

The Acanthodesmioidea have been widely recognized (Goll 1968, 1969, 1972a, b, 1976, 1978, 1980; Goll & Bjørklund 1980, 1985), but there still remains many undescribed genera and species worldwide. In particular, few names have been proposed for early to early middle Miocene Acanthodesmioidea in, but not limited to, Japan and surrounding areas. To understand the taxonomy several identification criteria are required, such as: 1) the MB, Ax- and A-rods; 2) the orientation of the specimen under both Type 1 and Type 2 coordinates; 3) the number and name codes of the pores; 4) the anatomical position of rods and arches; and 5) the arch names around the sagittal ring. In spite of the difficulties in determining an assignable genus, the species are easily identified after a correct orientation of shell has been confirmed.

The number of basal pores ranges from three to six, but the anatomical architecture is different even when the same number of basal pores are observed. The numbers of the basal pores and their anatomical position is better defined by the presence of five types of pore pattern: 1) Six basal pores forming a full set of double *J*-, *Ca*- and *Cerv*-pores from the dorsal side (Goll 1968: pl. 174, fig. 10). In some taxa, six basal pores are visible from the ventral side, but the double *J*-basal pore is obliquely located on the dorsal side (Goll 1968: pl. 175, figs 15, 16; 1969: pl. 56, fig. 8; 1972a: pl. 47, fig. 2, pl. 58, fig. 3). If this tendency is extreme, the basal ring appears to have only four basal pores, with double *Ca*- and *Cerv*-pores (Goll 1972a: pl. 41, fig. 3); 2) Four basal double pores, the small pair is formed by a double *Cerv*-pore and the larger pair correspond to the double *Ca*-pore (Goll 1968: pl. 175, figs 7, 8; 1969: pl. 55, fig. 7, pl. 57, fig. 3; 1972a: pl. 42, fig. 3, pl. 48, fig. 2, pl. 50, fig. 4); 3) Two basal pores, sometimes presented as a double pit-like pore originated from very large basal pores. These pores are related to the downward D-rod, and recognized as a double *Cerv*-pore and double *Ca*-pore (Goll 1972a: pl. 51, fig. 3). A double basal pore could also appear when the double *Ca*- and *J*- or *Cerv*-pores become degraded, resembling a double pit-like small pore near the base (Goll 1968: pl. 176, fig. 12), or when both *J*- and *Cerv*-pores are completely absent (Goll 1972a: pl. 37, figs 1-3). Another case is observed when the reduction of the double l-rod occurs and the pore is constructed with *a*-spinule of A-rod and a probable *j*-spinule of V-rod (Sugiyama 1998: pl. 6, figs 3b); 4) Three of three larger basal pores, the *V*-rod extends upwards from the basal ring and two *Cerv*-pores unite to become as a single pore (united *Cerv*-pore herein) and the remaining two pores pertain to the double *Ca*-pore (Goll 1972a: pl. 57, fig. 1); 5) Finally, the V-rod might be invisible, in this case, three basal pores and a double pit-like pore are found on the basal ring (Goll 1972a: pl. 62, fig. 3; Nishimura 1990: fig. 25.7), however, the double *J*-pore may be visible or invisible, appearing in this case a double pit (Goll 1969: pl. 56: fig. 8). Thus, double *Ca*-pores are generally the largest existing basal pores while double *J*-pores tend to disappear. However, little to nothing is known about the relationship between the taxonomic classification and the variability of basal pore patterns.

Family Acanthodesmiidae Haeckel, 1862

Acanthodesmida Haeckel, 1862: 237, 265-266 [as both family and tribe]; 1882: 445 [as a tribe]; 1887: 970, 973 [as a subfamily of Coronida]. — Zittel 1876-1880: 123 [rank unknown]. — Mivart 1878: 179 [as a subsection]. — Stöhr 1880: 86 [as an order].

Acanthodesmidae – Claus 1876: 158 [in suborder Thalassicollea].

Acanthodesmiden – Hertwig 1879: 196-200 [as a family].

Perispyrida Haeckel, 1882: 443 [as a subfamily]; 1887: 1092, 1095 [as a subfamily].

Triostephanida Haeckel, 1882: 445 [as a subfamily].

Circospyrida Haeckel, 1882: 443 [*nomen dubium*, as a tribe]; 1887: 1024, 1072.

Eucoronida Haeckel, 1882: 445 [as a tribe]; 1887: 970, 976 [as a subfamily].

Trissocyclida Haeckel, 1882: 446 [as a tribe]; 1887: 970, 982 [as a subfamily].

Monostephida Haeckel, 1882: 447 [*nomen dubium*, as a subfamily].

Tympanida Haeckel, 1887: 937, 987-991 [as a family]. — Bütschli 1889: 1978 [as a family]. — *nec* Rüst 1892: 177 [as a family]. — Anderson 1983: 29 [as a family].

Semantida Haeckel, 1887: 937, 953-956 [as a family]. — Bütschli 1889: 1977 [as a family]. — Anderson 1983: 29 [as a family].

Coronida Haeckel, 1887: 937, 967-970 [as a family]. — Bütschli 1889: 1977 [as a family]. — *nec* Rüst 1892: 176. — Anderson 1983: 29 [as a family].

Lithocircida Haeckel, 1887: 940 [as a subfamily].

Cortiniscida Haeckel, 1887: 956 [as a subfamily].

Protympanida Haeckel, 1887: 990, 991 [*nomen dubium*, as a subfamily].

Semantidae – Popofsky 1908: 267; Popofsky 1913: 297. — Schröder 1914: 87-88. — Clark & Campbell 1945: 29. — Chediya 1959: 169. — Cachon & Cachon 1985: 292.

Tympanidiidae [*sic*] – Poche 1913: 219 (= Tympaniidae).

Coronidiidae – Poche 1913: 219.

Semantididae [*sic*] – Poche 1913: 219 (= Semantidae). — Campbell 1954: D106. — Tan & Tchang 1976: 270. — Chen & Tan 1996: 152. — Tan & Chen 1999: 271. — Tan & Su 2003: 85.

Coronidae [*sic*] – Popofsky 1913: 300 (= Coronidiidae). — Schröder 1914: 87. — Chediya 1959: 171. — Tan & Tchang 1976: 270. — Cachon & Cachon 1985: 292.

Tympanidae – Popofsky 1913: 301. — Schröder 1914: 87. — Chediya 1959: 173. — Cachon & Cachon 1985: 292-293.

Acanthodesmiidae – Campbell 1954: D106. — Riedel 1967b: 296; 1971: 656. — Riedel & Sanfilippo 1970: 523; 1971: 1590. — Petrushevskaya 1971a: 260; 1971b: 990; 1981: 353-354. — Dumitrica 1973a: 840; 1979: 35. — Petrushevskaya & Kozlova 1972: 532-533. — Sanfilippo & Riedel 1973: 526. — Nakaseko *et al.* 1975: 173. — Nishimura 1990: 116, 118 (*sensu* emend.). — Takahashi 1991: 101. — van de Paverd 1995: 200-201. — Anderson *et al.* 2002: 1017. — De Wever *et al.* 2001: 230, 232. — Afanasieva *et al.* 2005: S305. — Afanasieva & Amon 2006: 155.

Lithocircinae – Campbell 1954: D106.

Semantidinae [*sic*] – Campbell 1954: D106 (= Semantinae).

Cortiniscinae – Campbell 1954: D106. — Chediya 1959: 170.

Acanthodesmiinae – Campbell 1954: D106-107. — Petrushevskaya 1981: 356-357. — Afanasieva *et al.* 2005: S305-306. — Afanasieva & Amon 2006: 156-157.

Eucoronidinae – Campbell 1954: D108.

Trissocyclinae – Campbell 1954: D108. — Chediya 1959: 172.

Protympaniinae – Campbell 1954: D108 [*nomen dubium*].

Perispyridinae – Campbell 1954: D116 (not from the Mesozoic *Perispyridium*). — Petrushevskaya 1981: 354. — Afanasieva *et al.* 2005: S305. — Afanasieva & Amon 2006: 155.

Circospyridinae – Campbell 1954: D114 [*nomen dubium*]. — Petrushevskaya 1981: 364-366. — Afanasieva *et al.* 2005: S305. — Afanasieva & Amon 2006: 155.

Lithocyrtinae [*sic*] – Chediya 1959: 168 (= Lithocircinae).

Acanthodesminae [*sic*] – Chediya 1959: 171 (= Acanthodesmiinae).

Eucoroninae [*sic*] – Chediya 1959: 172 (= Eucoronidinae).

Protympaninae [*sic*] – Chediya 1959: 173 [*nomen dubium*] (= Protympaniinae).

Circospyrinae [*sic*] – Chediya 1959: 181 [*nomen dubium*] (= Circospyridinae).

Perispyrinae [*sic*] – Chediya 1959: 184 (= Perispyridinae). — Tan & Su 1982: 166.

Trissocyclidae – Goll 1968: 1416-1417 (*sensu* emend.). — Hollis 1997: 83.

Spyridae [*sic*] – Boltovskoy 1998: 33 [*nomen nudum*] (= Spyrididae).

Type genus. — *Acanthodesmia* Müller, 1856: 485 [type species by subsequent designation (Campbell 1954: D107): *Lithocircus vinculatus* Müller, 1856: 484].

Included genera. — *Acanthodesmia* Müller, 1856: 485 (= *Acanthostephanus* **n. syn.**, *Octotympanum* **n. syn.**, *Tristephaniscus* **n. syn.**, *Tristephanium* **n. syn.**, *Triostephus* **n. syn.**, *Tympanura* **n. syn.**, *Zygostephus* **n. syn.**, *Zygostephanus* **n. syn.**; *Tympanium* synonymized by Nigrini & Lombari 1984: N75; *Lithocoronis* synonymized by Petrushevskaya 1971a: 274). — *Dictyospyris* Ehrenberg, 1846: 385 (= *Dictyospyrissa* synonymized by Petrushevskaya 1971a: 267; ? *Dictyospyrantha* **n. syn.**; *Dictyospyrella* synonymized by Kozlova 1999: 164). — *Eucoronis* Haeckel, 1882: 445 (= *Acrocoronis* with the same type species; *Acrocubus*, *Apocubus*, synonymized by Petrushevskaya 1971a: 267; *Coronidium* synonymized by Petrushevskaya 1981: 358). — *Lithocircus* Müller, 1856: 484 (= *Archicircus*, *Archistephus*, synonymized by Petrushevskaya 1971a: 269). — *Lithocubus* Haeckel, 1882: 446. — *Lithotympanium* Haeckel, 1882: 447. — *Semantis* Haeckel, 1887: 956 (= *Cortiniscus* **n. syn.**). — *Tricolospyris* Haeckel, 1882: 443 (= *Perispyris* **n. syn.**). — *Trissocyclus* Haeckel, 1882: 446 (= *Tricyclarium* with the same type species; *Tricirconium* **n. syn.**, *Tricyclonium* **n. syn.**; *Tricircarium*, *Trissocircus*, *Zygostephanium*, synonymized by Petrushevskaya & Kozlova 1972: 533). — *Tympanomma* Haeckel, 1887: 1004.

Nomina dubia. — *Circospyris*, *Dendrocircus*, *Dictyospyromma*, *Dipocoronis*, *Dipocubus*, *Hexacoronis*, *Monostephus*, *Plectocoronis*, *Podocoronis*, *Prismatium*, *Stephaniscus*, *Stephanolithis*, *Stylocoronis*, *Tetracoronis*, *Tetracubus*, *Tripocoronis*, *Tripocubus*, *Tympaniscus*, *Zygostephaniscus*.

Invalid name. — *Lithotympanum*, *Tympanidium*.

Diagnosis. — Acanthodesmiidae formed by a sagittal ring with twin cupola or twin set of body frames. The Lo-axis is parallel to Lg-axis while the Sh-axis is parallel to the Sg-axis. No significant skeleton developed below the basal ring. The basal ring is constructed of two to six basal pores. The endoplasm is situated within the space encapsulated by the sagittal ring. The space of the cupola is occupied by algal symbionts.

Stratigraphic occurrence. — Middle Paleocene-Living.

Remarks

This family is probably an artificial group. The very young form of *Lithocircus* closely resemble *Zygocircus* (Stephaniidae) but the former is considered to be a young stage of some acanthodesmioid genera. This family is distinguishable from the Cephalospyrididae by the presence of a significant skeleton below the basal ring and from the Paradictyidae in the Lo-axis parallel to the Sg-axis but not to Lg-axis. Living appearance and cytological ultrafine structure were illustrated in *Acanthodesmia* (Anderson 1983: fig. 1.2.C; Cachon & Cachon 1985: fig. 53.b; Matsuoka 1993a; fig. 2.9; 2017: fig. 16; Sugiyama & Anderson 1998b; Suzuki & Aita 2011: fig. 5.K; Suzuki & Not 2015; fig. 8.11.2; Matsuoka *et al.* 2017: Appendix B; Zhang *et al.* 2018: 10, figs 2.40-2.45, pl. 15, figs 4.22, 4.26) and *Lithocircus* (Probert *et al.* 2014: S2, VEPO-10). Algal symbionts of Acanthodesmia were identified as *Gymnoxanthella radiolariae*, the same dinoflagellate species as those of *Dictyocoryne elegans* (Euchitoniidae, Spumellaria) and *Dictyopodium* (originally *Pterocanium*, Lithochytrididae, Nassellaria in Yuasa *et al.* 2016). Meanwhile, algal symbionts of *Lithocircus* were identified as *Brandtodinium nutricula* by Probert *et al.* (2014).

Validity of genera

Acanthodesmia

The following combination has the same type species, respectively: *Tristephanium* and *Triostephus*; *Tympanium*, *Tympanidium* and *Tympanura*; and *Zygostephanus* and *Zygostephus*. The genera synonymized in this paper were classified into two families by Campbell (1954): "Acanthodesmidae" whose skeleton is formed by one sagittal ring (D-ring), a horizontal basal ring, and a well-developed vertical meridian ring (Campbell 1954: D106) and "Paratympanidae" whose skeleton is composed of one sagittal ring (D-ring), a horizontal basal ring, and two parallel vertical meridian rings (Campbell 1954: D108). The former is "twin *q*-ring" and the latter is "twin *z*-ring" parallel to "twin *q*-ring" in the sense of Petrushevskaya (1969: fig. 1.7). Both "family" specimens are actually found at least in the northeastern Indian Ocean (confirmed by Zhang Lanlan & Suzuki Noritoshi in the same slides). These specimens cannot be differentiated even at specific level by any other characters except by the number of vertical meridian rings. In consideration of this situation, the number of parallel vertical meridian rings is not applicable at not only a family level but also at genus level. These families are subdivided into several subfamilies by the number of gates (opening) in Campbell (1954). The definition of a "gate" is unclear because it is not defined by geometric rules. For example, *Acanthodesmia* belongs to the "Acanthodesmiinae" which are defined as having "*five large gates, or openings, between rings*" (Campbell 1954: D106), but as for the number of openings following geometric rules, *Acanthodesmia* has eight openings (not explained in detail here). According to Campbell (1954: D107-108), *Acanthodesmia* is characterized by partly latticed gates and *Lithocoronis* by armed rings with arborescent spines. The description of "partly latticed gates" in *Acanthodesmia* is wrong because the type-illustration has no latticed parts (Müller 1859b: pl. 1, fig. 7). A "Partly latticed gate" is visible in well-preserved fully-grown specimens. The genus name *Acanthostephanus* seems to appear only in the first description of Haeckel (1879: 705) and its type species is marked by thorny rings. There are many intermediate forms between *Acanthodesmia* through *Acanthostephanus* to *Lithocoronis* in same samples, suggesting ontogenetic variations. High variety in *Acanthodesmia* has already been commented by Petrushevskaya (1971a: 274). *Triostephus* is characterized by a sagittal ring (D-ring) and frontal rings (twin *q*-ring) of different sizes and forms whereas *Tristephaniscus* by a D-ring and twin *q*-rings alike (Campbell 1954: D108). Different shape and size between D-ring and twin *q*-ring depends highly on species, so it cannot be applied for genus criteria. The type-illustration of *Tristephus* (Haeckel 1887: pl. 93, fig. 9) is similar to that of *Acanthostephanus* (Haeckel 1879: pl. 16, fig. 7) with thorny rings but their differences are the presence of a twin *a-f* ring which is parallel to the basal ring and several feet on *Tristephus*. As shown in the support image for *Acanthostephanus*, the development of feet are intra- or infra-species variations. Several specimens display incomplete *a-f* ring and, thus, some species can present *Acanthostephanus*-forms to *Tristephus*-forms. This means that it is not necessary to separate *Tristephus* from *Acanthostephanus*. *Zygostephanus* is marked by a vertical ring without a sagittal constriction (Campbell 1954: D108). The meaning of "without sagittal constriction" is not understandable because no sagittal constrictions on vertical rings (in this case, D-ring and twin *q*-ring) are observed in *Acanthodesmia* (support image for *Acanthodesmia* in the Atlas). The type-illustration of *Zygostephanus muelleri*, the type species of *Zygostephanus* (Haeckel 1862: pl. 12, fig. 2), looks to lack a basal ring. As like the support image for *Acanthodesmia* in the Atlas, the basal ring is easily overlooked without special care. *Octotympanum* and *Tympanium* are characterized by the presence of parallel twin *q*-rings and twin *z*-rings forementioned because they were classified in the "Paratympanidae". According to Campbell (1954: D108), *Octotympanum* is marked by incomplete equatorial rings but this characteristic is meaningless for any identification even at species level due to differences in the ontogenetic growth. The type-illustrations of *Tympanium* as well as *Octotympanum* are nearly identical to the type-illustration of *Lithocoronis* within species or at species level, except for the presence/absence of twin *z*-rings. The basal ring has two or four polygonal pores depending on the development stage of doble l-rod (Goll 1972a: pl. 63, fig. 2 for two basal pores-type; Goll 1969: pl. 60, fig. 3 for four basal pores-type). The two basal pores type has two unified *Ca*- and *Cerv*-pores and the four basal pore type has very large twin *Ca*-pores and small twin *Cerv*-pores. *J*-pore is unknown. All the genera listed here are synonymized here like this way. The oldest available name *Acanthodesmia* is validated.

Dictyospyris

All the genera synonymized here belonged to the "Circospyridinae" *sensu* Campbell (1954: D114) but this diagnosis is too incomplete to permit to precisely identify them. Real type specimens for *Dictyospyris*, *Dictyospyrella* and *Dictyospyrissa* were re-discovered in the Ehrenberg collection (Ogane *et al.* 2009b: pl. 9, figs 2a, 2b for *Dictyospyris* [as a topotype], pl. 75, figs 3b, 3c for *Dictyospyrella*, and pl. 38, figs 1a, 1b for *Dictyospyrissa*). Lack of basal feet is a distinguishing character for the "Circospyridinae" according to Campbell (1954), but the most important common structure in them are the presence of a latticed cephalic wall with small pores and the absence of any spines derived from the initial spicule system. The basal ring of *Dictyospyrella* in the lectotype (Ogane *et al.* 2009b: pl. 75, figs 3b, 3c) comprises three large pores (twin *Ca*-pores and a unified *Cerv*-pore) and two tiny pores (twin *J*-pores). The drawing of *Dictyospyris fenestra* by Ehrenberg (1876: pl. 19, fig. 11), the type species of *Dictyospyrissa*, looks as having four large basal pores. The real specimen of the Ehrenberg's drawing shown in Ogane *et al.* (2009b: pl. 38, figs 1a, 1b) first confirmed that this specimen is obliquely oriented in the microscopic slide. Referred to the lectotype photo, these four large pores correspond to twin *J*-pores for the upper pores and twin *Ca*-pores for the lower pores. The *Cerv*-pores are invisible in the lectotype but the support image for *Dictyospyrissa* displays a unified *Cerv* pore in the lower side of two photos. The topotype of *Dictyospyris trilobata* (Ogane *et al.* 2009b: pl. 9, figs 2a, 2b), the type species of *Dictyospyris*, looks to have 3 large basal pores which correspond to twin *Ca*-pores and a unified *Cerv*-pore. Probable tiny twin *J*-pores are visible in the lower side of the specimen in the lower photo of the support image for *Dictyospyris*. These observations permit to conclude that *Dictyospyris* has five basal pores composed of large twin *Ca*-pores, a small to large unified *Cerv*-pore and small to large twin *J*-pores. If the unified *Cerv*-pore is large, the double *J*-pores are small. By contrast, if the unified *Cerv*-pore is small, the twin *J*-pore is large. Due to this pattern, the number of large basal pores changed as three or four among them. Large variation is only recognized in basal rings.

The type-illustration of *Dictyospyris stalactites* (Haeckel 1887: pl. 89, fig. 7), the type species of *Dictyospyrantha*, surely fits to the description of this genus as well as the diagnosis of "Circospyridinae" *sensu* Campbell (1954). A probable *Dictyospyrantha* specimen is illustrated by Goll (1968: pl. 173, figs 21-24; 1972b: pls 73-74). Four basal pores are present with relatively large twin *Ca*-pores besides MB and relatively smaller unified *Cerv*-pores besides the V-rod. A unified *J*-pore is large and placed on the dorsal side of the test. In consideration of this basal pore pattern *Dictyospyris* and *Dictyospyrantha* may be different genera, but there is no time possibility to fix a much better position of *Dictyospyrantha* in this Atlas. According to Campbell (1954: D114), *Dictyospyris*, *Dictyospyrissa* and *Dictyospyrella* are respectively characterized by a basal ring with four-heart shaped basal pores, four large basal pores and three large basal pores. Under the current taxonomic system for Nassellaria (De Wever *et al.* 2001), it is impossible to synonymize genera with different numbers of basal pores on the basal ring. On the other hand, if this variation is plausible, *Dictyospyris*, *Dictyospyrissa* and *Dictyospyrella* can be synonymized as a single genus. The oldest available name is *Dictyospyris* among them including *Dictyospyrantha*.

Eucoronis

The combination of *Eucoronis* and *Acrocoronis* and that of *Acrocubus* and *Apocubus* have respectively the same type species. As *Acanthodesmia*, the genera synonymized here are classified into the "Acanthodesmiidae" (*Coronidium*, *Eucoronis*) and the "Paratympanidae" (*Acrocubus*) *sensu* Campbell (1954: D107-108). The "Paratympanidae" are defined by two parallel rings but the reliability of the type-illustration for *Acrocubus* is suspected. Referred to real specimens and following the terminology in the remarks of the Acanthodesmioidea, the type-illustration of *Eucoronis* is a view from the lateral plane (Lt-plane) (Haeckel 1887: pl. 82, fig. 6; the support image for *Eucoronis* in the Atlas) and the type-illustration of *Coronidium* is a view from the supra side of the equatorial plane (Eq-plane). The support image for *Coronidium* in the Atlas is a view from the inferior side of the Eq-plane. The referable images shown in Goll (1968: pl. 175, figs 4, 5, 8, 9, pl. 176, figs 8, 10, 12; 1972a: pl. 69, fig. 3) display four basal pores in the basal ring. Four basal pores comprise relatively small twin *Cerv*-pores and very large twin *Ca*-pores. A tiny twin *J*-pore is placed on the lateral side of the shell. The principle of these basal pores is common for both *Acanthodesmia* and *Dictyospyris*. Campbell (1954) characterized *Coronidium* by four open lateral gates, *Eucoronis* by six large gates, absence of large basal feet, simple gates and armed rings with short thorns, and *Acrocubus* by lack of an equatorial ring and basal ring without feet. All these diagnoses, whoever, are helpless to characterize this genus. *Eucoronis*, *Acrocoronis* and *Acrocubus* were simultaneously published in Haeckel (1882: 445, 445 and 446 in ascending order). In respect to the first revision by Petrushevskaya (1971a: 267), *Eucoronis* is validated here. The relationships among *Eucoronis*, *Trissocyclus* and *Tympanomma* need more studies.

Lithocircus

Archistephus has the same type species as *Archicircus*. *Archicircus* has already been synonymized with *Lithocircus* by Petrushevskaya (1971a: 269), but this genus is mixed with juvenile forms of *Acanthodesmia*, *Semantis*, *Tricolospyris* (Acanthodesmiidae), *Zygocircus* (Stephaniidae) and many genera of the Cephalospyrididae. It is practically impossible to differentiate a true *Lithocircus* from a young form of some Acanthodesmioidea.

Semantis

Both *Semantis* and *Cortiniscus* were classified in the "Semantididae" whose skeleton is composed of a vertical sagittal and a horizontal basal ring (Campbell 1954: D106). They are mixed with not only the true *Semantis* and *Cortiniscus* but also with young forms of some Acanthodesmioidea. This definition is not based on basal pore patterns and construction of the initial spicular system. As a strict differentiation at genus level based on these characters will need more time, we simply synonymized both these genera for a practical usage. These two genera were simultaneously published in Haeckel (1887: 956 for *Semantis* and 963 for *Cortiniscus*). *Semantis* is validated among them in consideration of realistic type specimen images (Haeckel 1887: pl. 92, fig. 2).

Tricolospyris

Campbell (1954: D116) characterized *Tricolospyris* as "lattice complete on all sides, otherwise like *Perispyris*". The "complete lattice" is obviously the supplemental skeletal part by secondary growth mode defined in Ogane *et al.* (2009c). The basal pore parallel to the equatorial plane is two basal pores (Goll 1972b: pl. 1, figs 4, 5, pl. 3, fig. 1, pl. 4, fig. 3, pl. 6, fig. 4, pl. 7, fig. 4, pl. 9, fig. 12). These two basal pores are very large: the Japanese rice spatula-shaped twin *Ca*-pore. The large twin *Cerv*-pore is also visible at an oblique angle from the inferior view (the basal view). The large twin *J*-pore is also present at an oblique angle from the basal view. The presence of robust double *l*- and *L*-rods to form twin *Ca*-pores is common with *Ceratospyris*, suggesting phylogenetic relationships. *Tricolospyris* and *Perispyris* were simultaneously published in Haeckel (1882: 443 for both genera). *Tricolospyris* is selected here as a valid name because real specimens are recognized within this genus.

Trissocyclus

The combinations of *Trissocyclus* and *Tricyclarium* and that of *Trissocircus* and *Tricircarium* have respectively the same type species. The genera synonymized here are classified into the "Zygostephaninae" (*Zygostephanium*) with four lateral gates and the "Trissocyclinae" (*Trissocyclus*, *Tricyclonium*, *Trissocircus*, *Tricirconium*) with eight large gates in Campbell (1954: D108). The differences among the four genera in "Trissocyclinae" are the relative size differences of the sagittal rings (D-ring), the simplicity of the "gates" and the latticed conditions. According to Campbell (1954), *Trissocyclus* and *Tricyclonium* are different from *Trissocircus* and *Tricirconium*, the latter having simple gates. However, no obvious differences are recognizable in the type-illustrations of these four genera. Referred to the relative size differences of the sagittal ring, the combination of *Trissocyclus* and *Trissocircus* and that of *Tricyclonium* and *Tricirconium* are indicate their respective synonymy. Real specimens of *Trissocyclus* are commonly found but any real specimens identifiable as *Tricyclonium* or *Tricirconium* have not been encountered so far. As in previous genera, the difference between *Trissocyclus* and *Tricyclonium* being only the relative difference in size of their sagittal ring, we synonymize all these four genera until real *Tricyclonium* or *Tricirconium* representatives can be illustrated. The basal ring illustrated by Goll (1968: pl. 175, figs 1-5, 7-9) shows four pores which comprise larger rectangle twin *Ca*-pores and small elliptical twin *Cerv*-pores. *J*-pores are unknown. *Zygostephanium* is considered to have four lateral gates but not eight. We suspect an incorrect recognition of the number of gates so that this genus is also synonymized with the remaining genera until a new study can be conducted. Two oldest available names were simultaneously published in Haeckel (1882: 446 for *Trissocyclus* and *Trissocircus*). As real specimens are found for *Trissocyclus stauroporus*, *Trissocyclus* is validated.

Family Cephalospyrididae Haeckel, 1882 n. stat.

Cephalospyrida Haeckel, 1882: 441 [as a tribe].

Archiphatnida Haeckel, 1882: 429 [*nomen dubium*, as a tribe].

Acrospyrida Haeckel, 1882: 441 [as a tribe]; 1887: 1085 [as a subfamily].

Brachiospyrida Haeckel, 1882: 441 [as a tribe].

Dipodospyrida Haeckel, 1882: 441 [*nomen dubium*, as a tribe].

Triospyrida Haeckel, 1882: 441 [*nomen dubium*, as a subfamily].

Taurospyrida Haeckel, 1882: 442 [as a tribe].

Aegospyrida Haeckel, 1882: 442 [*nomen dubium*, as a tribe].

Phormospyrida Haeckel, 1882: 442 [as a tribe]; Haeckel 1887: 1021 1084-1085 [as a family]. — Bütschli 1889: 1981 [as a family]. — Anderson 1983: 29 [as a family].

Polyspyrida Haeckel, 1882: 442 [*nomen dubium*, as a subfamily]; Haeckel 1887: 1024, 1059 [as a subfamily].

Tetraspyrida Haeckel, 1882: 442 [*nomen dubium*, as a subfamily]; Haeckel 1887: 1024, 1043 [as a subfamily].

Therospyrida Haeckel, 1882: 442 [*nomen dubium*, as a tribe]; Haeckel 1887: 1024, 1055 [as a subfamily].

Gorgospyrida Haeckel, 1882: 443 [as a tribe].

Petalospyrida Haeckel, 1882: 443 [as a tribe].

Zygostephanida Haeckel, 1882: 446 [*nomen dubium*, as a tribe]; Haeckel 1887: 970 [as a subfamily].

Semantiscida Haeckel, 1887: 956 [*nomen dubium*, as a subfamily].

Tholospyrida Haeckel, 1887: 1021, 1077-1078 [as a family]. — Bütschli 1889: 1981 [as a family]. — Anderson 1983: 29 [as a family].

Zygospyrida Haeckel, 1887: 1021, 1022-1024 [*nomen dubium*, as a family]. — Bütschli 1889: 1980 [as a family]. — Anderson 1983: 29 [as a family].

Dipospyrida Haeckel, 1887: 1024, 1035 [*nomen dubium*, as a subfamily].

Hexaspyrida Haeckel, 1887: 1024, 1046 [*nomen dubium*, as a subfamily].

Lophospyrida Haeckel, 1887: 1078 [as a subfamily].

Tiarospyrida Haeckel, 1887: 1078 [as a subfamily].

Pylospyrida Haeckel, 1887: 1078 [*nomen dubium*, as a subfamily].

Rhodospyrida Haeckel, 1887: 1085, 1087 [as a subfamily].

Androspyrida Haeckel, 1887: 1090-1092 [as a family]. — Bütschli 1889: 1982 [as a family]. — Anderson 1983: 29 [as a family].

Lamprospyrida Haeckel, 1887: 1092 [as a subfamily].

Archiphaenida Haeckel, 1887: 1133, 1158, 1173 [*nomen dubium*, as a subfamily].

Tholospyriden – Haecker 1907: 123-124 [as a family].

Phormospyriden – Haecker 1907: 124 [as a family].

Zygospyridae [*sic*] – Haecker 1908: 445 [*nomen dubium*] (= Zygospyrididae). — Popofsky 1908: 269; 1913: 304. — Schröder 1914: 142. — Clark & Campbell 1942: 53; 1945: 29. — Campbell & Clark 1944a: 33; 1944b: 21. — Chediya 1959: 177. — Tan & Su 1982: 164. — Chen & Tan 1996: 152. — Tan & Chen 1999: 272. — Tan & Su 2003: 86. — Chen *et al.* 2017: 167.

Phormospyridae [*sic*] – Haecker 1908: 446 (= Phormospyrididae). — Popofsky 1913: 310. — Chediya 1959: 183. — Cachon & Cachon 1985: 293. — Chen & Tan 1996: 152. — Tan & Su 2003: 97.

Rhodospyrinae [*sic*] – Haecker 1908: 446 (= Rhodospyridinae). — Chediya 1959: 183.

Androspyridae [*sic*] – Popofsky 1908: 270 (= Androspyrididae); Popofsky 1913: 311. — Chediya 1959: 184. — Tan & Su 1982: 166. — Cachon & Cachon 1985: 293. — Chen & Tan 1996: 152. — Tan & Chen 1999: 278. — Tan & Su 2003: 99.

Tholospyridae [*sic*] – Popofsky 1908: 270 (= Tholospyrididae); Popofsky 1913: 309. — Tan & Su 1982: 165. — Cachon & Cachon 1985: 293. — Chen & Tan 1996: 152. — Tan & Su 2003: 92. — Chen *et al.* 2017: 170.

Zygospyrididae – Poche 1913: 221 [*nomen dubium*].

Tholospyrididae – Poche 1913: 221. — Campbell 1954: D114.

Androspyrididae – Poche 1913: 221. — Campbell 1954: D116.

Cyrtostephanidae Popofsky, 1913: 288-289. — Campbell 1954: D106.

Dipospyrinae [*sic*] – Clark & Campbell 1942: 55 [*nomen dubium*] (= Dipospyridinae). — Chediya 1959: 177.

Tetraspyrinae [*sic*] – Clark & Campbell 1942: 55 [*nomen dubium*] (= Tetraspyridinae). — Chediya 1959: 178.

Hexaspyrinae [*sic*] – Clark & Campbell 1942: 56 [*nomen dubium*] (= Hexaspyridinae); Clark & Campbell 1945: 31. — Chediya 1959: 179.

Therospyrinae [*sic*] – Clark & Campbell 1942: 58 [*nomen dubium*] (= Theospyridinae). — Chediya 1959: 180.

Polyspyrinae [*sic*] – Clark & Campbell 1942: 59 (= Polyspyridinae). — Campbell & Clark 1944a: 36. — Clark & Campbell 1945: 33. — Chediya 1959: 181.

Semantiscinae – Clark & Campbell 1945: 29 [*nomen dubium*]. — Chediya 1959: 169.

Triospyridae [*sic*] – Frizzell & Middour 1951: 27-28 [*nomen dubium*] (= Triospyrididae). — Petrushevskaya & Kozlova 1972: 529.

Dipodospyrinae [*sic*] – Frizzell & Middour 1951: 28 [*nomen dubium*] (= Dipospyridinae).

Zygostephaninae – Campbell 1954: D108 [*nomen dubium*]. — Chediya 1959: 171.

Dipodospyridinae [*sic*] – Campbell 1954: D112 [*nomen dubium*] (= Dipodospyridinae). — Petrushevskaya 1981: 341-342. — Afanasieva *et al.* 2005: S304. — Afanasieva & Amon 2006: 154.

Tetrarrhabdinae Campbell, 1954: D112 [*nomen dubium*].

Tripospyrididae – Campbell 1954: D112 [*nomen dubium*]. — Blueford 1988: 242.

Hexaspyridinae – Campbell 1954: D113 [*nomen dubium*].

Petalospyridinae Campbell, 1954: D114.

Therospyridinae – Campbell 1954: D114 [*nomen dubium*].

Androspyridinae – Campbell 1954: D116. — Petrushevskaya 1981: 350-351. — Afanasieva *et al.* 2005: S305. — Afanasieva & Amon 2006: 155.

Phormospyrididae – Campbell 1954: D116.

Phormospyridinae – Campbell 1954: D116.

Rhodospyridinae – Campbell 1954: D116.

Tiarospyridinae – Campbell 1954: D116.

Spyridobotryidinae Campbell, 1954: D116 [*nomen dubium*].

Archiphatninae – Campbell 1954: D119 [*nomen dubium*].

Tholocpyridae [*sic*] – Chediya 1959: 182 (= Tholospyrididae).

Lamprospyrinae [*sic*] – Chediya 1959: 184 (= Lamprospyridinae).

Archiphaeninae – Chediya 1959: 196 [*nomen dubium*].

Triospyrididae – Petrushevskaya 1971a: 243-251 [*nomen dubium*] (*sensu* emend.); 1971b: 990; 1981: 328-329. — Kozlova 1999: 162. — De Wever *et al.* 2001: 229-230. — Afanasieva *et al.* 2005: S304. — Afanasieva & Amon 2006: 154. — Matsuzaki *et al.* 2015: 39.

Triospyrididinae – Petrushevskaya 1981: 330 [*nomen dubium*].

Tholospyridinae – Petrushevskaya 1981: 347. — Afanasieva *et al.* 2005: S304. — Afanasieva & Amon 2006: 154.

Zygosmyridae [*sic*] – Cachon & Cachon 1985: 293 [*nomen dubium*] (= Zygospyrididae).

Triospyridinae – Afanasieva *et al.* 2005: S304 [*nomen dubium*]. — Afanasieva & Amon 2006: 154.

Type genus. — *Cephalospyris* Haeckel, 1882: 441 [type species by subsequent designation (Campbell 1954: D112): *Cephalospyris cancellata* Haeckel, 1887: 1035] = junior subjective synonym of *Platybursa* Haeckel, 1882: 429 [type species by subsequent monotypy: *Cantharospyris platybursa* Haeckel, 1887: 1051].

Included genera. — *Androspyris* Haeckel, 1887: 1092. — *Ceratospyris* Ehrenberg, 1846: 385 (= *Liriocyrtis* synonymized by Matsuzaki *et al.* 2015: 41). — *Corythospyris* Haeckel, 1882: 443. — *Dendrospyris* Haeckel, 1882: 441. — *Desmospyris* Haeckel, 1882: 443 (= *Phormospyris* synonymized by Caulet 1979: 136). — *Dorcadospyris* Haeckel, 1882: 441 (= *Brachiospyris*, *Gamospyris* synonymized by Petrushevskaya & Kozlova 1972: 532). — *Elaphospyris* Haeckel, 1882: 442 (= *Giraffospyris* with the same type species). — *Gorgospyris* Haeckel, 1882: 443 (= *Gorgospyrium* with the same type species). — *Lamprospyris* Haeckel, 1882: 441 (= ? *Eulophospyris* **n. syn.**). — *Liriospyris* Haeckel, 1882: 443 (= *Petalospyromma* synonymized by Petrushevskaya 1981: 332). — *Lophospyris* Haeckel, 1882: 443 (*nec* Haeckel, 1887) (= ? *Semantrum* **n. syn.**). — *Pentaspyris* Haeckel, 1882: 442 (= *Taurospyris* **n. syn.**). — *Petalospyris* Ehrenberg, 1846: 385 (= *Anthospyris* **n. syn.**, *Rhodospyris* **n. syn.**, *Sepalospyris* **n. syn.**; *Patagospyris* synonymized by Ling 1975: 272; *Petalospyrantha*, *Petalospyrissa* synonymized by Petrushevskaya 1981: 335; *Petalospyrella* synonymized by Petrushevskaya & Kozlova 1972: 532). — *Platybursa* Haeckel, 1882: 429 (= *Cephalospyris*, *Cyrtostephanus* synonymized by Petrushevskaya 1971a: 257; *Clathrobursa* synonymized by Haeckel 1887: 1045; *Tessarospyris* synonymized by Petrushevskaya 1971a: 259). — *Thamnospyris* Haeckel, 1882: 443. — *Tholospyris* Haeckel, 1882: 441 (= *Tholospyrium* with the same type species; *Tholospyridium* **n. syn.**; *Tristylospyris, Tristylospyrula*, synonymized by De Wever *et al.* 2001: 230). — *Tiarospyris* Haeckel, 1882: 443. — *Triceraspyris* Haeckel, 1882: 441 (= *Acrospyris* **n. syn.**, *Tripospyrella* **n. syn.**; *Triospyrium* synonymized by Petrushevskaya 1971a: 248).

Invalid names. — *Archiphaena*, *Calpophaena*, *Coronophaena*, *Dipospyris*, *Pylospyris*, *Stephanophaena*, *Tripospyris*.

Nomina dubia. — *Acrocorona*, *Aegospyris*, *Archiphatna*, *Cantharospyris*, *Calpocapsa*, *Cladocorona*, *Cladophatna*, *Clathrocircus*, *Clathrospyris*, *Coronophatna*, *Dipodospyris*, *Hexaspyridium*, *Hexaspyris*, *Polyspyris, Semantidium*, *Semantiscus*, *Spyridobotrys*, *Stephanophatna*, *Stephanospyris*, *Tetrarhabda*, *Tetraspyris*, *Therospyris*, *Triospyridium*, *Triospyris*, *Tripodospyris*, *Tripospyrantha, Tripospyrissa*, *Tripospyromma*, *Zygospyris*.

Junior homonyms. — *Lophospyris* Haeckel, 1887 (= *Elaphospyris*) *nec* Haeckel, 1882; *Stephanospyris* Haeckel, 1882 (= *Dorcadospyris*) *nec* Haeckel, 1862.

Diagnosis. — Skeleton having a sagittal ring with twin cupolas or twin set of body frames. Two or more feet, a coronal skirt and/or a thorax are developed. In addition, the Lo-axis is parallel to the Lg-axis while the Sh-axis is parallel to the Sg-axis. The basal ring is marked by two to six basal pores. Protoplasm was identified in *Lophospyris*. A spherical endoplasm is located around the center of the sagittal ring while a brownish matter of unknown composition is aggregated below the spherical endoplasm and attached to the MB. Algal symbionts scattered in and out of the skeleton area. A gelatinous matter is found wrapping the endoplasm, the algal symbionts and the skeleton. The algal symbionts are scattered all over. Radiated pseudopodia are visible inside the gelatinous matter.

Stratigraphic occurrence. — Middle Paleocene-Living.

Remarks

The family name "Triospyridae" has been used hitherto but cannot be upheld as a practical valid status. This is due to the absence of an illustrated type species of *Triospyris*. Amongst the potential candidate for family-names in Haeckel (1882) (Acrospyrida, Brachiospyrida, Cephalospyrida, Phormospyrida, and Gorgospyrida) we retain Cephalospyrididae as a valid family name, considering the best figured and described specimen representing the type genus (*Cephalospyris cancellata* Haeckel, 1887). However, little is known about the basal pore patterns and the relationship of the feet with the cephalic initial spicular system. Thus, this family concept may be artificial. "Living" and protoplasm images are illustrated for *Lophospyris* (Krabberød *et al.* 2011: fig. 1.O; Matsuoka 2017: fig. 18; Zhang *et al.* 2018: 10, figs 2.12, 2.14-2.16) and *Platybursa* (Aita *et al.* 2009: pl. 32, fig. 7; Zhang *et al.* 2018: 10, fig. 2.20). *Ceratospyris* is known to be infected with Marine Alveolata Group I (Ikenoue *et al.* 2016). Evolution for *Dorcadospyris* was illustrated (Kling 1978: 238-239; Riedel & Sanfilippo 1981: fig. 12.9).

Validity of genera

Ceratospyris

The reason for a synonymy with *Liriocyrtis* is written in Matsuzaki *et al.* (2015: 41). The basal ring structure comprises four basal pores: large, long rectangle, twin *Ca*-pores and small twin *Cerv*-pores divided by the V-rod (Goll 1972a: pl. 50, figs 1-4). Twin *J*-pores are very large, developed on the lateral side of the lobate shell. This basal pore pattern is similar to that of *Dictyospyris*. Three feet are directly connected with D- and double L-rod. No downward rod below the V-rod.

Desmospyris

The basal ring of *Desmospyris* comprises five to six basal pores (Goll 1968: pl. 173, figs 12, 13, 20; Goll 1972a: pl. 53, figs 3, 4). The *J*-pore is subdivided as twin *J*-pores by the D-rod (Goll 1968: pl. 173, fig. 20) or a unified *J*-pore looks as two pores with a downwardly oriented D-rod (Goll 1968: pl. 173, fig. 13; Goll 1969: pl. 53, figs 3, 4). Other basal pores are the large twin *Ca*-pores and relatively large twin *Cerv*-pores. The type-illustration of *Phormospyris tricostata* (Haeckel 1887: pl. 83, fig. 15) looks "strange" but the most similar specimens to this species (Caulet 1979: pl. 5, fig. 2) show identical skeletal structures. *Desmospyris* and *Phormospyris* were simultaneously published in Haeckel (1882: 443 for the former and 442 for the latter). Although Caulet (1979) did not mention the synonymy between *Desmospyris* and *Phormospyris*, this paper applied the name *Desmospyris* for them, implying the first reviser's decision. The whole structure of *Thamnospyris* is similar to *Desmospyris* but they are not synonymized due to insufficient examination.

Dorcadospyris

The genera synonymized herein belonged to the "Diplospyridinae" *sensu* Campbell (1954: D112) which are defined by two lateral basal feet. *Brachiospyris* is marked by unbranched feet with lateral spines and no apical horn, *Dorcadospyris* by feet with lateral spines and a single apical horn and *Gamospyris* by two unbranched feet forming a ring and a single horn. Sanfilippo *et al.* (1985: fig. 10) illustrated these differences as an evolutionary change at species level. The basal ring structure shown in *Ceratospyris ocellata*, the type species of *Brachiospyris*, drawn by Ehrenberg (1876: pl. 20, fig. 5) is not precise when referred to the real sketch of this specimen in the Ehrenberg collection (Ogane *et al.* 2009b: pl. 77, figs 4a-c). Petrushevskaya (1981: fig. 531) illustrated four basal pores in the basal ring. The basal pore consists of a unified *J*-pore, twin *Ca*-pores and a unified *Cerv*-pore. Two feet do not directly connect with any initial spicular system. *Dorcadospyris* in the sense of Sanfilippo *et al.* (1985) includes species with three feet. The basal ring of *Dorcadospyris* with three feet is also illustrated in Petrushevskaya (1981: fig. 533). Differing from the species with two feet, the basal ring comprises five pores: a tiny twin *J*-pore, a large twin *Ca*-pore and a relatively larger unified *Cerv*-pore (Goll 1972a: pl. 62, fig. 3). The third foot is directly connected with the D-rod. It is unclear whether the difference of *J*-pore related with the presence of the third feet from the D-rod has a value as genus criteria or not. *Dorcadospyris*, *Brachiospyris* and *Gamospyris* were simultaneously published in Haeckel (1882: 441 for all genera). As *Dorcadospyris dentata*, the type species of *Dorcadospyris*, is commonly found, this genus name is selected as a valid name for them.

Elaphospyris

The basal ring is not part of the initial spicular system (Goll 1972a: pl. 47, figs 2-4), because MB is obviously above the basal ring. D-, V-, double L- and double l-rods are downwardly oriented to connect the basal ring. Six "pores" are visible but they are not the true basal pores and, thus, there are no *J*-, *Ca*- and *Cerv*-pores. D-rod only is directly connected with a basal foot and all the remaining feet are not directly connected with any initial part of the spicular system. Many papers applied the genus name *Giraffospyris* to several species, but this is taxonomically problematic. Both genera were erected the same year by Haeckel (1882: 442). The first reviser for sure is Campbell (1954: D114). This revision is however, erroneous (Nigrini, personal com.). As written in the Atlas, Campbell (1954: D114) erroneously considered *Elaphospyris* to be an objective synonym of *Giraffospyris*, and then he designated *Ceratospyris heptaceros* as the type species of *Giraffospyris* and only by inference of *Elaphospyris*. Therefore, we consider the type species designation of *Ceratospyris heptaceros* Ehrenberg to date from Chediya (1959: 180). It is clear if we check Haeckel (1887: 1056-1057) who erected the genus *Elaphospyris* with two subgenera *Elaphospyris* and *Corythospyris*.

Gorgospyris

The real specimens perfectly corresponding to the type-illustration of *Gorgospyris medusa* (Haeckel 1887: pl. 87, fig. 1), the type species of *Gorgospyris*, are rare (the support image for *Gorgospyris* in the Atlas). The basal ring structure in these specimens is different from that shown in Haeckel (1887: pl. 87, fig. 2). *Gorgospyris* is an available name older than *Gorgospyrium*.

Lamprospyris

The illustrated specimen of *Lamprospyris darwinii*, the type species of *Lamprospyris*, looks to have a free D-ring (sagittal ring) inside the cephalic lobe (Haeckel 1887: pl. 89, fig. 13). Real specimens identifiable as this species, however, have three feet which are directly connected with D- and double L-rods (the support image for *Lamprospyris*). *Lamprospyris* characteristically develops a latticed shell over the junction between the A-rod and the AV-arch. As this kind of lattice shell is rarely known in this family, *Elaphospyris* is synonymized with *Lamprospyris* herein. This synonymy needs to be confirmed in the future by an evolutionary connection between the type species of both these genera. *Lamprospyris* is an available name older than *Eulophospyris*.

Liriospyris

Goll (1968) identified his specimens as "*Liriospyris clathrata* (Ehrenberg)" (Goll 1968: pl. 175, figs 12, 13, 16, 17) but the specimen found in the Ehrenberg collection (Ogane *et al.* 2009b: pl. 38, figs 5a-c) is quite different from the drawing in Ehrenberg (1854c: pl. 36, fig. 25). The specimen shown in Ogane *et al.* (2009b) follows the indication by Ehrenberg himself so it is not possible to ignore this specimen. But this specimen is obviously different from the current usage of "*Liriospyris clathrata* (Ehrenberg)" and is also impossible to use for determining taxonomic morphological features. "*Liriospyris clathrata* (Ehrenberg)" is the type species of *Stephanospyris*. If this specimen is regarded as a valid name, *Stephanospyris* must be validated instead of *Liriospyris* because the former was published in Haeckel (1862: 295) while the latter in Haeckel (1882: 443). Real structure of *Liriospyris* can be understood from Goll (1968: pl. 175, figs 12, 13, 16, 17; 1969: pl. 57, figs 1-4). The basal ring comprises four basal pores: large twin *Ca*-pores and relatively larger twin *Cerv*-pores. A unified *J*-pore has a large size and is placed on the lateral side of the bilobate test. Four of six basal feet are directly connected with the double L-rod, the D-rod and an un-coded rod below the V-rod. The remaining two basal feet are present near the double l-rods but are not directly connected with them. The basal structure of *Petalospyromma* is shown in Goll (1969: pl. 57, figs 11, 12, 15-17). Differing from the basal structure of *Liriospyris*, the basal pores consist of two very large twin pores and tiny twin pores. As it is not possible to specify the D-rod and double *l*-rod from this sketch, the relevant code of *J*-, *Ca*- and *Cerv*-pores is not specified for them. *Petalospyromma* is tentatively synonymized with *Liriospyris* for a simple practical identification. *Liriospyris* is similar to *Ceratospyris*, but the former has small twin *Cerv*-pores and no un-coded downward rod below the V-rod. *Liriospyris* is an older available name than *Petalospyromma*.

Lophospyris

The basal ring of *Lophospyris* has two pores which are very large, polygonal, twin *Ca*-pores (Goll 1972a: pl. 58, figs 1-3). Both twin *J*-pores and twin *Cerv*-pores are also polygonal in shape, the former being placed on the dorsal lateral side of the test whereas the latter is placed on the ventral lateral side of the test. Goll (1976) has already proved that *Semantrum quadrifore*, the type species of *Semantrum*, is a young specimen of *Lophospyris* (Goll 1976: pl. 13, figs 5, 6). *Lophospyris* is an older available name than *Semantrum*.

Pentaspyris

No exactly fit specimen of *Pentaspyris* has ever been so far reported. The morphospecies most similar to *Pentaspyris* was illustrated as "*Lophospyris pentagona hyperborea*" by Goll (1976: pl. 15, figs 1-12). As Goll (1976) classified this morphotype as a subspecies of "*Lophospyris pentagona*", this morphotype has exactly the same basal ring structure as *Ceratospyris pentagona*, the type species of *Lophospyris* (Goll 1976: pl. 15, figs 3, 7). No *Taurospyris* specimens are also so far reported. The most similar morphotypes of *Taurospyris* were illustrated as "*Phormospyris stabilis capoi*" by Goll (1976: pl. 7, fig. 5) but the number of basal feet is quite different. Under such suspect conditions, both these genera are synonymized as to reduce the number of "un-realistic genera" from the valid genus list. *Pentaspyris* and *Taurospyris* were simultaneously established by Haeckel (1882: 442 for both genera). *Pentaspyris* is validated among them in consideration of its type-illustration more realistic than that of *Taurospyris*.

Petalospyris

The genera listed here are artificially synonymized for simplicity of practical identification. The basal structure of *Petalospyrissa* and *Petalospyrantha* is a basal ring which is not directly connected with the initial spicular system below MB (Goll 1968: pl. 174, figs 5-8, 10). They have six "openings" without any arches directly connected with any D-, V-, double L- and double l-rods, and subsequently have no *J*-, *Ca*- and *Cerv*-pores. This basal structure is similar to that of *Elaphospyris*. However, the basal structure in ? *Petalospyrella* (Goll 1969: pl. 56, figs 9-11) and *Patagospyris* (Goll 1969: pl. 58, fig. 11) has a basal ring directly connected with the initial spicular system. Their basal structure has three "large" basal pores with nearly the same size: the twin *Ca*-pores and a unified *Cerv*-pore. Tiny twin *J*-pores are also visible. Although all these genera synonymized here have many feet, none of these feet are directly connected with the initial spicular system. Although the *Petalospyrissa*-type basal structure is different from the *Patagospyris*-type one at genus or family level, it is practically impossible to apply this difference for real specimens with their current knowledge. Due to this reason, we prioritize a practical usage based on the similarity of the whole appearance until they are better studied in the future.

In the sense of Campbell (1954), all the genera with the exception of *Sepalospyris* belonged to the "Triospyrididae" whose shell is composed of a cephalis and its apophyses and no thorax (*Petalospyris*, *Petalospyrantha*, *Petalospyrella*, *Petalospyrissa* and *Anthospyris*) (Campbell 1954: D112) or to the "Phormospyrididae" which have a thorax (*Rhodospyris* and *Patagospyris*) (Campbell 1954: D116). These two "families" are differentiated by the presence/absence of a thorax. As there are many intermediate forms between them, this family criterion is not applicable for these genera. Regardless of different "families", the definition of subfamilies is the same among them (Campbell 1954: D112 for the "Petalospyridinae" and D116 for the "Rhodospyridinae"). The criterion for establishing a subfamily rank is also meaningless. The differences among *Petalospyris*, *Petalospyrella* and *Petalospyrissa* (Campbell 1954: D114) are based on the number of large basal pores on the basal ring. Since the number of basal pores has not yet been examined in the type species of all these genera, it is difficult to positively apply this criterion for the current taxonomy. The remaining character written in Campbell (1954) is the number of apical horns. One apical horn characterizes *Petalospyris*, *Petalospyrantha*, *Petalospyrella*, *Petalospyrissa* and *Patagospyris*. Three apical horns are found in *Anthospyris* and *Rhodospyris*. These genera can be divided into two groups but not in seven genera. It is not necessary to separate them by the number of apical horns. Differing from these genera, *Sepalospyris* has an apical cupola (Campbell 1954: D116). Although the presence of a cupola is not a sure criterion for genus or species definition, we synonymized this genus with *Petalospyris* because no real specimens identifiable as *Sepalospyris* have been found so far. The oldest available name among them is *Petalospyris*.

Platybursa

Clathrobursa has the same type species as *Tessarospyris*. *Cyrtostephanus* was classified into the "Cyrtostephanidae" of the superfamily "Stephaniicae" (Campbell 1954: D105-106). Following this classification, *Cyrtostephanus* is characterized by an incomplete ring, a latticed sagittal ring (D-ring) or a netlike fan of repeated anastomosed spines and a skeleton formed of a sagittal ring without a basal tripod. This definition, however, does not partly correspond to the type-illustration and the support image for *Cyrtostephanus* in the Atlas. The type-illustration (Popofsky 1913: pl. 28, figs 4, 5) is a basal view (a view from the bottom of the test) as the supra view (the apical view) is not known. The right photography of the support images for *Cyrtostephanus* in the Atlas appears to show an AV arch free in the latticed cephalic lobe. The remaining three genera belong to the "Triospyrididae" of the "superfamily Triospyridicae" whose shell is composed of a cephalis and its apophyses, a binocular cephalis with a sagittal constriction, the absence of an apical cupola or dome or thorax. All these characters, however, are not recognized as superfamily criteria by the molecular phylogeny results (Sandin *et al.* 2019). The three genera were classified into different three "subfamilies": the "Triospyridinae" with three basal feet for *Cephalospyris* (Campbell 1954: D112), the "Tetrarrhabdinae" with two lateral and two sagittal feet for *Tessarospyris* (Campbell 1954: D112), and the "Hexaspyridinae" with six basal feet for *Platybursa* (Campbell 1954: D114). These subfamily criteria are suspect because of the indistinguishable robustness of the feet and lengths among them. Real specimens of these type species (support images for *Platybursa*, *Cephalospyris* and *Clathrobursa* in the Atlas) seem to have less numbers or more numbers of "basal feet". If this subfamily criterion would be accepted for these genera, more genera and subfamilies must be established. Following ignorance of these "subfamily" differences, *Cephalospyris* is characterized by an apex with an instum and sinistram apical hole (a right and left apical hole), *Tessarospyris* by the absence of apical horns, and *Platybursa* by the absence of apical horns, according to Campbell (1954: D112, 114). There are no reasons to separate *Tessarospyris* and *Platybursa* anymore. No distinguishing marker for *Cephalospyris* exists in any real specimens. These observations conclude that they should be regarded as a same genus. Some concerns remain about this synonymy. The basal rings are confirmed in *Platybursa*, *Cephalospyris* and *Tessarospyris*, but not in *Cyrtostephanus*. A complete ring is present in only *Cyrtostephanus*. These concerns should be solved in the future. All the genera, except *Cyrtostephanus,* were simultaneously published in Haeckel (1887: 429 for *Clathrobursa* and *Platybursa*, 441 for *Cephalospyris*, 442 for *Tessarospyris*). In respect to the first reviser, *Platybursa* is regarded as a valid genus among them.

Tholospyris

The combination of *Tholospyris* and *Tholospyrium* and that of *Tristylospyris* and *Tristylospyrula* are respectively based on the same type species. Under the scheme of Campbell (1954: D112, 114), *Tristylospyris* and *Tholospyris* have in common three unbranched basal feet and no thorax. The "difference" among these genera relies on the definition of the family. *Tristylospyris* belonged to the "Triospyrididae" whose shell is characterized by the presence of a cephalis and its apophyses and the absence of an apical cupola (Campbell 1954: D112) whereas *Tholospyris* belonged to the "Tholospyrididae" whose shell includes a cephalis with an apical cupola (Campbell 1954: D114). The main difference is the presence/absence of "an apical cupola" but type images as well as support images for *Tholospyris* and *Tristylospyris* in the Atlas show the presence of "an apical cupola" in both genera. According to Campbell (1954), *Tristylospyris* lacks an apical horn and apical holes and *Tholospyris* has an apical horn. This difference depends on the development stage of the apical horn so it is not useful for genus criterion. "Apical holes" exist in both genera.

The basal ring (Goll 1969: pl. 56, figs 3-6, 8) comprises four pores: very large, Japanese rice spatula-shaped twin *Ca*-pores and large twin *Cerv*-pores. Twin *J*-pores are visible from a base view, but they are obliquely oriented on the dorsal side (A-rod side) of the test. Three basal feet are directly connected with D- and double L-rods. The size of the twin *Cerv*-pores is obviously larger than in *Ceratospyris*, but the independency of both these genera has to be re-evaluated. *Tholospyris* and *Tristylospyris* were simultaneously published in Haeckel (1882: 441 for both genera). *Tholospyris* has already been selected as a valid genus by the first reviser (De Wever *et al.* 2001: 230) although no explanations were given.

Triceraspyris

Following Campbell's concept (Campbell 1954: D112, D116), the genera listed here can be placed into a group with one apical or simple horn (*Triospyrium*, *Tripospyrella*, *Acrospyris*) and a group with three apical horns (*Triceraspyris*). Other differences given are absence of thorax for the "Triospyrididae" for *Triceraspyris*, *Triospyrium* and *Tripospyrella*, and presence of thorax for the "Phormospyrididae" as *Acrospyris*. The "thorax" of the type-illustration of *Acrospyris* (Haeckel 1887: pl. 95, fig. 17) is represented by supplementary meshes connecting the adjacent feet and, thus, this "genus" has no true thorax. The lectotypes of *Ceratospyris didiceros* (Ogane *et al.* 2009b: pl. 39, figs 1a-c) and *Ceratospyris furcata* (Ogane *et al.* 2009b: pl. 39, figs 5a-d), the typical species of *Triceraspyris* and type species of *Triospyrium*, show nearly the same morphology except for the developmental stage of the three apical horns and the distal ends of the three feet. These differences are not significant to separate them into two genera. The basal structure was only documented for *Tripospyrella*, which comprises three "large" basal pores (Campbell 1954: D112). The support image for *Tripospyrella* cited from Haeckel (1887: pl. 95, fig. 2) shows twin *Ca*-pores (coded as *k* in Haeckel 1887) and a unified *Cerv*-pore (*i* in Haeckel 1887). A very tiny twin *J*-pore is as well drawn in this figure. If this is correct, this structure is identical to that of *Dictyospyris* and *Dorcadospyris* at a family level. *Triceraspyris* and *Acrospyris* were simultaneously published in Haeckel (1882: 441 for these two genera). Real specimens identifiable as *Triceraspyris* are found so that this genus is selected as a valid genus.

Family Paradictyidae Haeckel, 1882 n. stat. *sensu* Petrushevskaya (1981)

Paradictyida Haeckel, 1882: 444 [as a tribe].

Nephrospyrida Haeckel, 1887: 1092, 1099 [as a subfamily].

Nephrospyrinae [*sic*] – Chediya 1959: 185 (= Nephrospyridinae).

Paradictyinae – Campbell 1954: D116. — Petrushevskaya 1981: 369-370. — Afanasieva *et al.* 2005: S306. — Afanasieva & Amon 2006: 157.

Nephrospyridinae – Petrushevskaya 1981: 352-352. — Afanasieva *et al.* 2005: S305. — Afanasieva & Amon 2006: 155.

Type genus. — *Paradictyum* Haeckel, 1882: 444 [type species by absolute tautonomy: *Nephrospyris paradictyum* Haeckel, 1887: 1102] = junior subjective synonym of *Nephrodictyum* Haeckel, 1882: 444 [type species by subsequent designation (Campbell 1954: D106): *Nephrospyris renilla* Haeckel, 1887: 1101].

Included genera. — *Amphispyris* Haeckel, 1882: 443 (= *Amphispyrium* with the same type species; *Amphispyridium* **n. syn.**, *Microcubus* **n. syn.**, *Toxarium* **n. syn.**, *Toxellium* **n. syn.**, *Toxidiella* **n. syn.**, *Toxonium* **n. syn.**, ? *Tricyclidium* **n. syn.**). — *Nephrodictyum* Haeckel, 1882: 444 (= *Nephrospyris* with the same type species; *Paradictyum* synonymized by Goll & Bjørklund 1985: 115). — *Psychospyris* Riedel & Sanfilippo, 1971: 1591. — *Sphaerospyris* Haeckel, 1887: 1099.

Nomen dubium. — *Protympanium*.

Junior homonym. — *Toxidium* Haeckel, 1887 (= *Toxidiella*) *nec* Le Conte, 1860.

Diagnosis. — Main skeleton forming a sagittal ring with twin cupolas or twin set of body frames. The Lo-axis is parallel to Sg-axis and the Sh-axis is parallel to the Pl-axis. No significant skeleton developed below the basal ring. The basal ring is constructed of three or six basal pores. Basal pores are partly, or fully, covered with fine polygonal meshes in some members. The endoplasm is spherical and situated in the area inside the sagittal ring. Both cupolas are almost occupied with tens to a hundred number of algal symbionts in *Amphispyris*. In *Nephrodictyum*, a hundred algal symbionts are exclusively distributed in the periphery or in the peripheral lobes of the shell. No algal symbionts are located outside the shell.

Stratigraphic occurrence. — Late Paleocene-Living.

Remarks

Nephrodictyum and related genera were hitherto included in the Acanthodesmiidae (De Wever *et al.* 2001: 231-232), but the orientation of the axes under Type 2 to Type 1 coordinates is fundamentally different between the Paradictyidae and the Acanthodesmiidae. Differing from the Paradictyidae, the Acanthodesmiidae have the Lo-axis parallel to the Lt-axis. The protoplasm, living status and cytological ultrafine structure were documented for *Amphispyris* (Sugiyama & Anderson 1998b; Suzuki & Not 2015; fig. 8.11.4; Zhang *et al.* 2018: 10, figs 2.11), *Nephrodictyum* (Cachon & Cachon 1985: fig. 53.d; Zhang *et al.* 2018: 10, fig. 2.18), and the *Paradictyum* form of *Nephrodictyum* (Aita *et al.* 2009; pl. 5, fig. 1a-2b; pl. 31, fig. 7).

Validity of genera

Amphispyris

Amphispyris is different from *Tricolospyris* at the family level as written in remarks and diagnosis of the Acanthodesmiidae and Paradictyidae, and this difference is well illustrated in Goll (1968: pl. 176, fig. 13; 1972b: pls 1-16), Petrushevskaya (1969: figs 4.IV, 4.V) and Tan & Su (1981: pls 1-3). The following genus combinations share the same type species: *Amphispyris* and *Amphispyrium*; *Toxarium* and *Toxellium*; and *Toxidium* and *Toxidiella*. In Campbell (1954) and Haeckel (1887) there is a very strong link in the Nassellaria at a suborder level and family-rank. Four genera (*Microcubus*, *Toxarium*, *Toxonium*, *Tricyclidium*) are classified in the "Division Plectellari" (Campbell 1954: D103) and two genera in the "Division Cyrtellari" (Campbell 1954: D111). As the "division" was situated between the "Nassellaria" and the "superfamily" in Campbell (1954), this rank is now equal to the suborder rank. "Plectellari" is defined by "without complete skeleton" whereas "Cyrtellari" is defined by "complete lattice shell". The fundamental framework of the genera listed here is the same. Due to this reason, these divisional schemes do not reflect difference in real specimens. The next link in a classic study is the family rank. These genera were then classified into different superfamilies, families and subfamilies but these descriptions were logically wrongly applied: the anatomical orientation and apparent orientation under the absolute Cartesian coordinates for the former and relative Cartesian coordinates for the latter (see remarks of the Acanthodesmioidea). However, these coordinates were confused in the Paradictyidae (see diagnosis and remarks of the Paradictyidae). *Amphispyris* and *Amphispyridium* were classified into the "Androspyrididae" of the "superfamily Triospyridicae" by presence of a thorax and cephalis with an apical cupolar at family level (Campbell 1954: D116) and existence of a bilocular cephalis with a sagittal constriction at the superfamily level (Campbell 1954: D112). These criteria are meaningless because recognizing cephalis, thorax and apical cupolar can be wrong, owing to a wrong recognition of the absolute orientation of the shell. Thus, the distinguishing criteria for subfamily and any higher levels are not any longer valuable for the Paradictyidae.

Once the link at suborder level and family-rank dissolved, synonym discussion becomes easy. Goll (1972b) identified "*Tholospyris devexa devexa*" and "*Tholospyris devexa finalis*" successively for specimens with incomplete latticed shells (Goll 1972b: pl. 10 for the former and pl. 12, figs 9-12 for the latter) and complete latticed shells (Goll 1972b: pl. 11 for the former and pl. 13 for the latter). The incomplete latticed forms can be identified as *Toxarium* or *Toxonium* if the type-illustrations of these genera are referred to. The definition of these two genera is based on the number of columellae, basal ring, equatorial ring, and thoracic bows (Campbell 1954: D108 for *Toxarium* and D109 for *Toxonium*), but it is unable to be reworded by the current terminology. A complete latticed shell can be identified as *Amphispyris* or *Amphispyridium*. These two genera have in common a shell with two transvers strictures and a latticed structure only complete in the frontal ring (Campbell 1954: D116 for both genera). Although the true meaning of the "frontal ring" is unclear, this description fits with real specimens. *Amphispyris* has three pairs of large annular meshes on each side of the ring-plane whereas *Amphispyridium* has four pairs instead of three pairs, but this difference cannot be recognized in the type-illustrations of these two genera (Haeckel 1887: pl. 88, fig. 4 for *Amphispyris* and pl. 88, fig. 2 for *Amphispyridium*). Thus, four genera *Toxarium*, *Toxonium*, *Amphispyris* and *Amphispyridium* are a same genus.

The specimen identifiable as *Tricyclidium* based on the genus definition by Campbell (1954: D108) is identified as a specimen of *T. devexa devexa* in Goll (1976: pl. 10, fig. 1) and that of *Microcubus* is named as "*Tholospyris devexa dusenburyi*" (Goll 1976: pl. 12, figs 1-8). These images indicate that *Tricyclidium* and *Microcubus* are different as ontogenetic growth stages at the species level. *Amphispyris*, *Microcubus* and *Tricyclidium* were simultaneously published in Haeckel (1882: 443 for *Amphispyris*, 446 for *Microcubus* and *Tricyclidium*). Real specimens corresponding to *Amphispyris* were found at many locations so that this genus is selected as a valid genus.

Family Stephaniidae Haeckel, 1882

Stephanida Haeckel, 1882: 444 [as a family]; 1887: 937-940 [as a family]. — Lankester 1885: 849 [as a family]. — Bütschli 1889: 1976 [as a family]. — *nec* Rüst 1892: 176. — Anderson 1983: 29 [as a family].

Stephida – Lankester 1885: 850 [as a family].

Cortinida Haeckel, 1887: 940, 950 [as a subfamily].

Stephaniidae – Poche 1913: 219. — Campbell 1954: D106. — Petrushevskaya 1981: 371; 1986: 132. — Afanasieva *et al.* 2005: S305. — Afanasieva & Amon 2006: 155.

Stephanidae [*sic*] – Popofsky 1913: 283-284 (= Stephaniidae). — Schröder 1914: 87. — Chediya 1959: 167. — Tan & Tchang 1976: 269. — Cachon & Cachon 1985: 291-292. — Chen & Tan 1996: 152. — Tan & Chen 1999: 270. — Tan & Su 2003: 83. — Chen *et al.* 2017: 165.

Stephaniinae – Campbell 1954: D106.

Cortiniae – Chediya 1959: 169.

Type genus. — *Stephanium* Haeckel, 1887: 952 [type species by subsequent designation (Campbell 1954: D106): *Stephanium quadrupes* Haeckel, 1887: 952] = junior subjective synonym of *Zygocircus* Bütschli, 1882: 496 [type species by monotypy: *Lithocircus productus* Hertwig, 1879: 197].

Included genus. — *Zygocircus* Bütschli, 1882: 496 (= *Cortina* **n. syn.**, *Plagiocarpa* **n. syn.**, *Stephanium* **n. syn.**).

Diagnosis. — The skeleton consists of only a sagittal ring. The Lo-axis is parallel to the Pl-axis while the Md-axis is parallel to Sg-axis. The endoplasm is spherical and located in the area encircled by the sagittal ring. Algal symbionts may or may not be present. Even if present, algal symbionts are uncommon and densely distributed around the endoplasm within the area of the sagittal ring.

Stratigraphic occurrence. — early Middle Eocene-Living.

Remarks

In the case of very young Acanthodesmioidea, it is nearly impossible to differentiate them from the true *Zygocircus*. "Living" and protoplasm images were illustrated for *Zygocircus* (Cachon & Cachon 1985: fig. 53.a; Matsuoka 1993a: fig. 2.3; Suzuki *et al.* 2009b: figs 3I, 3J; Suzuki & Not 2015: fig. 8.11.3; Matsuoka *et al.* 2017: Appendix B). The Stephaniidae have been overlooked due to their small size and their transparent protoplasm observed in plankton studies. *Zygocircus* has simply been identified as *Zygocircus productus* Hertwig 1879, even if real specimens may be completely different from the type-illustration in Hertwig (1879). However, this should be avoided as algal symbiont-bearing *Zygocircus* possesses a different morphology to that of the *Zygocircus* without algal symbionts.

Validity of genera

Zygocircus

The *Zygocircus*-form includes not only fully-grown forms but also very young stages of Acanthodesmioidea, being unable to clearly differentiate them. For a simply practical identification, *Zygocircus* includes here into a single genus the morphotypes with a complete or incomplete D-ring, three or more basal feet directly extending from the initial spicular system and no arches except for the D-ring. *Zygocircus* was published by Bütschli (1882: 496), the same year as *Plagiocarpa* by Haeckel (1882: 424). *Zygocircus* is selected as the valid genus because its type species was illustrated only in 1882.

Phylogenetic Molecular Lineage III (Sandin *et al.* 2019)

Diagnosis. — Lineage III encompasses one or two segmented Nassellaria with a skirt or a skirt-like thorax. The cephalic initial spicular system is characterized by the development of variable arches and by the reduction of some major rods (e.g., l-rod in Plagiacanthoidea, MB in Archipilioidea). The basal ring completely merged with the shell wall as part of the pore frame. It may also be partly embedded in the shell wall or completely absent.

Remarks

Lineage III includes the superfamilies Archipilioidea, Theopilioidea, Stichopilioidea, Plagiacanthoidea and Pylobotrydoidea. Lineage III is clearly separated from Lineage IV with 100% PhyML bootstrap values having 10 000 replicates (BS) and > 0.99 posterior probabilities (PP). Except for the Plagiacanthidae and Ximolzidae Dumitrica, nom. nov., the presence of an arch is a common structure in Lineage III. The Archipilioidea have arches as part of the cephalic wall while the Theopiliidae of the Theopilioidea have a perforated cephalic wall instead of disarrayed arches. The cephalis of the Pylobotrydoidea is divided into three lobes with systematically arranged arches in the cephalic cavity whereas the cephalic arches of the Plagiacanthoidea are either largely buried in the cephalic wall (Phaenocalpididae, Dimelissidae). The cephalic arches of Plagiacanthoidea may also be largely free in the cephalic cavity (Ceratocyrtidae, Pseudodictyophimidae Suzuki, n. fam.) or exposed with a complete loss of the shell wall (Plagiacanthidae, Ximolzidae Dumitrica, nom. nov.).

Superfamily Archipilioidea Haeckel, 1882 *sensu* Sandin, Not & Suzuki *in* Sandin *et al.* (2019)

Archipilida Haeckel, 1882: 427 [as a tribe]; 1887: 1133, 1134 [as a subfamily].

Archipiliicae – Campbell 1954: D117 [as a superfamily]. — Nakaseko 1957: 27 [as a superfamily]. — Dieci 1964: 185 [as a superfamily].

Archipiliilae – Campbell 1954: D117 [as a subsuperfamily]. — Nakaseko 1957: 27 [as a subsuperfamily]. — Dieci 1964: 185 [as a subsuperfamily].

Archipiliacea – Loeblich & Tappan 1961: 228 [as a superfamily].

Archipilioidea – Afanasieva *et al.* 2005: S291. — Afanasieva & Amon 2006: 138. — Sandin, Not & Suzuki *in* Sandin *et al.* 2019: 201.

Diagnosis. — Archipilioidea are composed of practically single segmented shell, although upper and lower parts may be recognized by the position of the MB. The initial spicular system is characterized by a very short or missing MB, forming a three-pointed initial spicular system and a significant basal ring that is completely merged with the shell wall as part of the pore frame. The cephalic wall includes many arches or an arch-like meshwork.

Remarks

This superfamily consists of the Archipiliidae and the Theophormididae, and was established in consistency with the molecular phylogeny analyses of Sandin *et al.* (2019). These analyses documented 100% PhyML bootstrap values with 10 000 replicates (BS) and >0.99 posterior probabilities (PP). The morphological commonality between *Archipilium* and *Enneaphormis* is very limited.

Family Archipiliidae Haeckel, 1882 *sensu* Sandin *et al.* (2019)

Archipilida Haeckel, 1882: 427 [as a tribe]; 1887: 1133, 1134 [as a subfamily].

Trissopilida Haeckel, 1882: 427 [*nomen dubium*, below a tribe].

Archipiliidae – Campbell 1954: D117. — Petrushevskaya 1986: 132. — Kozlova 1999: 108. — Afanasieva *et al.* 2005: S291. — Afanasieva & Amon 2006: 138.

Archipiliinae – Campbell 1954: D117. — Afanasieva *et al.* 2005: S291. — Afanasieva & Amon 2006: 138.

Archipilinae [*sic*] – Clark & Campbell 1942: 62 (= Archipiliinae); 1945: 33. — Campbell & Clark 1944a: 38. — Chediya 1959: 188. — Petrushevskaya 1981: 247-248.

Nothotripodiscinidae Deflandre, 1972: 231.

Archipilidiae [*sic*] – Sandin *et al.* 2019: 201 (= Archipiliidae).

Type genus. — *Archipilium* Haeckel, 1882: 427 [type species by subsequent designation (Campbell 1954: D117): *Archipilium orthopterum* Haeckel, 1887: 1139].

Included genus. — *Archipilium* Haeckel, 1882: 427 (= *Nothotripodiscinus* synonymized by Petrushevskaya 1975: 584).

Nomen dubium. — *Trissopilium*.

Diagnosis. — Archipiliidae are identified by having only one segment, three feet, and short skirt extension. A three-pointed star rod system and a significant circular frame around the aperture. The cephalic initial spicular system consists of A-, D-, double L- and Ax-rods. The MB is very short or partly degraded. Double l-rod and V-rod are absent. The basal ring is large and significant. It is directly connected to the D- and double L-rods forming three collar pores. These three rods develop into external feet. The basal ring completely merges with the shell's pore frame. One bifurcated rod may emerge from each of the basal ring's A- and double L-rod connecting points. These rods form variable arches with other supplemental rods to create the pore frame of the cephalic wall in younger forms. The rods become completely embedded in the thick cephalic wall in fully grown forms. A short skirt-like frame develops and an endoplasm occupies the internal space of the shell. The A-rod, or a pointed MB, are sometimes missing or dissolved.

Stratigraphic occurrence. — Late Oligocene-Living.

Remarks

The overall shape of the Archipiliidae is generally similar to that of genera with three feet, one segment, configurations such as Dimelissidae or Phaenocalpididae. However, Archipiliidae are different from these latter two families by the absence or near absence of an MB and the presence of a significant basal ring. The cephalis is covered by a thick wall in normal *Archipilium*-specimens but a mesh-like texture similar to the cephalic part of *Enneaphormis* appears in very young forms of *Archipilium* (Takahashi 1991: pl. 36, fig. 7; O'Connor 1999: fig. 4.K). A quality image of the cephalic initial spicular system was only published in Nishimura (1990: fig. 21.2) while a schematic illustration was shown in Sandin *et al.* (2019: supplement 1). A "Living" specimen of *Archipilium* was illustrated in Suzuki & Not (2015: fig. 8.10.20).

Family THEOPHORMIDIDAE Haeckel, 1882 *sensu* Suzuki emend. herein

Theophormida Haeckel, 1882: 436 [as a tribe]; 1887: 1313, 1366 [as a subfamily].

Sethophormida Haeckel, 1882: 432 [*nomen dubium*, as a tribe]; 1887: 1192, 1242, 1243 [as a subfamily].

Sethophorminae [*sic*] – Clark & Campbell 1942: 72 [*nomen dubium*] (= Sethophormidinae). — Frizzell & Middour 1951: 29. — Chediya 1959: 205.

Sethophormidae [*sic*] – Frizzell & Middour 1951: 29 (= Sethophormididae). — Nishimura 1990: 95 (*sensu* emend.). — Sugiyama 1994: 3-4. — van de Paverd 1995: 225. — Sugiyama 1998: 233.

Theophorminae [*sic*] – Clark & Campbell 1942: 81 (= Theophormidinae); 1945: 43. — Campbell & Clark 1944a: 47; 1944b: 31. — Chediya 1959: 217.

Sethophormididae – Riedel & Campbell 1952: 667, 669 [*nomen dubium*]. — Campbell 1954: D124. — Petrushevskaya 1971a: 65-66; 1971b: 988; 1981: 127; 1986: 133. — Dumitrica 1979: 28. — Takahashi 1991: 108. — Kozlova 1999: 118. — De Wever *et al.* 2001: 236. — Afanasieva *et al.* 2005: S293-294. — Afanasieva & Amon 2006: 141.

Sethophormidinae – Riedel & Campbell 1952: 669 [*nomen dubium*]. — Campbell 1954: D124. — Petrushevskaya 1981: 130; 1986: 133. — Afanasieva *et al.* 2005: S294. — Afanasieva & Amon 2006: 141.

Theophormididae – Campbell 1954: D132.

Theophormidinae – Campbell 1954: D132.

Enneaphormidinae Petrushevskaya, 1981: 127-128; 1986: 132. — Afanasieva *et al.* 2005: S294. — Afanasieva & Amon 2006: 141-142.

Theophormidae [*sic*] – Nishimura 1990: 105 (*sensu* emend.) (= Theophormididae).

TYPE GENUS. — *Theophormis* Haeckel, 1882: 436 [type species by subsequent designation (Campbell 1954: D132): *Theophormis callipilium* Haeckel, 1887: 1367].

INCLUDED GENERA. — *Enneaphormis* Haeckel, 1882: 432. — *Theophormis* Haeckel, 1882: 436 (= *Astrophormis* **n. syn.**). — *Velicucullus* Riedel & Campbell, 1952: 669.

INVALID NAME. — *Leptarachnium*.

NOMINA DUBIA. — *Octophormis*, *Sethophormis*, *Tetraphormis*.

DIAGNOSIS. — A two-segmented, flat shell with a significantly large basal ring that is completely merged, becoming part of the shell's skeletal frame. A cephalic wall with an arch-like meshwork is observed. The cephalic initial spicular system consists of MB, A-, D-, V-, double L-, and Ax-rods. The double l-rod is absent while the MB is very short or partly degraded. The A-rod is very short, keeping the cephalic wall flat. The V-rod is absent in some members. The D-, V- and double L-rods are horizontally situated, and are near the same height level as MB. Likewise, the basal ring is also horizontally situated close to the MB's height level. The presence or absence of MB and V-rod limits the number of pores in the basal ring; three collar pores by direct connection to the D- and double L-rods (*Enneaphormis*), or four collar pores by direct connection with D-, V- and double L-rods (*Theophormis* and *Velicucullus*). This results in a three- or four-leafed clover outline. In the case of three collar pores, three rods are arranged at 120 degree-intervals and four rods cross each other orthogonally at angles of 90 degrees. The endoplasm transparent, very small, and is situated within the basal ring. Algal symbionts are found near or within the space inside the basal ring in *Theophormis* but no algal symbionts are detected in *Enneaphormis*.

STRATIGRAPHIC OCCURRENCE. — Middle Paleocene-Living.

REMARKS

The cephalic initial spicular system of all known three genera was photographed for *Enneaphormis* (Nakaseko & Nishimura 1982: pl. 46, figs 4a-5b; Yeh & Cheng 1990: pl. 4, fig. 5; Sugiyama 1998: pl. 3, figs 5; O'Connor 1999: pl. 3, figs 1-4), *Theophormis* (Nishimura 1990: figs 21.1, 21.2; Takahashi 1991: pl. 32, fig. 10, 12; Sugiyama 1994: pl. 1, fig. 7), and *Velicucullus* (Nishimura 1992: pl. 3, fig. 7; O'Connor 1999: pl. 3, figs 1-4). The interpretation of Nishimura (1992: pl. 3, fig. 7) indicated the presence of an MB, double L- and an un-coded rod, but this should be necessary reinterpreted as a D-rod instead of an MB and an un-coded rod instead of a V-rod if we refer to Sugiyama (1994: pl. 1, fig. 7). "Living" and protoplasm images were observed in *Enneaphormis* (Suzuki & Not 2015; fig. 8.11.30) and *Theophormis* (Zhang *et al.* 2018: 10, figs 2.34-2.37).

VALIDITY OF GENERA

Theophormis

Astrophormis was classified into "Sethophormidinae of the Sethophormididae within subsuperfamily Sethopiliilae", and *Theophormis* was classified into "Theophormidinae of the Theophormididae within subsuperfamily Theopiliilae" *sensu* Campbell (1954). Sethophormididae and Theophormididae are both defined by the presence of four to nine or more radial apophyses (Campbell 1954: D124 for the former and D132 for the latter). Both have the same basal shell mouth open (Campbell 1954: D124 for the former and D132 for the latter). Thus, the major difference between the genera *Astrophormis* and *Theophormis* is at the subsuperfamily level. "Sethopiliilae" is defined by the division of its shell by a transverse stricture into the cephalis and thorax (Campbell 1954: D122), whereas the "Theopiliilae" shell is divided by two transverse strictures into the cephalis, thorax, and abdomen (Campbell 1954: D129). The supporting illustration of *Theophormis* shows a thorax that resembles a gown with a very wide skirt (Nishimura & Yamauchi 1984: pl. 26, fig. 5), which suggests later growth in the type-illustration. According to Campbell (1954), *Astrophormis* has 12 to 20 or more radial ribs on a flat, nearly discoidal thorax and the absence of an apical horn (Campbell 1954: D124). *Theophormis* has a flat, dilated abdomen with an open mouth and numerous radial ribs (Campbell 1954: D132). The type-illustrations and supporting images for *Theophormis* and *Astrophormis* demonstrate their very similar appearance. The name *Theophormis* was used earlier than *Astrophormis*.

Superfamily THEOPILIOIDEA Haeckel, 1882 n. stat. *sensu* Suzuki emend. herein

Theopilida Haeckel, 1882: 435 [as a tribe]; 1887: 1313, 1315 [as a subfamily].

Theopiliilae – Campbell 1954: D129 [as a subsuperfamily]. — Nakaseko 1957: 27 [as a subsuperfamily].

Neosciadiocapsaceae O'Dogherty, 1994: 227 [as a superfamily].

Diagnosis. — Skeleton having a very shallow hat-shaped to hat-shaped shell with two segments. The thoracic pore frames of the thorax are systematically distributed in both longitudinal and lateral directions. The distal end of the thorax is associated with a velum, a latticed frame, many feet and other ornaments.

Remarks

This superfamily consists of the Anthocyrtididae and Theopiliidae. The taxonomic position of the Theopilioidea is based on the molecular phylogenetic position of *Eucecryphalus* (Lineage III, Sandin *et al.* 2019). They correspond to nassellarians characterized by a very shallow hat-shaped shells, classified into family Anthocyrtididae (= Neosciadiocapsidae in De Wever *et al.* 2001: 233-235) or Theopiliidae (De Wever *et al.* 2001: 238-239). However, molecular phylogenetic data placed a close related morphological group, the Cycladophoridae (based on *Cycladophora*) into Lineage IV (Sandin *et al.* 2019). At that time, it was impossible to conceptualize a higher classification position for the Anthocyrtididae. The Lampromitridae may also belong to this superfamily (see remarks for Lampromitridae).

Family Anthocyrtididae Haeckel, 1882 *sensu* Caulet emend. herein

Anthocyrtida Haeckel, 1882: 430 [below tribe]; Haeckel 1887: 1192, 1241-1242 [as a family]. — Bütschli 1889: 1988 [as a family].

Anthocyrtiden – Haecker 1907: 125-126 [as a family].

Anthocyrtidae [*sic*] – Popofsky, 1908: 285 (= Anthocyrtididae); 1913: 359. — Schröder 1914: 100. — Clark & Campbell 1942: 72; 1945: 38. — Dogiel & Reshetnyak 1955: 48. — Chediya 1959: 205. — Tan & Tchang 1976: 280. — Tan & Su 1982: 172. — Nishimura 1990: 145 (*sensu* emend.). — Chen & Tan 1996: 153. — Tan & Chen 1999: 313. — Tan & Su 2003: 113, 155. — Chen *et al.* 2017: 198.

Anthocyrtididae – Poche 1913: 221.

Anthocyrtinae [*sic*] – Orlev 1959: 455 (= Anthocyrtidinae).

Neosciadiocapsidae Pessagno, 1969: 392-394; 1976: 45-46; 1977b: 935. — Petrushevskaya & Kozlova 1972: 540. — Dumitrica 1979: 31-32. — De Wever 1982b: 284. — Kozur 1984: 65. — O'Dogherty 1994: 277. — Hollis 1997: 72. — O'Connor 1999: 13 (*sensu* emend.). — De Wever *et al.* 2001: 233, 235.

Neosciodiocapsidae [*sic*] – Tochilina 1989b: 61 (= Neosciadiocapsidae).

Neosciadiocapsinae – Afanasieva *et al.* 2005: S294. — Afanasieva & Amon 2006: 141.

Type genus. — *Anthocyrtis* Ehrenberg, 1846: 385 [type species by monotypy: *Anthocyrtis mespilus* Ehrenberg, 1847: 55].

Included genera (Cenozoic only). — *Anthocyrtis* Ehrenberg, 1846: 385 (= *Anthocyrtella* with the same type species; *Anthocyrtarium* **n. syn.**, *Anthocyrtium* **n. syn.**, *Clathrocyclas* **n. syn.**, *Clathrocyclia* **n. syn.**, *Coniforma* **n. syn.**). — *Eurystomoskevos* Caulet, 1991: 536. — *Microsciadiocapsa* Pessagno, 1969: 403 (= *Lipmanium* synonymized by Petrushevskaya 1981: 152; *Scyphiforma* synonymized by Petrushevskaya 1981: 153; *Squinabolella* synonymized by O'Dogherty 1994: 227).

Diagnosis. — Anthocyrtididae can be viewed as Theopilioidea with a ventral tube or with a trace of it on the cephalis. The development status of the apical horn is variable among genera. The aperture is always open. The cephalic initial has MB, A-, V-, D-, double L-, and double l-rods. The Ax-rod may be present or absent by cause of an infra-species variation. The basal ring is completely merged with the shell wall, and in certain cases its inner edge is recognizable in the cephalis. The basal ring is directly connected with D-, V-, double L- and double l-rods. However, the arches (double Dl-arch) of the basal ring's apical side are missing, partly merged with the shell wall, or completely merged on the shell wall as relatively large pores. This variation changes the number of visible collar pores from four to six. The D-rod extends downward while the V-rod rises up. The A-rod side of the basal ring is bended downward along the double l-rod, while the V-side of the basal ring is bended upwards along the double L-rod. The MB is extended from the center to the A-rod side of the cephalic cavity. The A-rod is free in the cephalic cavity and extends vertically relative to MB. The ventral tube opens below the V-rod. The D- and double L-rods form a rod-like wing in some members. The triple-branched terminal parts of the L- and l-rod are visible from the aperture view.

Stratigraphic occurrence. — Early Berriasian-Late Oligocene.

Remarks

It appears difficult distinguish the Anthocyrtididae from the Theopiliidae and Cycladophoridae due to homeomorphy. Differing from the Anthocyrtididae, both the Theopiliidae and Cycladophoridae lack a ventral tube or a semblance of its trace. The Anthocyrtididae are commonly found in the late Cretaceous while Cenozoic members are uncommon. The relationship among the three families is not yet fully understood. This can be attributed to the nearly identical cephalic structure between the Theopiliidae and Cycladophoridae, regardless of them being distant families at Lineage level (Sandin *et al.* 2019; See also remarks for Theopiliidae and Cycladophoridae). Tochilina & Vasilenko (2015, 2018b) identified Anthocyrtididae's overall resemblance to Cycladophoridae as opposed to the Theopiliidae. The cephalic structure was illustrated for Cretaceous "Neosciadiocapsidae" (Pessagno 1969: pl. 24, figs 1, 2, pl. 27, figs 1, 2, pl. 30, figs 1, 2, pl. 34, figs 1, 2, pl. 35, figs 1, 2, pl. 35, fig. 7, pl. 36, figs 1, 2, pl. 37, figs 3, 6, pl. 38, figs 1, 2), for Paleocene *Anthocyrtis* (Nishimura 1992: pl. 4, figs 6, 9) and for Eocene *Anthocyrtis* (O'Connor 1999: pl. 2, figs 12-22). Based on the stable position of the Ax-rod, the codes indicated by Pessagno (1969) may lead to confusion . The "a" in pl. 24, fig. 1 and "c" in pl. 30, figs 1 and 2 are V-rod. The cephalis and upper part of the thorax are covered by an imperforated thick siliceous wall in most Anthocyrtididae. In some Cenozoic members, these parts are not covered with a wall. In such cases, the double Dl-arch extends as a part of the thoracic pore frame (e.g., Nishimura 1992: pl. 4, figs 6b, 9b).

Validity of genera

Anthocyrtis

The following genus combinations share the same type species: *Anthocyrtis* and *Anthocyrtella*, *Anthocyrtium* and *Anthocyrtarium*, and *Clathrocyclas* and *Clathrocyclia*. Like *Astrophormis* and *Theophormis*, *Anthocyrtium* and *Anthocyrtis* were classified into "Sethophormidinae of the Sethophormididae within subsuperfamily Sethopiliilae" (Campbell 1954: D122, 124-126), whereas *Clathrocyclas* was classified into "Theophormidinae of the Theophormididae within subsuperfamily Teopiliilae" (Campbell 1954: D129, 132) *sensu* Campbell (1954). As discussed in detail, the taxa subsuperfamily, family, and subfamily are meaningless for these genera. *Anthocyrtium* is characterized by 12 or more feet (Campbell 1954: D125); *Anthocyrtis* has a distinctive cephalis from the thorax, and only 6 feet (Campbell 1954: D125-126); and *Clathrocyclas* features a conical shell and a single terminal corona of feet (Campbell 1954: D132). One difference among species is the prominence of the stricture between the cephalis and thorax; however, this difference is less distinctive at the genus level. The number of feet differs among genera, but the lectotype of *Anthocyrtis mespilus*, the type species of *Anthocyrtis*, does not have six feet. Although the number of feet has not been confirmed for other type species using real specimens, this difference is insufficient to distinguish specimens at the genus level. *Coniforma* is a late Cretaceous genus with a corona-like skirt and many very short feet, which are characteristics that are phylogenetically associated with *Anthocyrtis*. It is unnecessary to maintain *Coniforma* as an independent genus within this family. The oldest available name for these specimens is *Anthocyrtis*.

Family Theopiliidae Haeckel, 1882 *sensu* Caulet emend. herein

Theopilida Haeckel, 1882: 435 [as a tribe]; 1887: 1313, 1315 [as a subfamily].

Theopilinae [*sic*] – Clark & Campbell 1942: 80 (= Theopiliinae). — Campbell & Clark 1944a: 46; 1944b: 29. — Chediya 1959: 213.

Theopiliidae – Campbell 1954: D130. — De Wever *et al.* 2001: 238, 239. — Matsuzaki *et al.* 2015: 60.

Theopiliinae – Campbell 1954: D130. — Petrushevskaya 1981: 134-137; 1986: 134. — Afanasieva *et al.* 2005: S294. — Afanasieva & Amon 2006: 141.

Type genus. — *Theopilium* Haeckel, 1882: 435 [type species by subsequent designation (Campbell 1954: D130): *Theopilium tricostatum* Haeckel, 1887: 1322] = junior subjective synonym of *Eucecryphalus* Haeckel, 1861b: 836 [type species by subsequent designation (Haeckel 1887: 1221): *Eucecryphalus gegenbauri* Haeckel, 1861b: 836].

Included genera. — *Clathrocycloma* Haeckel, 1887: 1388. — *Eucecryphalus* Haeckel, 1861b: 836 (= *Eucecryphalium* with the same type species; *Cecryphalium*, *Corocalyptra* synonymized by Petrushevskaya 1971a; 146; *Theopilium* synonymized by Sanfilippo & Riedel 1992: 31).

Nomina dubia. — *Eucyrtomphalus*, *Theocalyptra*.

Diagnosis. — Theopilioidea with two cephalic spines (rod-like apical and ventral horns). No feet are observed. The cephalis has pores. The thorax is constructed by a fragile, polygonal pore frame and it is generally conical with a straight outline. The thorax may or may not have a weak neck on its upper part. The width of the pore frames is equivalent to the bars between the adjacent pores as well as to the junction points among the pores. In some members, a velum or velum-like periphery develops around the thorax aperture. The cephalic initial spicular system consists of MB, A-, V-, D-, double L-rods. The double l-rod merges into the shell wall. The basal ring is absent. The MB is generally located at a similar height to the cephalic constriction and is horizontally or obliquely oriented. The length of the MB is one-third to one-half of the cephalis diameter. The A-rod is long, and rises almost vertically to penetrate the cephalic wall forming a rod-like apical horn. The V-rod is relatively long and forms a ventral horn. No ventral tube is observed. In some members, the D-rod extends almost horizontally to become a spine, outside the shell. The double L-rod extends relatively downward and protrudes as spine from the shell wall. In other cases, the distal part of the double L-rod has three branches on the cephalic wall, forming a part of the pore frame.
The endoplasm is transparent to light amber in color. Its size is too small and it is located above the neckline on the upper part of the thorax. The terminal projection is visible but the axial projection is absent.

Stratigraphic occurrence. — early Early Miocene-Living.

Remarks

The cephalic initial spicular system was illustrated for both *Clathrocycloma* (Sugiyama & Furutani 1992: pl. 18, fig. 4) and *Eucecryphalus* (Nishimura 1990: figs 20.1, 26.4, 26.5; Sugiyama *et al.* 1992: pl. 21, fig. 7). Matsuzaki *et al.* (2015: 60) documented the cephalic initial spicular system of the *Eucecryphalus* in detail. Sandin *et al.* (2019: supplement 1) drew a schematic image of this genus, although this schematic drawing omits the double l-rod. The presence of two apical spines and the absence of a ventral tube in Theopiliidae easily distinguish them from the Anthocyrtididae. *Eucecryphalus* was once grouped with *Cycladophora* (Cycladophoridae) due to similarity in their cephalic initial spicular system (Matsuzaki *et al.* 2015: 60), but this grouping was discarded by a distinctive separation in molecular phylogeny at the lineage level (Sandin *et al.* 2019). As highlighted in the remarks for the Cycladophoridae in this paper, significant differences between the Theopiliidae and Cycladophoridae have not yet been confirmed. Typical Theopiliidae are characterized by a fragile thorax with a conical straight outline and many polygonal pores with same width frames. On the other hand, the Cycladophoridae likely have a robust thorax with a smaller number of rounded pores whose frames tend to widen around the junction of three of more pores. Cycladophoridae also tend to have a well-necked upper thorax ("pedestal" by Popova 1989). This tendency, however, is not so clear and some of these features may simply be lacking at species level. Most species introduced by Lombari & Lazarus (1988) seem to belong to *Clathrocycloma*. "Living" and protoplasm images were published for *Eucecryphalus* (Sashida & Kurihara 1999: figs 11.8, 11.13, 11.19; Zhang *et al.* 2018: 17, fig. 7.13, p. 18, figs 7.13-7.16; Ichinohe *et al.* 2018: fig. 2.B, C).

Superfamily Stichopilioidea Haeckel, 1882 n. stat.

Stichopilida Haeckel, 1882: 439 [as a tribe]; 1887: 1435, 1436 [as a subfamily].

Triacartilae – Campbell 1954: D136 [as a subsuperfamily]. — Nakaseko 1957: 27 [as a subsuperfamily]. — Dieci 1964: 188 [as a subsuperfamily].

Diagnosis. — Same as the family.

Remarks

Sandin *et al.* (2019) placed *Ectotoxon* (originally *Extotoxon* [*sic*]) in the same clade as the Artostrobiidae. However, this placement is wrong due to a misidentification. Thus, there is no molecular support to determine the higher classification position of the Stichopiliidae and the independency of the superfamily Stichopilioidea.

Family Stichopiliidae Haeckel, 1882 *sensu* Petrushevskaya (1986)

Stichopilida Haeckel, 1882: 439 [as a tribe]; Haeckel, 1887: 1435, 1436 [as a subfamily].

Artopilida Haeckel, 1882: 437 [as a tribe].

Stichopilinae [*sic*] – Campbell & Clark 1944b: 36 (= Stichopiliinae). — Frizzell & Middour 1951: 31. — Chediya 1959: 226.

Stichopiliidae – Frizzell & Middour 1951: 31. — Petrushevskaya 1986: 133.

Triacartidae Campbell, 1954: D136.

Triacartinae Campbell, 1954: D136.

Type genus. — *Stichopilium* Haeckel, 1882: 439 [type species by subsequent designation (Frizzell & Middour 1951: 32): *Stichopilium bicorne* Haeckel, 1887: 1437].

Included genera. — *Artopilium* Haeckel, 1882: 437 (= *Trictenartus* with the same type species). — *Ectotoxon* Sugiyama, 1994: 6. — *Lophoconus* Haeckel, 1887: 1403. — *Stichopilium* Haeckel, 1882: 439 (= *Triacartus* with the same type species).

Homonym. — *Pterocorythium* Haeckel, 1887 (= *Artopilium*, synonymized by Campbell 1954: D136) *nec* Haeckel, 1882.

Diagnosis. — Stichopiliidae consist of two or three segments, with or without discrete wings. An additional undulated extension might be present in some members. The shell wall is thin, fragile and consists of a very fine grid-like structure. Two significant apical horns with a similar development and three wings are observed. Two of the three wings extend parallelly to these two significant horns and the remaining wing extends vertically. The cephalic initial spicular system consists of MB, A-, V-, D- and double L-rods. The double l-rod and cephalic basal ring absent. These rods are so robust and straight that MB, A- and V-rods are well visible under light microscopy. The MB is generally parallel to the segment boundary. The small endoplasm is located in the cephalon-thoracic part. A single, very long pseudopodium (axial projection) extends more than eight times the total length of the shell. A bundle of pseudopodia forms a cone shape. No algal symbionts are reported.

Stratigraphic occurrence. — Late Oligocene-Living.

Remarks

The cephalic initial spicular system was illustrated for *Artopilium* (Nishimura 1990: figs 18.1, 18.2; Sugiyama 1994: pl. 3, fig. 5), *Ectotoxon* (Sugiyama 1994: pl. 3, fig. 4, pl. 4, figs 1, 2) and *Stichopilium* (Nishimura & Yamauchi 1984: pl. 35, fig. 14; Sugiyama 1998: pl. 6, fig. 2). All genera belonging to the Stichopiliidae were not treated by De Wever *et al.* (2001). The arches of the cephalic initial spicular system seem to be different at the genus or species level. The Mesozoic families Foremanellinidae Dumitrica 1982a and Cuniculiformidae De Wever 1982a are similar to the Stichopiliidae except for the presence of double l-rods in the Mesozoic families. These families both have two significant apical horns related to the A- and V-rods and also share a similarity in the segmentation or undulation patterns associated with Stichopiliidae. If these families are phylogenetically connected to the Stichopiliidae, fossil records from the Berriasian (Early Cretaceous) to the early Oligocene are missing. A "Living" image has been illustrated for "*Dictyocodon*" *prometheus* by Sugiyama *et al.* (2008: figs 2, 8) but no appropriate genus name currently exists for this species. The evolution of the Stichopiliidae has not been studied, probably due to many undescribed species (e.g., Lazarus 1992: pl. 9, figs 9-17).

Validity of genera

Artopilium

Campbell (1954: D136) incorrectly validated *Trictenartus* as an objective synonym of *Artopilium*. Nigrini (pers. comm.) left notes indicating that Campbell (1954: D136) had designated *Artopilium elegans* Haeckel, 1887 as the type species of *Trictenartus* solely by the inference of *Artopilium*. Therefore, we consider the type species designation of *Artopilium* to date from Chediya (1959: 226).

Stichopilium

Campbell (1954: D136) validated *Triacartus* as an objective synonym of *Stichopilium*. However, Frizzell & Middour (1951: 31-32) had already validated *Stichopilium*, but not *Triacartus*. Therefore, following the first reviser rule, *Stichopilium* is the valid genus name.

Superfamily Plagiacanthoidea Hertwig, 1879

Plagiacanthiden [*sic*] Hertwig, 1879: 200-202 (= Plagiacanthidae) [as a family].

Cystidiicae [*sic*] – Campbell 1954: D103 (= Cystidioidea) [as a superfamily].

Plagoniicae [*sic*] – Campbell 1954: D103 [*nomen dubium*] (= Plagonioidea) [as a superfamily].

Sethopiliilae Campbell, 1954: D122 [*nomen dubium*, as a subsuperfamily]. — Nakaseko 1957: 27 [as a subsuperfamily]. — Dieci 1964: 187 [as a subsuperfamily].

Plagoniacea [*sic*] – Loeblich & Tappan 1961: 227 [*nomen dubium*] (= Plagonioidea) [as a superfamily].

Plagiacanthoidea – Petrushevskaya 1971a: 57-65; 1971b: 988; 1975: 589; 1981: 61-62; 1986: 132. — Petrushevskaya & Kozlova 1972: 534. — Goll 1979: 379 (*sensu* emend.). — Matsuzaki *et al.* 2015: 42. — Sandin & Suzuki *in* Sandin *et al.* 2019: 201 (*sensu* emend.).

Diagnosis. — Plagiacanthoidea having one or two segments and several arches. The cephalic initial spicular system consists of MB, A-, V-, double L- and Ax-rods. The double l-rods are generally absent. The V-rod may be degraded in intra-genera or infra-genus variations. The presence or absence of other main rods of the cephalic initial spicular system, as well as the presence of arches is highly variable depends on taxa within this superfamily. These cephalic arches may be free inside the cephalic cavity, embedded in the cephalic wall, or both.

Remarks

The Plagiacanthoidea consist of the Ceratocyrtidae, Dictyocryphalidae Suzuki, n. fam., Dimelissidae, Phaenocalpididae, Plagiacanthidae, Pseudodictyophimidae Suzuki, n. fam., Tripodisciidae and Ximolzidae Dumitrica, nom. nov. The taxonomic position of all families, except the Tripodisciidae, is based on molecular phylogeny analyses of Sandin *et al.* (2019). The taxon names at family-, genus- and species-levels for Plagiacanthoidea are the most difficult to determine among Nassellaria. This is due to several problems: a) the different published schematic drawings of the cephalic initial spicular system for the same genus, or even for the same species; b) the technical difficulties to identify the representatives of this superfamily under transmitted light microscopy; and c) the existence of many undescribed genera and species in this superfamily.

The evolution of nassellarians through time has shown the importance of the cephalic initial spicular system for the classification at the family rank. However, this principle does not apply to the Plagiacanthoidea. The principal distinguishing feature of Plagiacanthoidea at the genus level is the presence or absence of rods and/or arches of the cephalic initial spicular system (Petrushevskaya 1971a; Sugiyama 1992a, 1993, 1994; O'Connor 1997b). Essentially, this difference requires that rods and/or arches must vary amongst genera, leading to the logical conclusion that the cephalic initial spicular system is unstable at the genus level in the Plagiacanthoidea. This was written in several papers (e.g., Funakawa 1995a, b; O'Connor 1997a, b, 1999). Furthermore, detailed studies indicate that the architecture and combination of the arches are variable within the same genus (Funakawa 1994, 2000).

Several papers published very different schematic drawings for the same genus or even the same species, proning the users to confusion. Sugiyama (1998) mentioned that several papers erroneously drew a combination of cephalic initial spicular systems. Thus, the evidence images must be carefully examined by the users. This discrepancy can be partially explained by the differences among major studies of Funakawa, O'Connor and Sugiyama. Sugiyama focused on identifying the commonalities in the cephalic initial spicular system at the genus level, whereas Funakawa concentrated on the differences at the species or intra-species level. The methodology followed by O'Connor is a combination of both approach of Japanese researchers. Nishimura (1990) occasionally observed nearly invisible rods of the cephalic initial spicular system and hypothesized that some of these were buried in the cephalic wall during the ontogenesis. This hypothesis should be treated carefully as few to no objective evidence was presented in many cases.

Most taxonomic studies on Plagiacanthoidea were based on scanning electron microscopy (SEM) images; hence the problem for identification of Plagiacanthoidea under transmitted light microscopy. Funakawa and Sugiyama, specialists of the Plagiacanthoidea, explained the process of identifying the specimens to one of the authors (N.S.). They stressed that the identification of the Plagiacanthoidea at species and genus levels is in fact possible under a light microscope (see for example the new taxa described in the Southern Ocean by Renaudie & Lazarus 2012; 2013; 2015; 2016).

Even if it is possible to identify Plagiacanthoidea under a light microscope, anatomical knowledge is essential in understanding their taxonomy. An accurate taxonomy for the Plagiacanthoidea should consider the following aspects: 1) the collar stricture between cephalis and thorax which is independently determined from the position of MB; 2) the presence of a cephalic wall; 3) a cephalic initial spicular system consisting of MB, A-, D-, V-, double L-, double l-, Ax-rods, and several arches; 4) the presence/absence of rods and arches, and their development, which are also important in identifying similar genera but not as critical in many cases due to preexisting knowledge of infra-generic variation; 5) the overall similarity among species that may lead to critical misidentifications; 6) the spinules on each rod that are coded as (a) "*a*", "*m*" and "*g*" on A-rod from the near end of MB, (b) "*j*" and "*f*" on V-rod from the near end of MB, (c) "*p*" and "*d*" on L-rod from the near end of MB, (d) "*c*" on D-rod, and (e) "*t*" on l-rod; 7) the name of the arch can be coded with major rods names (e.g., AV-arch) when the exact position is not necessary to be signaled; however, if the exact position of the arch is needed, the arch must be coded with the code of spinules (e.g., *aj*-arch but not AV-arch); 8) the presence of additional arches, occasionally developed on other arches; and 9) stress the differences between "primary arch" (if both ends of the arch arise from the coded rods) from "secondary arch" (if only one end is arising from the coded spinules) and "third arch" (if neither of the two ends are arising from any coded spinules).

This superfamily was ranked at the family level (Petrushevskaya 1971a; Sugiyama 1994; 1998; Funakawa 1994). This group was also raised at the superfamily level to include Mesozoic member (Petrushevskaya 1981). Later, this superfamily was disassembled again (De Wever *et al.* 2001). Molecular phylogenetic results (Sandin *et al.* 2019) classified one distinctive group as Clade G (100% PhyML bootstrap values with 10 000 replicates (BS) and >0.99 posterior probabilities) including *Archiscenium* (Phaenocalpididae), *Ceratocyrtis* and *Lipmanella* (Ceratocyrtidae), *Archiperidium*, *Peromelissa* and *Lithomelissa* (Dimelissidae), *Dictyocryphalus* and *Pseudodictyophimus* (Pseudodictyophimidae Suzuki, n. fam.), *Protoscenium* (Ximolzidae Dumitrica, nom. nov.), and *Pseudocubus* (Plagiacanthidae). The aforementioned genera cannot be separated within Clade G due to the small values in BS or PP. This indicates that the morphological differences are larger than the molecular difference for the complete 18S and partial 28S sequences (D1-D2 region). This suggests that (a) these genera should be regarded as a single group and that (b) an approach with morphological differences should be prioritized for the Clade G. Clade G is assigned to the superfamily level in consideration of taxonomic hierarchy consistency for Mesozoic families of Nassellaria.

Plagiacanthoidea are the most diversified Nassellaria in both environmental DNA (Sandin *et al.* 2019) and relative year-round abundance (Motoyama *et al.* 2005; Ikenoue *et al.* 2015) at every latitude (Boltovskoy *et al.* 2010) and depth (Boltovskoy 2017). Despite this diversity and abundance, the establishment of a taxonomic framework has not been completed yet.

Family Ceratocyrtidae Petrushevskaya, 1981 n. stat. *sensu* Caulet emend. herein

Ceratocyrtinae Petrushevskaya, 1981: 108-109. — Afanasieva *et al.* 2005: S295. — Afanasieva & Amon 2006: 143-144.

Type genus. — *Ceratocyrtis* Bütschli, 1882: 536 [type species by subsequent designation (Petrushevskaya 1971a: 98): *Cornutella*? *cucullaris* Ehrenberg, 1874: 221].

Included genera. — *Ceratocyrtis* Bütschli, 1882: 536 (= *Bathrocalpis* synonymized by Petrushevskaya 1971a: 98; *Helotholus* synonymized by Petrushevskaya 1975: 587). — *Entepipedus* Sugiyama, 1994: 6. — *Gomisterna* Sugiyama, 1994: 8. — *Gondwanaria* Petrushevskaya, 1975: 584. — *Lipmanella* Loeblich & Tappan, 1961: 226. — ? *Periarachnium* Haeckel, 1882: 430. — ? *Phlebarachnium* Haeckel, 1882: 430.

Junior homonym. — *Dictyoceras* Haeckel, 1862 (= *Lipmanella*) *nec* Eichwald, 1860.

Diagnosis. — Ceratocyrtidae are described as Plagiacanthoidea with a very small cephalis and a large thorax or relevant shell. Apical horn and wings may be present or absent. No feet are observed. The collar stricture is located above the MB's level. The MB generally rises to the apical side with the double L-rod that extends horizontally. The double l-rod is present in most members. The double AL-arch forms part of the collar stricture or appears as a horizontal line near the bottom of the cephalic wall. The architecture of the cephalic initial spicular system is variable within the family: a crowned ring above MB, made of double VL- and AL-arches is present in *Ceratocyrtis, Gomisterna* and *Gondwanaria*; while a basal ring, made of double LV- and Ll-arches, is found free from the shell wall in *Lipmanella*. The transparent to colored endoplasm forms long lobes below the cephalis. A gelatinous matter covers the shell in *Phlebarachnium*. No algal symbionts are found in *Ceratocyrtis* and *Lipmanella*, while plenty of algal symbionts surround the shell of *Phlebarachnium*.

Stratigraphic occurrence. — Late Paleocene-Living.

Remarks

All the genera, except for *Ceratocyrtis*, were not treated in De Wever *et al.* (2001). Petrushevskaya (1981) established the subfamily "Ceratocyrtinae" with the following members *Antarctissa*, *Ceratocyrtis*, *Gondwanaria*, *Periarachnium*, *Phlebarachnium* and *Pseudodictyophimus*. *Antarctissa* and *Pseudodictyophimus* were excluded herein based on the different architecture of their cephalic initial spicular system. In contrast, *Entepipedus*, *Gomisterna* and *Lipmanella* with double l-rod or double AL-arch that form a horizontal line in the lower part of the cephalis were included.

The cephalic initial spicular system has been well documented in *Ceratocyrtis* (Petrushevskaya 1986: pl. 1, fig. 1; Sugiyama 1993: figs 20.4-20.6, 23.1; Sugiyama & Furutani 1992: pl. 18, fig. 6; pl. 20, fig. 2; Sugiyama *et al.* 1992: pl. 15, figs 2-3; Funakawa 1994: fig. 7.1; 1995a; pl. 1, figs 4, 5), *Entepipedus* (Sugiyama 1994: pl. 4, fig. 4), *Gomisterna* (Sugiyama 1994: pl. 5, fig. 1), *Gondwanaria* (Nishimura 1990: fig. 17.4-17.6; Sugiyama *et al.* 1992: pl. 21, fig. 9; Funakawa 2000: pl. 1, figs 1-3; pl. 2, figs 1-3), *Lipmanella* (Nishimura & Yamauchi 1984: pl. 35, fig. 3; Sugiyama & Furutani 1992: pl. 17, fig. 1; Funakawa 2000: pls 3-6), and *Periarachnium* (Aita *et al.* 2009: pl. 5, fig. 7c). *Entepipedus* has a very particular cephalic initial spicular system, thus, its exact taxonomic position is unknown.

"Living" or protoplasmic images were reported for *Ceratocyrtis* (Sashida & Kurihara 1999: fig. 12.9; Zhang *et al.* 2018: 15, fig. 3? , 4), *Lipmanella* (Matsuoka *et al.* 2001: pl. 1, fig. 3; Matsuoka 2007: fig. 5c; Sashida & Kurihara 1999: fig. 11.3; Suzuki & Aita 2011: fig. 5O; Suzuki & Not 2015: figs 8.4.2, 8.10.6; Zhang *et al.* 2018: 15, fig. 15, p. 21, fig. 7, p. 23, fig. 12), and *Phlebarachnium* (Aita *et al.* 2009: pl. 30, figs 5a-5d, p. 32, fig. 4; Zhang *et al.* 2018: 21, fig. 13).

Validity of genus

Ceratocyrtis

The taxonomic confusion problem between *Bathrocalpis*, *Ceratocyrtis* and *Helotholus* sometimes arises in questions. The discussion in Matsuzaki *et al.* (2015) was based on the "lectotype" of *Helotholus histricosus* by Dolven *et al.* (2014). This "lectotype" was different from the type-illustration of Jørgensen (1905) because it lacks a neck at cephalis position. An important Southern Ocean species, "*Helotholus vema*", does not belong to *Helotholus* or *Ceratocyrtis* but is similar to *Steganocubus*. Sugiyama (1993: 69) had already noticed the necessity of further studies to resolve these taxonomic inconsistencies.

Family Dictyocryphalidae Suzuki, n. fam.

urn:lsid:zoobank.org:act:C897A495-6E6C-4149-84CE-1324AF0AF58C

Lophophaenida Haeckel, 1882: 430 [*nomen dubium*, below tribe].

Lithobotryida Haeckel, 1887: 1107, 1111-1112 [*nomen dubium*, as a family]. — Bütschli 1889: 1983 [as a family]. — Anderson 1983: 29 [as a family].

Lithobotryidae Poche, 1913: 222 [*nomen dubium*]. — Schröder 1914: 143. — Chediya 1959: 186. — Cachon & Cachon 1985: 295. — Chen *et al.* 2017: 173.

Lophophaenidae – Campbell 1954: D128 [*nomen dubium*]. — Petrushevskaya & Kozlova 1972: 534. — Dumitrica 1979: 30. — Blueford 1988: 246. — Nishimura 1990: 85, 87 (*sensu* emend.). — Sugiyama 1993: 51. — Dumitrica 1995: 28. — van de Paverd 1995: 217. — Sugiyama 1998: 233. — De Wever *et al.* 2001: 224, 226. — Matsuzaki *et al.* 2015: 42.

Lophophaeninae – Campbell 1954: D128 [*nomen dubium*]. — Dieci 1964: 187. — Petrushevskaya 1971a: 86-91; 1971b: 989; 1981: 87-88. — Takahashi 1991: 96. — Hollis 1997: 55. — Afanasieva *et al.* 2005: S292. — Afanasieva & Amon 2006: 139.

Type genus. — *Dictyocryphalus* Haeckel, 1887: 1308 [type species by subsequent designation (Campbell 1954: D128): *Cornutella*? *obtusa* Ehrenberg, 1844a: 77].

Included genera. — *Antarctissa* Petrushevskaya, 1967: 85. — *Botryopera* Haeckel, 1887: 1108 (= *Trisulcus* synonymized by Petrushevskaya 1975: 591). — *Dictyocryphalus* Haeckel, 1887: 1308 (= ? *Cephaluspinus* **n. syn.**). — *Nomina dubia*. — *Lithobotrys*, *Lophophaena*, *Lophophaenoma*, *Lophophaenula*.

Junior homonyms. — *Dictyocephalus* Ehrenberg, 1861 (= *Dictyocryphalus*, Ehrenberg 1861b) *nec* Leidy, 1859; *Discocephalus* Ehrenberg, 1861 (= *Dictyocryphalus*, Ehrenberg 1861b) *nec* Ehrenberg *in* Hemprich & Ehrenberg, 1829.

Diagnosis. — Dictyocryphalidae Suzuki, n. fam. are two segmented Plagiacanthoidea. The thoracic part with a neck or a suture is generally present. No feet and rarely three spinule-like wing rods from A- and double L-rods are present. The shell is subdivided at variable degrees into a post-lobe on the most apical side of the A-rod, a eucephalic lobe in the space between the A- and V-rods, and an ante-lobe on the more ventral side of the V-rod. In well-developed specimens, the eucephalic lobe is bounded by two arches from both the post- and ante-lobes. The level of the neck and the boundary of the eucephalic lobe are always located above the MB's level. Both post- and ante-lobes usually develops between the MB and the thoracic part. The cephalic spicular system consists of MB, A-, V-, D-, double L- and Ax-rods. The double l-rod is generally absent. The MB is very short or degrades, becoming a pointed connection (PC) with D- and double L-rods. The PC (or MB) is located in the center of the cephalic cavity. The V-rod is rarely absent at genus or species levels. A basal ring does not exist. Instead, a cephalic basal ring-like structure is connected by the A-rod, V-rod, and several supplemental connecting rods that arise from both the double L-rod and D-rod. Due to the development of basal ring-like structure, true double AL- and double LV-arches are absent. In this case, the arches are coded as A', double L', l'-rod. This basal ring-like structure is isolated from the cephalic wall that is joined by many rods around the basal ring. The Ax-rod is very short, except for in the case of *Antarctissa*. No tubes are found on the cephalis. A-rod is merged to the cephalis. It may also be partly or fully free in the cephalic cavity. If the AL'- and L'V-arches are merged with the shell wall, sutures form on both sides of the eucephalic lobe.
The protoplasm was examined in *Dictyocryphalus*. The endoplasm is transparent or brown, yields multi nuclei, and occupies the cephalis, and part of the thorax depending on specimens. If present, algal symbionts are scattered outside the shell. No axopodial projection was found so far.

Stratigraphic occurrence. — early Middle Eocene-Living.

Remarks

Except for *Dictyocryphalus*, the genera of the Dictyocryphalidae Suzuki, n. fam. have stable, cephalic initial spicular and arch system components. The Dictyocryphalidae Suzuki, n. fam. are characterized by the presence of a basal-ring like structure and a retrograding MB or three-pointed AC. *Dictyocryphalus* has variable systems at the species or infra-species level with the presence of a basal ring that is directly connected with the D- and double L-rods, - the presence of double Al- and double DL-arches, - the presence of double VL-arch instead of DL-arch, - the rare presence of an l-rod, - or the absence of lobes. Some unstable characters found in *Dictyocryphalus* are also observed in representatives of *Dimelissidae*. The Dictyocryphalidae Suzuki, n. fam. is easily distinguished from the Pseudodictyophimidae Suzuki, n. fam. by the absence of three feet.

There was some confusion among the genera of the Dictyocryphalidae Suzuki, n. fam., and between the *Dimelissidae* and the Dictyocryphalidae Suzuki, n. fam. (e.g., *Dictyocryphalus* vs *Lithomelissa*; *Botryopera* vs *Amphimelissa*). Rapid examinations of the presence of a cephalic basal-ring structure and an absence of AL- and DL-arches are unrealistic. The A-rod is not free in the cephalic cavity of *Dictyocryphalus* whereas it is free in the cephalic cavity of *Lithomelissa* (Dimelissidae). Three lobate cephalis are similar in *Botryopera* and in *Amphimelissa* (Pylobotrydidae). Differing from *Botryopera*, *Amphimelissa* develops a double l-rod and a multicamerate cephalis that is larger than the thorax. As with the Dimelissidae, all the genus members of the Dictyocryphalidae Suzuki, n. fam. except *Antarctissa* (Petrushevskaya 1986) remain unconfirmed by the stratigraphic distribution of these genera and species. Moreover, many genera and species remain undescribed.

The cephalic initial spicular system was documented in *Antarctissa* (Petrushevskaya 1986: pl. 1, fig. 9), *Botryopera* (Sugiyama 1993: figs 14-17), *Dictyocryphalus* (Caulet 1974: pl. 9, figs 4-6? ; Nishimura 1990: figs 17.1-17.3, 18.3? ; Sugiyama *et al.* 1992: pl. 16, figs 6, 7; Sugiyama 1993: fig. 23.2; 1994: pl. 5, figs 3, 4? ; Funakawa 1994: figs 8.1, 8.2, 8.4; 2000: pl. 1, fig. 4 [wrong plate number is indicated on the true plate 1]; Nishimura & Yamauchi 1984: pl. 32, fi. 6; O'Connor 1997a: pl. 6, figs 6, 7, 8? , 9). Living or protoplasm images were illustrated for *Dictyocryphalus* (Matsuoka 1993a: fig. 2.6; Ogane *et al.* 2010: figs 1.6, 1.7; Suzuki & Aita 2011: fig. 5L; Matsuoka 2017: fig. 22; Matsuoka *et al.* 2017: appendix B; Zhang *et al.* 2018: 10, figs 6, 8, p. 19, fig. 28).

The taxonomic validity of the "Lophophaenidae" involves very complex problems which include the (A) validity of the type species of *Dictyocryphalus* Haeckel 1887; the (B) validity of the type species of *Lophophaena* Ehrenberg 1847; and (C) the possible designation of a neotype for *Lophophaena*. The type species of *Dictyocryphalus* is *Cornutella*? *obtusa* Ehrenberg 1844a designated as such by Campbell (1954: D128) as an objective synonym of *Dictyocephalus*. The name-bearing specimen was first published by Ehrenberg (1854c: pl. 22, fig. 40). The type locality of *D. obtusus* (Ehrenberg) is Caltanisetta, West of Sicily (Ehrenberg 1844a: 77), and thus the type specimens were expected to be preserved in Ehrenberg's slide tray K28B06 (Suzuki *et al.* 2009c: 88) in the Ehrenberg collection. The slide series of "Caltanisetta" (K28B06) was highly damaged and many slides of the Caltanisetta are missing. For this reason, Suzuki *et al.* (2009c) examined all the pieces of the slides, including two-millimeter fragments, and took photographs of all the encountered radiolarian specimens, published in pls 1-21 of Suzuki *et al.* (2009c). Following this observation, the type specimens appear to be completely missing. Instead, the most similar morphotypes are illustrated in pl. 20, figs 13b-14 of Suzuki *et al.* (2009c), but their designation of neotype was unlikely because the slides in K28B06 almost completely missing. No raw samples are archived in NfM. The sample locality information is noted in Ehrenberg (1839: 78), but the specification of the locality was unhelpful. Some papers illustrated radiolarians from Sicily (Riedel & Sanfilippo 1978b; Sanfilippo *et al.* 1978, 1985; Cortese & Bjørklund 1999). The morphotype that most closely resembles *D. obtusus* from Caltanisetta was illustrated in Cortese & Bjørklund (1999: figs 21.P-21.R). If we compare pls 1-21 of Suzuki *et al.* (2009c) with the figures 20-22 of Cortese & Bjørklund (1999), the fauna appears to be nearly identical, and it may be tentatively concluded that figs 21.P-21.R of Cortese & Bjørklund (1999) represent the true *D. obutsus* as a potential neotype.

A second encountered problem is the type species of *Lophophaena*. The genus *Lophophaena* was established by Ehrenberg (1847) without any included species, and the first assigned species was "*Lophophaena Galea Orci*" as a monotype (Ehrenberg 1854b: 245). Thus, this species automatically becomes the type species of *Lophophaena*. The name-bearing specimen was noted as "Ex abysso 12000 ped" in the description (Ehrenberg 1854b), meaning "from 12,000 fathoms in deep". The fact that the sample information written in Ehrenberg (1854a: table) is noted as 8160' and not 12000' is bizarre. The mismatch of type locality is another new problem. Putting aside a sample mismatch, the exact sample locality for "*Lophophaena Galea Orci*" are the samples from "42 41'N, 24 35'W, 18 July, 1360 Fath-6480'" or "54 17'N, 22 33'W 22 Aug. 2000 Fath-12000'" (Ehrenberg 1854a: 60). Based on these disparate localities, a new problem arises. Following these papers as well as the internal documents in NfM, potential type series could be found in "Meersgrund II (K27B02)" or "Meersgrund II (K27B03)" (Suzuki *et al.* 2009c: 90). All the specimens assigned by Ehrenberg himself are photographed on pl. 30 for K27B02 and pls 31-36 for K27B03 in Suzuki *et al.* (2009c). The exact sample information is specified on these trays (K27B02 and K27B03). Congruently, any type-bearing specimens for "*Lophophaena Galea Orci*" could not be found in the slides. An additional problem stems from the publication. Campbell (1954: D128) falsely indicates "*Lophophaena galea* Ehrenberg, 1854a" as the subsequent type species of *Lophophaena*. This species has not been formally described and is therefore a *nomen nudum*. Some papers cite pl. 8, figs 12 of Ehrenberg (1876) as "*Lophophaena galea*" but the name on the plate explanation is "*Lophophaena*? *galeata*" which was first described by Ehrenberg (1874: 242-243). In addition, the specimen illustrated in Ehrenberg (1876: pl. 8, fig. 12) is from Barbados and it is not from the true locality of "*L. Galea Orci*." Thus, the correct name-bearing specimen has not been illustrated and has not been preserved in the Ehrenberg collection, resulting in the assigned status as *nomen dubium*.

Validity of genera

Dictyocryphalus

The translated diagnosis from the original Spanish for *Cephaluspinus* follows. "*Shell campanulate sub-divided into cephalis and thorax. Surface perforated by sub-circular pores of different size and irregularly distributed. Cephalis with many spines, some larger than others, some of which are apparently broken in the analyzed specimen. The other part of the shell is smooth, except for the basal part, which has spines, or feet, that are in fact externally prolonged terminations of the pore frames. These feet are numerous, approximately 20, and shorter than the cephalic spines.*" Petrushevskaya (1981: 90) considered *Cephaluspinus* a subjective synonym of *Lophophaena* because its morphological characteristics correspond entirely to that of *Lophophaena*. As *Lophophaena* (*sensu* Petrushevskaya 1981) corresponds to *Dictyocryphalus* under the strict ruling under the Code (see the remarks in the Dictyocryphalidae Suzuki, n. fam.), the synonymy has been simply replaced by *Dictyocryphalus*. However, this synonymy cannot be precisely determined because the initial spicular system of *Cephaluspinus* is unknown.

Family Dimelissidae Petrushevskaya, 1981 n. stat. *sensu* Caulet emend. herein

Dimelissinae Petrushevskaya, 1981: 82; 1986: 132. — Afanasieva *et al.* 2005: S292. — Afanasieva & Amon 2006: 139.

Sethopilida Haeckel, 1882: 431 [*nomen dubium*, as a tribe]; Haeckel 1887: 1192, 1194, 1195 [as a subfamily].

Spongolarcida Haeckel, 1887: 606, 613 [*nomen dubium*, as a subfamily]. — Schröder 1909: 52 [as a subfamily].

Sethopilinae [*sic*] – Clark & Campbell 1942: 65 [*nomen dubium*] (= Sethopiliinae); Clark & Campbell 1945: 37. — Campbell & Clark 1944a: 41; 1944b: 23. — Chediya 1959: 199. — Tan & Tchang 1976: 274. — Chen *et al.* 2017: 182.

Spongolarcinae – Campbell 1954: D96 [*nomen dubium*]. — Chediya 1959: 152.

Sethopiliidae – Campbell 1954: D122 [*nomen dubium*].

Sethopiliinae – Campbell 1954: D122 [*nomen dubium*]. — Petrushevskaya 1981: 74-75. — Afanasieva *et al.* 2005: S292. — Afanasieva & Amon 2006: 139.

Type genus. — *Dimelissa* Campbell, 1951: 529 [type species by subsequent designation according to ICZN 1999, art. 67.8 (Campbell 1951: 529): *Lithomelissa thoracites* Haeckel, 1861b: 836] = junior subjective synonym of *Peromelissa* Haeckel, 1882: 433 [type species by subsequent designation (Campbell 1954: D124): *Peromelissa phalacra* Haeckel, 1887: 1236].

Included genera. — *Arachnocorys* Haeckel, 1861b: 837 (= *Arachnocoronium* with the same type species; *Acanthocoronium* **n. syn.**). — *Archiperidium* Haeckel, 1882: 429. — *Cryptogyrus* Sugiyama, 1993: 65. — *Lithomelissa* Ehrenberg, 1847: 54 (= *Acromelissa* synonymized by Petrushevskaya 1975: 592). — *Peromelissa* Haeckel, 1882: 433 (= ? *Dicorys* synonymized by Petrushevskaya 1981: 84; ? *Micromelissa* Haeckel, 1882 *nec* Haeckel, 1887, *Psilomelissa* synonymized by Petrushevskaya 1971a: 133; *Dimelissa* synonymized by Matsuzaki *et al.* 2015: 44). — *Phormacantha* Jørgensen 1905: 132. — *Plectacantha* Jørgensen, 1905: 131.

Invalid name. — *Amphicryphalus.*

Nomina dubia. — *Acanthocorallium*, *Acanthocorythium*, *Acanthocorys*, *Amphicentria*, *Amphiplecta*, *Arachnocorallium*, *Arachnocorythium*, *Mitrocalpis*, *Peridarium*, *Peridium*, *Sethomelissa*, *Sethopilium*, *Spongolarcus*.

Junior homonym. — *Micromelissa* Haeckel, 1887 (= *Dimelissa*) *nec* Haeckel, 1882.

Diagnosis. — Anatomically, Dimelissidae are two-segmented Plagiacanthoidea with a well-developed first segment (cephalis) and a less developed, sometimes absent, second segment (thorax). The cephalis, mono-chambered, is separated from the thorax and bears

well-developed A, V, and double L-rod. No cephalic lobes develop. The cephalic initial spicular system consists of MB, A-, V-, D-, and double L-rods. The double l-rod is generally absent. The MB is very short or degraded at a pointed connection (PC). The PC tends to be located on the apical side of the test. The MB, if present, is located near the apical side. The D- and double L-rods are oriented at an even angle at 180 degrees from PC. The most constricted level (neck) of the shell is always located above the MB's level. The A-rod merges into the cephalic wall, or may be partly or fully free in the cephalic cavity. Double AL- and double LV-arches are generally present. As both A- and V-rods are oriented upward, both double AL-arches and double LV-arches also rise upward. AL-arches and VL-arches merge with the cephalic wall or are freely located inside the cephalic cavity. However, these arches never form sutures on the cephalic wall. If AL-arches merged with the cephalic wall, they tend to form larger pores than other pores found on the shell. The Ax-rod is present. A basal ring rarely develops in some species and is directly connected with the D- and double L-rods to form three collar pores. In this case, the basal ring is located below the MB's level.
Protoplasm was observed in *Arachnocorys*, *Cryptogyrus*, *Peromelissa* and *Plectacantha*. The endoplasm is transparent to yellowish transparent and located within the cephalis (at variable degrees) and at least in the upper part of the thorax. In some species including *Arachnocorys*, multi nuclei are observed. Algal symbionts are present inside the cephalis of *Arachnocorys*, but no algal symbionts are found in *Cryptogyrus*, *Peromelissa* and *Plectacantha*.

Stratigraphic occurrence. — late Middle Eocene-Living.

Remarks

Differing from the Pseudodictyophimidae Suzuki, n. fam., the Dimelissidae lack a cephalic structure such as a basal ring. This family can be divided into three groups: In the first instance, the cephalis is well-developed, sometimes with an open upper part and an arachnoid wall (*Arachnocorys*, *Archiperidium*, *Cryptogyrus*, *Phormacantha*, *Plectacantha*). The cephalis also bears strong extensions of the main rods arising from MB. The thorax is short, considerably reduced, and mostly constituted by extensions of the D- and double L-rods. In the second, the cephalis is globular and closed, with a wall perforated by small circular pores (*Lithomelissa*, *Peromelissa*). No robust feet are present. A strong horn is inserted mostly laterally. The thorax is more developed, with pores and D- and double L-rods both present. Finally, the third instance included *Archiperidium*, *Cryptogyrus* and *Phormacantha*). It is extremely difficult to differentiate the Dimelissidae from the Pseudodictyophimidae Suzuki, n. fam. due to an extensive similarity in overall shape. True feet are not developed in Dimelissidae; however, this character is also observed in some genera of Pseudodictyophimidae Suzuki, n. fam. (*Pseudodictyophimus* and *Tripodocyrtis*). The most significant difference between the Dimelissidae and the Pseudodictyophimidae Suzuki, n. fam. is the absence of lobes in the cephalis. The Dimelissidae lack cephalic lobes. However, some lobes are absent or poorly developed in several genera of the Pseudodictyophimidae Suzuki, n. fam. (*Steganocubus* and *Syscioscenium*).

The cephalic internal spicular system of many genera in this family was illustrated but the genus names used must be revised. This revision is necessary due to the complex internal structures, the wrongly recognized type-species, and the use of a genus name that was defined by un-illustrated type species. After our re-examination of the genus position, the cephalic internal spicular system of the following genera has been well illustrated: "*Amphicryphalus*" (Funakawa 1995a: pl. 1, figs 1-3), "*Amphiplecta*" (Nishimura 1990: fig. 14.6-14.8, 19.4?; Funakawa 1994: figs 6, 7.2-7.3; Nishimura & Yamauchi 1984: pl. 24, fig. 2), *Archiperidium* (Nishimura & Yamauchi 1984: pl. 23, figs 1-3), *Arachnocorys* (Nishimura & Yamauchi 1984: pl. 24, figs 10, 11; Nishimura 1990: figs 14.1-14.4, 16.2, 16.3? , 16.4? ; Takahashi 1991: pl. 26, fig. 6; Sugiyama *et al.* 1992: pl. 18, fig. 4), *Cryptogyrus* (Sugiyama 1993: figs 19.1-19.5, 20.1-20.2), "*Helotholus histricosa*" (Dumitrica 1973a: pl. 12; Lazarus 1990: pl. 7, figs 1-5; Nishimura & Yamauchi 1984: pl. 24, fig. 9), *Lithomelissa* (Nishimura & Yamauchi 1984: pl. 32, fig. 5; Nishimura 1990: figs 15.1, 15.2, 15.4-15.8, 16.1, 16.5? ; Takahashi 1991: pl. 26, fig. 3? ; Sugiyama *et al.* 1992: pl. 17, fig. 1; Funakawa 1995b: figs 10.3, 10.4; O'Connor 1999: pl. 2, figs 23-27), "*Peridium*" (Funakawa 1994: fig. 11.1, 11.2; Nishimura 1990: fig. 13.8-13.11; Takahashi 1991: pl. 26, fig. 4; Funakawa 1995a: pl. 2, figs 1-4, pl. 3, figs 1-4), *Peromelissa* (Nishimura & Yamauchi 1984: pl. 24, fig. 7, pl. 32, fig. 4) and *Plectacantha* (Nishimura & Yamauchi 1984: pl. 22, figs 11-13). However, the generic combination of the Dimelissidae has not been supported by any form of objective phylogenetic evidence. Furthermore, molecular phylogenetic studies do not provide a sufficient resolution to resolve this issue, and as of yet, many genera remain undescribed. "Living" or protoplasm image were illustrated for *Arachnocorys* (Zhang *et al.* 2018: 9, figs 23, 24), *Cryptogyrus* (Sashida & Kurihara 1999: figs 11.7, 11.16; Suzuki & Aita 2011: fig. 5M; Zhang *et al.* 2018: 15, fig. 6, p. 19, fig. 18), *Peromelissa* (Sashida & Kurihara 1999: figs 11.4, 12.10; Suzuki & Not 2015: fig. 8.11.9; Matsuoka 2017, fig. 21; Zhang *et al.* 2018: 15, figs 7, 17, 18, p. 21, figs 14-17), and *Plectacantha* (Suzuki *et al.* 2009b: figs 2K, 2L). *Lithomelissa* may be infected with Marine Alveolata Group I (Ikenoue *et al.* 2016).

Validity of genera

Arachnocorys

Arachnocorys is characterized by a shell enveloped by a web-like network (Campbell 1954: D126), whereas the *Acanthocoronium* shell is enveloped by a simple network (Campbell 1954: D125). A web-like network around the cephalis is not always present in *Arachnocorys* specimens, which indicates intraspecific variation in ontogenetic growth. *Arachnocorys* is the oldest available name among all synonyms.

Family Phaenocalpididae Haeckel, 1887
sensu Caulet emend. herein

Phaenocalpida Haeckel, 1887: 1133, 1157-1158 [as a family]. — Bütschli 1889: 1984 [as a family]. — *nec* Rüst 1892: 179 [as a family].

?Archiperida Haeckel, 1882: 429 [as a tribe]; 1887: 1133, 1134, 1146 [as a subfamily]. — Wisniowski 1889: 686 [as a subfamily].

Phaenocalpididae – Poche 1913: 220.

Phaenocalpidae [*sic*] – Popofsky 1913: 331 (= Phaenocalpididae). — Schröder 1914: 91. — Clark & Campbell 1942: 64; 1945: 34. —

Campbell & Clark 1944a: 39; 1944b: 21. — Dogiel & Reshetnyak 1955: 47. — Chediya 1959: 192. — Tan & Chen 1999: 291. — Tan & Su 2003: 113, 120. — Chen *et al.* 2017: 178.

?Archiperinae – Campbell 1954: D118. — Chediya 1959: 190.

Clathromitrinae Petrushevskaya, 1971a: 69-71; 1981: 63. — Funakawa 1995b: 211. — Afanasieva *et al.* 2005: S291-292. — Afanasieva & Amon 2006: 138.

Clathromitridae – Petrushevskaya 1981: 62-63.

TYPE GENUS. — *Phaenocalpis* Haeckel, 1887: 1173 [type species by subsequent designation (Campbell 1954: D120): *Phaenocalpis petalospyris* Haeckel, 1887: 1173].

INCLUDED GENERA. — ? *Archipera* Haeckel, 1887: 1155. — *Archiscenium* Haeckel, 1882: 429 (= *Euscenium* **n. syn.**; *Euscenarium* **n. syn.**, *Plectoscenium;* **n. syn.**). — *Clathromitra* Haeckel, 1882: 431. — *Conicavus* Takahashi, 1991: 117. — *Genetrix* Sugiyama, 1994: 5. — *Periplecta* Haeckel, 1882: 424. — *Phaenocalpis* Haeckel, 1887: 1173. — *Pteroscenium* Haeckel, 1882: 429 (= *Verticillata* synonymized by Nishimura 1990: 114). — *Spongomelissa* Haeckel, 1887: 1209. — *Tripophaenoscenium* Campbell & Clark, 1944a: 38.

NOMINA DUBIA. — *Cladoscenium*, *Dictyocircus*, *Euscenidium*, *Phaenoscenium*.

DIAGNOSIS. — The Phaenocalpididae consist of a pyramidal one-segmented shell with a single, long apical horn and three long, robust feet. The cephalis is latticed with several arches emerging from the cephalic initial spicular system or is exclusively made of these arches. Each double AL-arch forms a regular suture or a deep-depression suture on the cephalis. Another vertical suture is visible from the apical horn side view that corresponds to the AD-arch. In some members, (e.g., *Tripophaenoscenium*), double Al- and AD-arches extend outside the cephalic wall. The A-rod directly arises from the MB to form a straight, free, apical spine on the cephalis. The V-rod forms a significant ventral spine outside the cephalis or may extend horizontally or downwardly. In the latter cases, the extended V-rod forms a short foot or another external spine. Certain members develop more arches. The basal ring directly connects to the D- and double L-rods. These three rods are oriented downward placing the basal ring below the MB. A skirt-like thorax with or without several feet develop in some members, but these feet are generally disconnected from the basal ring. The endoplasm is transparent and located in a space surrounded by the double AL-arch and the basal ring. No algal symbionts have yet been observed in the examined specimens.

STRATIGRAPHIC OCCURRENCE. — Middle Paleocene-Living.

REMARKS

This family name substitutes the commonly used family name "Clathromitridae". The genus composition of the Phaenocalpididae differs drastically between references. The family characters mainly refer to *Clathromitra* and not *Phaenocalpis* due to limited availability of information for the latter genus. Petrushevskaya (1971a: 69-70) established a new subfamily "Clathromitrinae" with members of *Archiscenium*, *Clathromitra*, *Pteroscenium* (= *Verticillata* in original) and *Tripophaenoscenium*. Later, Petrushevskaya (1981: 63-72) further added several valid Mesozoic genera (not shown here) and genera such as *Corythomelissa*, *Euscenium*, *Tripodiscium* (originally *Tripodisculus* and *Tripodiscinus*), *Phaenocalpis* and *Spongomelissa*. De Wever *et al.* (2001: 236-238) included "*Clathromitra joergenseni*" among the figures included for the family Sethoperidae (De Wever *et al.* 2001: figs 151.1, 151.6); however, the genus name was not included in list of genera included in Sethoperidae. In addition, all the genera assigned by Petrushevskaya (1971a, 1981), except *Pteroscenium*, were excluded from the list of genera by De Wever *et al.* (2001). This could mean that *Clathromitra* was not a member of the Sethoperidae *sensu* De Wever *et al.* (2001) and, thus, the "Clathromitridae" *sensu* Petrushevskaya (1981) was eliminated from the list of De Wever *et al.* (2001). Petrushevskaya (1971a, 1981) documented the characteristics of the Phaenocalpididae in detail but did not indicate arches on the figures, thereby not confirming them. The cephalic initial spicular system was shown for *Clathromitra* (Sashida & Kurihara 1999: fig. 11.14), the *Euscenarium*-form of *Archiscenium* (Nishimura & Yamauchi 1984: pl. 24, fig. 6; Nishimura 1990: figs 23.3-23.5; Takahashi 1991: pl. 24, figs 1-4; Sugiyama & Furutani 1992: pl. 18, fig. 1; Sugiyama *et al.* 1992; pl. 15, figs 6, 7; Funakawa 1994: fig. 15.1, 15.2; Sugiyama 1994: pl. 2, figs 4, 5, 7, 8), *Genetrix* (Sugiyama 1994: pl. 3, figs 1-3), *Tripophaenoscenium* (Funakawa 1994: fig. 15.3), *Periplecta* (Nishimura & Yamauchi 1984: pl. 24, fig. 3), and the *Verticillata*-form of *Pteroscenium* (Nishimura & Yamauchi 1984: pl. 29, figs 1-8; Nishimura 1990: figs 24.3-24.5). Referring to these photos, some explanations of Petrushevskaya (1981) need to be changed in order to convey an accurate interpretation. The protoplasm was seen in *Archiscenium* (Zhang *et al.* 2018: 19, fig. 7.17), *Clathromitra* (Sashida & Kurihara 1999: fig. 11.14) and in the *Verticillata*-form of *Pteroscenium* (Zhang *et al.* 2018: 18, figs 7.5? , 7.17). Considering these cephalic structures, *Conicavus* may belong to the Ceratocyrtidae. However, no detailed information regarding this issue has been provided.

Except for critical cases, the Phaenocalpididae can be distinguished from the Sethoperidae by the presence of sutures on the cephalis, a ventral rod extending from the cephalis, the absence of a wired screen on cephalis and thorax, and by not having three wing extensions. *Euscenarium*, *Periplecta* and *Pteroscenium* are sometimes misidentified as a member of the Sethoperidae. They can be differentiated from the member of the Sethoperidae by the presence of a double AL-arch and the absence of straight *a*-spinules on the A-rod as well as the presence of secondary arches along A- and double L-rods.

VALIDITY OF GENERA

Archiscenium

The initial spicular system is the same among *Archiscenium*, *Euscenium*, and *Euscenarium*. Their differences include the form of the arches connecting the initial spicules, which can resemble A-, double L-, or D-rods, with sizes varying among genera. The exact synonymy requires further study. *Archiscenium* is the oldest available name among these genera.

Family PLAGIACANTHIDAE Hertwig, 1879 *sensu* Dumitrica (2004)

Plagiacanthiden [*sic*] Hertwig, 1879: 200-202 (= Plagiacanthidae) [as a family].

Triplagida Haeckel, 1882: 423 [as a tribe]; 1887: 908 [as a subfamily].

Plagonida Haeckel, 1882: 423 [*nomen dubium*, as a subfamily]; 1887: 906-908 [as a family]. — Bütschli 1889: 1975 [as a family]. — Anderson 1983: 29 [as a family].

Tetraplagida Haeckel, 1882: 423 [*nomen dubium*, as a tribe]: 1887: 908, 911 [as a subfamily].

Plectanida Haeckel, 1882: 424 [as a subfamily]; 1887: 906, 919-921 [as a family]. — Anderson 1983: 29 [as a family].

Polyplagida Haeckel, 1882: 424 [*nomen dubium*, as a tribe]; 1887: 908, 917 [as a subfamily].

Polyplectida Haeckel, 1882: 424 [as a tribe]; 1887: 921, 929 [as a subfamily].

Tetraplectida Haeckel, 1882: 424 [*nomen dubium*, as a tribe]; 1887: 921, 923 [as a subfamily].

Triplectida Haeckel, 1882: 424 [*nomen dubium*, as a tribe]; 1887: 921 [as a subfamily].

Cystidina [*sic*] – Haeckel 1884: 30 (= Cystidiidae) [as a family].

Nassellida Haeckel, 1887: 896 [*nomen dubium*, as a family]. — Anderson 1983: 29 [as a family].

Hexaplagida Haeckel, 1887: 908, 915 [*nomen dubium*, as a subfamily].

Hexaplectida Haeckel, 1887: 921, 927 [*nomen dubium*, as a subfamily].

Nasselida [*sic*] – Bütschli 1889: 1975 (= Nassellidae) [as a family].

Plectanidae – Popofsky 1908: 262; 1913: 277. — Schröder 1914: 72. — Wailes 1937: 12. — Chediya 1959: 166. — Tan & Tchang 1976: 269. — Tan & Chen 1999: 268. — Tan & Su 2003: 81.

Plagoniidae – Poche 1913: 219 [*nomen dubium*]. — Campbell 1954: D103. — Riedel 1967b: 295 (*sensu* emend.); 1971: 655-656. — Sanfilippo & Riedel 1973: 529. — Nakaseko *et al.* 1975: 173. — Nakaseko & Sugano 1976: 129. — Riedel & Sanfilippo 1977: 869-870. — Petrushevskaya 1981: 97. — Anderson 1983: 40. — Boltovskoy 1998: 33. — Anderson *et al.* 2002: 1005. — Afanasieva *et al.* 2005: S293. — Afanasieva & Amon 2006: 140.

Plagonidae [*sic*] – Popofsky 1908: 262 [*nomen dubium*] (= Plagoniidae). — Schröder 1914: 72. — Chediya 1959: 164. — Cachon & Cachon 1985: 291 (*sensu* emend.).

Nassellidae – Poche 1913: 219 [*nomen dubium*]. — Chediya 1959: 163.

Plagoniinae – Campbell 1954: D103 [*nomen dubium*].

Cystidiidae – Campbell 1954: D103. — Petrushevskaya 1981: 98. — Afanasieva *et al.* 2005: S293. — Afanasieva & Amon 2006: 140.

Triplagiinae – Campbell 1954: D104.

Plectaniidae – Campbell 1954: D104. — Chen & Tan 1996: 152. — Chen *et al.* 2017: 164.

Plectaniinae – Campbell 1954: D104. — Petrushevskaya 1981: 72. — Afanasieva *et al.* 2005: S292. — Afanasieva & Amon 2006: 139.

Tetraplagiinae – Campbell 1954: D104 [*nomen dubium*].

Tetraplectinae – Campbell 1954: D104 [*nomen dubium*]. — Chediya 1959: 166. — Petrushevskaya 1981: 304-305. — Afanasieva *et al.* 2005: S293. — Afanasieva & Amon 2006: 140.

Triplectinae – Campbell 1954: D104 [*nomen dubium*]. — Chediya 1959: 166. — Tan & Tchang 1976: 269.

Enneaplegmatinae Campbell, 1954: D105.

Triplaginae – Chediya 1959: 164.

Hexaplaginae – Chediya 1959: 165 [*nomen dubium*].

Polyplaginae [*sic*] – Chediya 1959: 165 [*nomen dubium*] (= Polyplagiidae).

Polyplectinae – Chediya 1959: 167.

Hexaplectinae – Chediya 1959: 167 [*nomen dubium*].

Plagiacanthidae – Petrushevskaya 1971a: 69 (*sensu* emend.); 1971b: 988-989 (*sensu* emend.); 1981: 73-74; 1986: 132. — Dumitrica 1979: 28, 30; 2004: 198-199 (*sensu* emend.). — Goll 1979: 383 (*sensu* emend.). — Takahashi 1991: 92. — Hollis 1997: 55. — Sugiyama 1998: 233. — Kozlova 1999: 104. — De Wever *et al.* 2001: 219. — Afanasieva *et al.* 2005: S268 (*sensu* emend.). — Afanasieva & Amon 2006: 100.

Plagiacanthinae – Petrushevskaya 1971a: 147-149; 1971b: 990; 1981: 91-92. — Takahashi 1991: 92. — De Wever *et al.* 2001: 219, 221. — Dumitrica 2004: 216. — Afanasieva *et al.* 2005: S269. — Afanasieva & Amon 2006: 102.

Plagiacanthida [*sic*] – Nishimura 1990: 81 (= Plagiacanthidae) (*sensu* emend.).

Type genus. — *Plagiacantha* Claparède in Müller, 1856: 500 [type species by monotypy: *Acanthometra arachnoides* Claparède, 1855: 675].

Included genera. — *Arachnocalpis* Haeckel, 1882: 427. — *Cystidium* Hertwig, 1879: 214 (= *Paracystidium* **n. syn.**). — *Dumetum* Popofsky, 1908: 264 (= *Pentaplagia* synonymized by Dumitrica 2004: 216). — *Enneaplegma* Haeckel, 1882: 424 (= *Polyplecta* with the same type species). — *Jeanpierria* Dumitrica, 2004: 217. — *Neosemantis* Popofsky, 1913: 298 (= *Deflandrella* synonymized by Dumitrica 1978: 240). — *Plagiacantha* Claparède in Müller, 1856: 500 (= *Plagoniscus* **n. syn.**; *Triplagia* synonymized by Dumitrica 2004: 199; *Triplagiacantha* synonymized by Petrushevskaya 1981: 96). — *Plectagonidium* Cachon & Cachon, 1969: 236. — *Plectanium* Haeckel, 1882: 424 (= *Plectaniscus* **n. syn.**). — *Pseudocubus* Haeckel, 1887: 1010 (= ? *Drepotadium* **n. syn.**; *Rhizoplecta* synonymized by Dumitrica 1973a: 836; *Talariscus* synonymized by Petrushevskaya 1971a: 149).

Invalid name. — *Hexaplecta*.

Nomina dubia. — *Hexaplagia*, *Hexaplegma*, *Nassella*, *Plagonidium*, *Plagonium*, *Plectophorina, Polyplagia*, *Tetraplagia*, *Tetraplecta*, *Triplecta.*

Junior homonyms. — *Campylacantha* Jørgensen, 1905 (= *Neosemantis*) *nec* Scudder, 1897; *Obeliscus* Popofsky, 1913 (= *Talariscus*) *nec* Beck, 1837; *Plectophora* Haeckel, 1882: 424 (= *Plectophorina*) *nec* Gray 1834: captions for pl. 42, fig. 2.

Diagnosis. — The skeleton is exclusively made of bladed, initial spicules. No arch develops between A- and V-rods (e.g., AV-arch) Sagittal ring is absent, unlike other genera of Acanthodesmioidea. Protoplasm was observed in *Cystidium*, *Neosemantis*, *Plagiacantha* and *Pseudocubus*. The yellowish to brown endoplasm is located within the spicules' area. In fully grown specimens, the endoplasm extends beyond this area. Except for *Cystidium,* no algal symbionts are observed in any known genera. Fine pseudopodia radiate around the endoplasm in *Cystidium* and *Neosemantis*. The terminal cone is visible from the base of the *Pseudocubus'* cephalic part. No axial projection is observed.

Stratigraphic occurrence. — late Middle Eocene-Living.

Remarks

This taxon is rarely illustrated in references. However, the spicular system of the following genera is examinable in references: ? *Dumetum* (Sugiyama 1992a: pl. 1, fig. 5), *Neosemantis* (Nishimura & Yamauchi 1984: pl. 22, figs 7, 10; Nishimura 1990: fig. 13.1, 13.2, 12.4, 12.6; Takahashi 1991: pl. 27, fig. 12; Sugiyama *et al.* 1992: pl. 20, fig. 2), *Plagiacantha* (Nishimura 1990: fig. 13.3?), and *Pseudocubus* (Sugiyama *et al.* 1992: pl. 18, figs 1-3; Sugiyama 1993: figs 7.1-7.3, 8.1; Funakawa 1995a: pl. 4, figs 1-3, pl. 5, figs 1-3). The shell is too small and too transparent to observe in seawater, as such Plagiacanthidae can only be identified at higher magnifications (40x or 60x objective lens) with a phase-contrast microscope or a Nomarski differential interference contrast microscope. Under such constraints, "living images" were illustrated for *Cystidium* (Anderson 1977: pl. 1, figs 1, 2; Probert *et al.* 2014: S1, SES 28), *Neosemantis* (Matsuoka 2017: fig. 17), *Plagiacantha* (Sashida & Kurihara 1999: fig. 11.18; Suzuki *et al.* 2009b: figs 3A, 3B; Zhang *et al.* 2018: 13, fig. 25), and *Pseudocubus* (Sashida & Uematsu 1994: figs 3.8, 3.9; Sashida & Kurihara 1999: fig. 12.12; Matsuoka 2007: fig. 4d; Suzuki & Not 2015: fig. 8.11.11; Zhang *et al.* 2018: 15, fig. 19). Algal symbionts of *Cystidium* were identified as *Brandtodinium nutricula* by Probert *et al.* (2014). Ultrafine cellular structure was documented for *Cystidium* (Anderson 1977).

Validity of genera

Cystidium

The original French description for *Paracystidium* is translated as follows: "Paracystidium *has all the characteristics of* Cystidium*, except for the occurrence of a very small spicule, free in the protoplasm surrounding the central capsule and located at its aboral pole.*" *Cystidium* is a type of naked Nassellaria; the differences specified in its description are minor and could indicate either different ontogenetic stages or different species. The name *Cystidium* is older than *Paracystidium*.

Plagiacantha

According to the type-illustrations, *Plagiacantha* (Claparède & Lachmann 1858: pl. 22, fig. 9), *Triplagia* (Haeckel 1887: pl. 91, fig. 2), and *Triplagiacantha* (Hertwig 1879: pl. 7, fig. 6) appear to have only three robust rods, but as the supporting image for *Plagiacantha* (Dumitrica 1973b: pl. 22, figs 2, 4) shows, the main rods are identified as A-, D-, and double L-rods; thus, these genera have four rods in principle. It is likely that a short D-rod was overlooked in these type-illustrations. *Triplagia* and *Triplagiacantha* have been synonymized with *Plagiacantha* in previous studies. The architecture of *Plagoniscus* is identical to that of *Plagiacantha*, except for a long D-rod that has variable length among species. *Plagiacantha* is the oldest available name among these genera.

Plectanium

Plectanium has six radial spines that arise in two opposite groups from poles of the common central rod (Campbell 1954: D104). *Plectaniscus* has four radial spines that arise from the common central point, and its apical spine differs from three basal spines (Campbell 1954: D104-105). Specimens identifiable as *Plectanium* (the supporting image for *Plectanium* in the Atlas) possess four bladed rods, not six. It is unnecessary to differentiate these groups at the genus level. If the type-illustration (Haeckel 1887: pl. 91, fig. 11) is accurate, then the two opposite groups arising from poles of the common central rod illustrated in Haeckel (1887) appear similar to the initial spicular system of the conjoined individuals shown in Dumitrica (2013b: fig. 2.2). The name *Plectanium* is older than *Plectaniscus*.

Family Pseudodictyophimidae Suzuki, n. fam.

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Tripocalpida Haeckel, 1882: 428 [*nomen dubium*, below tribe]; 1887: 1133-1135 [as a family]. — Wisniowski 1889: 686 [as a family]. — Bütschli 1889: 1983 [as a family]. — *nec* Rüst 1892: 178 [as a family]. — *nec* Cayeux 1894: 206, 2111.

Tripocalpidae – Popofsky 1908: 271 [*nomen dubium*]; 1913: 327. — Schröder 1914: 91. — Clark & Campbell 1942: 62; 1945: 33. — Campbell & Clark 1944a: 38. — Chediya 1959: 188. — Tan & Tchang 1976: 273. — Tan & Su 1982: 169. — Nishimura 1990: 107 (*sensu* emend.). — van de Paverd 1995: 212. — Chen & Tan 1996: 153. — Tan & Chen 1999: 288. — Tan & Su 2003: 113, 114. — Chen *et al.* 2017: 173.

Tripocalpididae – Poche 1913: 220 [*nomen dubium*].

Type genus. — *Pseudodictyophimus* Petrushevskaya, 1971a: 91 [type species by monotypy: *Dictyophimus gracilipes* Bailey, 1856: 4].

Included genera. — ? *Chitascenium* Sugiyama, 1994: 4. — ?*Corythomelissa* Campbell 1951: 529. — *Pseudodictyophimus* Petrushevskaya, 1971a: 91. — *Steganocubus* Sugiyama, 1993: 56 (= *Marimoum* **n. syn.**). — *Syscioscenium* Sugiyama, 1992c: 216. — *Tripodocyrtis* Funakawa, 1994: 473.

Nomina dubia. — *Dictyophimus*, *Pterocanium*, *Tripocalpis*, *Tripodoconus*, *Tripodonium*.

Junior homonym. — *Sethomelissa* Haeckel, 1887 (= *Corythomelissa*) *nec* Haeckel, 1882.

Diagnosis. — Anatomically, Pseudodictyophimidae Suzuki, n. fam. are practically two-segmented Plagiacanthoidea with a well-developed first segment (cephalis) and a developed, sometimes lacking, second segment (thorax). A large part of the cephalis is the eucephalic lobe located between the A- and V-rods. The postcephalic lobe and antecephalic lobe are located between the lowest part of the eucephalic lobe and the middle to lower part of the thorax. The suture and boundary of the eucephalic lobe are always situated above the MB's level. The cephalic spicular system consists of MB, A-, V-, D-, double L- and Ax-rods. The double l-rod is generally absent. The MB is very short or retrogrades to become a pointed connection (PC) with the D- and double L-rods. The PC (or MB) is located at the center of the cephalic cavity. The V-rod is rarely absent at the genus or species levels. An anatomical basal ring composed of LL- and double AL- (or AD-) arches is present. All these arches convex upward to form a suture between the cephalis and the thorax. A large part of LL- and double AL- (or AD-) arches merges with the shell wall or is located very close to the shell wall. The Ax-rod is very short. No tubes are present on the cephalis. The feet that are directly connected to the D- and double L-rods may be present. The A-rod

is merged to the cephalis. The cephalis may also be partly or fully free in the cephalic cavity. The sutures and the most constricted part of the shell are always located above the MB or PC.
A protoplasm was observed in *Pseudodictyophimus*. The endoplasm is transparent and located inside the cephalis. Depending on specimens, the endoplasm may also be observed in part of the thorax. No algal symbionts are observed. No axopodial projection has been found as of yet.

Stratigraphic occurrence. — Late Eocene-Living.

Remarks
The diagnosis given above excludes *Steganocubus* as this genus possesses a typical, but very small basal ring-like structure and does not have three feet. Poor development of connecting bars between the basal ring-like structure and shell wall in *Steganocubus* seem to regard it as an intermediate form, between the Dictyocryphalidae Suzuki, n. fam. and the Pseudodictyophimidae Suzuki, n. fam. The Pseudodictyophimidae Suzuki, n. fam. is distinguished from the Dictyocryphalidae Suzuki, n. fam. by the presence of an anatomical basal ring with the LL- and double AL-arches, instead of a basal ring-like structure.

Differing from the Dimelissidae, no true arches directly connected to the D-rod exist. The overall appearance of *Steganocubus* is almost identical to *Syscioscenium*. However, the former possesses a typical but very small, basal ring-like structure whereas the latter develops LL- and double AD-arches that merge with the shell wall. Both *Chitascenium* and *Corythomelissa* are difficult to distinguish from *Archipilium* (Archipiliidae), several genera belonging to the Phaenocalpididae, some genera in the Dimelissidae, and the *Tripocyrtis*-form of *Clathrocanium* (Sethoperidae). Sandin *et al.* (2019) considered *Chitascenium* a member of the Archipiliidae. The Phaenocalpididae can be distinguished from *Chitascenium* and *Corythomelissa* by the presence of a suture with the AD-arch, a well-developed ventral spine and a true basal ring. The Dimelissidae differ from both these genera by the absence of the cephalic lobe, the eccentric position of the PC or short MB, the presence of a double LV-arch. The *Tripocyrtis*-form of *Clathrocanium* differs from *Chitascenium* and *Corythomelissa* by the presence of a true basal ring, several free arches in the cephalic cavity, no sutures related to the arches, and a very small ventral tube.

The stratigraphic distribution of species belonging to Pseudodictyophimidae Suzuki, n. fam. is poorly documented; in addition, many genera and species remain undescribed. The cephalic initial spicular system is documented for *Chitascenium* (Sugiyama 1994: pl. 1, figs 4, 6), *Corythomelissa* (Funakawa 1994: fig. 14.1), *Pseudodictyophimus* (Caulet 1974: pl. 5, figs 3-6; Poluzzi 1982: pl. 24, fig. 9? ; Nishimura 1990: fig. 16.6-16.10, 18.5; Sugiyama *et al.* 1992: pl. 17, figs 2-4; Sugiyama 1993: fig. 23.3; Funakawa 1994: figs 12.1-12.3; 1995a: pl. 6, figs 1-2? , pl. 7, figs 2, 3, pl. 8, figs 1-6), *Syscioscenium* (Sugiyama 1992c: pl. 21, figs 1-4, pl. 22, figs 1-4; 1994: pl. 1, fig. 5), *Steganocubus* (Sugiyama 1992a: pl. 1, fig. 3? ; 1993: figs 10-12; Funakawa 1994: figs 9.1-9.4; 1995a: pl. 9, figs 1-7, pl. 10, figs 1-4), and *Tripodocyrtis* (Nishimura 1990: fig. 17.7; Funakawa 1994: figs 13.1, 13.2; 1995a: pl. 10, figs 5, 6). "Living" or protoplasm images are illustrated for *Pseudodictyophimus* (Sashida & Uematsu 1994: fig. 3.6; Sashida & Kurihara 1999: fig. 11.5; Suzuki & Not 2015: fig. 8.11.7; Zhang *et al.* 2018: 19, fig. 19, p. 23, fig. 14).

Validity of genera
Steganocubus
After these genera were published, the authors who named *Steganocubus* and *Marimoum* agree that these are the same genus (interview from Funakawa and Sugiyama by NS in 1995). The name *Steganocubus* is older than *Marimoum*.

Family Tripodisciidae Haeckel, 1882 n. stat.

Tripodiscida Haeckel, 1882: 428 [below tribe].

Type genus. — *Tripodiscium* Haeckel, 1882: 427 [type species by subsequent designation (Campbell 1954: D117): *Tripodiscium tristylospyris* Haeckel, 1887: 1143].

Included genera. — *Tridictyopus* Hertwig, 1879: 203. — *Tripodiscium* Haeckel, 1882: 427 (= *Tripodiscinus* with the same type species; *Tripodisculus* **n. syn.**, *Tristylospyrium* **n. syn.**). — ? *Tristylocorys* Haeckel, 1887: 1140.

Diagnosis. — One segment with three feet and no apical horn.

Stratigraphic occurrence. — Living.

Remarks
This family is simply used to maintain *Tripodiscium* as a valid genus in this review; however, the consistency of Tripodisciidae needs to be confirmed by retrieving good specimens of the genera included in this family. *Tridictyopus* is very similar to *Conicavus*. Broken specimen of *Periplecta* (Phaenocalpididae) and the *Tripocyrtis*-form of *Clathrocanium* (Sethoperidae) are nearly identical to *Tripodiscium*.

Validity of genera
Tripodiscium
Although the type-illustrations of *Tripodiscium* (Haeckel 1887: pl. 52, fig. 22), *Tripodisculus* (Haeckel 1887: pl. 52, fig. 21), and *Tristylospyrium* (Haeckel 1887: pl. 52, fig. 23) are very similar, Campbell (1954) placed these genera within different superfamilies. *Tristylospyrium* was classified into "Triospyridinae of the Triospyrididae within superfamily Triospyridicae" (Campbell 1954: D112), whereas *Tripodiscium* and *Tripodisculus* were classified into "Archipiliinae of the Archipiliidae within subsuperfamily Archipiliilae within superfamily Archipiliicae" (Campbell 1954: D117). Superfamily "Triospyridicae" is defined by a bilocular cephalis with sagittal constriction, whereas superfamily "Archipiliicae" is defined by a cephalis that is neither bilocular nor lobate; these morphological characters cannot be specified in the type-illustrations. Triospyrididae is defined by a shell composed of cephalis and its apophyses, without apical cupola or dome or thorax, but this definition is applicable to *Tristylospyrium*, *Tripodiscium*, and *Tripodisculus*. Strangely, "three basal feet" is used to identify the subfamily Triospyridinae but also to distinguish among different ranks

within family Archipiliidae. Thus, these taxonomic ranks are meaningless among *Tristylospyrium*, *Tripodiscium*, and *Tripodisculus*. Subfamily "Archipiliinae" within family Archipiliidae is defined as having the basal shell mouth open, which is not included as a character for subfamily "Triopsyridinae" of the Triospyrididae in the superfamily "Triospyridicae", which represents another direct contradiction. Differences among these three genera are definitely not related at the family or higher taxonomic rank; therefore, it is sufficient to consider their morphological characters directly at the genus level, even *sensu* Campbell (1954). *Tristylospyrium* is characterized by an apex without a horn, *Tripodiscium* by three unbranched solid feet, and *Tripodisculus* by branched or forked feet (Campbell 1954: D112, 117, and 118). However, the type-illustration of *Tripodiscium* has branched or forked feet, not unbranched solid feet (Haeckel 1887: pl. 52, fig. 22). Because the apex without horn and branched or forked feet are the only common features among these three genera, they need not be separated at the superfamily level. The oldest available name is *Tripodiscium*.

Family XIMOLZIDAE Dumitrica, nom. nov.

Ximolzasinae O'Dogherty, Carter, Dumitrica, Goričan, De Wever, Hungerbühler, Bandini & Takemura, 2009b: 218 [*nomen nudum*, nomen correct act]. — O'Dogherty *et al.* 2011: 112. — Bragina 2016: 541.

Zamolxinae Dumitrica, 1982b: 402-404 [unavailable name]; Dumitrica 2004: 205. — De Wever *et al.* 2001: 219. — Afanasieva *et al.* 2005: S292. — Afanasieva & Amon 2006: 138-139.

TYPE GENUS. — *Ximolzas* Dumitrica, 2007: 207 [type species by original designation: *Zamolxis corona* Dumitrica, 1982b: 407].

INCLUDED GENERA (CENOZOIC ONLY). — *Daniplagia* Dumitrica 2004: 208. — *Protoscenium* Jørgensen 1905: 133. — *Rhabdolithis* Ehrenberg 1847: 50 (= *Xiphostylomma* **n. syn.**).

DIAGNOSIS. — The skeleton is exclusively made of massive, un-bladed, initial spicules.

STRATIGRAPHIC OCCURRENCE. — Early Coniacian-Living.

REMARKS

This newly designated family is simply conceived in order to validate the family name under the Code. This family name is derived from the genus name *Ximolzas* Dumitrica 2007, replacing the junior homonym name: *Zamolxis* Dumitrica, 1982 (Dumitrica 1982b). The family name "Ximolzasinae" appeared in O'Dogherty *et al.* (2009b, 2011) and Bragina (2016). The family name was published in O'Dogherty *et al.* (2009b: 218) as "*nomen correctum* herein"; however, the *nomen correctum* act is not defined in the English versions of any historical codes (Blanchard *et al.* 1905; ICZN 1926, 1964, 1985, 1999; Schenk & McMasters 1956) or previous rules of zoological nomenclature (Strickland 1878; Melville 1995). This word appeared in an instruction book as a "change of spelling, e.g., -somidae to -somatidae because of [an] incorrect spelling of [the] stem form" for "*nomen correctum*" act (e.g., Winston 1999:142, table 7.1). Thus, the "*nomen correct*" act cannot be read as "new replacement name" (or *nomen novum*). Legal acts for name published after 1999 is mentioned in Article 16 ("every new name published after 1999, including new replacement names (*nomina nova*), must be explicitly indicated as intentionally new"). In addition (Article 16.2), it requires, as an inevitable act, that "a new family-group name published after 1999 must be accompanied by citation of the name of the type genus." Article 16 not only includes the "new family" but also the "*nomen novum*" (see Recommendation 16A") the Article 16.2 also includes the "*nomen novum*" for family.

The skeletal architecture of Neogene taxa belonging to the Ximolzidae Dumitrica, nom. nov. has only been illustrated for *Protoscenium* (Nishimura & Yamauchi 1984: pl. 23, fig. 6? ; Sugiyama 1992c: pl. 22, fig. 5). The taxonomic position of *Rhabdolithis* is still in discussion.

VALIDITY OF GENERA

Rhabdolithis

Xiphostylomma is clearly the same genus as *Rhabdolithis*. Campbell (1954) did not consider *Rhabdolithis*.

Superfamily PYLOBOTRYDOIDEA Haeckel, 1882 n. stat.

Pylobotrida Haeckel, 1882: 440 [as a subfamily].

Cannobotrydicae – Campbell 1954: D143 [*nomen dubium*, as a superfamily].

Cannobotryoidea – Petrushevskaya 1971a: 154 [*nomen dubium*] (*sensu* emend.); 1971b: 988; 1975: 588; 1981: 307-309; 1986: 136. — Petrushevskaya & Kozlova 1972: 554. — Yeh 1987: 86 (*sensu* emend.). — Afanasieva *et al.* 2005: S303. — Afanasieva & Amon 2006: 153.

Cannobotryoida [*sic*] – Amon 2000: 61 [*nomen dubium*] (= Cannobtrydoidea) [as an order].

DIAGNOSIS. — Monotype superfamily. See the diagnosis of the family Pylobotrydidae.

REMARKS

The Pylobotrydidae (originally Cannobotryidae) are placed within the clade of the superfamily Plagiacanthoidea by molecular phylogenetic analysis, (Sandin *et al.* 2019). According to the hierarchy and consistency in Eukaryotes (Cavalier-Smith *et al.* 2018; Adl *et al.* 2019), the order rank for this taxon is unacceptable at the present time.

Family PYLOBOTRYDIDAE Haeckel, 1882 *sensu* Sugiyama (1998)

Pylobotrida Haeckel, 1882: 440 [as a subfamily].

Cannobotrida Haeckel, 1882: 440 [*nomen dubium*, as a subfamily].

Pylobotryida – Haeckel 1887: 1107, 1119-1120 (*sensu* emend.) [as a family]. — Bütschli 1889: 1983 [as a family]. — Anderson 1983: 29 [as a family].

Cannobotryida – Haeckel 1887: 1107-1108 [*nomen dubium*, as a family]. — Bütschli 1889: 1982 [as a family]. — Anderson 1983: 29 [as a family].

Botryocellida Haeckel, 1887: 1112 [as a subfamily].

Botryopylida Haeckel, 1887: 1112 [*nomen dubium*, as a subfamily].

Botryocampida Haeckel, 1887: 1120 [as a subfamily].

Botryocyrtida Haeckel, 1887: 1120 [as a subfamily].

Cannobotryidae [*sic*] – Poche 1913: 222 [*nomen dubium*] (= Cannobotrydidae). — Schröder 1914: 143. — Chediya 1959: 185. — Riedel 1967b: 296 (*sensu* emend.); 1971: 657-658. — Riedel & Sanfilippo 1970: 536; 1971: 1601. — Petrushevskaya 1971a: 154-159; 1981: 315. — Sanfilippo & Riedel 1973: 532. — Nakaseko *et al.* 1975: 174. — Nakaseko & Sugano 1976: 131. — Pessagno 1976: 54. — Dumitrica 1979: 35. — Cachon & Cachon 1985: 295. — Sanfilippo *et al.* 1985: 704. — Yeh 1987: 86 (*sensu* emend.). — Nishimura 1990: 169 (*sensu* emend.). — Takahashi 1991: 133. — Boltovskoy 1998: 33-34. — Sugiyama 1998: 233. — Kozlova 1999: 133. — Tan & Chen 1999: 282. — Anderson *et al.* 2002: 1018. — De Wever *et al.* 2001: 243-245. — Tan & Su 2003: 106. — Afanasieva *et al.* 2005: S303-304. — Afanasieva & Amon 2006: 153. — Chen *et al.* 2017: 171, 233.

Pylobotryidae [*sic*] – Poche 1913: 222 (= Pylobotrydidae). — Schröder 1914: 143. — Chediya 1959: 187.

Acrobotrusidae Popofsky, 1913: 314 [*nomen dubium*].

Neobotryisidae [*sic*] – Popofsky 1913: 319-400 (= Neobotrydidae).

Cannobotrydidae – Campbell 1954: D143 [*nomen dubium*].

Glycobotrydidae Campbell, 1954: D143. — Tan & Tchang 1976: 272. — Tan & Su 1982: 167; 2003: 108. — Tan & Chen 1999: 283.

Botryocampinae – Campbell 1954: D144. — Chediya 1959: 187.

Pylobotrydidae – Campbell 1954: D144. — Tan & Su 1982: 168; 2003: 111. — Chen & Tan 1996: 153. — Tan & Chen 1999: 286. — Chen *et al.* 2017: 172.

Pylobotrydinae [*sic*] – Campbell 1954: D144 (= Pylobotrydinae). — Tan & Su 1982: 168. — Chen *et al.* 2017: 172.

Botryocellinae – Chediya 1959: 186.

Botryopylinae – Chediya 1959: 186 [*nomen dubium*].

Botryocyrtinae [*sic*] – Chediya 1959: 187 (= Botryocyrtidinae).

Cannobotrythidae [*sic*] – Riedel & Sanfilippo 1977: 879 [*nomen dubium*] (= Cannobotrydidae).

Botryocyrtididae – Petrushevskaya 1981: 309. — Amon 2000: 61-62. — Afanasieva *et al.* 2005: S303. — Afanasieva & Amon 2006: 153.

Type genus. — *Pylobotrys* Haeckel, 1882: 440 [type species by subsequent designation (Campbell 1954: D144): *Pylobotrys putealis* Haeckel, 1887: 1121].

Included genera. — *Amphimelissa* Jørgensen, 1905: 136 (= *Bisphaerocephalina* synonymized by Petrushevskaya 1971a: 158; *Bisphaerocephalus* synonymized by Petrushevskaya 1971a: 165; ? *Glycobotrys* **n. syn.**). — *Botryocampe* Ehrenberg, 1861b: 829 (= *Saccospyris* synonymized by Matsuzaki *et al.* 2015: 59). — *Botryocella* Haeckel, 1887: 1116. — *Botryocyrtis* Ehrenberg, 1861b: 829 (= ? *Acanthobotrys* synonymized by Petrushevskaya & Kozlova 1972: 554). — *Centrobotrys* Petrushevskaya, 1965: 113. — *Lithocorythium* Ehrenberg, 1847: 54 (= ? *Phormobotrys* **n. syn.**). — *Monotubus* Popofsky, 1913: 322. — *Neobotrys* Popofsky, 1913: 320 (= *Xiphobotrys* **n. syn.**). — *Pylobotrys* Haeckel, 1882: 440 (= *Acrobotrissa* **n. syn.**, *Ceratobotrys* **n. syn.**; *Acrobotrella* synonymized by Petrushevskaya 1981: 319).

Nomina dubia. — *Acrobotrantha*, *Acrobotromma*, *Acrobotrusa*, *Acrobotrys*, *Botryopyle*, *Cannobotrys*, *Cannobotrantha*, *Cannobotrella*, *Cannobotrissa*, *Cannobotromma*, *Cannobotrusa*, *Diauletes*.

Junior homonyms. — *Acrobotrissa* Popofsky, 1913 (= *Acrobotrissa*) *nec* Haeckel, 1887; *Lithobotrys* Haeckel, 1887 (= *Glycobotrys*) *nec* Ehrenberg, 1844 (Ehrenberg 1844a).

Diagnosis. — Pylobotrydidae consist of two to three segments and a complex cephalis. The cephalic part is subdivided in ante-, eu-, and postcephalic lobes. The antecephalic lobe appears as an inflated part on the ventral side, between the V- and double L-rods; the eucephalic lobe is observed as an inflated space in the central part between the A- and V-rods, while the postcephalic lobe appears as an inflated space in the apical side, between the A- and D-rods. The eucephalic lobe is noticeably larger than the postcephalic lobe. The cephalic initial spicular system consists of MB, A-, V-, D-, double L-, double l-, and Ax-spines. Double l-rods are well developed and protrude as spines from the shell wall. The basal ring is developed. Double *ap*-arch (a kind of AL-arch) and double *pj*-arch (a kind of LV-arch) are both developed. A deep distinctive suture generally develops between the lobes and in some members, a flat divider made of arches is also visible between the postcephalic and eucephalic lobes. A tube located between the eu- and antecephalic lobes, is closely related to the V-rod.
The arrangement of the protoplasm and algal symbionts, as well as the color of the endoplasm, are variable among genera. The ante- and postcephalic lobes are occupied by algal symbionts in *Pylobotrys*, *Amphimelissa* and *Centrobotrys*, whereas the algal symbionts are located on the distal end of the endoplasm in *Botryocyrtis* and *Monotubus*.

Stratigraphic occurrence. — late Middle Eocene-Living.

Remarks

The definition of ante-, eu- and post-cephalic lobes is that employed by Sugiyama (1998: fig. 3). This family was originally called Cannobotrydidae. However, owing to the *nomen dubium* status of the type genus of Cannobotrydidae, it has been replaced with valid family name: Pylobotrydidae. The stem of the genitive singular of *Pylobotrys* is Pylobotryd-. According to Article 29.3.1, if the stem ends in -id, those letters may be elided before adding the family-group suffixes. Although the grammatic spelling of the family derived from *Pylobotrys* may be "Pylobotryidae", prevailing usage "Pylobotrydidae" (Tan & Su 2003: 111; Chen *et al.* 2017: 172) is hereby retained in accordance with Article 29.5 (maintenance of current spelling). Sugiyama (1998: 233) pointed out the morphological similarity of this family with Dimelissidae (= Lophophaenidae in original) due to the small size, the similar development of arches, and the similarity in the cephalic initial spicular system (concerning the presence or absence of the double l-rods). This view was supported by molecular phylogenic studies because *Pylobotrys* falls into the same clade as the Plagiacanthoidea, Clade G (Sandin *et al.* 2019). In fact, *Entepipedus* (Ceratocyrtidae) has an intermediate form which consists of the presence of double l-rods and the absence of cephalic lobes.

A genus belonging to the Pylobotrydidae is identifiable by: 1) the recognition of the A- and V-rods; 2) the relative position between MB and the collar stricture development, defined by the position of the lobes; and 3) the spines and wings derived from the cephalic initial spicular system. A comprehensive examination of the Pylobotrydidae was conducted under light microscopy by Petrushevskaya (1964, 1965, 1968), and was partly confirmed in scanning electron microscopy (SEM) and through other observation methods. SEM images were provided for *Pylobotrys* (Nishimura 1990: figs 37.1-37.3), *Amphimelissa* (Bjørklund & Swanberg 1987: figs 3, 4), *Botryocella* (O'Connor 1999: pl. 1, figs 21-24), *Lithocorythium* (Sugiyama 1994: pl. 5, fig. 2), and *Neobotrys* (Nishimura & Yamauchi 1984: pl. 41, fig. 3). The sutures between the lobes result from the position of the arches, although this is not well illustrated in these photos. "Living" and protoplasm images were published for *Amphimelissa* (Sashida & Uematsu 1994: fig. 3.11? ; Suzuki & Not 2015: fig. 8.11.15), *Pylobotrys* (Zhang *et al.* 2018: 9, fig. 2.34), *Botryocyrtis* (Matsuoka 2017: fig. 30; Zhang *et al.* 2018: 9, fig. 2.35) and *Monotubus* (Zhang *et al.* 2018: 9, fig. 2.36). Little is known about the evolutionary history of this family, except for visual hypotheses of *Centrobotrys* (Riedel & Sanfilippo 1981: fig. 12.10) and the family's genus level (Petrushevskaya 1968).

Validity of genera

Amphimelissa

Large numbers of *Amphimelissa setosa*, the type species of this genus, have been illustrated from topotypic regions (Bjørklund & Swanberg 1987; Bjørklund *et al.* 2015) to clarify the morphological variation within the genus. This species includes a morphotype with three or more rods derived from the initial spicular system (Bjørklund & Swanberg 1987: figs 4.Q, 4.S, 4.W) and a tube or tube-like structure with a free V-rod (Bjørklund & Swanberg 1987: figs 4.C, 4.W, 4.X). Petrushevskaya (1981: 326) revised the definition of *Bisphaerocephalina* as follows, translated using terminology from Sugiyama (1998):" *Postcephalic lobe* [note: lobe between A- and D-rods] *slightly higher than the eucephalic lobe* [note: lobe between A- and V-rods]*; it may differentiate into a small tubule. Antecephalic lobe* [note: lobe between V- and double L-rods] *slightly differentiated* [...] *V-rod may be linked to a small tube* [...] *The apical horn and the appendages related to the D- and double L-rods may be well developed* [...] " These characters fall within the range of variation in *Amphimelissa.* The original description of *Bisphaerocephalus* by Popofsky (1908) is translated as follows: " [...] *Cephalis smooth, no horn, well differentiated from the thorax, which bears three laterally directed spines* [note: spines directly connected from A- and double L-rods] *in the collar area. Cephalis separated into two parts* [note: postcephalic and eucephalic lobes] *by a vertical stricture* [...] *From the upper part of the thorax to the lower part of the cephalis, the collar area is covered by a secondary mesh* [note: antecephalic lobe, ...] ". Popofsky (1908) reported no apical horn, but Petrushevskaya (1965: figs 9.1-9.3) shows wide variety in the lengths of the apical horn and appendages (see supporting image for *Bisphaerocephalus*). These characters are also within the range of morphological variation in *Amphimelissa*. *Glycobotrys* was proposed by Campbell (1951) to replace *Lithobotrys* Haeckel 1887 *nec* Ehrenberg 1844a, using the type species of *Lithobotrys geminata*. Campbell (1954: D143-144) explained that this genus has tubules and a fenestrated thorax. The topotype was identified in the Ehrenberg collection as *L. geminata* by Ehrenberg himself (Ogane *et al.* 2009b: pl. 19, figs 7a-c), and surely can be identified as this species in the modern sense. The description by Campbell (1954) does not match either this topotype or the type-illustration (Ehrenberg 1876: pl. 3, fig. 19). Foreman (1968: text-figs 11a-c) illustrated the cephalis structure of *L. geminata*. Based on these specimens, *Glycobotrys* lacks outcropped rods from the initial spicular system, except for the A-rod, but this genus has a larger postcephalic lobe than eucephalic lobe and a very small antecephalic lobe, as also seen in *Amphimelissa* at the genus level. *Amphimelissa* is the oldest available name among these genera.

Lithocorythium

The type-illustrations of both *Lithocorythium* (Ehrenberg 1854c: pl. 22, fig. 29a, 29b) and *Phormobotrys* (Haeckel 1887: pl. 96, fig. 26) are in ventral view (showing V- and double L-rods), because the eucephalic lobe (smaller, between A- and V-rods) and postcephalic lobe (larger, between A- and D-rods) are both clearly visible. The first description was written in Latin by Ehrenberg (1847: 54) and is translated as follows: "*Shell with more than one stricture. Last segment whole. With no median appendages. Aperture latticed.*" The next description was written in German by Haeckel (1862: 330) and is translated as follows: "*Multi-segmented lattice shell, subdivided into three or more superposed irregular segments by two or more circular constrictions, with no lateral appendages and a constricted aperture covered by a lattice.*" The type-illustration of *Lithocorythium* demonstrates that these descriptions are incorrect: the postcephalic lobe is larger and without apical horn or appendages. The type-illustrations likely display the A-rod, which does not protrude from the cephalic wall, and D- and double L-rods, which are merged with the thoracic wall. The supporting image for *Lithocorythium*, cited by Sanfilippo *et al.* (1978: pl. 1, figs 4, 5), may not belong to *Lithocorythium* because the A-, D-, and double L-rods are extruded from the wall. The revised definition of *Phormobotrys* by Petrushevskaya (1981: 322) using the terminology of Sugiyama (1998) is translated as follows: "*Postcephalic lobe somewhat higher than the eucephalic lobe, with its length passing into a tube* [...] *No apparent apical horn or other appendages. Thorax well differentiated, but final segment rudimentary. Segments separated by deep internal septa. Aperture on the final segment enclosed by mesh.*" A comparison of the definition and type-illustrations of *Lithocorythium* and *Phormobotrys* shows that the only differences between these genera are the segments separated by deep internal septa and final segment rudimentary in the latter genus; however, both of these characters are inappropriate as genus criteria. Haeckel (1887: 1124), the author of *Phormobotrys*, mentioned the presence of a tube. As *Lithocorythium* does not appear to have a tube, their synonymy is in doubt. Phylogenetic studies are required to resolve this issue. The name *Lithocorythium* is older than *Phormobotrys*.

Neobotrys

Campbell (1954: D144) described *Neobotrys* as having an inner trellis consisting of a sagittal ring and appended spines. The sagittal ring is unusual; this description was probably derived from original remarks by Popofsky (1913: 320), whose definition of *Neobotrys* is translated as follows: "*Neobotrysidae with an inner spicule, composed of a sagittal ring supporting A-, D-, and double L-rods. The rods are enveloped by tubes* [...] *has two or three cephalic chambers. Based on these chambers, it should be related to the spyrids, after Haeckel* [...] ". As shown in specimens of the type species *Neobotrys quadritubolosa* (supporting image for *Neobotrys* in the Atlas), the sagittal ring *sensu* Popofsky (1913: pl. 30, fig. 4) corresponds to a deep constriction between the postcephalic lobe (between the A- and D-rods) and eucephalic lobe (between the A- and V-rods). The postcephalic and eucephalic lobes of the Pylobotrydidae have an A-rod, associated arches related with the A- and double L-rods, a double *ap*-arch that connects the L-rod and Al-arch within or attached to the wall (Sandin *et al.* 2019: supplement). The illustrated specimen provided in Popofsky (1913) is in slightly oblique right dorsal side view, which overlooks several arches within the cephalis, which probably led to the incorrect description of a sagittal ring supporting A-, D-, and double L-rods. *Xiphobotrys* has a significant apical spine and appendages that are similar to those of *Neobotrys*. Unlike *Neobotrys*, *Xiphobotrys* lacks tubes in association with the very long A-, D-, V-, and double L-rods. Considering the close phylogenetic relationship between these two genera, they should be synonymized as a single genus. The name *Neobotrys* is older than *Xiphobotrys*.

Pylobotrys

The genera synonymized with *Pylobotrys* differ in the size and development of the postcephalic lobe (between A-and D-rods), antecephalic lobe (between V- and double D-rods), and tubes or appendages in the suture between the postcephalic lobe and thorax (terminology from Sugiyama 1998). Petrushevskaya (1981: 319) synonymized *Acrobotrella*, *Acrobotrissa*, and *Neobotrys* with *Acrobotrys*, but they require re-interpretation because the validated *Acrobotrys* is *nomen dubium*, and the type species have not been illustrated.

Acrobotrissa has two homonyms defined by Haeckel (1887: 1114; type species *Acrobotrissa trisolenia*) and Popofsky (1913: 321; type species *Acrobotrissa cribrosa*); their type images are documented in the Atlas. The validity of *Acrobotrissa* is discussed hereafter based on the former type species. Petrushevskaya (1981: 319-320) commented that *Acrobotrys* is a subjective synonym of *Acrobotrissa* because their characters are similar, and revised the definition of *Acrobotrys*, translated as follows: "[...] *Postcephalic lobe with a long tube larger than the eucephalic lobe. Height of the eucephalic lobe with its own septa* [...] *Height of the antecephalic lobes slightly smaller than that of the eucephalic lobe, with a long tube on the ventral side. A rod crossing approx. the middle part of the postcephalic lobe. Collar structure differentiated, but not always very distinct. Tubes other than those of the A- and V-rods may be differentiated, i.e., tubes that are not connected to an internal spicule (in the suture between the postcephalic lobe and thorax)* [...] ". This description matches the type-illustration of *Acrobotrissa* (Haeckel 1887: pl. 96, fig. 8), and therefore is considered the practical description of *Acrobotrissa*. Unlike *Acrobotrissa*, *Acrobotrella* is defined by the presence of two divergent tubes (apical and sternal) (Haeckel 1887: 1114). This definition excludes morphospecies with a tube in the suture between the cephalic lobe and thorax (cf. type-illustration, Haeckel 1887: pl. 96, fig. 10). However, *Acrobotrys trisolenia* (Haeckel 1887: pl. 96, fig. 8) and *Acrobotrys disolenia* (Haeckel 1887: pl. 96, fig. 10) differ only in the presence of this tube. These two species presumably have a direct ancestral relationship; therefore, these genera should be merged into a single genus.

The definition of *Pylobotrys* was revised by Petrushevskaya (1981: 320), translated as follows: "*The postcephalic lobe, and also the galea, are subdivided into upper and lower parts. If the antecephalic lobe is well developed, and if the eucephalic lobe is divided into a collar and an upper part, then the cephalis may appear to be composed of multiple chambers, as reflected in the Haeckelian description and name*." This description of multiple chambers is probably the result of the complex initial spicular system. Petrushevskaya (1981: 320) noted that *Pylobotrys* is differentiated from *Acrobotrissa* (originally *Acrobotrys*) in its shorter tubes and the structure of the cephalis, which is not separated from the thorax by a clear external constriction. Once *Acrobotrella* was synonymized with *Acrobotrissa*, the clear external constriction was removed as a genus criterion. The tube length is also insufficient for differentiating among these genera.

Ceratobotrys was established according to differences from *Acrobotrissa* (originally *Acrobotrys*) including having apical and dorsal spines and two hollow latticed lateral spines, except for A-, D-, and double L-tubes (Nishimura 1990: 169). The presence of these distinctive tubes, which are probably related to double L-rods, clearly differs from *Acrobotrissa*; however, if this character is applied for genus classification, the taxonomy of the Pylobotrydidae becomes complex, requiring the definition of many new genera. These characters are similar to those of *Neobotrys*, but the fundamental difference is that *Neobotrys* has distinctive A-, D-, and double L-rods outside the test. This difference does not allow to synonymize *Ceratobotrys* with *Neobotrys*. A remaining concern is that according to Popofsky (1913), *Acrobotrissa cribrosa* can be classified into *Pylobotrys*, with one or no tube on the postcephalic lobe; thus, this junior homonym is a synonym of *Pylobotrys*. No known specimens of *A. cribrosa* have a tube on the postcephalic lobe; therefore, the absence of a tube on the postcephalic lobe is a stable character. However, *Acrobotrys chelinobotrys*, described by Takahashi (1991: pl. 45, figs 22-24), is very similar to *Ceratobotrys riedeli*, the type species of *Ceratobotrys*, except for a closed postcephalic lobe in *A. chelinobotrys*. Considering this species-level difference, it is unlikely that *A. cribrosa* represents a separate genus from *Acrobotrissa*.

The oldest available genus among these groups is *Pylobotrys*, although the type species of *Pylobotrys*, *P. putealis* (Haeckel 1887: pl. 96, fig. 21), has not been seen and was illustrated based solely on its first description by Haeckel.

Phylogenetic Molecular Lineage IV
Sandin *et al.* (2019)

Diagnosis. — The shell is generally robust with a completely grown last segment (either abdomen or thorax), which is very large relative to the cephalic size. The collar stricture is easily observable.

Remarks
Lineage IV includes four superfamilies Cycladophoroidea, Sethoperoidea, Lithochytridoidea, and Pterocorythoidea. For all superfamilies, not including the Sethoperoidea, the placement in the Lineage IV relies upon molecular phylogeny (Sandin *et al.* 2019), although PhyML bootstrap values (10 000 replicates, BS) and posterior probability (PP) score as >90% and >0.90, respectively. The diagnosis written above is mainly based on the common structures among the Cycladophoroidea, Lithochytridoidea and Pterocorythoidea, which are well recognized as members of a distinct molecular group.

Superfamily Cycladophoroidea
Suzuki *in* Sandin, Pillet, Biard, Poirier, Bigeard, Romac, Suzuki & Not, 2019 n. stat.

Cycladophoridae Suzuki *in* Sandin, Pillet, Biard, Poirier, Bigeard, Romac, Suzuki & Not, 2019: 201-202.

Diagnosis. — Same as the family.

Remarks
This superfamily is established so as to maintain consistency at the superfamily rank in Lineage IV.

Family Cycladophoridae Suzuki *in* Sandin, Pillet, Biard, Poirier, Bigeard, Romac, Suzuki & Not, 2019

Cycladophoridae Suzuki *in* Sandin, Pillet, Biard, Poirier, Bigeard, Romac, Suzuki & Not, 2019: 201-202.

Type genus. — *Cycladophora* Ehrenberg, 1846: 385 [type species by subsequent monotypy: *Cycladophora*? *davisiana* Ehrenberg, 1862: 297].

Included genera. — *Cycladophora* Ehrenberg, 1846: 385 (= *Cyclamptidium* with the same type species; *Diplocyclas* synonymized by Bjørklund & De Ruiter 1987: 274; *Spuroclathrocycla* synonymized by Lombari & Lazarus 1988: 108). — ? *Valkyria* O'Connor, 1997a: 74.

Diagnosis. — Cycladophoridae consist of a helmet-conical shell with two-segments, with or without a frill-like fringe. The cephalis is small, spherical, and may be found pore-less or with relict pores. The thorax is robust and tends to be "well-necked" in its upper part. The thoracic pore frames are generally polygonal-rounded or simply rounded. The width of pore frames is variable in places. Three wing-like rods or rims are visible on upper thoracic wall. The cephalic initial spicular system consists of MB, A-, V-, D-, double l-, double L- and dot-like Ax-rods. A tubular, cephalic horn is absent. Two apical horns emerge from the A-rod, and from the obliquely oriented V-rod. A double Ll-arch develops horizontally and double LV-arch extend at a large angle. The double Dl-arch is of a very small size. Most parts of Ll- and LV-arches are buried in the shell wall whereas the Dl-arch is almost merged with the shell wall to form a tiny clear double hole. The endoplasm is located in the cephalis and upper part of the thorax. No endoplasm is present in the lower half of the test. The occurrence of pseudopodia has not been confirmed as of yet. No algal symbionts are present.

Stratigraphic occurrence. — Late Eocene-Living.

Remarks
The Cycladophoridae differ from the Lithochytrididae by having the latter three distinctive rims or relevant structures related to the V-and double L-rods. The Cycladophoridae are easily distinguished from the Pterocorythoidea by having the latter a cephalic structure with special lobes (pterocorythid-type). The genus composition of the Cycladophoridae results from the molecular phylogeny (Sandin *et al.* 2019), but the position of *Valkyria* is problematic. First, the genus *Valkyria* is a monotypic genus from the Oligocene to the lowest Miocene (O'Connor 1997a: text-fig. 2) and no descendants have been reported. Secondly, Sandin *et al.* (2019) tentatively identified it as "*Valkyria* ?" because the most similar morphotype representative of the genus presented a phylogenetic disconnection with the *Valkyria*-species. Nevertheless, the cephalic structure of the paratype *Valkyria pukapuka* (O'Connor 1997a: text-fig. 7, pl. 7, figs 11, 12) is identical to that of *Cycladophora* (Nakaseko & Nishimura 1982: pl. 48, fig. 2; Nishimura & Yamauchi 1984: pl. 36, figs 8a, 8b; Poluzzi 1982: pl. 23, fig. 13; Sugiyama *et al.* 1992: pl. 21, fig. 3). As repeatedly admitted (Matsuzaki *et al.* 2015; Sandin *et al.* 2019), the morphological difference between the Theopiliidae and the Cycladophoridae remains unclear (see remarks in Theopiliidae). A polygonal frame on the thorax and a fragile shell wall are common in Theopiliidae (see remarks in Theopiliidae). The robust shallow-hat shaped nassellarians with polygonal frames were mainly described in the northwestern Pacific and Sea of Japan (e.g., *Cycladophora sphaeris* (Popova, 1989); *Cycladophora urymensis* (Popova, 1989); *Cycladophora nakasekoi* Motoyama, 1996; *Cycladophora funakawai* Kamikuri, 2010, in published year order). Excepting the difference in polygonal frame, these species share a common structure to *Cycladophora*. The evolutionary phylogenetic studies, based on species with a continuous stratigraphic record in the aforementioned areas, conclude that *Cycladophora davisiana*, the type species of *Cycladophora*, directly evolved from *Cycladophora sphaeris* (Popova, 1989) (originally *Cycladophora sakaii*), which in turn is the direct descendant of *C. funakawai* (Motoyama 1997; Kamikuri 2010). This suggests that a robust skeleton is also a key distinguishing feature for the Cycladophoridae. Other Cycladophoridae taxa are found in these areas and some attempts were made to reconstruct the evolution of the traditional Cycladophoridae which diverged, or evolved, from the *Coniforma*-form of *Anthocyrtis* (originally *Coniforma*; Late Cretaceous), *Anthocyrtis* (Eocene), the *Clathrocyclas*-form of *Anthocyrtis* (end of Eocene to Oligocene), the *Spuroclathrocyclas*-form of *Cycladophora* (*Spuroclathrocyclas* in original; Miocene to Pliocene), and *Cycladophora* (Pliocene-Pleistocene), respectively (Tochilina & Vasilenko 2015, 2018b). If this reconstruction could be supported at a species level, the Anthocyrtididae would then belong to the same superfam-

ily as the Cycladophoridae, or would become synonym of Cycladophoridae. The "Living" appearance of *Cycladophora* has been well documented (Suzuki & Not 2015: figs 8.10.8, 8.10.9, 8.11.21; Zhang *et al.* 2018: 19, figs 7.26, 7.27).

VALIDITY OF GENERA

Cycladophora

The type designation for *Cycladophora* has a complex history because three species, *Cycladophora davisiana*, *Cycladophora stiligera*, and *Cycladophora tabulata* were each selected as the type species in different publications. The genus name was proposed without any assigned species in 1846. The species name was first applied as "*Cycladophora*? *davisiana*" by Ehrenberg (1862: 297), but this is not accepted as the first named species of *Cycladophora* according to the Code (ICZN 1999), article 67.2.5 of which states, "*A nominal species is deemed not to be originally included if it was doubtfully or conditionally includes* [...]". The next applications of *Cycladophora* were as *Cycladophora davisiana* and *Cycladophora tabulata* in Ehrenberg (1873b: 288-289, pl. 2, fig. 11; p. 145, 288-289, pl. 4, fig. 18 for the latter). Thus, according to ICZN (1999) article 67.2.2, the type species must be selected from Ehrenberg (1873b). Because Ehrenberg had already placed *davisiana* within *Cycladophora*, *Cycladophora davisiana* takes precedence over *Cycladophora tabulata* as the type species, even if the first application was questionably assigned. Unfortunately, the type specimen of *Cycladophora tabulata* is missing from the Ehrenberg collection. Thus, *Cycladophora tabulata* is considered *nomen dubium*, and the type designation of *Cycladophora tabulata* by Foreman (1973b: 434) is unlikely. Unaware of the recommendations of ICZN (1926) article 30:III-q, stating that, all else equal, "*show preference to a species which the author of the genus actually studied at or before the time he* [sic] *proposed the genus*," Campbell (1954: D132) wrongly designated *Cycladophora stiligera* as the type species of *Cycladophora*. *Cycladophora stiligera* was described by Ehrenberg (1874), and therefore cannot be selected as the type species according to ICZN (1999) article 67.2.2, which states, "*If a nominal genus* [...] *was established before 1931* [...] *without included nominal species, the nominal species that were first subsequently and expressively included in it are deemed to be the only originally included nominal species*." Thus, *Cycladophora davisiana* is the only valid type species of *Cycladophora*.

Cyclamptidium has the same type species as *Cycladophora*. *Diplocyclas* was previously synonymized with *Cycladophora* by Bjørklund & De Ruiter (1987: 274). The type species of *Spuroclathrocyclas*, *Clathrocyclas semeles*, was placed in *Cycladophora* by Lombari & Lazarus (1988); thus, *Spuroclathrocyclas* is potentially a synonym of *Cycladophora*, although this genus was established in 1989, 1 year later than Lombari & Lazarus (1988). Therefore, the taxonomic characters of *Spuroclathrocyclas* require evaluation.

Spuroclathrocyclas was defined by Popova (1989: 72), translated as "*Three-segmented shell with an aperture with peristome. First segment spherical and well differentiated, with two apical cylindrical or side horns as external extensions of the A- and V-rods. On the opposite side to the first and second horns is another horn formed by external extension of the single internal rod, which is rarely preserved. Second segment sometimes designated as a pedestal, sub-cylindrical, slightly wider than the first segment. Third segment bell-shaped. First segment smooth, not separated from the second (pedestal) by a constriction. Sharp constriction with an internal septum between the second and third segments. Third segment swollen. Aperture slightly constricted or as wide as the widest part of the last segment. Inner peristome sometimes bearing apophyses of considerable length. Pores are medium on the first and second segments, and wider and quincuncially distributed on the third segment. Walls of most segments are uniformly thin. Basal spines have large pores and are not always preserved*." *Spuroclathrocyclas* differs from *Cycladophora davisiana* in four ways: bell-shaped abdomen, ambiguous separation between the cephalis and thorax (pedestal), sharp constriction with an internal septum between the thorax and abdomen, and aperture slight constricted. The species best fitting these characters is *Spuroclathrocyclas sphaeris*, which is a senior synonym of *Cycladophora sakaii*; however, based on high-resolution biostratigraphy (Motoyama 1997), this species is the direct ancestor of *Cycladophora davisiana*. Based on this analysis, *Cycladophora davisiana* and *Cycladophora sphaeris* should belong to the same genus. Among these genus names, *Cycladophora* is the oldest.

Superfamily SETHOPEROIDEA Haeckel, 1882 n. stat.

Sethoperida Haeckel, 1882: 433 [as a tribe]; 1887: 1192, 1194, 1232 [as a subfamily].

DIAGNOSIS. — Same as the family.

REMARKS

The independency of this superfamily and its relationship to other Lineage IV superfamilies has not been recognized due to the lack of molecular phylogenic data for the Sethoperidae. The complexity of the cephalis and the mono-segmentation resemble that of the Plagiacanthoidea.

Family SETHOPERIDAE Haeckel, 1882 *sensu* Suzuki emend. herein

Sethoperida Haeckel, 1882: 433 [as a tribe]; 1887: 1192, 1194, 1232 [as a subfamily].

Archicorida Haeckel, 1882: 427 [*nomen dubium*, as a tribe]; 1887: 1133, 1179, 1180 [as a subfamily]. — Wisniowski 1889: 687.

Callimitrida Haeckel, 1882: 431 [below tribe].

Sethophatnida Haeckel, 1882: 433 [as a tribe].

Sethophaenida – Haeckel 1887: 1192, 1242, 1285 [*nomen dubium*, as a subfamily].

Tripocyrtida Haeckel, 1887: 1192-1194 [as a family]. — Bütschli 1889: 1986 [as a family]. — *nec* Rüst 1892: 181 [as a family]. — *nec* Cayeux 1894: 212.

Tripocyrtidae – Haecker 1908: 448. — Popofsky 1908: 274; 1913: 333. — Schröder 1914: 100. — Wailes 1937: 13. — Clark & Campbell 1942: 65; 1945: 37. — Campbell & Clark 1944a: 41; 1944b: 23. — Chediya 1959: 199. — Tan & Tchang 1976: 274. — Tan & Su 1982: 169; 2003: 113. — Chen & Tan 1996: 153. — Tan & Chen 1999: 296. — Chen *et al.* 2017: 182.

Sethoperinae – Haecker 1908: 448-451. — Campbell 1954: D124. — Chediya 1959: 203. — Petrushevskaya 1971a: 76-80; 1971b: 989-990 (*sensu* emend.); 1981: 295. — Tan & Tchang 1976: 279. — Afanasieva *et al.* 2005: S293. — Afanasieva & Amon 2006: 140. — Chen *et al.* 2017: 198.

Archicorinae – Clark & Campbell 1942: 65 [*nomen dubium*]; 1945: 35. — Campbell & Clark 1944a: 40; 1944b: 22. — Chediya 1959: 196.

Sethoperidae – Petrushevskaya & Kozlova 1972: 535 (*sensu* emend.); Petrushevskaya 1975: 589; 1981: 291-295. — Dumitrica 1979: 30. — Takahashi 1991: 98. — De Wever *et al.* 2001: 236, 238. — Afanasieva *et al.* 2005: S293. — Afanasieva & Amon 2006: 140.

Tripocyrtididae – Poche 1913: 220.

Sethophatninae – Campbell 1954: D128 [*nomen dubium*].

Sethophaeninae – Chediya 1959: 208 [*nomen dubium*].

Sethophatnidae – Loeblich & Tappan 1961: 228 [*nomen dubium*].

Type genus. — *Sethopera* Haeckel, 1882: 433 [type species by subsequent designation (Campbell 1954: D124): *Sethopera tricostata* Haeckel, 1887: 1232] = junior subjective synonym of *Clathrocanium* Ehrenberg, 1861b: 829 [type species by subsequent designation (Campbell 1954: D122): *Clathrocanium squarrosum* Ehrenberg, 1873a: 303].

Included genera. — *Callimitra* Haeckel, 1882: 431 (= *Arachnothauma* **n. syn.**). — *Clathrocanium* Ehrenberg, 1861b: 829 (= *Clathrocanidium* with the same type species; *Arachnopilium*, *Clathrocorona*, *Clathrolychnus* synonymized by Petrushevskaya 1971a: 80; *Tripocyrtis* synonymized by Petrushevskaya 1981: 300; *Sethopera* **n. syn.**). — *Clathrocorys* Haeckel, 1882: 431. — *Dictyocodoma* Haeckel, 1887: 1335. — *Dictyocodon* Haeckel, 1882: 435 (= *Dictyocodella* with the same type species). — *Pteropilium* Haeckel, 1882: 435 (= *Clathropilium* with the same type species).

Invalid name. — *Sethophaena.*

Nomina dubia. — *Archibursa*, *Archicorys*, *Sethophatna*.

Diagnosis. — Sethoperidae consist of a one- to two- segmented, rounded pyramidal shell with one long apical horn and three long feet (or wings). The cephalis is latticed. A wired screen develops between the apical horn and each of the feet, (or wings) and/or between the feet (or wings) and thorax. The thorax varies from a three-sided, rounded pyramid to a basket-like from. The cephalic initial spicular system consists of MB, A-, V-, D-, and the double-L rods. Double l-rod absent. The basal ring is directly connected to the D- and double L-rods forming three collar pores. Several arches develop freely in the cephalic cavity, or are attached on the inner side of the cephalic wall. However, but these do not form sutures on the cephalic wall. The combination and connecting ends of the arches such as AD-arch, *ap*-arch (one of AL-arch), *ac*-arch (one of AD-arch) and *pj*-arch (one of VL-arch) are variable. A straight double *a*-spinule extends laterally as a part of the *ap*-arch, a second double arch named the *m*-(*ap*) arch, may develop between the *m*-position on the A-rod and the *ap*-arch. A further second double arch may be present between the *g*-position of the A-rod and the *m*-(*ap*) arch. The V-rod is present but never protrudes through the cephalic wall. In its place, a very small ventral tube exists. The protoplasm is observed in *Callimitra* and *Clathrocanium*. The endoplasm with multi-nuclei or a single nucleus is very small, transparent, and located in the cephalic cavity. Several algal symbionts are located inside and/or just below the cephalis.

Stratigraphic occurrence. — Late Eocene-Living.

Remarks

The taxonomic position of the Sethoperidae at the superfamily and lineage levels, as well as the taxonomic differences between the Phaenocalpididae and Sethoperidae require additional studies. *Tripocyrtis* appear to be a synonym of *Periplecta* (Phaenocalpididae) while *Dictyocodoma* and *Clathropilium* appear to be members of the Stichopiliidae and Ceratocyrtidae, respectively. In most cases, the Sethoperidae are distinguished from the Phaenocalpididae by the presence of a wired screen in the cephalis and thorax. However, in some critical cases, a detailed examination of the cephalic initial spicular system is necessary (*Tripocyrtis* vs *Periplecta*). The cephalic initial spicular system of the Phaenocalpididae is broadly similar to that of the Sethoperidae. The differences between the Sethoperidae and the Phaenocalpididae are: 1) the development a second arch along D- and double L-rods outside of the basal ring in Sethoperidae; 2) the lack of developed sutures on the cephalis with cephalic arches in Sethoperidae; and 3) the presence of a straight a-spinule and arches that are related to m- and g-positions on the A-rod forming a "segmented" appearance inside the cephalis from dorsal or ventral view in Sethoperidae. The type-illustration of *Dictyocodoma* is probably obtained from the dorsal or ventral view of Stichopiliidae. This view allows the user to find a single apical horn if the supporting image is indeed correct. However, this observation is structurally impossible as the view with the three wings should be also associated with the identification of both apical and ventral horns. A *Pteropilium* species was previously identified as a member of *Lipmanella* (Nishimura & Yamauchi 1984: pl. 34, fig. 7). However, if the cephalic initial spicular system defined by Funakawa (2000) is considered, *Pteropilium* is completely different from *Lipmanella*.

The cephalic initial spicular system has been well illustrated for *Callimitra* (Nishimura 1990: figs 22.3, 22.4; Takahashi 1991: pl. 27, fig. 3), *Clathrocanium* (Poluzzi 1982: pl. 29, figs 1-3; Takahashi 1991: pl. 26, figs 12; Sugiyama *et al.* 1992: pl. 15, fig. 4), *Clathrocorys* (Nishimura 1990: figs 21.3, 22.1, 22.2, 23.5; Sugiyama 1994: pl. 2, figs 1, 2), *Pteropilium* (Nishimura & Yamauchi 1984: pl. 34, fig. 7), and *Tripocyrtis* (Nishimura 1990: figs 23.1, 23.2, 23.4). These genera have small size and they are frequently overlooked in many plankton studies. Nonetheless, some living images were illustrated for *Callimitra* (Anderson 1983: fig. 1.2.G; Matsuoka 1999: pl. 1, fig.1; 2017: fig. 20; Zhang *et al.* 2018: 9, fig. 33; pl. 10, figs 31, 46, 47) and *Clathrocanium* (Suzuki *et al.* 2009b: figs 2O, 2P; Zhang *et al.* 2018: 10, fig. 4, p. 13, fig. 21).

Validity of genera

Callimitra

The precise anatomical description of *Callimitra* was written by Petrushevskaya (1981: 301) and revised by Goll (1979:

386) as follows: "[...] *characterized by 3 large lattice panels extending laterally from the tip of the apical apophysis to the tips of each of the frontal and primary lateral apophyses*." *Arachnothauma* was described as follows: "*Shell cupola- or helm-shaped with three delicate convex appendages downwardly curved. From them originate pairs of divergent small lateral apophyses* [...] *From the top of the cephalis originates a similar appendage* [...] *with also lateral apophyses. Between them are distributed extremely thin threads that are linked again to other oblique threads. This structure gives the impression that a very small spider web has covered a very elegant beam structure*" (translation from Zacharias 1906: 566-567). This description of *Arachnothauma* and the type-illustration (Zacharias 1906: fig. 19) match those of *Callimitra*. Zacharias (1906) did not compare *Arachnothauma* to *Callimitra*. They are indeed clearly synonyms. The name *Callimitra* is older than *Arachnothauma*.

Clathrocanium
Clathrocanidium has the same type species as *Clathrocanium*. *Clathrocanium*, *Clathrocorona*, *Arachnopilium, Clathrolychnus*, *Sethopera*, and *Tripocyrtis* are defined in terms of their ontogenetic growth stages. *Clathrocanium* (Suzuki *et al.* 2009c: pl. 54, figs 5a-d), *Sethopera* (Haeckel 1887: pl. 97, fig. 11), and *Tripocyrtis* (Haeckel 1887: pl. 60, fig. 10) represent the youngest stage, without a perforated apical horn. *Clathrocorona* (Haeckel 1887: pl. 64, fig. 2), with perforated apical horn and three perforated basal feet, represents the next growth stage, and is illustrated in the Atlas as a supporting image for *Clathrocanidium*. The next growth stages are *Clathrolychnus* (Haeckel 1887: pl. 64, fig. 5), with a perforation connecting the apical horn and basal feet, followed by *Arachnopilium* (Haeckel 1887: pl. 64, fig. 7), with the development of a perforated thin cover around the three gates between the basal feet. *Arachnopilium* is illustrated as a supporting image for *Clathrocorona* and *Clathrolychnus* in the Atlas.

Superfamily LITHOCHYTRIDOIDEA Ehrenberg, 1846 n. stat.

Lithochytrina Ehrenberg, 1846: 385 [as a family]; 1847: 53 [as a family].

Lychnocanioidea – Petrushevskaya 1986: 132-132. — Afanasieva *et al.* 2005: S295-296. — Afanasieva & Amon 2006: 144.

DIAGNOSIS. — Lithochytridoidea consist of two- to three-segmented Nassellaria with a stout vertical apical horn, a spherical cephalis, a conical or globular thorax, as well as three feet or a relevant structure. The feet are principally connected to the D- and double L-rods of the cephalic initial spicular system. Expect for a few exceptions, an aperture is present.

REMARKS
The Lithochytridoidea consists of the Bekomidae and Lithochytrididae. Based on the results of the molecular phylogeny, *Lamprotripus* and *Dictyopodium* (= *Pterocanium* in original) form a tight, single group (Sandin *et al.* 2019).

Family BEKOMIDAE Dumitrica *in* De Wever, Dumitrica, Caulet, Nigrini & Caridroit, 2001

Bekomidae Dumitrica *in* De Wever, Dumitrica, Caulet, Nigrini & Caridroit, 2001: 284. — Matsuzaki *et al.* 2015: 63-64.

Bekominae – Afanasieva *et al.* 2005: S296. — Afanasieva & Amon 2006: 145.

TYPE GENUS. — *Bekoma* Riedel & Sanfilippo, 1971: 1592 [type species by monotypy: *Bekoma bidarfensis* Riedel & Sanfilippo, 1971: 1592].

INCLUDED GENERA. — *Bekoma* Riedel & Sanfilippo, 1971: 1592. — *Bekomiforma* Sanfilippo & Riedel, 1974: 1020. — *Lamprotripus* Haeckel, 1882: 431. — *Orbula* Foreman, 1973a: 437.

NOMINA DUBIA. — *Stichocampe*, *Stichopterium*.

DIAGNOSIS. — Bekomidae consist of two-segmented Lithochytridoidea (exclusive of *Orbula*) with six collar pores that form the basal ring of the cephalis, two free A- and V-rods in the cephalic cavity, and three feet. Except in the case of *Lamprotripus*, the cephalis is covered with a thick siliceous wall. The cephalic initial spicular system consists of A-, V-, D-, double l-, and double L-rods. A combination of A- and V-rods, or solely A-rod, forms one or more significant cylindrical apical horn(s). D- and double L-rods protrude from the cephalis and form three feet or rims on the thorax. The MB is located in the center of the basal aperture of the cephalis. The basal ring is directly connected to the D-, double l- and double L-rods. The basal ring tends to be located horizontally in the cephalic cavity. Although the basal ring is generally merged to the shell wall, it is well visible in older forms (*Bekoma* and *Bekomiforma*) but degraded in a younger form (*Lamprotripus*).
A protoplasm is observed in *Lamprotripus*. The endoplasm is opaque dark grey, filling the upper part of the shell at the level where three rod wings are separated from the shell. No algal symbionts are present.

STRATIGRAPHIC OCCURRENCE. — Middle Paleocene-Living.

REMARKS
The Bekomidae are distinguishable from the Lithochytrididae. The latter lack the double l-rod and have four collar pores instead of six and their MB is oblique to the collar stricture. The cephalic initial spicular system was illustrated for *Bekoma* (Nishimura 1992: pl. 5, figs 4, 5, 9, 11; pl. 8, fig. 5?), *Bekomiforma* (Sugiyama *et al.* 1992: pl. 20, fig. 1) and *Lamprotripus* (Nishimura & Yamauchi 1984: pl. 31, fig. 1; Nishimura 1990: figs 26.6, 26.7, 29.6; Sugiyama *et al.* 1992: pl. 22, fig. 1). The diagnosis written above excludes the characteristics of "*Lamprotripus*" *mawsoni* (Riedel 1958). As this species lacks the double l- and V-rods (Sugiyama *et al.* 1992: pl. 16, figs 4, 5), it cannot be placed in *Lamprotripus*. This species is also grouped with *Dictyopodium* (= *Pterocanium* in original) but not *Lamprotripus* in the Clade I (Sandin *et al.* 2019). "*L.*" *mawsoni* has three collar pores as opposed to four. Sugiyama *et al.* (1992: 18-19) conceptualized it as a new genus. The living appearance of *Lamprotripus* is documented (Suzuki & Not 2015: fig. 8.10.15).

Family LITHOCHYTRIDIDAE Ehrenberg, 1846 *sensu* Suzuki *in* Matsuzaki *et al.* (2015)

Lithochytrina Ehrenberg, 1846: 385 [as a family]; 1847: 53 [as a family]. — Schomburgk 1847: 124, 125 [as a family]. — Ehrenberg 1876: 156.

Lychnocanida Haeckel, 1882: 432 [below tribe].

Lithornithida Haeckel, 1882: 436 [*nomen dubium*, below tribe].

Lychnocaniinae – Petrushevskaya 1971a: 227-228; 1981: 239-240. — Afanasieva *et al.* 2005: S296. — Afanasieva & Amon 2006: 144.

Lychnocaniidae – Petrushevskaya & Kozlova 1972: 552. — Petrushevskaya 1975: 583; 1981: 229-230; 1986: 133. — Dumitrica 1979: 34. — Kozlova 1999: 127. — Afanasieva *et al.* 2005: S296. — Afanasieva & Amon 2006: 144. — Suzuki *in* Matsuzaki *et al.* 2015: 50.

Lithochytridinae – Petrushevskaya 1981: 244. — Afanasieva *et al.* 2005: 296. — Afanasieva & Amon 2006: 144.

Type genus. — *Lithochytris* Ehrenberg, 1846: 385 [type species by subsequent designation (Campbell 1954: D132): *Lithochytris vespertilio* Ehrenberg, 1874: 239].

Included genera. — *Dictyopodium* Ehrenberg, 1847: 54 (= *Pterocanarium* **n. syn.**; *Pterocanidium* and *Pleuropodium* synonymized by Riedel & Sanfilippo 1970: 529; *Lychnodictyum* synonymized by Lazarus *et al.* 1985: 196). — *Inversumbella* Nigrini & Caulet, 1992: 150. — *Lithochytris* Ehrenberg, 1846: 385 (= *Lithochytridium* with the same type species; *Sethochytris* synonymized by Petrushevskaya 1981: 247). — *Lychnocanissa* Haeckel, 1887: 1226 (= *Acerahedrina*, *Acerocanium*, *Lychnocanoma* synonymized by Riedel & Sanfilippo 1970: 529; *Podocyrtecium* **n. syn.**). — *Lychnocanium* Ehrenberg, 1846: 385 (= *Dictyophimium* with the same type species; *Lithochytrodes* synonymized by Petrushevskaya 1975: 583; *Lychnocanella* **n. syn.**). — ? *Verutotholus* O'Connor, 1999: 13.

Invalid name. — *Tetrahedrina*.

Nomina dubia. — *Lithornithium*, *Tetraedrina*.

Nomen nudum. — *Fenestracanthia*.

Diagnosis. — Lithochytrididae consist of two or three segmented Lithochytridoidea with four collar pores on the cephalic basal ring, a free A-rod in the cephalic cavity, and a very short to very long apical horn on the spherical cephalis. Three (rarely two) feet or wings are always present. The cephalic initial spicular system consists of MB, A-, D-, V- and double L-rods. No l-rods are observed. The basal ring is directly connected to the apical side end of MB, V-, and the double L-rods. Furthermore, the basal ring is sharply bended along the line, with the double L-rods. The apical side of the basal ring is merged with the shell wall but all four collar pores are easily recognizable. The V-rod occasionally extends outward from the cephalic wall. The MB is oriented slightly toward to the apical side. The double *mp*-arch (upper arch of the double AL-arch in the cephalis) is embedded in the cephalic wall and is occasionally visible, near the uppermost A-rod on the cephalis, under light microscopy. The D- and double L-rods merge with the shell wall, forming wall rims. These rods are also connected with each foot.
A protoplasm is observed in *Dictyopodium*. The endoplasm is transparent and appears as four lobes below the cephalis. The size of the lobe is variable, from very small near the cephalis to large close to the aperture. Many algal symbionts are distributed around the lobes. The endoplasm is observed inside or outside the shell. The pseudopodia are found radiating around the thorax. An axial projection is absent.

Stratigraphic occurrence. — Early Paleocene-Living.

Remarks

The problem in defining Lithochytrididae originates from the poorly reported cephalic structure in the type genus *Lithochytris* and its closest genus *Lychnocanium*. The cephalic structure was only reported for *Lithochytris* (Nishimura 1990: figs 28.2, 28.3) and *Lychnocanium* (Nishimura 1990: fig. 28.1). By contrast, the cephalic structure was repeatedly illustrated in *Dictyopodium* (Dumitrica 1973a: pl. 13, figs 3-6; Nishimura & Yamauchi 1984: pl. 30, figs 7, 9; Nishimura 1990: fig. 29.7; Sugiyama *et al.* 1992: pl. 24, figs 5-8, pl. 25, figs 1, 3, 4). To the best of our knowledge, the detailed structure of *Dictyopodium* is nearly the same as that of *Lychnocanium* but the former displays the most representative characters of Lithochytrididae. The cephalic structure of *Lychnocanissa* (originally *Lychnocanium*) was only observed in the late Eocene to early Miocene specimens (O'Connor 1997a: pl. 9, figs 9-12; 1999; pl. 4, figs 12-15, pl. 4, figs 22-27). However, their cephalic base is completely separate from the shell test while the basal ring is affixed to the shell test by numerous short radial beams. These characters are typical for the Theoperidae. High species diversity is documented in *Lychnocanissa* (originally *Lychnocanoma*) (Riedel & Sanfilippo 1970; Petrushevskaya 1981). Nonetheless, several species may not belong to this genus. *Verutotholus* is tentatively included in the Lithochytrididae though this genus has a double AL-arch, six collar pores and the presence of double l-rods (O'Connor 1999: pl. 2, figs 16, 20, 22b), more closely resembling the Bekomidae. An endemic *Lychnocanissa* with only two feet was originally described as *Acerahedrina* (Vinassa de Regny 1900). In regard to the cephalic structure of the *Acerahedrina*-form of *Lychnocanissa* (Nishimura 1990: figs 27.4-27.6; Sugiyama & Furutani 1992: pl. 17, fig. 2), the character of the cephalic base is similar to that of *Dictyopodium* and, thus, this form evidently belongs to the Lithochytrididae. The two feet of the *Acerahedrina*-form of *Lychnocanissa* are aligned parallel to the plane that includes MB-, D-, and V-rods. One of the feet appears to be connected with the D-rod while the other is disconnected from any initial rod.

The members of the Lithochytrididae and the valid genera names in the Lithochytrididae were historically misunderstood. As for the family, all Lithochytrididae genera except for "*Lychnocanoma*" and "*Pterocanium*" (the valid names are *Lychnocanissa* and *Dictyopodium* in this paper) were not treated in De Wever *et al.* (2001). De Wever *et al.* (2001) placed *Dictyopodium* in the Mesozoic family Ultranaporidae Pessagno 1977a. The current usage of the latter name has been already discussed and resolved by Matsuzaki *et al.* (2015: 49-50). The valid genus name and correct type species for *Lychnocanium* (Sanfilippo *et al.* 1973: 221; Petrushevskaya 1981: 242), "*Lychnocanoma*" (Riedel & Sanfilippo 1970: 529; Petrushevskaya & Kozlova 1972: 553; Petrushevskaya 1981: 241; Nishimura 1990: 132-133; O'Connor 1997a: 77-78; 1999: 24), and "*Pterocanium*" (the valid genus name is *Dictyopodium* in this paper) (Riedel & Sanfilippo 1970: 529; Petrushevskaya 1981: 237) were not fully agreed among previous researchers. The main argument concerned whether *Lychnocanium lucerna* Ehrenberg 1847 or *Lychnocanium falciferum* Ehrenberg, 1854 was the correct type species of *Lychnocanium*. A similar problem occurred between *Pterocanium proserpinae* Ehrenberg 1859 and *Lithocampe aculeata* Ehrenberg 1844b for the correct type species of *Pterocanium*.

The Lithochytrididae are commonly found from late Eocene sediments to the modern ocean, but the study of their evolution is limited. The evolutionary history of the genus *Dictyopodium* (= *Pterocanium* in original) was documented (Lazarus *et al.* 1985). One solution for the evolution of *Lithochytris-Lychnocanium* was proposed (Kling 1978: 234; Riedel & Sanfilippo 1981: fig. 12.11).

Knowledge of the living status of the Lithochytrididae is mainly based on *Dictyopodium* (Matsuoka 1993a: fig. 2.5; 1993b: pl. 5, figs 1, 2; 2017: fig. 23; Suzuki & Aita 2011: fig. 5N; Suzuki & Not 2015: fig. 8.11.17). Algal symbionts of *Dictyopodium praetextum* (Ehrenberg) were identified as *Gymnoxanthella radiolariae* but *Brandtodinium nucleate* remained absent. The identified symbiont is the same dinoflagellate species as those found in *Acanthodesmia* (Acanthodesmiidae) and *Dictyocoryne* (Euchitoniidae, Spumellaria) (Yuasa *et al.* 2016).

Validity of genera

Dictyopodium

The concept of the valid genus *Dictyopodium* is equivalent to the current usage of *Pterocanium* because *Dictyopodium trilobum*, the type species of *Dictyopodium*, has been classified under the current concept of *Pterocanium* for more than 130 years (Haeckel 1887). The type species of *Pterocanarium* is *Pterocanium proserpinae*, which has been classified in *Pterocanium* for over a century, but was synonymized with *Podocyrtis charybdea* by Petrushevskaya (1971a). Lazarus *et al.* (1985) reconstructed the phylogeny of late Neogene *Pterocanium* to include *Pterocanium charybdeum* and *Pterocanium trilobum* (originally *P. charybdeum trilobum*); subsequently, *Pterocanarium* was synonymized with *Dictyopodium*, and the genera *Pterocanidium*, *Pleuropodium*, and *Lychnodictyum* were synonymized with *Dictyopodium*. Among these, the oldest available name is *Dictyopodium*.

Lychnocanissa

In the Atlas, *Lychnocanissa* corresponds to *Lychnocanoma sensu* Foreman (1973b: 437), Sanfilippo *et al.* (1973: 221), Morley & Nigrini (1995: 80), and Suzuki in Matsuzaki *et al.* (2015: 50) and to *Lychnocanium sensu* Riedel & Sanfilippo (1970: 529), Petrushevskaya & Kozlova (1972: 553), Petrushevskaya (1981: 242), Nishimura (1990: 132-133), Kozlova (1999: 128), and O'Connor (1997a: 77-78; 1999: 24). Our concept is also equivalent to a combination of *Lychnocanium* and *Lychnocanoma*, *sensu* Tochilina & Vasilenko (2018a: 23). The type-illustration of *Podocyrtecium* shows three segmentations (Haeckel 1887: pl. 72, fig. 1), but this is likely incorrect because no three-segmented specimens similar to *Lychnocanoma* have been found. *Lychnocanissa*, *Lychnocanoma*, and *Podocyrtecium* were simultaneously published in Haeckel (1887: 1226 for *Lychnocanissa*, 1229 for *Lychnocanoma* and 1339 for *Podocyrtecium*). Selecting a valid genus is problematic. Campbell (1954: D124) considered *Lychnocanissa* the nominate subgenus of *Lychnocanium*. However, the type species of *Lychnocanium*, *Lychnocanium lucerna*, was not originally included in *Lychnocanissa*. Species included at that time included *Lychnocanium falciferum*, *Lychnocanium fenestratum*, *Lychnocanium fortipes*, *Lychnocanium sigmopodium*, *Lychnocanium tetrapodium*, *Lychnocanium trichopus*, and *Lychnocanium tuberosum*. Campbell (1954) did not designate a type species for *Lychnocanissa*. Therefore, we newly designated *Lychnocanium falciferum* as a type species in the Atlas. *Lychnocanium falciferum* was designated as the type species of *Lychnocanium* by Campbell (1954: D124), but many authors have commented that this designation is incorrect. One of the authors of the present study (NS) suggested that *Lychnocanoma* be validated several times over a period of 2 years; however, the final consensus is that *Lychnocanissa* is a valid genus. The validation of *Lychnocanissa* over *Lychnocanoma* obviously violates ICZN (1999) article 23.9, which states, "*23.9.1. Prevailing usage must be maintained when the following conditions are both met: 23.9.1. The senior synonym* [...] *has not been used as a valid name after 1899, and 23.9.1.2. The junior synonym* [...] *has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years*."

Lychnocanium

There are two concepts of *Lychnocanium*, one based on the designation of *Lychnocanium falciferum* as the type species by Campbell (1954: D124), and the other based on the designation of *Lychnocanium lucerna*, the first species assigned to *Lychnocanium*, as the type species by Ehrenberg (1847). This confusion has continued since the early 1970s (Riedel & Sanfilippo 1970; Sanfilippo *et al.* 1973; Petrushevskaya 1981; O'Connor 1997a; Tochilina & Vasilenko 2018a). The only correct solution is for *Lychnocanium lucerna* to be designated as the type species, according to ICZN (1999) article 69.3, which states, "*Type species by subsequent monotypy. If only one nominal species was first subsequently included in a nominal genus or subgenus without included species, that nominal species is automatically fixed as the type species, by subsequent monotypy.*" Under this monotypy, the concept of *Lychnocanium sensu* Riedel & Sanfilippo (1970: 529), Petrushevskaya & Kozlova (1972: 553), Petrushevskaya (1981: 241), Nishimura (1990: 132-133), Kozlova (1999: 128) and O'Connor (1997a: 77-78; 1999: 24), and Tochilina & Vasilenko (2018a: 23) is incorrect.

Under the correct type species, *Lychnocanium* is synonymized with *Lithochytrodes* and *Lychnocanella*. *Dictyophimium* has the same type species as *Lychnocanium*. *Lychnocanella* was defined by Kozlova (1999: 127) and is translated as follows: "*Three-segmented shell with three well-developed feet, protruding from the base of the thorax. This genus differs from* Lychnocanium *Ehrenberg* [note: type species *L. lucerna* in this case] *only by a pear-shaped thorax with an elongated proximal part.*" This difference is a major distinguishing feature at the species level but not at the genus level. Petrushevskaya (1981: 241) strongly disagreed with the relationship between *Lychnocanium* and *Lychnocanella*, but this opinion was based on the incorrect type species, *L. falciferum*, not *L. lucerna*. *Lithochytrodes* was synonymized with *Lychnocanella* by Petrushevskaya (1975: 583). Later comments by Petrushevskaya (1981: 256) are translated as follows: "*Characteristics similar to those of* Lychnocanella. *Differences include a more precise distinction between the second and third segments* [...] *about 10-20 longitudinal rows of pores* [...] Lithochytrodes *is proposed as a subjective synonym of* Lychnocanella." Among these groups, *Lychnocanium* is the oldest available name.

Superfamily PTEROCORYTHOIDEA Haeckel, 1882 *sensu* Suzuki emend. herein

Pterocorida Haeckel, 1882: 435 [below a tribe].

Pterocoryacea – Kozur & Mostler 1984: 122.

Pterocorythoidea – Suzuki *in* Matsuzaki *et al.* 2015: 49-50.

DIAGNOSIS. — Pterocorythoidea consist of three segmented Nassellaria with a stout, vertical apical horn, a spherical or elongated cephalis, a truncated conical thorax, and a very variable size last segment. Generally, no feet extend from the abdomen. If feet are present and extend from the abdomen, they remain disconnected from any rods of the cephalis spicular system. An aperture is observable except in the case of a few exceptions. The A-rod side of the MB is positioned very close to the shell wall or may be merged, becoming a part of the shell wall. The V-rod side of the MB is generally located at the center of the cephalic basal aperture. The V-rod is oriented upward at an angle of 30-45 degrees from the horizontal plane. The stability of the cephalis spicular system varies throughout families.

REMARKS

The Pterocorythoidea include the Lophocyrtiidae, Pterocorythidae, Theocotylidae and Theoperidae. As the Pterocorythidae is the only family with living genera (*Anthocyrtidium*, *Pterocorys*, and *Theocorythium*), the taxonomic position of the remaining three families is only based on morphological data. Matsuzaki *et al.* (2015) also included the Lithochytrididae (originally Lychnocaniidae) but did not conclude Lophocyrtiidae, Theocotylidae and Theoperidae as these families were not encountered in their study. Herein, the diagnosis is altered in order to align with these Cenozoic families. As three families of the Pterocorythoidea are extinct, the evolution between them can only be reconstructed by examining the fossil evidence. From an anatomical perspective, the *Spongiopodium*-form of *Paralampterium* has characters that resemble a combination of those found in Lophocyrtiidae and Theoperidae. *Calocyclas* has a mix of characters found in the Pterocorythidae and the Theocotylidae.

Family LOPHOCYRTIIDAE Sanfilippo & Caulet *in* De Wever, Dumitrica, Caulet, Nigrini & Caridroit, 2001

Lophocyrtiidae Sanfilippo & Caulet *in* De Wever, Dumitrica, Caulet, Nigrini & Caridroit, 2001: 283-284. — Afanasieva *et al.* 2005: S300-301. — Afanasieva & Amon 2006: 150.

TYPE GENUS. — *Lophocyrtis* Haeckel, 1887: 1410 [type species by subsequent designation (Campbell 1954: D134): *Eucyrtidium stephanophorum* Ehrenberg, 1874: 233].

INCLUDED GENERA. — *Aphetocyrtis* Sanfilippo & Caulet, 1998: 16. — *Apoplanius* Sanfilippo & Caulet, 1998: 12. — *Clinorhabdus* Sanfilippo & Caulet, 1998: 19. — *Cyclampterium* Haeckel, 1887: 1379 (= *Polyalacorys* **n. syn.**). — *Lophocyrtis* Haeckel, 1887: 1410. — *Paralampterium* Sanfilippo, 1990: 307 (= *Spongiopodium* **n. syn.**). — *Sciadiopeplus* Sanfilippo, 1990: 310.

DIAGNOSIS. — Lophocyrtiidae are commonly three-segmented, cylindrical to conical shell. The cephalis is spherical in shape and may or may not have pores. The cephalic initial spicular system consists of MB, A-, V-, double l-, double L-, and Ax-rods. The double *mp*-arch (one of AL-arch) freely develops in the cephalic cavity. The A-rod is generally visible and free in the cephalic cavity. It may also be attached to the cephalic wall. The thorax is of a rounded conical shape, thick-walled, and its pores are regularly quincuncially arranged. The abdomen is thick-walled to coarse-framed skirt-like. The abdomen's end is widely open. The feet, present in some members, are disconnected from the cephalic initial spicular system. The basal ring is directly connected to the apical end of the MB as well as to the double L- and V-rods, forming a frame that resembles a four-leafed clover. The basal ring sharply bends along the line with the double L-rods. The D- and double L-rods extend downward forming a rim on the internal wall of the thorax. These rods are completely merged. A double Dl-arch seems to be present as part of the thoracic wall, but the double l-rod is generally unrecognizable. No living form are known.

STRATIGRAPHIC OCCURRENCE. — Late Paleocene-early Middle Miocene.

REMARKS

The grammatically correct name is "Lophocyrtididae" but the current usage following Article 29.5 of the Code is maintained (Lophocyrtiidae). Three segmented, cylindrical Nassellaria similar to the Lophocyrtiidae are known in the Eucyrtidiidae (e.g., *Theocoronium*), Rhopalosyringiidae (e.g., *Rhopalosyringium*), and Pterocorythidae (e.g., *Calocyclas*, the *Podocyrtopsis*-form of *Podocyrtis*, the *Theoconus*-form of *Pterocorys*, *Theocorythium*). The most significant difference among them is the presence of a free double mp-arch in Lophocyrtiidae. *Theocoronium* is of a small size and is more fragile than the Lophocyrtiidae. *Rhopalosyringium* differs from the Lophocyrtiidae by its artostrobid-type cephalic structure. *Calocyclas* has a non-bladed, long, robust horn with a spherical and delicate thorax. Both *Pterocorys* and *Theocorythium* have a lobe-like, oblong, cephalic part with a complex internal structure. The cephalic structure of the *Spongiopodium*-form of *Paralampterium* (Lophocyrtiidae), similarly to Theoperidae, bears a connection structure between the cephalis and thorax.

According to Sanfilippo (1990), *Paralampterium* diverged from *Lophocyrtis* in the early Eocene; *Cyclampterium* separated around the Eocene-Oligocene boundary while *Sciadiopeplus* diverged from *Cyclampterium* just after the appearance of *Cyclampterium* in the early Oligocene. *Lophocyrtis* is also the direct ancestor of *Apoplanius*, this follows the analyses of the stratigraphic distribution as well as the geographic distribution at species level among *Lophocyrtis*, *Apoplanius*, *Aphetocyrtis* and *Clinorhabdus* (Sanfilippo & Caulet 1998). Takemura & Ling (1998) discussed the phylogeny of the Lophocyrtiidae with the same group of species treated in Sanfilippo & Caulet (1998). These species appear under the genus name *Theocorys* Haeckel 1882 (with a Mesozoic type species *Theocorys morchel-*

lula Rüst, 1885), as some photos appear to have a double *mp*-arch (Takemura & Ling 1998: fig. 3.19). Little is known about the ancestor of the Lophocyrtiidae.

The morphological change of the cephalic initial spicular system at species level was documented for *Aphetocyrtis*, *Apoplanius* and *Clinorhabdus* (Sanfilippo & Caulet 1998). The double *mp*-arch must be encrypted in the cephalic wall of some members as it remained unobserved in scanning electron microscopy (SEM) images (Takemura & Ling 1998: figs 5.7-5.12). The double *mp*-arch is recognizable as part of the thoracic wall in SEM illustrations of *Aphetocyrtis* (originally *Theocorys* in Takemura & Ling 1998: figs 5.11, 5.12), *Clinorhabdus* (originally *Theocorys* in Takemura & Ling 1998: figs 5.9, 5.10) and the *Spongiopodium* form of *Paralampterium* (Nishimura 1990: figs 27.1-27.3).

Validity of genera

Cyclampterium

Polyalacorys was first practically validated by Nishimura (1990: 142), who subsequently designated *Alacorys carcinus* as the type species of *Polyalacorys*, whereas *Cyclampterium* was transferred from a subgenus of *Cycladophora* (Haeckel 1887: 1379) to that of *Lophocyrtis* (Sanfilippo 1990: 304). Sanfilippo (1990) described *Cyclampterium* as having an apical horn usually short or absent and Nishimura (1990) described it as an apical spine prolonged from an A-rod. The length of the apical horn is the only difference in these descriptions. Sanfilippo (1990) considered the *Cyclampterium* lineage to start from *Lophocyrtis* (*Cyclampterium*) *hadra*. This species has a very long, stout apical horn that nearly reaches the same length as the apical horn of *Alacorys carcinus*, the type species of *Polyalacorys*. Based on the lineage reconstructed by Sanfilippo (1990), *Polyalacorys* must be synonymized with *Cyclampterium*. *Cyclampterium* has been raised to the rank of genus for practical usage due to its significant morphological differences, although this genus branches from *Lophocyrtis*.

Paralampterium

The main difference between the definitions of *Spongiopodium* and *Paralampterium* is a spongy wall structure and three or more foot-like projections for the former (Nishimura 1990: 135); the abdominal segment, the most conspicuous one, is very variable, with large-coarse meshes and three feet that are solid, incipiently latticed or pored for the latter (Sanfilippo 1990: 307). The definition of *Paralampterium* covers that of *Spongiopodium*, which raises the issue of splitting and lumping philosophies. The genus concept by Sanfilippo (1990) is based on stratigraphic and geographic distribution at the species level, whereas that by Nishimura (1990) is based on a spot sampling obtained in just one locality of the Pacific Ocean. As Sanfilippo's (1990) concept better reflects stratigraphic and geographic variation for this taxon, we support the lumping philosophy for this genus. Both genera were published in 1990; the formal publication dates were March 1990 for *Paralampterium* (*Marine Micropaleontology*, Volume 15 no. 3-4) and March 31, 1990, for *Spongiopodium* (*Science Reports of the Institute of Geoscience, University of Tsukuba, Section B: Geological Sciences*, Volume 11). Because there is no clear difference between these publication dates, we select *Paralampterium* as the valid name due its more comprehensive definition.

Family Pterocorythidae Haeckel, 1882

Pterocorida Haeckel, 1882: 435 [below a tribe].

Sethocorida Haeckel, 1882: 430 [as a tribe]; 1887: 1192, 1289 [as a subfamily].

Calocyclida Haeckel, 1882: 434 [below tribe].

Podocyrtida Haeckel, 1882: 435 [below tribe]; 1887: 1313, 1314-1315 [as a family]. — Bütschli 1889: 1990 [as a family]. — *nec* Rüst 1892: 183. — Nigrini 1967: 65 [as a family].

Sethocyrtida Haeckel, 1887: 1192, 1288-1289 [as a family]. — Bütschli 1889: 1989 [as a family]. — Rüst 1892: 182 [as a family]. — *nec* Cayeux 1894: 208.

Phormocyrtida Haeckel, 1887: 1313, 1365-1366 [as a family]. — Bütschli 1889: 1992 [as a family]. — Nigrini 1967: 65-66 [as a family].

Theocyrtida Haeckel, 1887: 1313, 1395-1396 [as a family]. — Wisniowski 1889: 689 [as a family]. — Bütschli 1889: 1992 [as a family]. — Rüst 1892: 183 [as a family]. — *nec* Cayeux 1894: 209. — Nigrini 1967: 66 [as a family].

Phormocampida Haeckel, 1887: 1435 [as a family]; 1887: 1453-1454 [as a family]. — Bütschli 1889: 1994 [as a family].

Phormocampiden – Haecker 1907: 126.

Phormocyrtiden – Haecker 1907: 126 [as a family].

Lamprocycladidae [*sic*] – Haecker 1908: 452-454 (= Lamprocyclidae).

Sethocyrtidae [*sic*] – Popofsky 1908: 287 (= Sethocyrtididae); 1913: 372. — Schröder 1914: 100, 113. — Clark & Campbell 1942: 75; 1945: 40. — Campbell & Clark 1944a: 43; 1944b: 26. — Chediya 1959: 208. — Tan & Tchang 1976: 282. — Tan & Su 1982: 175; 2003: 113, 170. — Chen & Tan 1996: 153. — Chen *et al.* 2017: 202.

Podocyrtidae [*sic*] – Popofsky 1908: 288 (= Podocyrtididae); 1913: 373. — Schröder 1914: 119. — Clark & Campbell 1942: 80. — Campbell & Clark 1944a: 46; 1944b: 29 (*sensu* emend.). — Dogiel & Reshetnyak 1955: 47. — Chediya 1959: 213. — Tan & Tchang 1976: 283. — Tan & Su 1982: 176; 2003: 113, 174-175. — Nishimura 1990: 125-126 (*sensu* emend.). — van de Paverd 1995: 238. — Chen & Tan 1996: 153. — Tan & Chen 1999: 323. — Chen *et al.* 2017: 207.

Phormocyrtidae [*sic*] – Popofsky 1908: 289 (= Phormocyrtididae); 1913: 395. — Schröder 1914: 127. — Clark & Campbell 1942: 81; 1945: 43. — Campbell & Clark 1944a: 47; 1944b: 31. — Chediya 1959: 217. — Chen & Tan 1996: 153. — Tan & Chen 1999: 336. — Tan & Su 2003: 113, 192. — Chen *et al.* 2017: 212.

Phormocampidae – Poche 1913: 221. — *nec* Khabakov 1937: 110. — Campbell & Clark 1944b: 37. — Chediya 1959: 228. — Tan & Su 2003: 113, 214.

Sethocyrtididae – Poche 1913: 221.

Theocyrtidae [*sic*] – Popofsky 1913: 397 (= Theocyrtididae). — Schröder 1914: 129. — Clark & Campbell 1942: 89; 1945: 47. — Campbell & Clark 1944a: 49; 1944b: 32. — Chediya 1959:

220. — Tan & Tchang 1976: 289. — Tan & Su 1982: 177; 2003: 113, 200. — Chen & Tan 1996: 154. — Chen *et al.* 2017: 218.

Sethocorinae [*sic*] – Clark & Campbell 1942: 75 (= Sethocorythinae); 1945: 40. — Campbell & Clark 1944a: 43; 1944b: 27. — Chediya 1959: 208.

Sethocyrtinae [*sic*] – Orlev 1959: 455-456 (= Sethocyrtididae).

Theocyrtinae [*sic*] – Orlev 1959: 457 (= Theocyrtidinae).

Phormocampinae – Orlev 1959: 459.

Pterocoryidae [*sic*] – Riedel 1967b: 296 (= Pterocorythidae) (*sensu* emend.); 1971: 657. — Riedel & Sanfilippo 1971: 1598. — Petrushevskaya & Kozlova 1972: 543. — Nakaseko *et al.* 1975: 174. — Nakaseko & Sugano 1976: 130. — Petrushevskaya 1981: 274-276. — Kozlova 1999: 144. — Amon 2000: 65-66. — Afanasieva *et al.* 2005: S300. — Afanasieva & Amon 2006: 149.

Pterocorydinae [*sic*] – Petrushevskaya 1971a: 230-231 (= Pterocorythinae); 1971b: 986.

Pterocorythidae – Moore 1972: 147 (*sensu* emend.). — Riedel & Sanfilippo 1977: 876. — Dumitrica 1979: 34. — Anderson 1983: 43. — Sanfilippo *et al.* 1985: 691. — Caulet & Nigrini 1988: 223. — Nigrini & Caulet 1988: 342. — Takahashi 1991: 123. — Hollis 1997: 65. — O'Connor 1997b: 108 (*sensu* emend.). — Boltovskoy 1998: 33. — Sugiyama 1998: 233. — Anderson *et al.* 2002: 1018. — De Wever *et al.* 2001: 258.

Calocyclinae [*sic*] – Petrushevskaya 1981: 226-227 (= Calocyclidinae). — Amon 2000: 64. — Afanasieva *et al.* 2005: S298. — Afanasieva & Amon 2006: 147.

Podocyrtiinae [*sic*] – Petrushevskaya 1981: 276 (= Podocyrtididae). — Afanasieva *et al.* 2005: S300. — Afanasieva & Amon 2006: 149.

Sethocorynae [*sic*] – Petrushevskaya 1981: 280 (= Sethocorythinae).

Pterocoryinae [*sic*] – Petrushevskaya 1981: 283 (= Pterocorythinae). — Afanasieva *et al.* 2005: S300. — Afanasieva & Amon 2006: 149.

Sethoconidae Nishimura, 1990: 124. — van de Paverd 1995: 229.

Lamprocyclidae – Tochilina 1997: 11-12.

Podocyrtinae [*sic*] – Amon 2000: 66 (= Podocyrtididae).

Sethocoryinae [*sic*] – Amon 2000: 67 (= Sethocorythinae). — Afanasieva *et al.* 2005: S300. — Afanasieva & Amon 2006: 149.

TYPE GENUS. — *Pterocorys* Haeckel, 1882: 435 [type species by subsequent designation (Campbell 1954: D130): *Pterocorys campanula* Haeckel, 1887: 1316].

INCLUDED GENERA. — *Albatrossidium* Sanfilippo & Riedel, 1992: 16. — *Anthocyrtidium* Haeckel, 1882: 430 (= *Anthocyrtissa*, *Sethocyrtis* synonymized by Caulet 1974: 239; *Anthocyrtura* synonymized by Petrushevskaya & Kozlova 1972: 545; *Phormocampe* synonymized by Petrushevskaya 1981: 282; *Sethocanium* **n. syn.**; *Sethocorys* synonymized by Caulet 1979: 132). — *Calocyclas* Ehrenberg, 1847: 54 (= *Calocyclissa* with the same type species; *Anthocyrtonium* synonymized by Petrushevskaya 1981: 280; *Calocycletta* **n. syn.**, *Calocyclior* **n. syn.**, *Calocyclissima* **n. syn.**, *Calocyclopsis* **n. syn.**). — *Calocycloma* Haeckel, 1887: 1384. — *Lamprocyclas* Haeckel, 1882: 434 (= *Lamprocyclia* with the same type species; *Androcyclas* synonymized by Petrushevskaya 1971a: 117; *Craterocyclas*, *Hexalodus*, *Theocorbis* synonymized by Petrushevskaya & Kozlova 1972: 544). — *Lamprocyrtis* Kling, 1973: 638. — *Lampterium* Haeckel, 1882: 434 (= *Alacorys*, *Tetralacorys*, ? *Lamptidium* synonymized by Petrushevskaya & Kozlova 1972: 543). — *Phormocyrtis* Haeckel, 1887: 1368. — *Podocyrtis* Ehrenberg, 1846: 385 (= *Podocyrtidium* with the same type species; *Podocyrtoges* **n. syn.**, *Podocyrtonium* **n. syn.**, *Podocyrtopsis* **n. syn.**). — *Pterocorys* Haeckel, 1882: 435 (= *Sethoconus* with the same type species, *Conarachnium* **n. syn.**; *Lithopilium*, *Theoconus*, *Theocorax*, synonymized by Petrushevskaya 1971a: 232). — *Tetracorethra* Haeckel, 1882: 429 (= *Hexacorethra* synonymized by Petrushevskaya 1971a: 234). — *Theocorythium* Haeckel, 1887: 1416 (= *Theocapsilla* synonymized by Petrushevskaya 1981: 286; *Theocapsura* synonymized by Petrushevskaya 1981: 287; ? *Theocorypha,* ? *Theocyrtis* **n. syn.**). — ? *Anthocyrtoma* Haeckel, 1887: 1268. — ? *Calocyclura* Haeckel, 1887: 1384 [errata 1764]. — ? *Theocorusca* Haeckel, 1887: 1407.

NOMINA DUBIA. — *Cyrtocorys*, *Ennealacorys*, *Lamprocycloma*, *Lamptonium*, *Phrenocodon*.

JUNIOR HOMONYM. — *Cyrtocoris* Haeckel, 1882 (= *Cyrtocorys*) *nec* White, 1842.

DIAGNOSIS. — Pterocorythidae consist of a small cephalis, a truncated, wide conical thorax, and a large abdomen. The aperture is always open and is associated with numerous feet, a circular rim on aperture, or a very coarse frame instead of abdomen. The cephalis varies from an elongated shape with a long apical horn to a thick-walled spherical shape with a robust apical horn. A pore, or pore-like depression, between the cephalis and thorax (sutural pore) is present (*Anthocyrtidium*, *Calocyclas*, *Theocorythium*) or absent (*Lamprocyclas*, *Lamprocyrtis*) as a stable character at the genus level. A sutural pore is always connected to the A-rod. In forms with an elongated cephalis, a free A-rod merges with the cephalic wall, constituting a rim, or part of a blade, along the apical horn. An alignment of several pores is visible on both sides of the A-rod on the cephalic surface. This alignment is found along the A-rod in *Calocyclas* and *Lamprocyrtis*. The elongated cephalis is divided into one larger unpaired lobe and two smaller lateral paired lobes separated by two directed arches AL that are obliquely oriented downward. The D-rod and double L-rod extend downward to merge with the thoracic wall but are never connected to the feet.

The cephalic initial spicular system consists of MB, A-rod, V-rod, double L-rod, and a double AL-arch. The A-rod is free near the basal ring and merges with the cephalic wall, becoming an apical horn. The V-rod is also free in the cephalic cavity and rarely penetrates the cephalic wall. Both the double l-rod and the distinguishing Ax-rod are present or absent. Three types of basal ring are recognized as an infra-species variation in most genera: (Type A) The basal ring is directly connected with the apical side end of MB, double L-rod, and V-rod to form four collar pores; (Type B) Differing from Type A, the basal ring is directly connected to the double l-rod, instead of the MB, forming four collar pores; and (Type C) a basal ring with six collar pores made of D-, V-, double l- and double L-rods. In the case of Type B, an additional very small double pore on the shell wall is formed by the D-rod, double l-rod and double Dl-arch. In the case of Type C, the double pores on the apical side of the basal ring are particularly very small.

A transparent endoplasm fills the cephalic cavity. Endoplasmic lobes of even sizes are present. Their size among specimens is variable but they never extend beyond the thorax. Algal symbionts are present and surround the endoplasmic lobes on the inner side of the shell test. Pseudopodia radiate throughout the test; a conical bundle of pseudopodia and a long robust thick pseudopodium (axial projection) extend outward from the aperture of the test. *Tetracorethra* has a degraded shell test. Living forms of *Tetracorethra* are also characterized by well-developed endoplasmic lobes and the absence of algal symbionts. The growth and development of pseudopodia remains still unknown in *Tetracorethra*.

STRATIGRAPHIC OCCURRENCE. — Late Paleocene-Living.

Remarks

The type genus of this family is *Pterocorys* and the genitive form is *Pterocorythos*, thus the stem is Pterocoryth-, and the family name should be Pterocorythidae (see Moore 1972: 147). Some species of Pterocorythidae with an absent lobe-like cephalis are occasionally misidentified as the Theocotylidae. This misidentification occurs regardless of the fundamental differences in the combination stability of the cephalic structure. The A-rod of the Pterocorythidae merges with the cephalic wall in most of the species, whereas the A-rod in Theocotylidae is free in the cephalic cavity and extends vertically to attach itself to the top of the cephalic cavity. The Pterocorythidae are generally distinguished by the presence of an elongated cephalis with an A-rod running along the cephalic wall (e.g., De Wever *et al.* 2001). However, this diagnosis cannot be rigidly applied for some genera such as *Calocyclas*, due to the variability of its cephalis which may be spherical (*Calocyclas sensu stricto*) to elongated (the *Calocycletta*-form of *Calocyclas*) or of an intermediate form (*Calocyclior*, *Calocyclissima* and the *Calocyclopsis*-form of *Calocyclas*). The genus *Calocyclas* (*sensu stricto*) differs from other Pterocorythidae by the A-rod position, which is variable and free in the cephalic cavity (Ogane *et al.* 2009b: pl. 94, fig. 7c). Other species assigned commonly to synonymies of *Calocyclas* (*Calocycletta*, *Calocyclior*, *Calocyclissima* and *Calocyclopsis*-forms) have an A-rod that merges with the cephalic wall (Moore 1972: pl. 1, fig. 1; pl. 2, fig. 5).

The cephalic structure has been described in *Anthocyrtidium* (Caulet 1974: pl. 9, figs 1-2; Nishimura & Yamauchi 1984: pl. 37, fig. 3; Nishimura 1990: figs 31.6, 31.9; Sugiyama *et al.* 1992: pl. 26, fig. 2; O'Connor 1997b: pl. 5, figs 9-13), *Calocyclas* (O'Connor 1997b: pl. 8, figs 2, 3; 1999: pl. 3, figs 5-11; Sugiyama & Furutani 1992: pl. 19, fig. 7), ? *Calocycloma* (Nishimura 1990: figs 30.3-30.5), *Calocyclura* (Sugiyama *et al.* 1992: pl. 20, figs 5, 6), *Lamprocyclas* (Nishimura & Yamauchi 1984: pl. 37, fig. 11; Nishimura 1990: figs 31.1, 31.2, 39.1; Sugiyama & Furutani 1992: pl. 18, fig. 5; Sugiyama *et al.* 1992: pl. 26, figs 5, 6; Tochilina 1997: pl. 1, fig. 2; pl. 2, figs 1-6; pl. 4, figs 2, 3; pl. 14, figs 14, 15; O'Connor 1999: pl. 4, figs 28-32), *Lamprocyrtis* (Caulet 1971: pls 3, 4; 1974: pl. 10, figs 5, 6; Nishimura 1990: fig. 38.1; Sugiyama *et al.* 1992: pl. 27, fig. 4), *Lampterium* (Nishimura 1990: figs 30.1, 30.2), *Pterocorys* (Nishimura & Yamauchi 1984: pl. 38, fig. 6), and *Theocorythium* (Nishimura & Yamauchi 1984: pl. 38, fig. 10; Sugiyama & Furutani 1992: pl. 19, fig. 1). The position of the A-rod, merged to the cephalic wall, is visible in the light microscopic image of *Phormocyrtis* (Ogane *et al.* 2009b: pl. 58, fig. 3f) and *Podocyrtis* (Ogane *et al.* 2009b: pl. 95, fig. 4b). The presence or absence of double l-rods varies at the species level, but not at the genus-, nor family-level. A good review of this difference was well illustrated in Tochilina (1997) and according to her, *Lamprocyclas* has basal rings of Type A (Tochilina 1997: pl. 4, fig. 5), Type B (Tochilina 1997: pl. 4, fig. 2), and Type C (Tochilina 1997: pl. 1, fig. 2; pl. 5, fig. 15).

The genus composition of the Pterocorythidae differs considerably among Petrushevskaya (1981: 275-276), De Wever *et al.* (2001: 258) and this catalogue. These divergences result from detailed investigation of the cephalic structure in 1990s. Additionally, our explanation is based on the first comprehensive integrated study of the cephalic structure anatomy and the molecular phylogeny. The overall appearance of *Tetracorethra* resembles the Plagiacanthoidea type, but the cephalic initial spicular system and protoplasmic structure of the former are identical to that of *Pterocorys* (Petrushevskaya 1971a: 234; 1981: 291). This opinion was supported by the molecular phylogenetic data of Sandin *et al.* (2019).

The three questionably assigned genera (*Anthocyrtoma*, *Calocyclura* and *Theocorusca*) were not treated in De Wever *et al.* (2001). Petrushevskaya (1981) placed *Anthocyrtoma* and *Calocyclura* in subfamilies "Lapmpromitrinae" and "Theocotylinae" (Petrushevskaya 1981: 104-105, 222), respectively. The taxonomic position of *Theocorusca* was not clearly mentioned in Petrushevskaya (1981: 316) but appears included in the Cannobotrydidae as the figure of this genus was placed with those of *Botryocylinder* and *Rhopalosyringium*. Herein, *Anthocyrtoma* is tentatively included in the Pterocorythidae. The complete form of *Anthocyrtoma* (Riedel & Sanfilippo 1973: pl. 3, fig. 5) is observed with a very large appendage consisting of many feet appearing below a giant thorax. Partially incomplete specimens of *Anthocyrtoma* (Riedel & Sanfilippo 1973: pl. 6, fig. 4) clearly display a free A-rod in the cephalic cavity and a probable V-rod along the left side of the cephalic cavity that resembles a dark line. This cephalic structure is more likely similar to that of the Theocotylidae than that of the Pterocorythidae. Other forms of *Anthocyrtoma* (Riedel & Sanfilippo 1973: pl. 6, figs 2, 3) appear further as synonyms of the genera *Clistophatna* Haeckel 1882 and *Clistophaena* Haeckel 1887 (Theocotylidae). If this observation is correct, the valid genus name for *Anthocyrtoma* is *Clistophatna*, and thus becomes a member of Theocotylidae. The taxonomic position of *Calocyclura* may also be placed in Theocotylidae due to the six collar pores in the basal ring, which is not directly adjoined to the D-rod. In addition, *Calocyclura* has a free D-rod near the MB, a vertical extending free A-rod, and has not sutural pore (Sugiyama *et al.* 1992: pl. 20, figs 5, 6). The appropriate position of *Theocorusca* is unclear.

The ultrafine protoplasmic structure of *Pterocorys* was documented by Sugiyama & Anderson (1997b: pl. 1, figs 2, 3, 5; pls 4, 5) through transmitted scanning microscope (TEM) images. A normal optical image of living specimens was given for *Anthocyrtidium* (Suzuki & Not 2015: fig. 8.11.17), *Pterocorys* (Sashida & Kurihara 1999: fig. 11.15; Matsuoka 2007: figs 4b, 5b; 2017: figs 26, 27; Matsuoka *et al.* 2017: Appendix b), *Tetracorethra* (Zhang *et al.* 2018: 15, fig. 24, p. 21, fig. 30) and *Theocorythium* (Matsuoka 2017: fig. 28).

The evolution of the Pterocorythidae at the family, genus and species levels was studied on the basis of a continuous stratigraphic distribution and a detailed geographic distribution. The evolution has been well documented at the family level (Sanfilippo & Riedel 1992), illustrated at genus level for the *Podocyrtis-Lampterium* lineage (Riedel & Sanfilippo 1981: fig. 12.7; Sanfilippo & Riedel 1990), and explained at species level for *Anthocyrtidium* (Nigrini & Caulet 1988) and *Calocyclas* (originally *Calocycletta* in Moore 1972: text-fig. 1; Riedel & Sanfilippo 1981: fig. 12.11).

The morphologic changes between *Podocyrtis sinuosa* and *Lampromitra mitra* were examined by landmark, outline semi-landmark and landmark-constrained outline analysis (Danelian & MacLeod 2019). *Lamprocyclas* may be infected with Marine Alveolata Group I (Ikenoue *et al.* 2016).

Validity of genera

Calocyclas

Calocyclissa has the same type species as *Calocyclas*. The validity of *Calocyclas* was complicated by a circumvention of the ICZN rules about the type species of *Cycladophora*. Campbell (1954: D132) incorrectly designated *Cycladophora stiligera* as the type species of *Cycladophora*. Riedel & Sanfilippo (1970: 529) followed this designation and also synonymized *Cycladophora stiligera* with *Calocyclas turris*, which is the type species of *Calocyclas*; thus, *Calocyclas* was considered a junior synonym of *Cycladophora sensu* Riedel & Sanfilippo (1970). Once the type species of *Cycladophora* was corrected to *Cycladophora davisiana* by Lombari & Lazarus (1988), *Calocyclas* was no longer considered a synonym of *Cycladophora*.

Sanfilippo & Riedel (1992) established *Calocyclior*, *Calocyclissima*, and *Calocyclopsis* as subgenera of *Calocycletta*; they are all monotypic subgenera with the following characters. *Calocyclissima* differs from the other subgenera in possessing longitudinal ribs between rows of thoracic pores, and very short cylindrical horns; *Calocyclopsis* is distinguished by its few broad shovel-shaped feet (Sanfilippo & Riedel 1992: 30); *Calocyclior* is defined by a larger and more inflated thorax, more delicate abdomen with a longer porous part, and short termination with triangular teeth (Sanfilippo & Riedel 1992: 31). However, there is no apparent need for the separation of these species into subgenera.

Petrushevskaya (1981: 279) revised the definition of *Calocycletta*, translated as follows: "*A helmet-shaped, typically pterocorythid cephalis basally narrowing. Cephalis height larger than its basal width. Collar area distinct. 'Neck' and lateral lobes well differentiated. Upper part of the shell cupola-shaped; lower part cylindrical. External constriction between the thorax and abdomen almost unmarked. Pores similar in size and shape. Shell wall of the thorax thicker than on the abdomen. Except for ribs on the thorax, all thickened parts mamillated. Wall of the abdomen hyaline near the aperture, but may be composed of long, flat, ribbon-shaped teeth, surrounding the wide-open aperture. Porous part of the abdomen not longer than the thorax, but with teeth, the abdomen may be much longer than the thorax.*" This revised definition covers the characters of *Calocyclas*. *Anthocyrtonium* was previously synonymized with *Calocyclas* by Petrushevskaya (1981: 280). Among these groups, the oldest available name is *Calocyclas*.

Lampterium

Lampterium was designated as a subgenus of *Podocyrtis* (Sanfilippo & Riedel 1992), but it is convenient to regard it as a genus for disambiguation from true *Podocyrtis*. *Tetralacorys* has the same type species as *Alacorys*. *Alacorys* and *Lamptidium* were previously synonymized by Petrushevskaya & Kozlova (1972: 543); thus, *Tetralacorys* was automatically synonymized with *Lampterium*. *Lampterium* and *Tetralacorys* were simultaneously published in Haeckel (1882: 434 for the former and 436 for the latter). *Lampterium* has generally been preferred to *Tetralacorys*; therefore, the former is selected as a valid name.

Podocyrtis

Podocyrtidium has the same type species as *Podocyrtis*. *Podocyrtoges* and *Podocyrtopsis* were established as subgenera of *Podocyrtis* by Sanfilippo & Riedel (1992). *Podocyrtopsis* is distinguished from *Podocyrtoges* by its larger thorax, lack of feet, and by abdominal pores being irregular in size and arrangement (Sanfilippo & Riedel 1992: 14). *Podocyrtonium* differs from *Podocyrtis* by having a larger and wider abdomen (Petrushevskaya 1981: 218). *Podocyrtoges* differs from *Podocyrtis* in having a larger abdomen than thorax. The thorax of *Podocyrtopsis* is larger than that of *Podocyrtoges* (Sanfilippo & Riedel 1992: 14). Sanfilippo & Riedel (1992) stressed that comparisons of single factors are much less satisfactory than considering entire subgeneric lineages, some of which contain diverse forms that cannot be briefly characterized. Thus, these groups should be considered a single genus, without subgenera; *Podocyrtis* is the oldest available name among them.

Pterocorys

Sethoconus and *Conarachnium* have the same type species, as do *Theoconus* and *Theocorax*. *Theoconus* was previously synonymized with *Pterocorys*; thus, *Theocorax* is also automatically synonymized with *Pterocorys*. *Eucyrtidium trochus* was examined by Ehrenberg himself, and designated the type species of *Conarachnium* and *Sethoconus*, based on specimens in the Ehrenberg collection (Suzuki *et al.* 2009c: pl. 55, figs 12a-c); the lectotype is a dorsal or ventral view of a young specimen of *Pterocorys zancleus*. In conclusion, these genera are synonymous. *Pterocorys* and *Conarachnium* were simultaneously published in Haeckel (1882: 430 for *Conarachnium* and 435 for *Pterocorys*). As the type species of *Pterocorys* is a better specimen than that of *Conarachnium*, the former is selected as the valid name.

Theocorythium

Theocorypha has the same type species as *Theocyrtis*. The original specimen of *Eucyrtidium barbadense* which was examined by Ehrenberg himself was found in the Ehrenberg collection (Ogane *et al.* 2009b, pl. 85, figs 7a-c) and was designated as the lectotype. This species is the type species of *Theocyrtis*. As shown in the supporting image for *Theocyrtis* in the Atlas, the real specimen is in very poor condition. *Theocorythium* is known from the late early Miocene, but the lectotype of *Theocyrtis* was dated to about the late Eocene. We tentatively synonymize *Theocyrtis* and *Theocorypha* with *Theocorythium*, but it should be considered *nomen dubium*. The genus name *Theocyrtis* has been used for important biostratigraphic marker species such as *Theocyrtis tuberosa*, but a new genus should be established for taxonomic stability.

Family Theocotylidae Petrushevskaya, 1981

Theocotylinae Petrushevskaya, 1981: 216-217. — Afanasieva *et al.* 2005: S298. — Afanasieva & Amon 2006: 147.

Theocotylidae – De Wever *et al.* 2001: 280.

Type genus. — *Theocotyle* Riedel & Sanfilippo, 1970: 524 [type species by original designation: *Theocotyle venezuelensis* Riedel & Sanfilippo, 1970: 524] = junior subjective synonym of *Axocorys* Haeckel, 1882: 434 [type species by subsequent monotypy: *Axocorys macroceros* Haeckel, 1887: 1420].

Included genera. — *Axocorys* Haeckel, 1882: 434 (= *Theocotyle* synonymized by Petrushevskaya 1981: 220; *Theocotylissa* **n. syn.**). — *Clistophatna* Haeckel, 1882: 433. — *Pentalacorys* Haeckel, 1882: 436 (= *Hexalacorys* **n. syn.**; *Octalacorys* synonymized by Sanfilippo & Riedel 1982: 175). — *Pterocodon* Ehrenberg, 1847: 54. — *Thyrsocyrtis* Ehrenberg, 1847: 54 (= *Podocyrtarium* synonymized by Petrushevskaya & Kozlova 1972: 542).

invalid name. — *Clistophaena*.

Diagnosis. — Theocotylidae consist of three segmented Pterocorythoidea with a small spherical cephalis and an abdomen that is usually two or three times larger than the thorax. The distal segment of the shell is always open. The cephalic initial spicular system consists of MB, A-, V-, D-, double L- and double l-rods. The basal ring is directly connected to the V-, double L- and double l-rods forming a four-leafed clover shape. Each of the double L- and double l-rods tend to be arranged into a straight line. The basal ring is bended along the line with the double l-rod. The A-rod is free and extends vertically to reach near the top of the cephalic cavity. The double AL-arch is visible under a light microscope near the top of the A-rod in the cephalic cavity and merge with the cephalic wall. The D-rod near MB is free from the shell wall and extends downward and is attached to the shell wall. The double L-rod is also free near the edge of the basal ring. These double L-rod extends downward, attaching itself to the shell wall. If present three feet are disconnected from the D- and double L-rods. Three or more feet appear disconnected from all parts of the cephalic initial spicular system. These feet are developed in some genera. Nothing is known about the protoplasmic characteristics.

Stratigraphic occurrence. — Middle Paleocene-early Middle Miocene.

Remarks

Some genera and species that possess a spherical cephalis in the Pterocorythidae (e.g., *Calocycloma*) may be misidentified as genera of the Theocotylidae (e.g., *Pentalacorys*). The Theocotylidae are distinguished from the Pterocorythidae by the presence of a free vertical A-rod in the cephalic cavity. All Pterocorythidae genera, except for *Calocyclas*, have an A-rod merged with the cephalic wall. The cephalic structure of the Theocotylidae is very similar to type B of the Pterocorythidae (with a basal ring and double l-rods, see remarks under Pterocorythidae). However, the former is always associated with double l-rods and a D-rod that is free from the shell wall near the MB. Another fundamental difference between both families is the stability of the cephalic structure. The combination of the cephalic initial spicular system varies, even in a same species of Pterocorythidae, yet it remains unchanged in the Theocotylidae. At the generic level, the differences in Theocotylidae is marked, between the *Theocotylissa*-form of *Axocorys* and *Pentalacorys*, by the geometric relationship of the cephalic basal ring to the shell wall. The basal ring of the *Theocotylissa*-form of *Axocorys* is distanced from the shell wall on the apical side of the MB, whereas in *Pentalacorys* the basal ring is connected to the shell wall. The cephalic initial spicular system was described in *Pentalacorys* (Nishimura 1990: figs 28.4-28.7, 30.7; O'Connor 1997a: pl. 9, figs 1-5) and in the *Theocotylissa*-form of *Axocorys* (Nishimura 1990: figs 26.8, 26.9) using scanning electron microscopy. However, the free vertical A-rod in the cephalic cavity is also visible using a light microscope in *Pentalacorys* (Ogane *et al.* 2009b: pl. 54, figs 1e, 2c, pl. 55, fig.1e, pl. 57, fig. 1e, pl. 91, fig. 3b, pl. 92, fig. 3a) and *Thyrsocyrtis* (Ogane *et al.* 2009b: pl. 56, figs 1e, 2d). The evolution between *Thyrsocyrtis* and *Pentalacorys* has been partially reported (Kling 1978: 234-235; Riedel & Sanfilippo 1982: pl. 3, figs 8-12; Sanfilippo & Riedel 1982).

Validity of genera

Axocorys

Theocotyle was previously synonymized with *Axocorys* by Petrushevskaya (1981: 220). Identical real specimens similar to the type-illustration of *Axocorys macroceros* (Haeckel 1887: pl. 68, fig. 1), the type species of *Axocorys*, have not been seen for over a century. The most similar specimen is illustrated in the supporting image for *Axocorys*; it has two segments, not three. The type-illustration of *Axocorys* is similar to *Theocotyle* in its deep constriction among segments and a fenestrated aperture. We tentatively synonymize *Theocotyle* with *Theocotylissa*. The best definition of *Theocotylissa* was written by Kozlova (1999: 161), and is translated as follows: "*Three-segmented shell, frequently very large, square or conical. Cephalis small, subspherical, with apical horn. Thorax conical or hemispherical, 2-2.5 times larger than cephalis. Abdomen is the widest segment. Thoracic and sub-abdominal pores large, distributed in alternate longitudinal rows, 13-25 rows on the visible half of the shell. Aperture shape narrower with triangular teeth, sharp thorns, or a smooth rim. External strictures between segments not always marked.*" Kozlova (1999) commented that *Theocotylissa* differs from *Theocotyle* in its larger size and more curved abdomen. These differences are not important at the genus level, but the lectotype of *Eucyrtidium ficus* (Ogane *et al.* 2009b: pl. 59, figs 2a, 2b) is marked by a smooth surface. Synonymy among these groups must be investigated in a future study; *Axocorys* is the oldest available name among them.

Pentalacorys

The living image of *Alacorys friderici* (Haeckel 1887: pl. 65, fig. 1) is implausible; its morphological characters are identical to those *Pentalacorys*. Until a living *Alacorys friderici* is found, this genus is synonymized with *Pentalacorys*. *Octalacorys* was previously synonymized with *Pentalacorys* by Sanfilippo & Riedel (1982: 175). *Pentalacorys* and *Hexalacorys* were simultaneously published in Haeckel (1882: 436 for both). As the type specimen of *Podocyrtis pentacantha* was examined by Ehrenberg himself in the Ehrenberg collection (Ogane *et al.* 2009b: pl. 93, figs 1a-d), *Pentalacorys* is selected as the valid name.

Family THEOPERIDAE Haeckel, 1882
sensu Suzuki emend. herein

Theoperida Haeckel, 1882: 435 [as a tribe]; 1887: 1313, 1325, 1354 [as a subfamily].

Rhopalocanida Haeckel, 1882: 437 [below tribe].

Artoperida Haeckel, 1882: 438 [as a tribe].

Theophaenida Haeckel, 1887: 1313, 1366, 1393 [as a subfamily].

Theoperinae – Clark & Campbell 1942: 81. — Campbell & Clark 1944b: 30. — Campbell 1954: D130, D132. — Chediya 1959: 216. — Petrushevskaya 1981: 231.

Theophaeninae – Chediya 1959: 219.

Theoperidae – Riedel 1967b: 296 (*sensu* emend.); 1971: 656. — Nakaseko & Sugano 1976: 130. — Riedel & Sanfilippo 1977: 870. — Anderson 1983: 40. — Sanfilippo *et al.* 1985: 666. — Blueford 1988: 244. — Takemura 1986: 43. — Takahashi 1991: 113. — Dumitrica 1995: 29. — Boltovskoy 1998: 33. — Cordey 1998: 118. — Sugiyama 1998: 233-234. — Takemura & Ling 1998: 159. — Kiessling 1999: 55. — Anderson *et al.* 2002: 1017. — De Wever *et al.* 2001: 282-283. — Suzuki H. *et al.* 2002: 180. — Suzuki & Gawlick 2003: 176. — Afanasieva *et al.* 2005: S297. — Afanasieva & Amon 2006: 146. — *nec* Suzuki H. *et al.* 2002: 105.

TYPE GENUS. — *Theopera* Haeckel, 1882: 436 [type species by subsequent designation (Campbell 1954: D130): *Theopera prismatica* Haeckel, 1887: 1357] = junior subjective synonym of *Rhopalocanium* Ehrenberg, 1846: 385 [type species by subsequent monotypy: *Rhopalocanium ornatum* Ehrenberg, 1847: 55].

INCLUDED GENERA. — *Clathropyrgus* Haeckel, 1882: 439. — *Cyrtopera* Haeckel, 1882: 439 (= *Artopera* Haeckel, 1882 *nec Artopera* Haeckel, 1887, with the same type species). — *Eusyringium* Haeckel, 1882: 437 (= *Eusyringartus* with the same type species; *Pterosyringium* synonymized by Petrushevskaya 1981: 218). — *Rhopalocanium* Ehrenberg, 1846: 385 (= *Artoperina* **n. syn.**, *Dictyatractus* **n. syn.**, *Rhopalatractus* **n. syn.**, *Rhopalocyrtis* **n. syn.**, *Theophaena* **n. syn.**; *Theopera* synonymized by Petrushevskaya 1981: 232). — *Stichopilidium* Haeckel, 1887: 1438.

INVALID NAME. — *Sethornithium.*

NOMINA DUBIA. — *Hexalatractus*, *Sestrornithium*.

JUNIOR HOMONYMS. — *Artopera* Haeckel, 1887 (= *Artoperina*) *nec* Haeckel, 1882; *Pteropilium* Haeckel, 1887 (= *Rhopalocyrtis*) *nec* Haeckel, 1882.

DIAGNOSIS. — Theoperidae consist of three segmented Pterocorythoidea with a thick-walled spherical cephalis, a truncated conical or globular thorax, and a well-defined abdomen and/or conical tube. Two or three undulations rarely develop on the abdomen. Three wings or feet extend from the D- and double L-rods between the upper part of the thorax and the thoracic-abdominal boundary. The wings are rarely absent.

The cephalic initial spicular system consists of MB, A-, V-, D-, and double L-rods. The basal ring directly connects to the apical side end of MB, double L- and V-rods, forming four collar pores. In some members, an additional twin pore connected to D- and double L-rods is present on the apical side of the basal ring. The basal ring is largely free from the shell wall or is attached to the shell with D- and double L-rods. The basal ring sharply bends along the line with double L-rods. An A-rod is free in the cephalic cavity and forms an apical horn on the cephalis. A free A-rod in cephalic cavity is connected to an apical horn. A free D-rod, close to the MB, merges to the shell test. Little to nothing is known regarding the protoplasm.

STRATIGRAPHIC OCCURRENCE. — Early Paleocene-early Middle Miocene.

REMARKS

The concept of the Theoperidae differs considerably among publications. The most widely applied concept was defined by Riedel (1967b: 296). In the Theoperidae family, he included nassellarians with simple cephalic structures enclosed in a small spherical cephalis, and with a "cyrtid" shell differentiated along a heteropolar axis. The "probable polyphyletic" character, noticed by Riedel (1967b) for the Theoperidae, has been against regarded as monophyletic (e.g., Sugiyama 1998: 233-234). Due to the nomenclature act following the Code, the taxonomic name Theoperidae was transformed into the concept of the superfamily Eucyrtidioidea (Petrushevskaya 1981: 200-202). However, the "probable polyphyletic" possibility appears to have been lost. Nishimura (1990: 125-126) insisted on using Podocyrtidae instead of Theoperidae as *Theopera* is a junior synonym of *Lithornithium*. This explanation is not only nonsensical but also an incorrect nomenclatural act due to the *nomen nudum* status of *Lithornithium*. The concept of "Podocyrtidae" mixes one family of Lineage I (Eucyrtidiidae in our catalogue) and five families of Lineage IV (Lithochytrididae, Lophocyrtiidae, Pterocorythidae, Theocotylidae and Theoperidae in our catalogue). Thus, the concept of "Podocyrtidae" must be rejected. Besides a very broad concept of the Theoperidae (Riedel 1967b; Nishimura 1990; Sugiyama 1998), the concept of "Theoperinae" adopted by Petrushevskaya (1981: 231) and of "Theoperidae" adopted by De Wever *et al.* (2001: 282-283) is further limited by the morphological commonality to the type genus *Theopera*. However, their concepts are slightly different in so far as to include *Pterocyrtidium* (Rhopalosyringiidae) and *Lamprotripus* (Bekomidae) from Petrushevskaya (1981). Conversely, *Lychnocanissa* (originally *Lychnocanoma*) and *Lychnocanium* (Lithochytrididae) are included in De Wever *et al.* (2001: 282). The improbable placement of these genera in the Theoperidae was explained in the remarks for *Lamprotripus*. Several species generally classified in *Lychnocanissa* (originally *Lychnocanoma*) (O'Connor 1997a: pl. 9, figs 9-12; 1; 1999: pl. 4, figs 11, 15) have a cephalic structure identical to that of the Theoperidae; this is marked by the presence of many rods around the cephalic base that join the basal ring and shell test. For O'Connor (1997a; 1999) these species develop a tube-like porous skirt, which is common to the thorax of the Theoperidae genera. *Lychnocanissa* is a very large group. Nonetheless, this does not suggest that all *Lychnocanissa* belong to the Theoperidae.

The cephalic initial spicular system was reported for *Cyrtopera* (Nishimura 1992: pl. 8, figs 2, 12; O'Connor 1999: pl. 4, figs 16-21), for some *Lychnocanissa* members (O'Connor 1997a: pl. 9, figs 9-12; 1999: pl. 4, figs 11, 15), *Rhopalocanium* (Nishimura 1990: fig. 27.10), and the "*Lychnocanissa*"-form of *Rhopalocanium* (Nishimura 1992: pl. 9, figs 12 16; O'Connor 1999: pl. 4, figs 1-15). The aforementioned explanations have a common cephalic structure with a few exceptions (Nishimura 1992: pl. 8, fig. 8).

Validity of genera

Rhopalocanium

Rhopalocyrtis and *Pteropilium* have the same type species. The genera listed here have common characters including two to three segments, inverted conical final segment, and wing-like lateral appendages that are directly connected with D- and L-rods. Apart from the final segment, the largest segment is cupola-shaped. Skeleton robust. In ignorance of the final segment, these genera may be subdivided into a two-segmented group (*Rhopalocanium*, *Artoperina*, *Dictyatractus*, *Rhopalatractus*, *Theopera*, and *Theophaena*) and a three-segmented group (*Rhopalocyrtis*). Apical horn on cephalis is variable, from very short (*Rhopalatractus*, *Theopera*, and *Theophaena*) to upwardly thickening hyaline cephalic wall (*Artoperina*), to very robust and long (*Rhopalocanium* and *Dictyatractus*). These continuous changes are insufficient for distinction at the genus level. The robustness and length of wing-like lateral appendages are also variable, but in a different way from the apical horn. Wing-like lateral appendages form ridges on the test, and its distal part is free from the test. Free lateral appendages sometimes develop poreless or latticed web from the test. The following differences are summarized in the Atlas for each genus based on type and supporting images: thoracic ribs and base of free lateral appendages on upper abdomen in *Dictyatractus* and *Rhopalocanium*; thoracic or thoracic to abdominal ribs and free lateral appendages with poreless web on upper abdomen or distal margin of abdomen in *Rhopalatractus*; thoracic to abdominal ribs as base of free lateral appendages in *Artoperina*; extended thoracic to abdominal ribs with very short lateral appendages from distal margin of abdomen in *Theopera*; and ribs vertically passing through thorax and free lateral appendages originating from abdomen in *Theophaena*. As the base and free parts of the lateral appendages overlap among these genera, these characters are inappropriate for genus classification. All genera have three lateral appendages, except *Theophaena*. No real specimens have been reported for *Theopera*. The final segments can be divided into three types: slender, inverted, conical in shape and a straight extending terminal tube in *Dictyatractus*, *Rhopalatractus*, and *Rhopalocanium*; inverted, conical in shape without opening in *Theopera* and *Theophaena*; short, truncated, inverted, conical in shape with fenestrated aperture at end of final segment in *Artoperina*; and short, truncated, slightly inverted, conical in shape with large aperture at end of final segment in *Dictyatractus* and *Rhopalatractus*. As described above, *Dictyatractus* and *Rhopalatractus* may have different final segments, in which case detailed differences in the final segment may represent intraspecific or infraspecific variation rather than genus differences. We have discarded all differences among all two-segmented genera described in previous studies (Haeckel 1882, 1887; Petrushevskaya 1981; Kozlova 1999) from the genus criteria. The remaining genus is *Rhopalocyrtis*, which was defined by Bütschli (1882: 526) and translated as follows: "*Four segments. Short apical horn. Well-developed abdomen and lateral appendages oriented slightly downward and to posterior, such that they originate from continuous second and third segments, which are strongly connected.*" We consider this description to be similar to that of two-segmented genera, except for the number of segments in *Rhopalocyrtis*. Among these groups, the oldest available name is *Rhopalocanium*.

Incertae familiae nassellarians

Included genus. — *Aspis* Nishimura, 1992: 358.

Stratigraphic occurrence. — Middle Paleocene-Late Paleocene.

Remarks

The cephalic structure of *Aspis* was only shown in Hollis (2002: pl. 5, fig. 11a). This genus is characterized by the absence of internal dividers and has a very complex cephalic initial spicular system. Dumitrica (1973b: pl. 3, figs 2-4) identified this genus as *Ceratocyrtis* at the time.

Orphaned nassellarian family ranks

Calodictya Ehrenberg, 1847: 54 [invalid name, as a family]; 1876: 156. — Schomburgk 1847: 124, 126 [as a family].

Cyrtiida Haeckel, 1862: 237-238, 272-290 [invalid name, as a family]. — Zittel 1876-1880: 120 [as a group].

Dicyrtida Haeckel, 1862: 238, 280, 296 [invalid name, as a tribe]; 1887: 1192 [as a section between suborder and family]. — Zittel 1876-1880: 121 [rank unknown]. — Stöhr 1880: 99 [as a family]. — Poche 1913: 220 [as a super-superfamily]. — Popofsky 1913: 333 [as a section between suborder and family]. — Schröder 1914: 91, 100 [as a group between suborder and family]. — Chediya 1959: 199 [as a group between superfamily and family].

Polycyrtida Haeckel, 1862: 238, 280, 341 [invalid name, as a tribe]. — Zittel 1876-1880: 123 [rank unknown].

Zygocyrtida Haeckel, 1862: 238, 280, 291 [invalid name, as a tribe]. — Zittel 1876-1880: 121 [rank unknown]. — Stöhr 1880: 97 [as a family].

Cyrlidae [*sic*] – Claus 1876: 159 [invalid name] (= Cyrtidae).

Cyrtiden – Hertwig 1879: 202-214 [invalid name, as a family].

Plectida Haeckel, 1882: 423 [invalid name, as a family]. — Lankester 1885: 850 [as a family].

Cyrtida – Haeckel 1882: 425 [invalid name, as a family]; 1884: 31 [as a family]. — Lankester 1885: 850 [as a family].

Dyocyrtida Haeckel, 1882: 430 [invalid name, as a subfamily].

Triocyrtida Haeckel, 1882: 434 [*nomen nudum*, as a subfamily]; 1887: 1313 [as a section between suborder and family].

Lophocorida Haeckel, 1882: 434 [invalid name, below a tribe].

Artocorida Haeckel, 1882: 437 [*nomen nudum*, as a tribe].

Tetracyrtida Haeckel, 1882: 437 [invalid name, as a subfamily].

Theophatnida Haeckel, 1882: 437 [*nomen nudum*, as a tribe].

Dyospyrida Haeckel, 1882: 441 [*nomen nudum*, as a subfamily].

Pentaspyrida Haeckel, 1882: 442 [invalid name, as a subfamily]; 1887: 1024, 1052 [as a subfamily].

Pleurospyrida Haeckel, 1882: 444 [*nomen nudum*, as a subfamily].

Stephida Haeckel, 1882: 444-445 [invalid name, as a family]. — Lankester 1885: 850 [as a family].

Dyostephanida Haeckel, 1882: 446 [*nomen nudum*, as a subfamily].

Dyostephida Haeckel, 1882: 446 [*nomen nudum*, as a subfamily].

Parastephida Haeckel, 1882: 446 [*nomen nudum*, as a subfamily].

Plectoida Haeckel, 1884: 30 [invalid name, as a family].

Cyrtoidea – Haecker 1908: 448 [invalid name, as a rank between suborder and family]. — Chediya 1959: 188 [as a superfamily]. — Pessagno 1977b: 933 [as a superfamily]. — Cachon & Cachon 1985: 294 [as a superfamily].

Pentaspyrinae – Clark & Campbell 1942: 57 [invalid name]; 1945: 32. — Campbell & Clark 1944a: 35. — Chediya 1959: 179.

Dicyrtoidea – Clark & Campbell 1942: 65 [invalid name, as a section above a family]; 1945: 36. — Campbell & Clark 1944a: 40 [as a section above a family]; 1944b: 23 [as a section].

Enneaplagiinae Campbell, 1954: D104 [*nomen nudum*].

Pentaspyridinae – Campbell 1954: D112 [invalid name].

Theophatninae Campbell, 1954: D134 [*nomen nudum*].

Cyrtoidae – Orlev 1959: 454 [invalid name, as a family].

Dicyrtoidae – Cachon & Cachon 1985: 294 [invalid name].

REMARKS

Families with no assigned species that can tentatively be placed in Nassellaria and are "*nomina nuda*" without any taxonomic information are simply listed herein. This list does not include higher ranks than the family-rank (e.g., suborder Cyrtida).

Order COLLODARIA Haeckel, 1882
Phylogenetic Molecular Lineage "Colonial collodarians" Biard *et al.* (2015)

Superfamily SPHAEROZOIDEA Müller, 1859

Sphaerozoen Müller, 1859a: 17 [as a family].

Sphaerozoeen – Hertwig 1879: 261 [as an order]. — Brandt 1885: 210-212.

Sphaerozoa – Lankester *et al.* 1909:145 [as an order].

Spheroidea – Calkins 1909: 40 [as an order].

Spherozoea – Calkins 1909: 40 [as an order].

Collosphaerinea – Poche 1913: 210 [as a suborder] (synonymized with Collosphaerida, Polycyttaria).

Sphaerozoidea – Bertolini 1937: 1267-1268 [as a group].

Collosphaeroidea – Bertolini 1937: 1268.

DIAGNOSIS. — For Colonial Collodaria, the colony consists of many collodarian cells which are embedded in a gelatinous support. A reticulated system of pseudopodia interconnects the collodarian cells inside the gelatinous substance. The cell is constituted of three zonal structure: the adipose droplet (oil droplet) in the center, the intracapsular zone with an endoplasm, and the extracapsular zone with ectoplasm. The intracapsular zone includes many small nuclei, pigmented spherules observed in light microscopy, and several small orthorhombic shaped crystals. The intracapsular zone is bounded from the extracapsular zone by the capsular wall. The extracapsular zone resembles a transparent clear thin zone and consists of the ectoplasm and pseudopodia. Anatomically, the pseudopodia are part of the endoplasm. The endoplasm extrudes from the intracapsular zone through the fusules, that is a special tunnel organelle on the central capsule. The extracapsular zone is bounded by the plasmalemma of the gelatinous material. The pseudopodia buried in gelatinous material radiate and appear as fibers of gelatinous matter. The algal symbionts are located in the ectoplasm or in the gelatinous matter. The boundary of the gelatinous matter is unknown. If present, the siliceous skeletons are wrapped with silicalemma. It is unknown whether the silicalemma is a part of the endoplasm and/or of the ectoplasm.

REMARKS

The Collodaria are conventionally divided into "colonial Collodaria" and "solitary Collodaria"; the former is commonly known as Sphaerozoidea. One of the most comprehensive studies of the Sphaerozoidea was performed by Strelkov & Reshetnyak (1971). The morphological terminology adopted in fig. 6 of Strelkov & Reshetnyak (1971) is a basis in understanding the Sphaerozoidea. The metabarcoding survey found that the coastal area populations are dominated by the Sphaerozoidae, while open ocean populations are dominated by the Collosphaeridae (Biard *et al.* 2017). Although the exact taxonomy of the host is unknown, amphipod species such as *Oxycephalusclausi*, *Streetsiaporcella* and *Hyperietta* stebbingi were found among Sphaerozoidea (Harbison *et al.* 1977; Zeidler 2016). The Sphaerozoidea consists of the Collophiidae, Collosphaeridae and Sphaerozoidae. The formation of superfamily names for this group needs some additional explanations. The Latin stem of *Sphaerozoum* is Sphaerozo-, thus Sphaerozo-oidea is grammatically correct. However, in this case, there is an old pronunciation problem. When one pronounces a double "oo", the result is not very nice for Latin, Italian, French and Spanish ears. In English the pronunciation can result as "ouuu" sound. There is just a big exception which is the Greek name "zoon" = zoo (identical in all European languages, even in Russian). The prevalent use in occidental languages is to remove the additional "o", so as not to pronounce this not phonetically nice "oo". Sphaerozoidae sounds better than Sphaerozooidae. Very often, many radiolarists have been using translations of such word in their native languages: Sphaerozoidés in French, Sphaerozoids in English and Sphaerozoiden in German (always without a double "o").

Family COLLOPHIDIIDAE Biard & Suzuki *in* Biard, Pillet, Decelle, Poirier, Suzuki & Not, 2015

Collophidiidae Biard & Suzuki *in* Biard, Pillet, Decelle, Poirier, Suzuki & Not, 2015: 384.

Collophidae – Ishitani *et al.* 2012 [no pages can be specified due to ambiguous indication, no type genus indication, and grammatic error in name formation, unavailable name].

Type genus. — *Collophidium* Haeckel, 1887: 26 [type species by subsequent designation (Campbell 1954: D44): *Collozoum serpentinum* Haeckel, 1887: 26].

Included genera. — *Collophidium* Haeckel, 1887: 26.

Nomen dubium. — *Colloprunum*.

Diagnosis. — Collophidiidae are Colonial Collodaria with a variable elongated, cylindrical, or spherical appearance. Each colony is comprised of a delicate gelatinous material that encompasses the scattered algal symbionts and the string-like aggregations. A string-like aggregation includes tens to a hundred collodarian cells within a firm gelatinous material. The central capsule is of an elongated cylindrical shape, with an endoplasm highly vacuolated.

Stratigraphic occurrence. — Living.

Remarks

The taxonomic independency of *Collophidium* was initially recognized by the studies of Anderson *et al.* (1999). This was achieved by the observation of ultrafine cellular structure and the publication of "living" images. Their results were later supported by a molecular phylogenetic study by Ishitani *et al.* (2012).

The microbial eukaryotes (0.8-20 μm) of the bathypelagic zone (3000-4000 m in water depth) in global oceans are dominated by *Collophidium*, suggesting the important role of this genus in the deep-ocean (Pernice *et al.* 2016). This family can be easily distinguished from the other collodarian families by the presence of cell-embedded sacks observed within the gelatinous matter. Many undescribed genera and species are encountered in plankton samples. Four *Collophidium* species were drawn in figs 10-13 of Strelkov & Reshetnyak (1971) but need to be described again as new species due to their identification based on the unillustrated species of Haeckel (1887).

Family Collosphaeridae Müller, 1859

Collosphaeren Müller, 1859a: 17 [as a family].

Collosphaerida – Haeckel 1862: 240, 530-531 [as both family and tribe]; 1882: 471 [as a family]; 1884: 29 [as a family]; 1887: 55, 92-94 [as a family]. — Mivart 1878: 179 [as a subsection]. — Brandt 1885: 252-254. — Bütschli 1889: 1949 [as a family]. — *nec* Rüst 1892: 140 [as a family]. — Afanasieva & Amon 2006: 157 [as a class].

Collosphaeridae – Claus 1876: 160. — Delage & Hérouard 1896: 203 [as a suborder]. — Enriques 1919: 57; 1932: 983. — Campbell 1954: D51. — Chediya 1959: 74. — Riedel 1967b: 294; 1971: 650. — Riedel & Sanfilippo 1971: 1586; 1977: 862. — Strelkov & Reshetnyak 1971: 329-332. — Dumitrica 1973a: 831. — Sanfilippo & Riedel 1973: 485. — Nakaseko *et al.* 1975: 166. — Nakaseko & Sugano 1976: 119. — Tan & Tchang 1976: 226. — Reshetnyak & Runeva 1978: 6-7. — Dumitrica 1979: 26-27. — Tan & Su 1982: 137. — Anderson 1983: 37, 71. — Cachon & Cachon 1985: 285. — Sanfilippo *et al.* 1985: 650. — Petrushevskaya 1986: 123. — Takahashi 1991: 53. — van de Paverd 1995: 35-37. — Chen & Tan 1996: 150. — Boltovskoy 1998: 30-31. — Tan 1998: 104. — Anderson *et al.* 2002: 1001. — De Wever *et al.* 2001: 169, 171. — Afanasieva *et al.* 2005: S306. — Chen *et al.* 2017: 93.

Acrosphaerida Haeckel, 1882: 471 [as a subfamily]; 1887: 94 [as a subfamily].

Clathrosphaerida Haeckel, 1882: 472 [as a subfamily]; 1887: 94, 118 [as a subfamily].

Collosphaeriden – Brandt 1905: 327-328 [as a family]. — Lankester *et al.* 1909: 145 [as a family]. — Popofsky 1917: 239 [as a family].

Collosphaerinae – Campbell 1954: D51.

Clathrosphaerinae – Campbell 1954: D52. — Chediya 1959: 77.

Acrosphaerinae – Chediya 1959: 74.

Collosphaerini – Strelkov & Reshetnyak 1971: 332.

Acrosphaerini – Strelkov & Reshetnyak 1971: 338-339

Siphonosphaerini Strelkov & Reshetnyak, 1971: 348.

Type genus. — *Collosphaera* Müller, 1855: 238 [type species by subsequent designation (Campbell 1954: D51): *Thalassicolla* (*Collosphaera*) *huxleyi* Müller, 1855: 238].

Included genera. — *Choenicosphaera* Haeckel, 1887: 102 (= *Choenicosphaerula* with the same type species; *Choenicosphaerium* **n. syn.**, *Coronosphaera* **n. syn.**, *Trypanosphaerium* **n. syn.**; *Trypanosphaera*, *Trypanosphaerula* synonymized by Menshutkin & Petrushevskaya 1989: 91). — *Clathrosphaera* Haeckel, 1882: 472 (= *Clathrosphaerula* with the same type species). — *Collosphaera* Müller, 1855: 238 (= *Dyscollosphaera* with the same type species; *Collodiscus* **n. syn.**, *Conosphaera* **n. syn.**, *Myxosphaera* **n. syn.**). — *Disolenia* Ehrenberg, 1861b: 831 (= *Solenosphaera*, *Tetrasolenia* synonymized by Haeckel 1887: 113, *Trisolenia* synonymized by Haeckel 1887: 114). — *Otosphaera* Haeckel, 1887: 116. — *Polysolenia* Ehrenberg, 1861b: 832 (= *Acrosphaera* synonymized by Nigrini 1967: 14; *Clathrosphaerium* synonymized by Matsuzaki *et al.* 2015: 4, *Mazosphaera* synonymized by Menshutkin & Petrushevskaya 1989: 93, *Odontosphaera* **n. syn.**). — *Siphonosphaera* Müller, 1859b: 59 (= *Holosiphonia* with the same type species; *Merosiphonia* synonymized by Riedel 1971: 651; *Solenosphactra* synonymized by Menshutkin & Petrushevskaya 1989: 95; *Solenosphenia* **n. syn.**, *Solenosphyra* **n. syn.**). — *Tribonosphaera* Haeckel, 1882: 471 (= *Buccinosphaera*, *Pharyngosphaera* synonymized by Menshutkin & Petrushevskaya 1989: 90).

Nomen nudum. — *Pentasolenia*

Nomina dubia. — *Caminosphaera*, *Eucollosphaera*, *Xanthiosphaera*.

Junior homonym. — *Pachysphaera* Brandt, 1902 *nec* Pilsbry in Tryon & Pilsbry, 1892.

Diagnosis. — Collosphaeridae consist of colonial Collodaria with tens, hundreds or more collodarian cells, depending on the size of the colony. Each collodarian cell has one or two, rarely more, spherical cortical shells. The intracapsular zone is always located inside the cortical shell. Each cell has multi-nuclei, at least in *Collosphaera* and *Disolenia*. Algal symbionts are observed within the cortical shell or outside of it, but little is known about their specific location at genus- or species- levels.

Stratigraphic occurrence. — early Early Miocene-Living.

Remarks

In sediments, the Collosphaeridae are identifiable at species level. Unfortunately, the Collosphaeridae are usually poorly preserved in sediments. A single colony contains variable morphotypes of one probable species. The morphological variations at the species level and taxonomic scheme at the genus level were repeatedly studied (Knoll & Johnson 1975; Menshutkin & Petrushevskaya 1989; Petrushevskaya &

Swanberg 1990). However, their contributions are difficult to apply for further studies. The first occurrences of *Collosphaera tuberosa* and *Tribonosphaera invaginata* are important in determining the RN16 (0.51±0.08 Ma at the base) and RN17 (0.34±0.11 Ma at the base) radiolarian biozones in the tropical region (Sanfilippo & Nigrini 1998). The first occurrence of *Siphonosphaera abyssi* is also key to determining the boundary of 1.80 Ma in the Northwest Pacific (Matsuzaki *et al.* 2014). Thus, the identification of these three species is critical. The critical identification was explained in detail in Matsuzaki *et al.* (2015: 5) for *S. abyssi* and the morphological changes of *Tribonosphaera* (originally *Buccinosphaera*) were stratigraphically recognized in Knoll & Johnson (1975). The determinable morphological character for *Tribonosphaera* is best illustrated in van de Paverd (1995: pl. 4, figs 2a, 4). Differing from other Collodaria families, the Collosphaeridae are the only family which provide a connection between our knowledge of living and fossil forms. In the fossil record, the evolution of *Polysolenia* (= *Acrosphaera* in original), *Collosphaera* and *Disolenia* (= *Trisolenia*) were recorded since the early Miocene (*c.* 20 Ma) (Bjørklund & Goll 1979). *Collosphaera* was used for biological research on ultrafine cellular structures (Anderson 1978a; 1983), assimilation of organic substances from algal symbionts using ^{14}C (Anderson 1978a; Anderson *et al.* 1983; 1985), binary fission on live (Anderson & Swanberg 1981; Anderson & Gupta 1998), and silicalemma containing granular masses forming the siliceous skeleton (Anderson 1981: figs 13.14-13.17). Moreover, the silicalemma function of Polycystinea was based on the study of *Collosphaera*. Collosphaeridae are relatively easy to identify at the genus level. Consequently, images of living specimens were published in many papers. "Living" images were illustrated for *Collosphaera* (Anderson 1978a: fig. 1; 1980: fig. 8; 1983: figs 1.5.E-1.5.F; Anderson & Gupta 1998: figs 1-7; Suzuki & Aita 2011: figs 5H, 5I; Probert *et al.* 2014: S1, PAC 2, 7; Suzuki & Not 2015: fig. 8.13.8, 8.13.9; Matsuoka *et al.* 2017: appendix A), *Otosphaera* (Suzuki & Not 2015: fig. 8.13.12), *Polysolenia* (Caron & Swanberg 1990: fig. 3.C), *Siphonosphaera* (Casey 1993: fig. 13.6: Suzuki & Not 2015: fig. 8.13.11), *Disolenia* (Anderson 1983: fig. 1.4.A; Caron & Swanberg 1990: fig. 3.A; Matsuoka 2007: fig. 5.b; Suzuki & Not 2015: fig. 8.13.13-8.13.15), and *Tribonosphaera* (Suzuki & Not 2015: fig. 8.13.10). The skeletal structure, including the growth line, was documented for *Polysolenia* (Nishimura 1986: figs 6.1-6.2), *Disolenia* (Nishimura 1986: fig. 6.3), *Tribonosphaera* (van de Paverd 1995: pl. 4, figs 2a, 4). These results are not applicable as a general rule for all Polycystinea due to the differences in skeletal formation of Nassellaria and Spumellaria. Though a powerful detection tool to define on-time silicification phenomena, PDMPO and HCK-123 failed to catch silicification phenomena for any collodarian specimens (not reported in Ogane *et al.* 2009c, 2010 because of negative results). Any results based on Collosphaeridae should not be overgeneralized in Polycystinea. From a historical point of view, the study of symbionts in Collosphaeridae is of particular interest. The algal symbionts and the nucleus of host were documented using DAPI dyeing epi-fluorescent observation for *Collosphaera* (Suzuki *et al.* 2009b: figs 1I-1K; Zhang *et al.* 2018: 11, fig. 4, p. 13, figs 1-4), *Mazosphaera* (Zhang *et al.* 2018: 13, figs 6-8), *Disolenia* (Suzuki *et al.* 2009b: figs 1L, 1M; Zhang *et al.* 2018: 11, figs 9, 10, p. 13, fig. 5), *Polysolenia* (Zhang *et al.* 2018: 11, fig. 21; p. 13, figs 9, 12, 13), *Otosphaera* (Zhang *et al.* 2018: 11, fig. 22; p. 13, figs 10, 11), *Polysolenia* (Zhang *et al.* 2018: 11, fig. 25), *Siphonosphaera* (Zhang *et al.* 2018: 13, figs 14-17). The algal symbionts of *Collosphaera* were identified as *Brandtodinium nutricula* by Probert *et al.* (2014). *Merodinium mendax* parasites in *Collosphaera* were reported by Chatton (1923) but integrative morpho- and molecular studies have not been conducted as of yet.

Validity of genera

Choenicosphaera

The combinations *Choenicosphaera* and *Choenicosphaerula*, and *Trypanosphaera* and *Trypanosphaerula* have the same type species. The genera listed here are subdivided into a group with poreless, hyaline shells (*Choenicosphaera* and *Trypanosphaera*) and a group with shells with pit-like pores (*Choenicosphaera*, *Coronosphaera*, and *Trypanosphaerium*). *Choenicosphaera* is defined by coronal radial spines around a large pore and a crown of spines around each pore (Campbell 1954: D52). These characteristics fit the type-illustration of *Coronosphaera diadema*, the type species of *Coronosphaera* (Haeckel 1887: pl. 7, fig. 3). *Coronosphaera* is characterized by pores prolonged outward in fenestrate tubules (Campbell 1954: D52). This difference is insufficient to separate them into two genera. According to Campbell (1954: D52), *Trypanosphaerium* is similar to *Coronosphaera*, but differs from the latter by solid walled tubules. This and the type-illustration of *Trypanosphaera coronata* (Haeckel 1887: pl. 5, fig. 3), the type species of *Trypanosphaerium*, fit the definition of *Choenicosphaerium*. *Trypanosphaera* has solid walled tubules and its pores all have tubules (Campbell 1954: D52). This explanation and the type-illustration of *Trypanosphaera trepanata*, the type species of *Trypanosphaera*, fit the characteristics of *Choenicosphaera*. Although it is unclear whether the genera with hyaline shells can be synonymized with the genera with pit-like pores on the shells, we tentatively synonymize all genera listed here. All of these genera were published simultaneously in Haeckel (1887: D102 for *Choenicosphaera*; D103 for *Choenicosphaerium*; D109 for *Trypanosphaera*; D110 for *Trypanosphaerium*; and D117 for *Coronosphaera*). There were no differences in taxonomic stability, thus the first genus was selected as the valid genus.

Collosphaera

The combinations *Collosphaera* and *Dyscollosphaera*, and *Myxosphaera* and *Collodiscus* each have the same type species. Müller (1855a: 238) described *Collosphaera* as "*a light-yellow cell surrounded by a fragile transparent spherical shell perforated by numerous circular pores*" (summary from the translation of Müller 1855a). Brandt (1885: 254) erected *Myxosphaera* for *Sphaerozoum coeruleum*, whose reproductive process differs from other Collosphaeridae and Sphaerozoidae. This original definition is useless for specifying any collodarian genera because no collodarian reproductive processes have been examined with modern techniques. Brandt (1885) noted other characteristics of *Myxosphaera*: "*the thickness of the central capsule wall; the appearance of blue pigmentation during swarmer formation; and no siliceous skeleton*" (translated from Brandt 1885). *Collosphaera* has a naked mode like *Myxosphaera*; consequently, they can be synonymized. *Collosphaera tuberosa* and *Buccinosphaera invaginata* seemed to have evolved from *Collosphaera orthoconus*, referring to Bjørklund & Goll (1979). *C. orthoconus* resembles *Conosphaera platyconus*, the type species of *Conosphaera* (Haeckel 1887: pl. 12, fig. 3); consequently, *Conosphaera* is a synonym of *Collosphaera*. The oldest name is *Collosphaera*.

Disolenia

The synonymized opinion on the four genera *Disolenia*, *Solenosphaera*, *Tetrasolenia*, and *Trisolenia* was already accepted in the 1880s (Haeckel 1887: 113; Strelkov & Reshetnyak 1971: 358; Bjørklund & Goll 1979: 1317-1318). However, the valid genus name is disputed and there are two problems. One is the type species for these four genera. *Solenosphaera* has the same type species as *Tetrasolenia* (*Tetrasolenia quadrata*). The type species of *Trisolenia* is *Trisolenia megalactis*, by subsequent monotypy. Matsuzaki *et al.* (2015: 6) subsequently designated *Trisolenia zanguebarica* as the type species of *Disolenia*, after radiolarians examined by Ehrenberg himself were found in the Ehrenberg collection. Thus, all of these genera are available taxonomic names. The second problem is which genus is the oldest; *Solenosphaera* used to be a valid genus, but this is obviously illegal because this genus was established in 1887 to "kill" Ehrenberg's *Disolenia*, *Tetrasolenia*, and *Trisolenia* (Haeckel 1887: 113). Ehrenberg's genera were published simultaneously in Ehrenberg (1861b: 831 for *Disolenia* and 833 for *Tetrasolenia* and *Trisolenia*). Campbell (1954: D52) and Nigrini (1967: 19) both validated *Disolenia* over *Tetrasolenia* and *Trisolenia*. As the first reviser's decision was retained under ICZN (1999), *Disolenia* was already a legal valid name.

Polysolenia

As noted in the remarks in the Atlas, the type species of *Acrosphaera* is not *Polysolenia setosa*, which was subsequently designated by Campbell (1954: D52). The correct type species is *Collosphaera spinosa*, a subsequent monotypy by Brandt (1885: 263). The controversy over whether *Acrosphaera* or *Polysolenia* is the valid name has existed since 1954 (see the historical review in Matsuzaki *et al.* 2015: 4), but this discussion was wasted because it started from the objective synonymy between *Acrosphaera* and *Polysolenia*. This is wrong logically, but the result is the same because *Collosphaera spinosa* was classified in *Polysolenia* (Matsuzaki *et al.* 2015: 4-5). *Mazosphaera* is obviously the same as *Polysolenia*. *Clathrosphaerium* differs from *Polysolenia* by the presence of a web-like mesh around the *Polysolenia*-form shell, which differs at intra- and infraspecific levels. *Odontosphaera* was tentatively synonymized with *Polysolenia* by the presence of a hooked spine on its pores, like *Collosphaera spinosa*. *Acrosphaera* was published in 1882. *Mazosphaera* and *Polysolenia*, the oldest available names, were published simultaneously in Ehrenberg (1861b: 832 for both genera). Since several papers use *Polysolenia*, this genus is validated here.

Siphonosphaera

Bjørklund & Goll (1979) considered *Siphonosphaera* a junior synonym of *Disolenia* (*Solenosphaera* originally). As the typical *Siphonosphaera* in a colony has a uniform morphotype, differing from the high variation in the number of tubules and shell shapes in *Disolenia* (Haeckel 1887: 113), we keep *Siphonosphaera* as an independent genus. *Holosiphonia* has the same type species as *Siphonosphaera*. *Merosiphonia* and *Solenosphactra* have already been synonymized (Riedel 1971: 651; Menshutkin & Petrushevskaya 1989: 95). *Solenosphyra* is marked by funnel-shaped, outwardly flaring tubules (Campbell 1954: D52). The most similar real specimen is shown in the support image for *Solenosphyra* in the Atlas. This specimen is very similar to *Siphonosphaera* and it is not necessary to separate it as an independent genus. An actual specimen identifiable as *Solenosphaera ascensionis*, the type species of *Solenosphenia*, has not been reported. This genus looks similar to *Disolenia*, but is tentatively synonymized with *Solenosphaera* considering the well-developed tubules and spherical cortical shell. The oldest available name is *Siphonosphaera*.

Family SPHAEROZOIDAE Müller, 1859

Sphaerozoen Müller, 1859a: 17 [as a family].

Sphaerozoida – Haeckel 1862: 240, 521-522 [as a family]; 1882: 472 [as a family]; 1884: 28 [as a family]; 1887: 10, 38-39 [as a family]. — Mivart 1878: 179 [as a subsection]. — Brandt 1885: 212-214 [rank unknown]. — Bütschli 1889: 1947 [as a family]. — *nec* Rüst 1892: 132 [as a family]. — Ludwig 1908: 17 [rank unknown]. — Anderson 1983: 23.

Collozoida Haeckel, 1862: 240, 522 [as a tribe]; 1882: 472 [as a family]; 1884: 28 [as a family]; 1887: 10, 23-24 [as a family]. — Bütschli 1889: 1947 [as a family]. — Ludwig 1908: 17 [rank unknown]. — Anderson 1983: 23.

Rhaphidozoida Haeckel, 1862: 240, 522, 525 [as a tribe].

Sphaerozoidae – Claus 1876: 160. — Delage & Hérouard 1896: 202 [as a suborder]. — Lankester *et al.* 1909: 145. — Enriques 1919: 57; 1932: 983. — Hollande & Enjumet 1953: 108. — Campbell 1954: D46. — Chediya 1959: 67. — Strelkov & Reshetnyak 1971: 317. — Nakaseko & Sugano 1976: 118. — Dumitrica 1979: 26. — Anderson 1983: 71. — Takahashi 1991: 61. — van de Paverd 1995: 34. — Tan 1998: 90 Tan & Chen 1999: 117. — De Wever *et al.* 2001: 173. — Afanasieva *et al.* 2005: S306.

Sphaerozoiden – Hertwig 1879: 158-160 [as a family]. — Brandt 1882: 388-400; 1905: 314-316 [as a family].

Collozoidae – Delage & Hérouard 1896: 201 [as a suborder]. — Campbell 1954: D44. — Chediya 1959: 66. — Tan 1998: 87. — Tan & Chen 1999: 114. — Anderson *et al.* 2002: 1001.

TYPE GENUS. — *Sphaerozoum* Meyen, 1834: 163 [type species by monotypy: *Sphaerozoum fuscum* Meyen, 1834: 164].

INCLUDED GENERA. — *Belonozoum* Haeckel, 1887: 39. — *Collozoum* Haeckel, 1862: 522 (= *Collodinium* with the same type species; *Coinozoum* **n. syn.**, *Collodastrum* synonymized by Haeckel 1887: 28, *Xantozoum* **n. syn.**). — *Rhaphidozoum* Haeckel, 1862: 529 (= *Rhaphidonactis* with the same type species; *Rhaphidoceras* synonymized by Popofsky 1920: 587; *Rhaphidonura* synonymized by Popofsky 1920: 567). — *Sphaerozoum* Meyen, 1834: 163 (= *Sphaerozonoceras* with the same type species; *Actinozoum* **n. syn.**; *Sphaerozonura* synonymized by Popofsky 1920: 568).

Nomina dubia. — *Jozoum*, *Sphaerozonactis*.

Diagnosis. — Sphaerozoidae consist of colonial Collodaria with isolated siliceous spicules. Each cell is surrounded by isolated siliceous spicules located inside a gelatinous matter. Algal symbionts generally surround each collodarian cell or are found scattered throughout the gelatinous matter. The shape of the colony changes within the same species. Each cell possesses many nuclei that are observable in the endoplasm.

Stratigraphic occurrence. — Living.

Remarks

Very small differences between isolated siliceous spicules, analyzed in molecular phylogeny by Biard *et al.* (2015), may reflect significant molecular differences. For fully grown spicules it may be possible to specify the small clades of Biard *et al.* (2015) but younger spicules share common shapes. Thus, it is impossible to determine the relevant clades of Biard *et al.* (2015). A colony in which isolated siliceous spicules are evenly distributed may be found in plankton samples. This is probably an intermediate condition between colonial and solitary forms and a part of the life stage (see remarks in Thalassicolloidea). Isolated siliceous spicules are occasionally encountered in rocks and sediments, but it is impossible to classify them as Thalassosphaeridae or Sphaerozoidae. If new research might prove that Thalassosphaeridae correspond to a different life stage of the Sphaerozoidae, the isolated siliceous spicules would be identified as fragments of Sphaerozoidae. *Collozoum* and *Sphaerozoum* are easily collected in shallow, warm waters; as such many living and fixed cells images were provided. “Living” images were illustrated for *Collozoum* (Anderson 1980: fig. 9; 1983: figs 1.5.A-1.5.B, 2.17; Swanberg & Harbison 1980: figs 2, 6; Swanberg & Anderson 1981: figs 1A-1D; De Wever *et al.* 1994: figs 6.a, 6.b; Matsuoka 2007: fig. 4.g; Suzuki & Aita 2011: figs 5F, 5G; Probert *et al.* 2014: S1, PAC 17, S2, SES 46, VEPO-14; Suzuki & Not 2015: figs 8.13.3-8.13.5), *Rhaphidozoum* (De Wever *et al.* 1994: fig. 14; Probert *et al.* 2014: S1, PAC 8; Suzuki & Not 2015: fig. 8.13.6), and *Sphaerozoum* (Anderson 1976b: pl. 1, figs 1, 2; 1983: figs 1.5.C-1.5.D; Suzuki & Aita 2011: fig. 5C, 5D; Probert *et al.* 2014: S1, SES 47; Yuasa & Takahashi 2014: figs 1A, 1B; Suzuki & Not 2015: fig. 8.13.7). Algal symbionts and nuclei were also illustrated with epi-fluorescent observation with DAPI dyeing for *Sphaerozoum* (Suzuki *et al.* 2009b: figs 1N, 1O; Zhang *et al.* 2018: 9, figs 4-6), *Rhaphidozoum* (Zhang *et al.* 2018: 11, figs 26, 27). *Collozoum* was used for studies on the ultrafine cellular structure (Anderson 1976c; 1983; Swanberg & Anderson 1981: Villar *et al.* 2018), food preference (Anderson 1980) and transcriptome analysis (Balzano *et al.* 2015). The ultrafine cellular structure (Anderson 1976b; 1981) and food preference of *Sphaerozoum* (Anderson 1980) has been well documented. One of the most important discover on *Sphaerozoum* has been the identification of the silicalemma, that is the cytokalymma in which the silica precipitate (Anderson 1981: fig. 13-13). The presence of crystals in a cell was already reported in *Collozoum* and *Sphaerozoum* by Haeckel (1862) (see Strelkov & Reshetnyak 1971: 305-306 for history of the study). The mineralogy in question is strontium sulfate and was found in reproductive swarmers of *Sphaerozoum* (Hollande 1974; Hollande & Martoja 1974) and ultrafine cellular structure (Yuasa & Takahashi 2014). From an historical point of view, the study of algal symbionts in Collosphaeridae are important because the *Zooxanthella nutricula* give the root of the common name “zooxanthella”. It was formally described for the first time in *Collozoum inerme* by Brandt (1882). Algal symbionts of *Collozoum*, *Rhaphidozoum* and *Sphaerozoum* were identified as *Brandtodinium nutricula* by Probert *et al.* (2014). The variety of symbiosis is largely documented in *Collozoum*. Hyperiid amphipod genus *Hyperietta* juveniles remain inside the gelatinous matter of *Collozoum longiforme* as an obligate parasite and they swim elsewhere after consuming the algal symbionts (Swanberg & Harbison 1980). A similar photography was captured in Biard *et al.* (2016: extended data fig. 3.d). A single *Hyperietta stephenseni* (Lestrigonidae) individual can hold a fan-shaped flat colony of *Collozoum pelagicum* because this amphipod uses the colony to paraglide water flows (Nakamura *et al.* 2019: fig.S2.d). Other parasites were reported from *Collozoum* as *Bod insidiosus* (Hollande & Enjumet 1953: 173-174), *Merodinium brandti* (Chatton 1923) and *M. belari* (Hollande & Enjumet 1953: 159-165; 1955: figs 3, 4), and also from *Sphaerozoum* as *Merodinium dolosum* and *M. asturum* (Chatton 1923). However, regardless of the efforts (Dolven *et al.* 2007; Bråte *et al.* 2012), little progress has been made regarding the molecular study of these parasites relative to the morpho-species.

Validity of genera

Collozoum

As no papers explained the definition of *Coinozoum*, we present a translated summary of this genus from Enriques (1919): “*Colony in vegetative mode is cylindrical with a length < 10 mm; width < 1-2 mm; vacuoles usually present, irregularly distributed; the colonies may appear segmented as if they were miniature C. inerme; plasmodia somewhat large as in C. radiosum; oil droplets colorless to very light yellow (only visible after squishing the colony).*” As this genus is defined by characteristics of the colony, not radiolarian cells, and *Coinozoum* was established as a subgenus of *Collozoum*, we simply synonymize this subgenus with *Collozoum*.

Xantozoum has not been explained in any papers. Enriques (1919: 21) erected this genus to apply only to *Collozoum fulvum*. The translated summary of Brandt’s (1885: 223) description of *C. fulvum* is as follows: “*Colony spherical or ellipsoidal with one large or many small vacuoles. Individuals spherical, slightly flattened with a circular outline. Central capsule delicate. Two layers of nuclei. Numerous yellow inclusions in the protoplasm.*” This genus was also established based on colony shape. Under the current taxonomic scheme, colony shape is useless for define species, genera, or other any taxonomic levels in Collodaria.

Collodastrum was defined as: "*form of the central capsules irregular and indefinite, variable, commonly polyhedral or polygonal, or amoeboid, often with irregular, finger-like processes*" (Haeckel 1887: 27). The type species is *Sphaerozoum pelagicum*, but this species lacks isolated siliceous spicules, so it belongs to *Collozoum*. The oldest available name is *Collozoum*.

Rhaphidozoum

Rhaphidonactis has the same type species as *Rhaphidozoum*, which is characterized by two to four shanks on radiate spicules, while *Rhaphidoceras* has complex spicules with rays at both ends, and in *Rhaphidonura*, "*complex spicules include both radiate type with rays from central point and branched type with rays at both ends*" (Campbell 1954: D46). The current concept of *Rhaphidozoum* is defined by: "*spicules partly simple and partly branched or radiate*" (Campbell 1954: D46). This definition covers the characteristics of *Rhaphidoceras* and *Rhaphidonura*. *Rhaphidozoum* is the oldest available name among them. However, molecular phylogenetic analyses revealed very high diversity in the current *Rhaphidozoum* at the genus and family levels (Biard *et al.* 2015).

Sphaerozoum

Sphaerozoum was studied mainly by Brandt (1885) and Strelkov & Reshetnyak (1971). Brandt (1885: 229) described this genus as: "*Skeletons always present and consist of numerous needle-like spines that are not connected and are distributed tangentially in individuals*" (translated from German by J.-P. Caulet). Strelkov & Reshetnyak (1971) described it as: "*This genus includes, as the only skeletal elements, double (paired-triradiate) spines as the main axis, bearing at the ends two, three, four, or more lateral branches. These branches can be simple and are most frequently smooth* (*Sphaerozoum punctatum*) *or ramified and covered with spinules* (*S. verticillatum*)" (translated from Russian by J.-P. Caulet). Enriques (1919: 61, 63) defines *Actinozoum* as: "*the main characteristic of this group is the greatest preponderance of complicate spicules*" (translated from Italian by J.-P. Caulet) and Haeckel (1887: 45) defines *Sphaerozonura* as: "*Spicules all geminate-radiate, but with different, variable numbers of shanks on each end of the middle rod.*" These characteristics are covered by Brandt's (1885) definition, rather than that of Strelkov & Reshetnyak (1971). *Sphaerozoum* is the oldest available name among them. As with *Rhaphidozoum*, molecular phylogenetic analyses revealed very high diversity in the current *Sphaerozoum* at the genus and family levels (Biard *et al.* 2015).

Phylogenetic Molecular Lineage "Solitary collodarians" Biard *et al.* (2015)

Superfamily THALASSICOLLOIDEA Müller, 1859

Thalassicollae Müller, 1859a: 28 [as a family].

Akeleta [*pars*] Zittel, 1876-1880: 118 [*nomen nudum*, as a group].

Collida [*pars*] Haeckel, 1862: 237, 244-246 [*nomen nudum*, as a family] (= Thalassicollidae + Thalassosphaeridae + Aulacanthidae). — Hertwig 1876: 75 [rank unknown]. — Mivart 1878: 179 [as a subsection]. — Calkins 1909: 40 [as an order].

Colliden – Hertwig 1879: 160-157 [*nomen nudum*, as a family].

Thalassicolleen – Hertwig 1879: 261 [as an order].

Thalassicollicae – Campbell 1954: D44 [as a superfamily].

Thalassosphaericae – Campbell 1954: D45 [as a superfamily].

Thalassosphaeracea – Loeblich & Tappan 1961: 221 [as a superfamily].

DIAGNOSIS. — Thalassicolloidea consist of solitary Collodaria with or without isolated siliceous spicules.

REMARKS

As explained in the remarks of Thalassicollidae, the superfamily Thalassicolloidea is an artificial morpho-group for practical purpose of plankton studies. This superfamily exactly corresponds to the "solitary Collodaria". The life, cytology, reproduction, algal symbionts and parasites of the Thalassicolloidea were well documented (Huth 1913; Hollande & Enjumet 1953). However, little is known about their studies. This may be attributed to a non-English understanding.

Family THALASSICOLLIDAE Müller, 1859

Thalassicollae Müller, 1859a: 28 [as a family].

Thalassicollida – Haeckel 1862: 237, 246 [as both family and tribe]; Haeckel 1882: 469 [as a family]; Haeckel 1884: 28 [as a family]; Haeckel 1887: 10-12 [as a family]. — Lankester 1885: 849 [as a family]. — Bütschli 1889: 1946 [as a family]. — Ludwig 1908: 17 [rank unknown]. — Anderson 1983: 23. — Boltovskoy 1998: 30 [as a family].

Thalassicollidae – Wallich 1869: 97-99. — Claus 1876: 158. — Delage & Hérouard 1896: 177 [as a suborder]. — Brandt 1902: 82. — Popofsky 1908: 203. — Lankester *et al.* 1909: 144. — Enriques 1932: 983. — *nec* Aberdeen 1940: 132-133. — Hollande & Enjumet 1953: 107, 108, 136-144. — Campbell 1954: D44. — Chediya 1959: 65. — Cachon & Cachon 1985: 284. — Anderson *et al.* 2002: 1000.

Brachiata Mivart, 1878: 179 [unavailable name, as a subsection] (including *Myxobrachia*).

Thalassophysidae Brandt, 1902: 82 [*nomen dubium*]. — Lankester *et al.* 1909: 144. — Hollande & Enjumet 1953: 108, 130-131, 144-150. — Cachon & Cachon 1985: 285.

Thalassophysiden – Huth 1913: 25 [*nomen dubium*, as a family].

Thalassicolliden – Huth 1913: 25-26 [as a family].

TYPE GENUS. — *Thalassicolla* Huxley, 1851: 433 [type species by subsequent designation (Haeckel 1887: 18): *Thalassicolla nucleata* Huxley, 1851: 435].

INCLUDED GENERA. — *Myxobrachia* Haeckel, 1870: 519. — *Procyttarium* Haeckel, 1879: 705 (= *Actissa* with the same type species). — *Thalassicolla* Huxley, 1851: 433 (= *Thalassicollidium* with the same type species). — *Thalassicollarium* Haeckel, 1887: 18. — *Thalassolampe* Haeckel, 1862: 253. — *Thalassopila* Haeckel, 1882: 469.

Nomina dubia. — *Actidiscus*, *Actilarcus*, *Actiprunum*, *Monocarion*, *Thalassophysa*.

Diagnosis. — Thalassicollidae consists of solitary Collodaria without a siliceous skeleton. A single large nucleus is present in the center and is surrounded with the endoplasm. Huge number of algal symbionts are present.

Stratigraphic occurrence. — Living.

Remarks

"*Thalassicolla*" is scattered among the Sphaerozoidae and Collosphaeridae clades in molecular phylogenetic studies (Biard *et al.* 2015). A life stage shift from "*Thalassophysa*" to *Collozoum* was reported by Hollande & Enjumet (1953: 136-144). Morphologic changes among *Myxobrachia*, *Thalassicolla* and *Thalassolampe* are ordinarily observable in a single cell within a several-day laboratory observation. In addition, many undescribed "genera" in Thalassicollidae are commonly found in plankton samples. The Thalassicollidae are an artificial group but should be maintained as a morphological family for convenience because "solitary collodarians" are abundantly and regularly found in plankton samples. *Thalassicolla* has long been regarded as a model organism of Spumellaria, but it is now understood that *Thalassicolla* has extremely endemic characters in terms of cytology, ecology, morphology and taxonomy (Suzuki & Aita 2011; Biard *et al.* 2015; Suzuki & Not 2015). The ultrafine cytologic structure is also quite different between Collodaria and spherical Spumellaria (Hollande & Enjumet 1960; Cachon & Cachon 1972b; 1972c; 1984). However, the protoplasmic illustrations in textbooks of Radiolaria, were referred to Thalassicollidae with or without certain modifications. Thus, they are useless in acquiring a basic knowledge of the majority of spherical Radiolaria (Campbell 1954: D12; Chediya 1959: 10; Orlev 1959: 376; Nakaseko *et al.* 1975: fig. 95; Nakaseko & Sugano 1976: fig. 7.1; Kling 1978: fig. 3.B; Margulis & Schwartz 1988; Nazarov 1988: figs 1, 2; Cachon *et al.* 1989: fig. 2). In particular, the bubble-like structure (named "glycocalyx" in Hollande & Hollande 1975) is a character unique to some members of the Thalassicollidae and Thalassosphaeridae. Due to its historic reputation as "a model Spumellaria", the biological knowledge of Thalassicollidae is substantial. "Living" images were illustrated for *Thalassicolla* (Huth 1913: figs 1-7; Anderson 1978b: fig. 1; 1983: fig. 1.1.A; Anderson & Botfield 1983: fig. 1: Caron & Swanberg 1990: fig. 3.D; Probert *et al.* 2014: S1, PAC 1, 3-6, 10-15; Suzuki & Not 2015: fig. 8.13.1; Biard *et al.* 2016: figs 3.a, 3.b, 3.e; Matsuoka *et al.* 2017: appendix A; Liu *et al.* 2019: fig. 1), *Thalassolampe* (Hollande & Enjumet 1953: fig. 8; Anderson 1993: fig. 4; 1996: fig. 1.F), *Thalassopila* (Biard *et al.* 2016: fig. 3.c) and "*Thalassophysa*" (Hollande & Enjumet 1953: figs 12-14, 37). The biology and ecology of *Thalassicolla* has been profusely documented with studied dealing with: ultrafine cellular structure (Hollande & Hollande 1975; Anderson 1976a, 1978b; Cachon & Cachon 1976; Anderson & Botfield 1983); feeding behavior, nutrition and reproduction (Anderson 1978b); optimal pH for enzyme activity and cellular specialization (Anderson & Botfield 1983); food preference in laboratory culture (Anderson 1980); ^{14}C isotopic evidence for assimilation of organic substances from algal symbionts (Anderson *et al.* 1983; 1985); and interaction of holobionts by transcriptome (Liu *et al.* 2019). The ultrafine cellular structures of *Thalassolampe* (Hollande & Cachon-Enjumet 1959; Cachon & Cachon 1977) and "*Thalassophysa*" (Hollande & Cachon-Enjumet 1959; Hollande *et al.* 1970) were also reported. Algal symbionts of *Thalassicolla* were identified as *Brandtodinium nutricula* by Probert *et al.* (2014). Fatal symbiosis by *Solenodinium* and *Caryotoma bernardi* was also documented in *Thalassicolla* (Hollande & Enjumet 1953: 166-173; Hollande & Corbel 1982). However, molecular studies concerning the morphological taxonomy for these fatal symbionts were not conducted.

Validity of genus

Procyttarium

Procyttarium has the same type species as *Actissa*. However, the practical definitions of these two genera were based on different species. *Procyttarium* is based on *Procyttarium primordial*, whereas *Actissa* is based on *Actissa princeps*. The definition of *Procyttarium* in Haeckel (1879: 705) is: "*globular cell (central capsule) with a central oil sphere surrounded by numerous small 'yellow vacuoles' radiating fine pseudopodia*" (translated from German by J.-P. Caulet). Since Haeckel (1887: 12) established *Actissa*, only Ludwig (1908) has studied *Actissa*. Ludwig (1908: 28) revised the definition of *Actissa* as: "*Thalassicollidae usually without spicules, usually without or with rare vacuoles in the extracapsular gelatinous sheath, which is more compact. Often very numerous algal symbionts. Smaller than* Thalassicolla. *Pigmented in red, yellow, or black. The central capsule wall is usually thick. In the vegetative stages, the chromatin usually borders a sphere built from 'ground matter'. The centrosome is observed at the beginning of anisospore formation. The macro- and microspores are usually inside the nucleus*" (translated from German by J.-P. Caulet). As these definitions show, these two "genera" differ. A new genus is needed for *Actissa* sensu Ludwig (1908).

Family Thalassosphaeridae Haeckel, 1862

Thalassosphaerida Haeckel, 1862: 237, 246, 255 [as both family and tribe]; 1882: 470 [as a family]; 1884: 28 [as a family]; 1887: 10, 29-30 [as a family]. — Bütschli 1889: 1947 [as a family]. — Ludwig 1908: 17 [rank unknown]. — Anderson 1983: 23. — Afanasieva & Amon 2006: 157 [as a class].

Thalassosphaeridae – Claus 1876: 158. — Delage & Hérouard 1896: 178 [as a suborder]. — Campbell 1954: D45. — Chediya 1959: 66. — De Wever *et al.* 2001: 171. — Afanasieva *et al.* 2005: S306. — Chen *et al.* 2017: 81.

Physematidae Brandt, 1902: 81-82 [*nomen dubium*]. — Hollande & Enjumet 1953: 107, 112, 129. — Cachon & Cachon 1985: 284.

Physematiidae – Lankester *et al.* 1909: 144 [*nomen dubium*].

Physematiden – Huth 1913: 25 [*nomen dubium*, as a family].

Bathysphaeridae Hollande & Enjumet, 1960: 127 [junior homonym]. — Cachon & Cachon 1985: 285.

Type genus. — *Thalassosphaera* Haeckel, 1862: 259 [type species by subsequent designation (Campbell 1951: 527): *Sphaerozoum bifurcum* Haeckel, 1861b: 845]

Included genera. — *Lampoxanthura* Haeckel, 1887: 38. — *Thalassosphaera* Haeckel, 1862: 259 (*nec* Haeckel, 1887) (= *Thalassoxanthomma* with the same type species). — *Thalassoxanthella* Haeckel, 1887: 31.

Nomina dubia. — *Calosphaera*, *Lampoxanthella*, *Lampoxanthium*, *Lampoxanthomma*, *Physematium*, *Thalassiosolen*, *Thalassorhaphis*, *Thalassoxanthium*.

Junior homonyms. — *Thalassoplancta* Haeckel, 1887 (= *Thalassorhaphis*) *nec* Haeckel, 1882; *Thalassosphaera* Haeckel, 1887 (= *Calosphaera*) *nec* Haeckel, 1862.

Diagnosis. — Thalassosphaeridae consist of solitary Collodaria. The protoplasm consists of a single central large nucleus surrounded by an endoplasm. A very high number of isolated siliceous spicules are scattered outside the endoplasm.

Stratigraphic occurrence. — Living.

Remarks

No molecular data was obtained but the Thalassosphaeridae are suspected to be one of the different living stages of Thalassicollidae (see remarks for Thalassicollidae). This family includes the first described polycystine genus in history, namely *Physematium*, but the original images in Meyen (1834) are too ambiguous, making it difficult to determine real specimens without a dose of interpretative imagination. However, the ecology of *Physematium* has been studied in wide area of open oceans. In this sense, there are several studies on the functional morphology of the colony (Anderson *et al.* 1986b), the trophic activity (Swanberg & Anderson 1985; Swanberg *et al.* 1986a), as well as their feeding preferences (Swanberg *et al.* 1986b). "Living" images were illustrated for *Lampoxanthura* (Anderson 1983: figs 1.2.C-1.2.D), *Thalassosphaera* (Suzuki & Aita 2011: fig. 5E; Suzuki & Not 2015: fig. 8.13.2), "*Physematium*" (Anderson 1983: figs.1.2.A-1.2.B; Anderson *et al.* 1986b: figs 1.1-1.2) and "*Thalassoxanthium*" (Hollande & Enjumet 1953: fig. 18). However, these "living images" were obtained for *nomina dubia* genera such as "*Physematium*" and "*Thalassoxanthium*". Many undescribed "genera" of Thalassicollidae are also commonly found in plankton samples.

Phylogenetic Molecular Lineage indet. (Nakamura *et al.* 2020)

Superfamily Oroscenoidea Haeckel, 1887 n. stat.

Oroscenida Haeckel, 1887: 1593 [as a subfamily].

Orosphaericae [*sic*] – Campbell 1954: D46 [*nomen dubium*] (= Orosphaeroidea) [as a superfamily in Collodaria].

Orosphaeridea – van de Paverd 1995: 33 [*nomen dubium*, as a suborder].

Diagnosis. — Oroscenoidea consist of a very large, single skeleton network, or of several rods radiating from a single point. The superficial area of the central capsule is very large.

Remarks

Due to its uniqueness, van de Paverd (1995) established the "Orosphaeridea" as a suborder of the Spumellaria. However, the type species of the genus *Orosphaera* is an un-illustrated species and, consequently the oldest available name (Oroscenoidea) is selected for family and superfamily ranks. The higher classification position of this superfamily is related to the position of the Oroscenidae in Collodaria; however, recent molecular studies (Nakamura *et al.* 2020) suggests a new and independent order.

Family Oroscenidae Haeckel, 1887 n. stat.

Oroscenida Haeckel, 1887: 1593 [as a subfamily]. — Borgert 1901: XV-9 [as a subfamily].

Orosphaerida Haeckel, 1887: 1541, 1590-1593 [*nomen dubium*, as a family]. — Bütschli 1889: 1997 [as a family]. — Borgert 1901: XV-2, XV-9 [as a family]. — Anderson 1983: 31 [as a family of Phaeodaria].

Oronida Haeckel, 1887: 1593 [*nomen dubium*, as a subfamily]. — Borgert 1901: XV-9 [as a subfamily].

Orosphaeridae – Haecker 1908: 408-428 [*nomen dubium*, in Collodaria]. — Lankester *et al.* 1909: 144. — Wetzel 1933: 5. — Hollande & Enjumet 1953: 107, 130 [in Collodaria]. — Campbell 1954: D46, 48 [in Collodaria]. — Dogiel & Reshetnyak 1955: 46 [in Spumellaria]. — Chediya 1959: 239 [in Phaeodaria]. — Friend & Riedel 1967: 221. — Riedel 1967b: 294; 1971: 650. — Nakaseko *et al.* 1975: 166. — Nakaseko & Sugano 1976: 118. — Riedel & Sanfilippo 1977: 861. — Dumitrica 1979: 19; 1984: 94-95. — Kozur & Mostler 1982: 410 [in Entactinaria]. — Anderson 1983: 37. — Petrushevskaya 1984: 125, 128 [in Collodaria]. — Cachon & Cachon 1985: 284 [in Sphaerocollina]. — Petrushevskaya 1986: 123 [in Collodaria]. — Gourmelon 1987: 35. — van de Paverd 1995: 33. — Kiessling 1999: 44 [in Entactinaria]. — Tan & Chen 1999: 120. — De Wever *et al.* 2001: 185 [in Entactinaria]. — Afanasieva *et al.* 2005: S276 [in Order Cancelliata]. — Afanasieva & Amon 2006: 115.

Orosphaerinae – Campbell 1954: D48 [*nomen dubium*].

Orosceninae – Campbell 1954: D48.

Type genus. — *Oroscena* Haeckel, 1887: 1597 [type species by subsequent designation (Campbell 1954: D48): *Oroscena gegenbauri* Haeckel, 1887: 1597].

Included genera. — *Orodapis* Friend & Riedel, 1967: 222. — *Orodendrum* Haeckel, 1887: 1598 (= *Oroplegma*, *Oroplegmium*, synonymized by Friend & Riedel 1967: 228). — *Oropelex* Friend & Riedel, 1967: 223 (= *Oropagis* **n. syn.**). — *Oroscena* Haeckel, 1887: 1597 (= *Oroscenium* with the same type species; *Orothamnus* **n. syn.**). — *Orostaurus* Friend & Riedel, 1967: 271.

Nomina dubia. — *Orodictyum*, *Orona*, *Oronium*, *Orosphaera*.

Diagnosis. — Oroscenidae consist of a one millimeter- to centimeter-sized empty spherical shell, made of polygonal frames. The present radial spines are club-shaped or form a finely-branched network. The radial spines and network extend in a downward direction in some genera. A single large central capsular, white in color, is located in the shell. No algal symbionts are present.

STRATIGRAPHIC OCCURRENCE. — Late Eocene-Living.

REMARKS

The family name "Orosphaeridae" is replaced by "Oroscenidae" due to the *nomen dubium* status of *Orosphaera*. The taxonomic position of the Oroscenidae has repeatedly changed among Collodaria (e.g., Haecker 1906; 1908; Hollande & Enjumet 1953; Petrushevskaya 1984), Spumellaria (e.g., Dogiel & Reshetnyak 1955), Phaeodaria (Chediya 1959) and Entactinaria (Kozur & Mostler 1982; Kiessling 1999; De Wever *et al.* 2001). Molecular study clearly indicates a close relationship to the Collodaria (Nakamura *et al.* 2020). Reports identify this group as a deep-water member (>200m). Nestell & Nestell (2010: 20, 22) included the late Guadalupian of the Permian (Capitanian) subfamily Polyedroentactiniinae into the Oroscenidae, but this grouping needs further study due to the stratigraphic gap between the Polyedroentactiniinae and the Cenozoic Oroscenidae. A "living" image is only obtained for *Orodendrum* (Suzuki & Zhang 2016: 39). Skeletal structure is illustrated for *Orodictyum* (Keany & Kennett 1972: fig. 4.6), *Orodendrum* (Nakamura *et al.* 2020: figs 2.G-2.I), and *Oroscena* (Kling 1978: fig.11).

VALIDITY OF GENERA

Orodendrum

Oroplegma has the same type species as *Oroplegmium*. Since Friend & Riedel (1967: 228) synonymized *Oroplegmium* with *Orodendrum*, *Oroplegma* is also automatically a synonym of *Orodendrum*. All were established simultaneously in Haeckel (1887: 1598 for *Orodendrum*, 1599 for *Oroplegma*, 1600 for *Oroplegmium*). Regarding the first revision between *Orodendrum* and *Oroplegmium*, *Orodendrum* is selected as the valid name.

Oropelex

Friend & Riedel (1967: 223), the authors of *Oropelex*, distinguished *Oropelex* from *Oropagis* in that its shell is single rather than double. At that time, the number of shells was applied systematically for genus, family, or higher taxonomic ranks without any concern about ontogenetic growth under Haeckel's system. The type photo of *Oropagis dolium*, the type species of *Oropagis*, illustrates the supplementary growth coverage, called the "outer shell" in Friend & Riedel (1967: 226). This does not necessitate separating them at the genus level. *Oropelex* and *Oropagis* were published simultaneously in Friend & Riedel (1967). *Oropelex* is selected as the valid name because the type specimen looks better.

Oroscena

The difference is the absence of pyramidal or tent-like elevations in *Orothamnus* and their presence in *Oroscena* (Campbell 1954: D48). These differences were applied for the subfamily levels distinguishing "Orosphaerinae" and "Orosceninae," in the type-illustration of *Oroscena arborescens* (Haeckel 1887: pl. 106, fig. 3); however, the type species of *Orothamnus* has obvious pyramidal or tent-like elevations. This difference is meaningless for these two genera. The subgenera in Orosphaerinae and Orosceninae were determined by whether the radial spines are branched, arborescent, or not. This difference is also seen at the species level. Both names were published simultaneously in Haeckel (1887: 1597 for *Oroscena*; 1596 for *Orothamnus*). *Oroscena* was selected as the valid name because real specimens have been photographed.

DOUBTFUL RADIOLARIA, NON-POLYCYSTINEA, BUT INITIALLY DESCRIBED AS POLYCYSTINEA

CORRESPONDING GENERA

Acanthometra Müller, 1855: 248 [Acantharia].

Campanula Alvira-Martín, 1972: 206 [*incertae sedis*].

Cannosphaeropsis Wetzel, 1933: 52 [Dinoflagellate].

Centrocolla Cachon & Cachon, 1985: 285 [*incertae sedis*].

Conostylus Popofsky, 1907: 702 [Siliceous sponge spicule].

Dystympanium Haeckel, 1887: 1006 [Silicoflagellate].

Enjumetia Özdikmen, 2009: 245 [*incertae sedis*].

Eutympanium Haeckel, 1882: 446 [*incertae sedis*].

Halicalyptra Ehrenberg, 1846: 385 [Silicoflagellate] (= *Acrocalpis*).

Hataina Huang, 1967: 178 [Siliceous sponge spicule].

Lithacanthus Popofsky, 1907: 699 [Siliceous sponge spicule].

Radiosphaera Jørgensen, 1905: 122 [Acantharia].

Prismozoon Burchardt, 1900: 788 [Diatom].

Rhaphiophorasphaera Clark & Campbell, 1945: 18 [Diatom]

Sethodisculus Haeckel, 1887: 423 [Siliceous sponge spicule].

Sticholonche Hertwig, 1877: 324 [Taxopodia].

Tetracina Loeblich & Tappan, 1961: 221 [Siliceous sponge spicule].

Zygacantha Müller, 1859b: 51 [Acantharia].

NOMINA DUBIA UNDER THE ICZN

Circotympanum, *Echinocalpis*, *Parastephanus*, *Paratympanium, Spongasteriscinus*.

INVALID NAME UNDER THE ICZN

Paratympanum.

JUNIOR HOMONYMS UNDER THE ICZN

Bathysphaera Hollande & Enjumet, 1960 (= *Enjumetia*) *nec* Beebe, 1932; *Spirillina* Ehrenberg, 1859 *nec* Ehrenberg, 1843; *Tetracanthus* Popofsky, 1907 (= *Tetracina*) *nec* Hope, 1834.

REMARKS

Non-Polycystinea genera listed herein present certain difficulties regarding the meaning of "taxonomic availability" as some of these are treated under the International Code of Nomenclature for Algae, Fungi, and Plants (ICN) (Turland *et al.* 2018). First, the concept of "type" is quite different between ICN and the International Code of Zoological Nomenclature (ICZN). The ICN mentions that the junior synonym of living "plants" prioritizes the senior synonym of fossil "plants". By contrast, the ICZN is applied independently of all other nomenclatural codes. It is for this reason that we simply present a list of genera which have repeatedly been questioned as radiolarians Polycystinea. One of the problems is posed by "*Hataina*" and "*Sethodiscus*" which are a siliceous ellipsoidal or spherical in shape and whose internal structures are made of radiated fine fibers. These forms belong to the Class Hexactinellidae of the Porifera (Rigby 2004: 444-445). It has been known as "OST" in Japan since 1949 (Morishima *et al.* 1949) and was originally thought of as a phaeodarian (Challengeridae). The origin of "OST" was specified by the discovery of ten-centimeter-colonies on the slope of Japan Trench, east of Tohoku region of Japan (Inoue & Iwasaki 1975). Several "OST" has been formally described as new genera (e.g., *Geodia* Lamarck, 1815; *Cydonium* Fleming, 1828; *Sethodisculus* Haeckel, 1887; *Hataia* Huang, 1967; *Silicosphaera* Hughes, 1985; *Concilaspongia* Robinson & Haslett, 1995; in chronological order); however, we did not provide valid name for any "OST" because they are not belonging to Polycystinea.

Radiosphaera was questionably regarded as a Collodaria, but this genus is a protoplasmic remain of acantharians after the dissolution of strontium sulfate. This can be recognized by the presence of myonemes, muscle-like fiber bundles on the periphery of some cell membranes (capsular membrane) observed under normal light microscopy (Hollande & Enjumet 1955: black bundles on fig. 10; Febvre 1981). "*Radiosphaera*" was definitely identified, by DAPI dyeing fluorescence microscopy, as an acantharian cell with multi-nuculi and many algal symbionts inside the cell membrane.

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Appendix 1. — Historical change of higher classification system.

Reference	Taxonomic Rank	Taxonomic Division						
Current higher classification	Infrakingdom	Rhizaria						
	Phylum	Retaria						
	Subphylum	Ectorea						
	Infraphylum	Sticholonchia						
	Class	Sticholonchea	Acantharea	Polycystinea				
	Order	Taxopodia	(not shown here)	Collodaria	Spumellaria			
Adl *et al.* (2019)	1st rank	Rhizaria						
	2nd rank	Retaria	Cercozoa					
	3rd rank		Thecofilosea					
	4th rank	Taxopodia	Acantharea	Polycystinea	Phaeodarea			
	5th rank		(not shown here)	Collodaria	Spumellaria		(not shown here)	
Cavalier-Smith *et al.* (2018)	Phylum	Retaria	Cercozoa					
	Subphylum	Ectorea	Monadofilosa					
	Infraphylum	Sticholonchia						
	Class	Sticholonchea	Acantharea	Polycystinea	Thecofilosea			
	Subclass							Phaeodaria
	Order	Taxopodia	(not shown here)	Collodaria	Spumellaria		(not shown here)	
Krabberød *et al.* (2017)	–	Rhizaria						
	–	Retaria						
	–							
	–	Taxopodia	Acantharia	Polycystina				
Suzuki & Not (2015)	Super-group	Rhizaria						
	1st rank							
	Order	Taxopodia	Acantharia	Collodaria	Spumellaria			
Adl *et al.* (2012)	1st rank	Rhizaria						
	2nd rank	Retaria	Cercozoa					
	3rd rank	Acantharia	Polycystina	Thecofilosea				
	4th rank	Taxopodia	(not shown here)	Collodaria	Spumellaria		Phaeodarea	
Adl *et al.* (2005)	Higher rank	eukaryotes						
	Super-group	Rhizaria						
	1st rank		Cercozoa					
	2nd rank	Taxopodida	Acantharia	Polycystinea	Phaeodaria			
	3rd rank	---	(not shown here)	Spumellaria		(not shown here)		
	4th rank	*Sticholonchea*		Collodaria	Sphaerellarina			
Cavalier-Smith (2003)	Infrakingdom	Rhizaria						
	Phylum	Retaria	Incertae sedis					
	Subphylum							
	Class	Sticholonchea	Acantharea	Polycystinea	Phaeodarea			
Cavalier-Smith (2002)	Infrakingdom		Rhizaria					
	Phylum		Retaria					
	(not defined)							
	(not defined)		Acantharians	Euradiolarians				

Appendix 1. — Continuation.

Reference	Taxonomic Rank	Taxonomic Division					
De Wever *et al.* (2001)	traditional name		sun animalcules	radiolarians			
	Superclass		Actinopodea				
	Class		Acantharia	Polycystinea	Phaeodaria		
	Order		(not shown here)	Collodaria	Spumellaria		(not shown here)
Cavalier-Smith (1999)	Infrakingdom		Retaria				
	(not defined)						
	(not defined)		acantharians	euradiolarians			
Cavalier-Smith (1998)	Infrakingdom	Actinopoda					
	Phylum						
	Subphylum	Spasmaria					
Cavalier-Smith (1998)	(not defined)	*Sticholonche*	acantharians	(Not specified in the paper)			
Cavalier-Smith (1993)	Parvkingdom	Actinopoda					
	Phylum						
	Subphylum	Spasmaria					
	Class	Sticholonchea	Acantharea	Polycystinea	Phaeodarea		
	Subclass		(not shown here)	Spumellaria		(not shown here)	
Cavalier-Smith (1987)	Superkingdom	Eukaryota					
	Kingdom	Protozoa					
	Subkingdom	Mitozoa					
	Branch	?					
	Subphylum	?	Acantharia				
	Class			Spumellaria		Phaeodaria	
Levine *et al.* (1980)	Superclass	Actinopoda					
	Class	Heliozoa	Acantharea	Polycystinea	Phaeodarea		
	Order	Taxopodida	(not shown here)	Spumellarida		(not shown here)	
	Suborder			Sphaerocollina	Sphaerellarina		
Honigberg *et al.* (1964)	Class	Actinopodea					
	Subclass	Heliozoia	Acantharia				
	Order		(not shown here)	Porulosida	Oculosida		
	Suborder						Phaeodarina
Poche (1913)	Class	Rhizopoda					
	Subclass						
	Superorder	Porulosa	Osculosa				
	Order	Sticholonchidea	Acantho-metridea	Sphaeridea	Monopylea	Tripylea	

Appendix 2. — Alphabetical list of Polycystinea families. Abbreviations, status: invalid name (**i.n.**); junior synonym (**syn.**); junior homonym (**hom.**); *nomen dubium* (**n.d.**); *nomen nudum* (**n.n.**); orders: Collodaria (**C**); Entactinaria (**E**); Nassellaria (**N**); Spumellaria (**S**); lineage: orphaned taxa (**Ø**); lineage indet. (**?**).

List of proposed family-group names (correct spelling)	Authorship	Status	Valid family name (senior synonym)	Type genus	Stem of the genitive single noun form	Highest original rank	Order	Lineage	Superfamily (grammatic correct name)
Acanthodesmiidae	Haeckel, 1862	valid	Acanthodesmiidae	*Acanthodesmia*	*Acanthodesmi-* (*not Acanthodesm-*)	family	N	II	Acanthodesmioidea
Acrobotrusidae	Popofsky, 1913	n.d.	Pylobotrydidae	*Acrobotrusa*	*Acrobotrus-*	family	N	III	Pylobotrydoidea
Acropyramididae	Haeckel, 1882	n.d.	Plectopyramididae	*Acropyramis*	*Acropyramid-* (*not Acropyram-*)	below tribe	N	II	Plectopyramidoidea
Acrosphaeridae	Haeckel, 1882	syn.	Collosphaeridae	*Acrosphaera*	*Acrosphaer-*	subfamily	C	–	Sphaerozoidea
Acrospyrididae	Haeckel, 1882	syn.	Cephalospyrididae	*Acrospyris*	*Acrospyrid-* (*not Arcospyr-*)	tribe	N	II	Acanthodesmioidea
Actinommidae	Haeckel, 1862	valid	Actinommidae	*Actinomma*	*Actinomm-*	tribe	S	IV	Haliommoidea
Actinosphaeridae	Mast, 1910	syn.	Rhizosphaeridae	*Actinosphaera*	*Actinosphaer-*	subfamily	E	III	Rhizosphaeroidea
Aegospyrididae	Haeckel, 1882	n.d.	Cephalospyrididae	*Aegospyris*	*Aegospyrid-* (*not Aegospyr-*)	tribe	N	II	Acanthodesmioidea
Amphibrachiidae	Pessagno, 1971	n.d.	Trematodiscidae	*Amphibrachium*	*Amphibrachi-* (*not Amphibrach-*)	subfamily	S	IV	Trematodiscoidea
Amphipyndacidae	Riedel, 1967b	valid	Amphipyndacidae	*Amphipyndax*	*Amphipyndac-*	family	N	I	Amphipyndacoidea
Amphisphaeridae	Suzuki in Matsuzaki *et al.*, 2015	n.d.	Stylatractidae	*Amphisphaera*	*Amphisphaer-*	family	S	?	Stylosphaeroidea
Amphistomidae	Dreyer, 1889	i.n.		no species are known	no stem	subfamily	S	Ø	
Amphistylidae	Haeckel, 1887	n.d.	Stylatractidae	*Amphistylus*	*Amphistyl-*	tribe	S	?	Stylosphaeroidea
Amphitholidae	Campbell, 1954	syn.	Amphitholidae	*Amphitholus*	*Amphithol-*	subfamily	S	IV	Phorticioidea
Amphitholidae	Haeckel, 1887	valid	Amphitholidae	*Amphitholonium*	*Amphitholoni-* (*not Amphiloholon-*)	subfamily	S	IV	Phorticioidea
Anaxoplastidae	Hollande & Enjumet, 1960	n.n.	Rhizosphaeridae	no species are known	no stem	superfamily	E	III	Rhizosphaeroidea
Androspyrididae	Haeckel, 1887	syn.	Cephalospyrididae	*Androspyris*	*Androspyrid-* (*not Androspyr-*)	family	N	II	Acanthodesmioidea
Anthocyrtididae	Haeckel, 1882	valid	Anthocyrtididae	*Anthocyrtis*	*Anthocyrtid-* (*not Anthocyrt-*)	below tribe	N	III	Theopilioidea
Arachnosphaeridae	Haeckel, 1862	syn.	Cladococcidae	*Arachnosphaera*	*Arachnosphaer-*	tribe	S	II	Cladococcoidea
Archaeodictyomitridae	Pessagno, 1976	valid	Archaeodictyomitridae	*Archaeodictyomitra*	*Archaeodictyomitr-*	family	N	I	Archaeodictyomitroidea
Archicorythidae	Haeckel, 1882	n.d.	Sethoperidae	*Archicorys*	*Archicoryth-* (*not Archicory-, Archicor-*)	tribe	N	IV	Sethoperoidea
Archidiscidae	Haeckel, 1887	n.d.	Amphitholidae	*Archidiscus*	*Archidisc-*	subfamily	S	IV	Phorticioidea
Archiperidae	Haeckel, 1882	syn.	Phaenocalpididae	*Archipera*	*Archiper-*	tribe	N	III	Plagiacanthoidea
Archiphaenidae	Haeckel, 1887	n.d.	Cephalospyrididae	*Archiphaena*	*Archiphaen-*	subfamily	N	II	Acanthodesmioidea
Archiphatnidae	Haeckel, 1882	n.d.	Cephalospyrididae	*Archiphatna*	*Archiphatn-*	tribe	N	II	Acanthodesmioidea
Archiphormididae	Haeckel, 1882	n.d.	Plectopyramididae	*Archiphormis*	*Archiphormid-* (*not Archiphorm-*)	tribe	N	II	Plectopyramidoidea
Archipiliidae	Haeckel, 1882	valid	Archipiliidae	*Archipilium*	*Archipili-* (*not Archipil-*)	tribe	N	III	Archipilioidea
Artiscidae	Haeckel, 1882	n.d.	Panartidae	*Artiscus*	*Artisc-*	subfamily	S	I	Lithocyclioidea
Artocapsidae	Haeckel, 1882	syn.	Eucyrtidiidae	*Artocapsa*	*Artocaps-*	tribe	N	I	Eucyrtidioidea
Artocorythidae	Haeckel, 1882	n.n.		*Artocorys*	*Artocoryth-*	tribe	N	Ø	
Artoperidae	Haeckel, 1882	syn.	Theoperidae	*Artopera*	*Artoper-*	tribe	N	IV	Pterocorythoidea
Artophatnidae	Haeckel, 1882	n.d.	Eucyrtidiidae	*Artophatna*	*Artophatn-*	tribe	N	I	Eucyrtidioidea
Artophormididae	Haeckel, 1882	syn.	Eucyrtidiidae	*Artophormis*	*Artophormid-*	tribe	N	I	Eucyrtidioidea
Artopiliidae	Haeckel, 1882	syn.	Stichopiliidae	*Artopilium*	*Artopili-* (*not Artopil-*)	tribe	N	III	Stichopilioidea
Artostrobiidae	Riedel, 1967b	valid	Artostrobiidae	*Artostrobium*	*Artostrobi-* (*not Artostrob-*)	family	N	II	Artostrobioidea
Astracturidae	Haeckel, 1882	valid	Astracturidae	*Astractura*	*Astractur-*	tribe	S	I	Lithocyclioidea
Astrosphaeridae	Haeckel, 1887	syn.	Cladococcidae	*Astrosphaera*	*Astrosphaer-*	family	S	II	Cladococcoidea
Axoprunidae	Dumitrica, 1985	valid	Axoprunidae	*Axoprunum*	*Axoprun-*	subfamily	E	III	Heliosaturnaloidea
Bekomidae	Dumitrica *in* De Wever *et al.*, 2001	valid	Bekomidae	*Bekoma*	*Bekom-*	family	N	IV	Lithochytridoidea
Botryocampidae	Haeckel, 1887	syn.	Pylobotrydidae	*Botryocampe*	*Botryocamp-*	subfamily	N	III	Pylobotrydoidea
Botryocellidae	Haeckel, 1887	syn.	Pylobotrydidae	*Botryocella*	*Botryocell-*	subfamily	N	III	Pylobotrydoidea
Botryocyrtididae	Haeckel, 1887	syn.	Pylobotrydidae	*Botryocyrtis*	*Botryocyrtid-* (*not Botryocyrt-*)	subfamily	N	III	Pylobotrydoidea
Botryopylidae	Haeckel, 1887	n.d.	Pylobotrydidae	*Botryopyle*	*Botryopyl-*	subfamily	N	III	Pylobotrydoidea
Brachiatidae	Mivart, 1877	n.n.	Thalassicollidae	no species are known	no stem	subsection	C	–	Thalassicolloidea
Brachiospyrididae	Haeckel, 1882	syn.	Cephalospyrididae	*Brachiospyris*	*Brachiospyrid-* (*not Brachiospyr-*)	tribe	N	II	Acanthodesmioidea
Callimitridae	Haeckel, 1882	syn.	Sethoperidae	*Callimitra*	*Callimitr-*	below tribe	N	IV	Sethoperoidea
Calocyclidae	Haeckel, 1882	syn.	Pterocorythidae	*Calocyclas*	*Calocycl-*	below tribe	N	IV	Pterocorythoidea
Calodictyidae	Ehrenberg, 1847	i.n.		no species are known	no stem	family	N	Ø	

Appendix 2. — Continuation.

List of proposed family-group names (correct spelling)	Authorship	Status	Valid family name (senior synonym)	Type genus	Stem of the genitive single noun form	Highest original rank	Order	Lineage	Superfamily (grammatic correct name)
Cannobotrydidae	Haeckel, 1882	n.d.	Pylobotrydidae	*Cannobotrys*	*Cannobotryd-* (*not Cannobotr-* *Cannobotry-*)	subfamily	N	III	Pylobotrydoidea
Carpocaniidae	Haeckel, 1882	valid	Carpocaniidae	*Carpocanium*	*Carpocani-* (*not Carpocan-*)	below tribe	N	II	Carpocanioidea
Carposphaeridae	Haeckel, 1882	n.d.	Haliommidae	*Carposphaera*	*Carposphaer-*	tribe	S	Ø	
Caryommidae	Haeckel, 1887	n.d.	Cladococcidae	*Caryomma*	*Caryomm-*	subfamily	S	II	Cladococcoidea
Caryosphaeridae	Haeckel, 1882	n.d.	Actinommidae	*Caryosphaera*	*Caryosphaer-*	tribe	S	IV	Haliommoidea
Caryostylidae	Haeckel, 1882	n.d.	Stylatractidae	*Caryostylus*	*Caryostyl-*	tribe	S	?	Stylosphaeroidea
Cenodiscidae	Haeckel, 1887	n.d.	Ethmosphaeridae	*Cenodiscus*	*Cenodisc-*	family	S	II	Cladococcoidea
Cenolarcidae	Haeckel, 1887	n.d.	Ethmosphaeridae	*Cenolarcus*	*Cenolarc-*	subfamily	S	II	Cladococcoidea
Cenosphaeridae	Deflandre, 1953	syn.	Haliommidae	*Cenosphaera*	*Cenosphaer-*	family	S	IV	Haliommoidea
Centroaxoplastidiadae	Cachon *et al.*, 1989	n.n.		no species are known	no stem	family	S	Ø	
Centrocollidae	Cachon & Cachon, 1985	n.d.		*Centrocolla*	*Centrocoll-*	family	S	Ø	
Centrocubidae	Hollande & Enjumet, 1960	valid	Centrocubidae	*Centrocubus*	*Centrocub-*	family	E	III	Centrocuboidea
Centrolonchidae	Campbell, 1954	valid	Centrolonchidae	*Centrolonche*	*Centrolonch-*	subfamily	E	III	Centrolonchoidea
Cephalospyrididae	Haeckel, 1882	valid	Cephalospyrididae	*Cephalospyris*	*Cephalospyrid-* (*not Cephalospyr-*)	tribe	N	II	Acanthodesmioidea
Ceratocyrtidae	Petrushevskaya, 1981	valid	Ceratocyrtidae	*Ceratocyrtis*	*Ceratocyrt-*	subfamily	N	III	Plagiacanthoidea
Chitonastridae	Kozur & Mostler, 1978	n.d.	Euchitoniidae	*Chitonastrum*	*Chitonastr-*	subfamily	S	I	Spongodiscoidea
Circodiscidae	Dumitrica, 1989	valid	Circodiscidae	*Circodiscus*	*Circodisc-*	subfamily	S	IV	Phorticioidea
Circospyrididae	Haeckel, 1882	n.d.	Acanthodesmiidae	*Circospyris*	*Circospyrid-* (*not Circospyr-*)	tribe	N	II	Acanthodesmioidea
Cladococcidae	Haeckel, 1862	valid	Cladococcidae	*Cladococcus*	*Cladococc-*	family	S	II	Cladococcoidea
Clathromitridae	Petrushevskaya, 1971a	syn.	Phaenocalpididae	*Clathromitra*	*Clathromitr-*	subfamily	N	III	Plagiacanthoidea
Clathrosphaeridae	Haeckel, 1882	syn.	Collosphaeridae	*Clathrosphaera*	*Clathrosphaer-*	subfamily	C	–	Sphaerozoidea
Coccodiscidae	Haeckel, 1862	syn.	Lithocycliidae	*Coccodiscus*	*Coccodisc-*	tribe	S	I	Lithocyclioidea
Coccolarcidae	Haeckel, 1887	n.d.	Ethmosphaeridae	*Coccolarcus*	*Coccolarc-*	subfamily	S	II	Cladococcoidea
Colliidae	Haeckel, 1862	i.n.		no species are known	no stem	family	C	Ø	
Collophidiidae	Biard & Suzuki *in* Biard *et al.*, 2015	valid	Collophidiidae	*Collophidium*	*Collophidi-* (*not Colloph-*)	family	C	–	Sphaerozoidea
Collosphaeridae	Müller, 1859a	valid	Collosphaeridae	*Collosphaera*	*Collosphaer-*	family	C	–	Sphaerozoidea
Collozoidae	Haeckel, 1862	syn.	Sphaerozoidae	*Collozoum*	*Collozo-*	tribe	C	–	Sphaerozoidea
Conocaryommidae	Lipman, 1969	valid	Conocaryommidae	*Conocaryomma*	*Conocaryomm-*	subfamily	S	IV	Phorticioidea
Conosphaeridae	Lipman, 1969	syn.	Collosphaeridae	*Conosphaera*	*Conosphaer-*	family	C	–	Sphaerozoidea
Cornutellidae	Takemura, 1986	syn.	Plectopyramididae	*Cornutella*	*Cornutell-*	family	N	II	Plectopyramidoidea
Coronidiidae	Haeckel, 1887	syn.	Acanthodesmiidae	*Coronidium*	*Coronidi-* (*not Coronid-*)	family	N	II	Acanthodesmioidea
Cortinidae	Haeckel, 1887	syn.	Stephaniidae	*Cortina*	*Cortin-*	subfamily	N	II	Acanthodesmioidea
Cortiniscidae	Haeckel, 1887	syn.	Acanthodesmiidae	*Cortiniscus*	*Cortinisc-*	subfamily	N	II	Acanthodesmioidea
Coscinommidae	Haeckel, 1887	n.d.	Hollandosphaeridae	*Coscinomma*	*Coscinomm-*	subfamily	S	I	Hexacromyoidea
Cristallosphaeridae	Popofsky, 1912	valid	Cristallosphaeridae	*Cristallosphaera*	*Cristallosphaer-*	family	S	IV	Spongopyloidea
Cromyommidae	Haeckel, 1882	syn.	Actinommidae	*Cromyomma*	*Cromyomm-*	tribe	S	IV	Haliommoidea
Cromyosphaeridae	Haeckel, 1882	syn.	Haliommidae	*Cromyosphaera*	*Cromyosphaer-*	tribe	S	IV	Haliommoidea
Cromyostylidae	Haeckel, 1882	n.d.	Stylatractidae	*Cromyostylus*	*Cromyostyl-*	tribe	S	?	Stylosphaeroidea
Cryptoaxoplastidae	Hollande & Enjumet, 1960	n.n.	Rhizosphaeridae	no species are known	no stem	superfamily	E	III	Rhizosphaeroidea
Cryptolarnaciidae	Dumitrica, 1989	valid	Cryptolarnaciidae	*Cryptolarnacium*	*Cryptolarnaci-* (*not Cryptolarnac-*)	subfamily	S	IV	Phorticioidea
Cubosphaeridae	Haeckel, 1887	syn.	Hexacromyidae	*Cubosphaera*	*Cubosphaer-*	family	S	I	Hexacromyoidea
Cubotholidae	Haeckel, 1887	n.d.	Amphitholidae	*Cubotholus*	*Cubothol-*	subfamily	S	IV	Phorticioidea
Cycladophoridae	Suzuki *in* Sandin *et al.*, 2019	valid	Cycladophoridae	*Cycladophora*	*Cycladophor-*	family	N	IV	Cycladophoroidea
Cyphantellidae	Loeblich & Tappan, 1961	hom.	Panartidae	*Cyphantella*	*Cyphantell-*	family	S	I	Lithocyclioidea
Cyphantidae	Campbell, 1954	hom.	Panartidae	*Cyphanta*	*Cyphant-*	family	S	I	Lithocyclioidea
Cyphinidae	Haeckel, 1882	n.d.	Panartidae	*Cyphinus*	*Cyphin-*	tribe	S	I	Lithocyclioidea
Cyrtidae	Haeckel, 1862	i.n.		no species are known	no stem	family	N	Ø	
Cyrtidosphaeridae	Cachon & Cachon, 1972	syn.	Ethmosphaeridae	*Cyrtidosphaera*	*Cyrtidosphaer-*	family	S	II	Cladococcoidea
Cyrtocalpididae	Haeckel, 1882	syn.	Carpocaniidae	*Cyrtocalpis*	*Cyrtocalpid-* (*not Cyrtocalpi-*)	below tribe	N	II	Carpocanioidea
Cyrtostephanidae	Popofsky, 1913	syn.	Cephalospyrididae	*Cyrtostephanus*	*Cyrtostephan-*	family	N	II	Acanthodesmioidea

Appendix 2. — Continuation.

List of proposed family-group names (correct spelling)	Authorship	Status	Valid family name (senior synonym)	Type genus	Stem of the genitive single noun form	Highest original rank	Order	Lineage	Superfamily (grammatic correct name)
Cystidiidae	Haeckel, 1884	syn.	Plagiacanthidae	*Cystidium*	*Cystidi-* (*not Cystid-*)	family	N	III	Plagiacanthoidea
Cytocladidae	Schröder, 1908	syn.	Thalassothamnidae	*Cytocladus*	*Cytoclad-*	family	E	III	Thalassothamnoidea
Desmocampidae	Haeckel, 1887	n.d.	Panartidae	*Desmocampe*	*Desmocamp-*	subfamily	S	I	Lithocyclioidea
Diacanthocapsidae	O'Dogherty, 1994	valid	Diacanthocapsidae	*Diacanthocapsa*	*Diacanthocaps-*	family	N	II	Carpocanioidea
Dictyocryphalidae n. fam.	Suzuki in Suzuki *et al.* (this paper)	valid	Dictyocryphalidae n. fam.	*Dictyocryphalus*	*Dictyocryphal-*	family	N	III	Plagiacanthoidea
Dicyrtidae	Haeckel, 1862	i.n.		no species are known	no stem	tribe	N	Ø	
Dimelissidae	Petrushevskaya, 1981	valid	Dimelissidae	*Dimelissa*	*Dimeliss-*	subfamily	N	III	Plagiacanthoidea
Diplosphaeridae	Stöhr, 1880	n.d.	Cladococcidae	*Diplosphaera*	*Diplosphaer-*	family	S	II	Cladococcoidea
Diplozonaridae	Haeckel, 1887	i.n.		no species are known	no stem	subfamily	S	Ø	
Dipodospyrididae	Haeckel, 1882	n.d.	Cephalospyrididae	*Dipodospyris*	*Dipodospyrid-* (*not Dipodospyr-*)	tribe	N	II	Acanthodesmioidea
Dipospyrididae	Haeckel, 1887	n.d.	Cephalospyrididae	*Dipospyris*	*Dipospyrid-* (*not Dipospyr-*)	subfamily	N	II	Acanthodesmioidea
Dipylissidae	Dumitrica, 1989	valid	Dipylissidae	*Dipylissa*	*Dipyliss-*	subfamily	S	IV	Larcospiroidea
Discidae	Haeckel, 1862	i.n.		no species are known	no stem	family	S	Ø	
Discopylidae	Haeckel, 1887	syn.	Pylodiscidae	*Discopyle*	*Discopyl-*	subfamily	S	IV	Larcospiroidea
Discospiridae	Haeckel, 1862	syn.	Trematodiscidae	*Discospira*	*Discospir-*	tribe	S	IV	Trematodiscoidea
Dorydiscidae	Campbell, 1954	n.d.	Axoprunidae	*Dorydiscus*	*Dorydisc-*	subfamily	E	III	Heliosaturnaloidea
Druppulidae	Haeckel, 1887	n.d.	Panartidae	*Druppula*	*Druppul-*	family	S	I	Lithocyclioidea
Dyocyrtidae	Haeckel, 1882	i.n.		no species are known	no stem	subfamily	N	Ø	
Dyosphaeridae	Haeckel, 1882	i.n.		no species are known	no stem	subfamily	S	Ø	
Dyospyrididae	Haeckel, 1882	n.n.		*Dyospyris*	*Dyospyrid-*	subfamily	N	Ø	
Dyostephanidae	Haeckel, 1882	n.n.		*Dyostephanus*	*Dyostephan-*	tribe	N	Ø	
Dyostephidae	Haeckel, 1882	n.n.		*Dyostephus*	*Dyosteph-*	subfamily	N	Ø	
Elatommidae	Haeckel, 1887	n.d.	Rhizosphaeridae	*Elatomma*	*Elatomm-*	tribe	E	III	Rhizosphaeroidea
Ellipsidiidae	Haeckel, 1887	n.d.	Stylatractidae	*Ellipsidium*	*Ellipsidi-*	family	S	?	Stylosphaeroidea
Enneaphormididae	Petrushevskaya, 1981	syn.	Theophormididae	*Enneaphormis*	*Enneaphormid-* (*not Enneaphorm-*)	subfamily	N	III	Archipilioidea
Enneaplagiidae	Campbell, 1954	n.n.		*Enneaplagia*	*Enneaplagi-*	subfamily	N	Ø	
Enneaplegidae	Campbell, 1954	syn.	Plagiacanthidae	*Enneaplegma*	*Enneapleg-* (*not Enneaplegm-*)	subfamily	N	III	Plagiacanthoidea
Entapiidae	Dumitrica *in* De Wever *et al.*, 2001	valid	Entapiidae	*Entapium*	*Entapi-* (*not Entap-*)	family	S	?	Stylosphaeroidea
Ethmosphaeridae	Haeckel, 1862	valid	Ethmosphaeridae	*Ethmosphaera*	*Ethmosphaer-*	family	S	II	Cladococcoidea
Euchitoniidae	Stöhr, 1880	valid	Euchitoniidae	*Euchitonia*	*Euchitoni-* (*not Euchiton-*)	subfamily	S	I	Spongodiscoidea
Eucoronididae	Haeckel, 1882	syn.	Acanthodesmiidae	*Eucoronis*	*Eucoronid-* (*not Eucoron-*)	tribe	N	II	Acanthodesmioidea
Eucyrtidiidae	Ehrenberg, 1846	valid	Eucyrtidiidae	*Eucyrtidium*	*Eucyrtidi-*	family	N	I	Eucyrtidioidea
Excentroconchidae	Hollande & Enjumet, 1960	valid	Excentroconchidae	*Excentroconcha*	*Excentroconch-*	family	E	III	Centrocuboidea
Flustrellidae	Campbell, 1954	syn.	Trematodiscidae	*Flustrella*	*Flustrell-*	subfamily	S	IV	Trematodiscoidea
Glycobotrydidae	Campbell, 1954	syn.	Pylobotrydidae	*Glycobotrys*	*Glycobotryd-* (*not Glycobotr-, Glycobotry-*)	family	N	III	Pylobotrydoidea
Gorgospyrididae	Haeckel, 1882	syn.	Cephalospyrididae	*Gorgospyris*	*Gorgospyrid-* (*not Gorgospyr-*)	tribe	N	II	Acanthodesmioidea
Haliommidae	Ehrenberg, 1846	valid	Haliommidae	*Haliomma*	*Haliomm-*	family	S	IV	Haliommoidea
Haliphormididae	Haeckel, 1882	n.d.	Hexacaryidae	*Haliphormis*	*Haliphormid-* (*not Haiphorm-*)	below tribe	S	I	Hexacromyoidea
Haplozonaridae	Haeckel, 1887	i.n.		no species are known	no stem	subfamily	S	Ø	
Heliasteridae	Hollande & Enjumet, 1960	hom.	Hollandosphaeridae	*Heliaster*	*Heliaster-*	family	S	I	Hexacromyoidea
Heliodiscidae	Haeckel, 1882	valid	Heliodiscidae	*Heliodiscus*	*Heliodisc-*	tribe	S	IV	Haliommoidea
Heliosestridae	Haeckel, 1887	syn.	Lithocycliidae	*Heliosestrum*	*Heliosestr-*	subfamily	S	I	Lithocyclioidea
Heliosphaeridae	Haeckel, 1862	syn.	Ethmosphaeridae	*Heliosphaera*	*Heliosphaer-*	tribe	S	II	Cladococcoidea
Heterosphaeridae	Mast, 1910	n.d.	Actinommidae	*Heterosphaera*	*Heterosphaer-*	subfamily	S	IV	Haliommoidea
Hexacaryidae	Haeckel, 1882	valid	Hexacaryidae	*Hexacaryum*	*Hexacary-* (*not Hexacar-*)	below tribe	S	I	Hexacromyoidea
Hexacontiidae	Haeckel, 1882	n.d.	Hexacromyidae	*Hexacontium*	*Hexaconti-* (*not Hexacont-*)	tribe	S	I	Hexacromyoidea

Appendix 2. — Continuation.

List of proposed family-group names (correct spelling)	Authorship	Status	Valid family name (senior synonym)	Type genus	Stem of the genitive single noun form	Highest original rank	Order	Lineage	Superfamily (grammatic correct name)
Hexacromyidae	Haeckel, 1882	valid	Hexacromyidae	*Hexacromyum*	*Hexacromy-* (*not Hexacrom-*)	tribe	S	I	Hexacromyoidea
Hexadoridae	Haeckel, 1882	n.d.	Hexacromyidae	*Hexadoras*	*Hexador-*	tribe	S	I	Hexacromyoidea
Hexalonchidae	Haeckel, 1882	n.d.	Hexacromyidae	*Hexalonche*	*Hexalonch-*	tribe	S	I	Hexacromyoidea
Hexaplagiidae	Haeckel, 1887	n.d.	Plagiacanthidae	*Hexaplagia*	*Hexaplagi-* (*not Hexaplag-*)	subfamily	N	III	Plagiacanthoidea
Hexaplecidae	Haeckel, 1887	n.d.	Plagiacanthidae	*Hexaplecta*	*Hexaplec-* (*not Hexaplect-*)	subfamily	N	III	Plagiacanthoidea
Hexapylidae	Haeckel, 1887	n.d.	Pylodiscidae	*Hexapyle*	*Hexapyl-*	subfamily	S	IV	Larcospiroidea
Hexaspyrididae	Haeckel, 1887	n.d.	Cephalospyrididae	*Hexaspyris*	*Hexaspyrid-* (*not Hexaspyr-*)	subfamily	N	II	Acanthodesmioidea
Hexastylidae	Haeckel, 1882	n.d.	Centrolonchidae	*Hexastylus*	*Hexastyl-*	tribe	S	I	Hexacromyoidea
Histiastridae	Dumitrica, 1989	valid	Histiastridae	*Histiastrum*	*Histiastr-*	subfamily	S	IV	Phorticioidea
Hollandosphaeridae	Deflandre, 1973	valid	Hollandosphaeridae	*Hollandosphaera*	*Hollandosphaer-*	family	S	I	Hexacromyoidea
Lamprocyclidae	Haecker, 1907	syn.	Pterocorythidae	*Lamprocyclas*	*Lamprocycl-*	family	N	IV	Pterocorythoidea
Lampromitridae	Haeckel, 1882	valid	Lampromitridae	*Lampromitra*	*Lampromitr-*	below tribe	N	II	Plectopyramidoidea
Lamprospyrididae	Haeckel, 1887	syn.	Cephalospyrididae	*Lamprospyris*	*Lamprospyrid-* (*not Lamprospyr-*)	subfamily	N	II	Acanthodesmioidea
Larcariidae	Haeckel, 1887	n.d.	Ethmosphaeridae	*Larcarium*	*Larcari-* (*not Larcar-*)	family	S	II	Cladococcoidea
Larcopylidae	Dreyer, 1889	syn.	Larcospiridae	*Larcopyle*	*Larcopyl-*	family	S	IV	Larcospiroidea
Larcospiridae	Haeckel, 1887	valid	Larcospiridae	*Larcospira*	*Larcospir-*	subfamily	S	IV	Larcospiroidea
Larnacalpididae	Haeckel, 1887	syn.	Phorticiidae	*Larnacalpis*	*Larnacalpid-*	subfamily	S	IV	Phorticioidea
Larnacillidae	Haeckel, 1887	syn.	Phorticiidae	*Larnacilla*	*Larnacill-*	subfamily	S	IV	Phorticioidea
Liosphaeridae	Haeckel, 1887	syn.	Ethmosphaeridae	*Liosphaera*	*Liosphaer-*	family	S	II	Cladococcoidea
Lithapiidae	Deflandre, 1953	syn.	Stylatractidae	*Lithapium*	*Lithapi-* (*not Lithap-*)	subfamily	S	?	Stylosphaeroidea
Litheliidae	Haeckel, 1862	valid	Litheliidae	*Lithelius*	*Litheli-* (*not Lithel-*)	family	S	IV	Lithelioidea
Lithobotrydidae	Haeckel, 1887	n.d.	Dictyocryphalidae n. fam.	*Lithobotrys*	*Lithobotryd-* (*not Lithobotr-, Lithobotry-*)	family	N	III	Plagiacanthoidea
Lithocampanidae	Petrushevskaya, 1981	n.d.	Rhopalosyringiidae	*Lithocampana*	*Lithocampan-*	subfamily	N	II	Artostrobioidea
Lithocampidae	Haeckel, 1887	syn.	Eucyrtidiidae	*Lithocampe*	*Lithocamp-*	family	N	I	Eucyrtidioidea
Lithochytrididae	Ehrenberg, 1846	valid	Lithochytrididae	*Lithochytris*	*Lithochytrid-*	family	N	IV	Lithochytridoidea
Lithocircidae	Haeckel, 1887	syn.	Acanthodesmiidae	*Lithocircus*	*Lithocirc-*	subfamily	N	II	Acanthodesmioidea
Lithocycliidae	Ehrenberg, 1846	valid	Lithocycliidae	*Lithocyclia*	*Lithocycli-* (*not Lithocycl-*)	family	S	I	Lithocyclioidea
Lithornithiidae	Haeckel, 1882	n.d.	Lithochytrididae	*Lithornithium*	*Lithornithi-* (*not Lithornith-*)	below tribe	N	IV	Lithochytridoidea
Lithostrobidae	Petrushevskaya, 1975	valid	Lithostrobidae	*Lithostrobus*	*Lithostrob-*	family	N	I	Eucyrtidioidea
Lophocoridae	Haeckel, 1882	i.n.		no species are known	no stem	tribe	N	Ø	
Lophocyrtiidae	Sanfilippo & Caulet in De Wever *et al.*, 2001	valid	Lophocyrtiidae	*Lophocyrtis*	*Lophocyrtid-* (*not Lophocyrti-*)	family	N	IV	Pterocorythoidea
Lophophaenidae	Haeckel, 1882	n.d.	Dictyocryphalidae n. fam.	*Lophophaena*	*Lophophaen-*	below tribe	N	III	Plagiacanthoidea
Lophospyrididae	Haeckel, 1887	syn.	Cephalospyrididae	*Lophospyris*	*Lophospyrid-* (*not Lophospyr-*)	subfamily	N	II	Acanthodesmioidea
Lychnocaniidae	Haeckel, 1882	syn.	Lithochytrididae	*Lychnocanium*	*Lychnocani-* (*not Lychnocan-*)	below tribe	N	IV	Lithochytridoidea
Lychnosphaeridae	Haeckel, 1882	syn.	Cladococcidae	*Lychnosphaera*	*Lychnosphaer-*	tribe	S	II	Cladococcoidea
Macrosphaeridae	Hollande & Enjumet, 1960	n.n.	Ethmosphaeridae	no species are known	no stem	family	S	II	Cladococcoidea
Monaxoniidae	Campbell, 1954	syn.	Euchitoniidae	*Monaxonium*	*Monaxoni-* (*not Monaxon-*)	subfamily	S	I	Spongodiscoidea
Monocyrtidae	Haeckel, 1862	i.n.		no species are known	no stem	tribe	N	Ø	
Monosphaeridae	Mast, 1910	syn.	Ethmosphaeridae	*Monosphaera*	*Monosphaer-*	subfamily	S	II	Cladococcoidea
Monosphaeridae	Haeckel, 1862	n.n.	Ethmosphaeridae	no species are known	no stem	above family	S	II	Cladococcoidea
Monostephidae	Haeckel, 1882	n.d.	Acanthodesmiidae	*Monostephus*	*Monosteph-*	subfamily	N	II	Acanthodesmioidea
Monostomidae	Dreyer, 1889	i.n.		no species are known	no stem	subfamily	S	Ø	
Monozoniidae	Campbell, 1954	n.d.	Zonariidae	*Monozonium*	*Monozoni-*	subfamily	S	IV	Larcospiroidea
Myelastridae	Riedel, 1971	syn.	Euchitoniidae	*Myelastrum*	*Myelastr-*	subfamily	S	I	Spongodiscoidea
Naninidae	Kozur & Mostler, 1982	syn.	Hexacromyidae	*Nanina*	*Nanin-*	subfamily	S	I	Hexacromyoidea
Nassellidae	Haeckel, 1887	n.d.	Plagiacanthidae	*Nassella*	*Nassell-*	family	N	III	Plagiacanthoidea

Appendix 2. — Continuation.

List of proposed family-group names (correct spelling)	Authorship	Status	Valid family name (senior synonym)	Type genus	Stem of the genitive single noun form	Highest original rank	Order	Lineage	Superfamily (grammatic correct name)
Neobotrydidae	Popofsky, 1913	syn.	Pylobotrydidae	*Neobotrys*	*Neobotryd-* (*not Neobotr-, Neobotry-*)	family	N	III	Pylobotrydoidea
Neosciadiocapsidae	Pessagno, 1969	syn.	Anthocyrtididae	*Neosciadiocapsa*	*Neosciadiocaps-*	family	N	III	Theopilioidea
Nephrospyrididae	Haeckel, 1887	syn.	Paradictyidae	*Nephrospyris*	*Nephrospyrid-* (*not Nephrospyr-*)	subfamily	N	II	Acanthodesmioidea
Nothotripodiscinidae	Deflandre, 1972	syn.	Archipiliidae	*Nothotripodiscinus*	*Nothotripodiscin-*	family	N	III	Archipilioidea
Ommatocampidae	Haeckel, 1887	syn.	Euchitoniidae	*Ommatocampe*	*Ommatocamp-*	subfamily	S	I	Spongodiscoidea
Ommatodiscidae	Stöhr, 1880	syn.	Litheliidae	*Ommatodiscus*	*Ommatodisc-*	family	S	IV	Lithelioidea
Oronidae	Haeckel, 1887	n.d.	Oroscenidae	*Orona*	*Oron-*	subfamily	C	–	Oroscenoidea
Oroscenidae	Haeckel, 1887	valid	Oroscenidae	*Oroscena*	*Oroscen-*	subfamily	C	–	Oroscenoidea
Orosphaeridae	Haeckel, 1887	n.d.	Oroscenidae	*Orosphaera*	*Orosphaer-*	family	C	–	Oroscenoidea
Palaeotetrapylidae	Dumitrica, 1989	valid	Palaeotetrapylidae	*Palaeotetrapyle*	*Palaeotetrapyl-*	subfamily	S	IV	Larcospiroidea
Panartidae	Haeckel, 1887	valid	Panartidae	*Panartus*	*Panart-*	family	S	I	Lithocyclioidea
Paradictyidae	Haeckel, 1882	valid	Paradictyidae	*Paradictyum*	*Paradicty-* (*not Paradict-*)	tribe	N	II	Acanthodesmioidea
Parastephidae	Haeckel, 1882	n.n.		*Parastephus*	*Parasteph-*	subfamily	N	Ø	
Patulibracchiidae	Pessagno, 1971	valid	Patulibracchiidae	*Patulibracchium*	*Patulibracchi-* (*not Patulibracch-*)	subfamily	S	?	Pseudoaulophacoidea
Pentapyloniidae	Dumitrica *in* De Wever *et al.*, 2001	syn.	Pseudoaulophacidae	*Pentapylonium*	*Pentapyloni-* (*not Pentapylon-*)	subfamily	S	?	Pseudoaulophacoidea
Pentaspyrinidae	Haeckel, 1882	i.n.		no species are known	no stem	subfamily	N	Ø	
Periaxoplastidae	Hollande & Enjumet, 1960	n.n.	Rhizosphaeridae	no species are known	no stem	superfamily	E	III	Rhizosphaeroidea
Perispyrididae	Haeckel, 1882	syn.	Acanthodesmiidae	*Perispyris*	*Perispyrid-* (*not Perispyr-*)	subfamily	N	II	Acanthodesmioidea
Petalospyrididae	Haeckel, 1882	syn.	Cephalospyrididae	*Petalospyris*	*Petalospyrid-* (*not Petalospyr-*)	tribe	N	II	Acanthodesmioidea
Phacodiscidae	Haeckel, 1882	valid	Phacodiscidae	*Phacodiscus*	*Phacodisc-*	subfamily	S	I	Lithocyclioidea
Phacopylidae	Dreyer, 1889	n.d.	Panartidae	*Phacopyle*	*Phacopyl-*	subfamily	S	I	Lithocyclioidea
Phaenocalpididae	Haeckel, 1887	valid	Phaenocalpididae	*Phaenocalpis*	*Phaenocalpid-* (*not Phaenocalp-*)	family	N	III	Plagiacanthoidea
Phaseliformidae	Pessagno, 1972	valid	Phaseliformidae	*Phaseliforma*	*Phaseliform-*	family	S	IV	Lithelioidea
Phormocampidae	Haeckel, 1887	syn.	Pterocorythidae	*Phormocampe*	*Phormocamp-*	family	N	IV	Pterocorythoidea
Phormocyrtididae	Haeckel, 1887	syn.	Pterocorythidae	*Phormocyrtis*	*Phormocyrtid-* (*not Phormocyrt-*)	family	N	IV	Pterocorythoidea
Phormospyrididae	Haeckel, 1882	syn.	Cephalospyrididae	*Phormospyris*	*Phormospyrid-* (not *Phormospyr-*)	tribe	N	II	Acanthodesmioidea
Phorticiidae	Haeckel, 1882	valid	Phorticiidae	*Phorticium*	*Phortici-* (*not Phortic-*)	subfamily	S	IV	Phorticioidea
Physematiidae	Brandt, 1902	syn.	Thalassosphaeridae	*Physematium*	*Physemati-* (*not Physemant-*)	family	C	–	Thalassicolloidea
Pipettaridae	Schröder, 1909	syn.	Panartidae	*Pipettaria*	*Pipettar-*	subfamily	S	I	Lithocyclioidea
Plagiacanthidae	Hertwig, 1879	valid	Plagiacanthidae	*Plagiacantha*	*Plagiacanth-*	family	N	III	Plagiacanthoidea
Plagoniidae	Haeckel, 1882	n.d.	Plagiacanthidae	*Plagonium*	*Plagoni-* (*not Plagon-*)	subfamily	N	III	Plagiacanthoidea
Plectaniidae	Haeckel, 1882	syn.	Plagiacanthidae	*Plectanium*	*Plectani-* (*not Plectan-*)	subfamily	N	III	Plagiacanthoidea
Plectidae	Haeckel, 1882	i.n.		no species are known	no stem	family	N	Ø	
Plectopyramididae	Haecker, 1908	valid	Plectopyramididae	*Plectopyramis*	*Plectopyramid-* (*not Plectopyram-*)	family	N	II	Plectopyramidoidea
Plegmosphaeridae	Haeckel, 1882	n.d.	Spongodrymidae	*Plegmosphaera*	*Plegmosphaer-*	tribe	S	I	Spongosphaeroidea
Pleurospyrididae	Haeckel, 1882	n.n.		*Pleurospyris*	*Pleurospyrid-*	subfamily	N	Ø	
Podocampidae	Haeckel, 1887	n.d.	Eucyrtidiidae	*Podocampe*	*Podocamp-*	family	N	I	Eucyrtidioidea
Podocyrtididae	Haeckel, 1882	syn.	Pterocorythidae	*Podocyrtis*	*Podocyrtid-* (*not Podocyrt-*)	below tribe	N	IV	Pterocorythoidea
Polycyrtidae	Haeckel, 1862	i.n.		no species are known	no stem	tribe	N	Ø	
Polyplagiidae	Haeckel, 1882	n.d.	Plagiacanthidae	*Polyplagia*	*Polyplagi-* (*not Polyplag-*)	tribe	N	III	Plagiacanthoidea
Polyplecidae	Haeckel, 1882	syn.	Plagiacanthidae	*Polyplecta*	*Polyplec-* (*not Polyplect-*)	tribe	N	III	Plagiacanthoidea
Polysphaeridae	Haeckel, 1882	i.n.		no species are known	no stem	subfamily	S	Ø	
Polyspyrididae	Haeckel, 1882	n.d.	Cephalospyrididae	*Polyspyris*	*Polyspyrid-* (*not Polyspyr-*)	subfamily	N	II	Acanthodesmioidea
Porodiscidae	Haeckel, 1882	hom.	Trematodiscidae	*Porodiscus*	*Porodisc-*	subfamily	S	IV	Trematodiscoidea
Protympaniidae	Haeckel, 1887	n.d.	Acanthodesmiidae	*Protympanium*	*Protympani-* (*not Potympan-*)	subfamily	N	II	Acanthodesmioidea
Prunobrachiidae	Pessagno, 1975	syn.	Histiastridae	*Prunobrachium*	*Prunobrachi-*	family	S	IV	Phorticioidea
Prunopylidae	Poche, 1913	valid	Prunopylidae	*Prunopyle*	*Prunopyl-*	family	S	IV	Spongopyloidea
Pseudoaulophacidae	Riedel, 1967a	valid	Pseudoaulophacidae	*Pseudoaulophacus*	*Pseudoaulophac-*	family	S	?	Pseudoaulophacoidea

Appendix 2. — Continuation.

List of proposed family-group names (correct spelling)	Authorship	Status	Valid family name (senior synonym)	Type genus	Stem of the genitive single noun form	Highest original rank	Order	Lineage	Superfamily (grammatic correct name)
Pseudodictyophimidae Suzuki, n. fam.	Suzuki in Suzuki *et al.* (this paper)	valid	Pseudodictyophimidae Suzuki, n. fam.	*Pseudo-dictyophimus*	*Pseudodictyophim-*	family	N	III	Plagiacanthoidea
Pterocorythidae	Haeckel, 1882	valid	Pterocorythidae	*Pterocorys*	*Pterocoryth-* (*not Pterocory-, Pterocor-*)	below tribe	N	IV	Pterocorythoidea
Pylobotrydidae	Haeckel, 1882	valid	Pylobotrydidae	*Pylobotrys*	*Pylobotryd-* (*not Pylobotr-, Pylobotry-*)	subfamily	N	III	Pylobotrydoidea
Pylocapsidae	Haeckel, 1882	n.n.		*Pylocapsa*	*Pylocaps-*	subfamily	S	Ø	
Pylodiscidae	Haeckel, 1887	valid	Pylodiscidae	*Pylodiscus*	*Pylodisc-*	family	S	IV	Larcospiroidea
Pyloniidae	Haeckel, 1882	n.d.	Zonariidae	*Pylonium*	*Pyloni-* (*not Pylon-*)	family	S	IV	Larcospiroidea
Pylophormidae	Haeckel, 1882	i.n.		no species are known	no stem	subfamily	S	Ø	
Pylospyrididae	Haeckel, 1887	n.d.	Cephalospyrididae	*Pylospyris*	*Pylospyrid-*	subfamily	N	II	Acanthodesmioidea
Pyramispongiidae	Kozur & Mostler, 1978	valid	Pyramispongiidae	*Pyramispongia*	*Pyramispongi-*	family	S	IV	Lithelioidea
Quinquecapsulariidae	Dumitrica in Baum-gartner *et al.*, 1995	valid	Quinquecapsulariidae	*Quinquecapsularia*	*Quinquecapsulari-* (*not Quinquecapsular-*)	family	E	III	Centrocuboidea
Rhaphidozoidae	Haeckel, 1862	syn.	Sphaerozoidae	*Rhaphidozoum*	*Rhaphidozo-* (*not Rhaphidoz-*)	tribe	C	–	Sphaerozoidea
Rhizosphaeridae	Haeckel, 1882	valid	Rhizosphaeridae	*Rhizosphaera*	*Rhizosphaer-*	tribe	E	III	Rhizosphaeroidea
Rhodospyrididae	Haeckel, 1887	syn.	Cephalospyrididae	*Rhodospyris*	*Rhodospyrid-* (*not Rhodospyr-*)	subfamily	N	II	Acanthodesmioidea
Rhopalocaniidae	Haeckel, 1882	syn.	Theoperidae	*Rhopalocanium*	*Rhopalocani-* (*not Rhopalocan-*)	below tribe	N	IV	Pterocorythoidea
Rhopalosyringiidae	Empson-Morin, 1981	valid	Rhopalosyringiidae	*Rhopalosyringium*	*Rhopalosyringi-* (*not Rhopaloryring-*)	family	N	II	Artostrobioidea
Saturnalidae	Deflandre, 1953	n.d.	Saturnulidae n. fam.	*Saturnalis*	*Saturnal-*	subfamily	E	III	Heliosaturnaloidea
Saturnulidae n. fam.	Suzuki in Suzuki *et al.* (this paper)	valid	Saturnulidae n. fam.	*Saturnulus*	*Saturnul-*	family	E	III	Heliosaturnaloidea
Semantidae	Haeckel, 1887	syn.	Acanthodesmiidae	*Semantis*	*Semant-*	family	N	II	Acanthodesmioidea
Semantiscidae	Haeckel, 1887	syn.	Cephalospyrididae	*Semantiscus*	*Semantisc-*	subfamily	N	II	Acanthodesmioidea
Sethoconidae	Nishimura, 1990	syn.	Pterocorythidae	*Sethoconus*	*Sethocon-*	family	N	IV	Pterocorythoidea
Sethocorythidae	Haeckel, 1882	syn.	Pterocorythidae	*Sethocorys*	*Sethocoryth-* (*not Sethocory-, Sethocor-*)	tribe	N	IV	Pterocorythoidea
Sethocyrtididae	Haeckel, 1887	syn.	Pterocorythidae	*Sethocyrtis*	*Sethocyrtid-* (*not Sethocyrt-*)	family	N	IV	Pterocorythoidea
Sethodiscidae	Chediya, 1959	syn.	Heliodiscidae	*Sethodiscus*	*Sethodisc-*	family	S	IV	Haliommoidea
Sethoperidae	Haeckel, 1882	valid	Sethoperidae	*Sethopera*	*Sethoper-*	tribe	N	IV	Sethoperoidea
Sethophaenidae	Haeckel, 1887	n.d.	Sethoperidae	*Sethophaena*	*Sethophaen-*	subfamily	N	IV	Sethoperoidea
Sethophatnidae	Haeckel, 1882	n.d.	Sethoperidae	*Sethophatna*	*Sethophatn-*	tribe	N	IV	Sethoperoidea
Sethophormididae	Haeckel, 1882	n.d.	Theophormididae	*Sethophormis*	*Sethophormid-* (*not Sethophorm-*)	tribe	N	III	Archipilioidea
Sethopiliidae	Haeckel, 1882	n.d.	Dimelissidae	*Sethopilium*	*Sethopili-* (*not Sethopil-*)	tribe	N	III	Plagiacanthoidea
Siphonosphaeridae	Strelkov & Reshetnyak, 1971	syn.	Collosphaeridae	*Siphonosphaera*	*Siphonosphaer-*	tribe	C	–	Sphaerozoidea
Soreumatidae	Haeckel, 1882	n.d.	Larcospiridae	*Soreuma*	*Soreumat-*	subfamily	S	IV	Larcospiroidea
Sphaeridae	Haeckel, 1882	i.n.		no species are known	no stem	family	S	Ø	
Sphaeropylidae	Dreyer, 1889	syn.	Actinommidae	*Sphaeropyle*	*Sphaeropyl-*	family	S	IV	Haliommoidea
Sphaerostylidae	Haeckel, 1882	n.d.	Stylatractidae	*Sphaerostylus*	*Sphaerostyl-*	tribe	S	Ø	
Sphaerozoidae	Müller, 1859a	valid	Sphaerozoidae	*Sphaerozoum*	*Sphaerozo-* (*not Sphaeroz-*)	family	C	–	Sphaerozoidea
Spirematidae	Haeckel, 1882	n.d.	Litheliidae	*Spirema*	*Spiremat-* (not *Spirem-*)	subfamily	S	IV	Lithelioidea
Spireumatidae	Haeckel, 1882	n.d.	Litheliidae	*Spireuma*	*Spireumat-* (*not Spirem-*)	subfamily	S	IV	Lithelioidea
Spongellipsidae	Haeckel, 1887	n.d.	Sponguridae	*Spongellipsis*	*Spongellips-*	subfamily	S	IV	Lithelioidea
Spongobrachiidae	Haeckel, 1882	valid	Spongobrachiidae	*Spongobrachium*	*Spongobrachi-* (not *Spongobrach-*)	tribe	S	I	Spongodiscoidea
Spongocycliidae	Haeckel, 1862	syn.	Litheliidae	*Spongocyclia*	*Spongocycli-* (not *Spongocycl-*)	tribe	S	IV	Lithelioidea
Spongodiscidae	Haeckel, 1862	valid	Spongodiscidae	*Spongodiscus*	*Spongodisc-*	tribe	S	I	Spongodiscoidea
Spongodruppidae	Haeckel, 1887	n.d.	Sponguridae	*Spongodruppa*	*Spongodrupp-*	subfamily	S	IV	Lithelioidea
Spongodrymidae	Haeckel, 1887	valid	Spongodrymidae	*Spongodrymus*	*Spongodrym-*	tribe	S	I	Spongosphaeroidea

APPENDIX 2. — Continuation.

List of proposed family-group names (correct spelling)	Authorship	Status	Valid family name (senior synonym)	Type genus	Stem of the genitive single noun form	Highest original rank	Order	Lineage	Superfamily (grammatic correct name)
SPONGOLARCIDAE	Haeckel, 1887	n.d.	DIMELISSIDAE	*Spongolarcus*	*Spongolarc-*	subfamily	N	III	PLAGIACANTHOIDEA
SPONGOLONCHIDAE	Afanasieva & Amon in Afanasieva *et al.* 2005	n.d.	SPONGODISCIDAE	*Spongolonche*	*Spongolonch-*	family	S	I	SPONGODISCOIDEA
SPONGOPHACIDAE	Haeckel, 1882	n.d.	TREMATODISCIDAE	*Spongophacus*	*Spongophac-*	tribe	S	IV	TREMATODISCOIDEA
SPONGOPYLIDAE	Dreyer, 1889	valid	SPONGOPYLIDAE	*Spongopyle*	*Spongopyl-*	subfamily	S	IV	SPONGOPYLOIDEA
SPONGOSPHAERIDAE	Haeckel, 1862	valid	SPONGOSPHAERIDAE	*Spongosphaera*	*Spongosphaer-*	tribe	S	I	SPONGOSPHAEROIDEA
SPONGOSTAURIDAE	Kozur & Mostler, 1978	n.d.	TREMATODISCIDAE	*Spongostaurus*	*Spongostaur-*	subfamily	S	IV	TREMATODISCOIDEA
SPONGOSTYLIDAE	Haeckel, 1882	n.d.	AXOPRUNIDAE	*Spongostylus*	*Spongostyl-*	subfamily	E	III	HELIOSATURNALOIDEA
SPONGOTROCHIDAE	Haeckel, 1882	syn.	SPONGODISCIDAE	*Spongotrochus*	*Spongotroch-*	tribe	S	I	SPONGODISCOIDEA
SPONGURIDAE	Haeckel, 1862	valid	SPONGURIDAE	*Spongurus*	*Spongur-*	family	S	IV	LITHELIOIDEA
SPYRIDAE	Ehrenberg, 1846	n.n.	ACANTHODESMIIDAE	no species are known	no stem	family	N	II	ACANTHODESMIOIDEA
SPYRIDOBOTRYDIDAE	Campbell, 1954	n.d.	CEPHALOSPYRIDIDAE	*Spyridobotrys*	*Spyridobotryd-*	subfamily	N	II	ACANTHODESMIOIDEA
SPYROIDAE	Haeckel, 1884	n.n.	ACANTHODESMIIDAE	no species are known	no stem	family	N	II	ACANTHODESMIOIDEA
STAUROCARYIDAE	Haeckel, 1882	syn.	ACTINOMMIDAE	*Staurocaryum*	*Staurocary-*	tribe	S	IV	HALIOMMOIDEA
STAUROCONTIIDAE	Haeckel, 1882	n.d.	HEXACROMYIDAE	*Stauracontium*	*Stauroconti-* (not *Staurocont-*)	tribe	S	I	HEXACROMYOIDEA
STAUROCROMYIDAE	Haeckel, 1882	n.d.	HEXACROMYIDAE	*Staurocromyum*	*Staurocromy-*	tribe	S	I	HEXACROMYOIDEA
STAUROCYCLIIDAE	Haeckel, 1882	syn.	LITHOCYCLIIDAE	*Staurocyclia*	*Staurocycli-* (not *Staurocycl-*)	tribe	S	I	LITHOCYCLIOIDEA
STAUROSTYLIDAE	Haeckel, 1882	n.d.	TUBOSPHAERIDAE N. FAM.	*Staurostylus*	*Staurostyl-*	tribe	S	?	STYLOSPHAEROIDEA
STAUROTHOLIDAE	Haeckel, 1887	n.d.	AMPHITHOLIDAE	*Staurotholus*	*Staurothol-*	subfamily	S	IV	PHORTICIOIDEA
STEPHANIIDAE	Haeckel, 1882	valid	STEPHANIIDAE	*Stephanium*	*Stephani-* (not *Stephan-*)	family	N	II	ACANTHODESMIOIDEA
STEPHIDAE	Haeckel, 1882	i.n.		no species are known	no stem	family	N	Ø	
STICHOCORYTHIDAE	Haeckel, 1882	syn.	EUCYRTIDIIDAE	*Stichocorys*	*Stichocoryth-*	tribe	N	I	EUCYRTIDIOIDEA
STICHOCYRTIDIDAE	Haeckel, 1862	n.d.	EUCYRTIDIIDAE	*Stichocyrtis*	*Stichocyrtid-*	tribe	N	I	EUCYRTIDIOIDEA
STICHOPERIDAE	Haeckel, 1882	n.d.	EUCYRTIDIIDAE	*Stichopera*	*Stichoper-*	tribe	N	I	EUCYRTIDIOIDEA
STICHOPHAENIDAE	Haeckel, 1887	syn.	EUCYRTIDIIDAE	*Stichophaena*	*Stichophaen-*	subfamily	N	I	EUCYRTIDIOIDEA
STICHOPHATNIDAE	Haeckel, 1882	syn.	EUCYRTIDIIDAE	*Stichophatna*	*Stichophatn-*	tribe	N	I	EUCYRTIDIOIDEA
STICHOPHORMIIDAE	Haeckel, 1882	syn.	EUCYRTIDIIDAE	*Stichophormium*	*Stichophormi-* (not *Stichophorm-*)	tribe	N	I	EUCYRTIDIOIDEA
STICHOPILIIDAE	Haeckel, 1882	valid	STICHOPILIIDAE	*Stichopilium*	*Stichopili-* (not *Stichopil-*)	tribe	N	III	STICHOPILIOIDEA
STIGMOSPHAERIDAE	Hollande & Enjumet, 1960	n.d.	CENTROLONCHIDAE	*Stigmosphaera*	*Stigmosphaer-*	family	E	III	CENTROLONCHOIDEA
STOMATOSPHAERIDAE	Campbell, 1954	syn.	ACTINOMMIDAE	*Stomatosphaera*	*Stomatosphaer-*	subfamily	S	IV	HALIOMMOIDEA
STREBLACANTHIDAE	Haeckel, 1887	syn.	LARCOSPIRIDAE	*Streblacantha*	*Streblacanth-*	subfamily	S	IV	LARCOSPIROIDEA
STREBLONIIDAE	Haeckel, 1887	n.d.	ZONARIIDAE	*Streblonia*	*Strebloni-* (not *Streblon-*)	family	S	IV	LARCOSPIROIDEA
STREBLOPYLIDAE	Haeckel, 1887	syn.	LARCOSPIRIDAE	*Streblopyle*	*Streblopyl-*	subfamily	S	IV	LARCOSPIROIDEA
STYLATRACTIDAE	Schröder, 1909	valid	STYLATRACTIDAE	*Stylatractus*	*Stylatract-*	family	S	?	STYLOSPHAEROIDEA
STYLOCYCLIIDAE	Haeckel, 1887	syn.	TREMATODISCIDAE	*Stylocyclia*	*Stylocycli-* (not *Stylocyc-*)	tribe	S	IV	TREMATODISCOIDEA
STYLODICTYIDAE	Haeckel, 1882	syn.	TREMATODISCIDAE	*Stylodictya*	*Stylodicty-*	tribe	S	IV	TREMATODISCOIDEA
STYLOSPHAERIDAE	Haeckel, 1887	valid	STYLOSPHAERIDAE	*Stylosphaera*	*Stylosphaer-*	family	S	?	STYLOSPHAEROIDEA
SUTTONIIDAE	Schaaf, 1976	valid	SUTTONIIDAE	*Suttonium*	*Suttoni-* (not *Sutton-*)	family	S	?	PSEUDOAULOPHACOIDEA
TAUROSPYRIDIDAE	Haeckel, 1882	syn.	CEPHALOSPYRIDIDAE	*Taurospyris*	*Taurospyrid-*	tribe	N	II	ACANTHODESMIOIDEA
TETRACYRTIDAE	Haeckel, 1882	i.n.		no species are known	no stem	subfamily	N	Ø	
TETRAPLAGIIDAE	Haeckel, 1882	n.d.	PLAGIACANTHIDAE	*Tetraplagia*	*Tetraplagi-* (not *Tetraplag-*)	tribe	N	III	PLAGIACANTHOIDEA
TETRAPLECIDAE	Haeckel, 1882	n.d.	PLAGIACANTHIDAE	*Tetraplecta*	*Tetraplec-* (not *Tetraplect-*)	tribe	N	III	PLAGIACANTHOIDEA
TETRAPYLONIIDAE	Campbell, 1954	n.d.	ZONARIIDAE	*Tetrapylonium*	*Tetrapyloni-* (not *Tetrapylon-*)	subfamily	S	IV	LARCOSPIROIDEA
TETRARHABDIDAE	Campbell, 1954	n.d.	CEPHALOSPYRIDIDAE	*Tetrarhabda*	*Tetrarhabd-*	subfamily	N	II	ACANTHODESMIOIDEA
TETRASPHAERIDAE	Enriques, 1932	syn.	SPONGODRYMIDAE	*Tetrasphaera*	*Tetrasphaer-*	family	S	I	SPONGOSPHAEROIDEA
TETRASPHAERIDAE	Haeckel, 1882	syn.	SPONGODRYMIDAE	*Tetrasphaera*	*Tetrasphaer-*	subfamily	S	I	SPONGOSPHAEROIDEA
TETRASPYRIDIDAE	Haeckel, 1882	n.d.	CEPHALOSPYRIDIDAE	*Tetraspyris*	*Tetraspyrid-* (not *Tetraspyr-*)	subfamily	N	II	ACANTHODESMIOIDEA
THALASSICOLLIDAE	Müller, 1859a	valid	THALASSICOLLIDAE	*Thalassicolla*	*Thalassicoll-*	family	C	–	THALASSICOLLOIDEA
THALASSOPHYSIDAE	Brandt, 1902	n.d.	THALASSICOLLIDAE	*Thalassophysa*	*Thalassophys-* (not *Thalassophy-*)	family	C	–	THALASSICOLLOIDEA
THALASSOSPHAERIDAE	Haeckel, 1862	valid	THALASSOSPHAERIDAE	*Thalassosphaera*	*Thalassosphaer-*	family	C	–	THALASSICOLLOIDEA
THALASSOTHAMNIDAE	Haecker, 1906	valid	THALASSOTHAMNIDAE	*Thalassothamnus*	*Thalassothamn-*	family	E	III	THALASSOTHAMNOIDEA
THEOCOTYLIDAE	Petrushevskaya, 1981	valid	THEOCOTYLIDAE	*Theocotyle*	*Theocotyl-*	subfamily	N	IV	PTEROCORYTHOIDEA

Appendix 2. — Continuation.

List of proposed family-group names (correct spelling)	Authorship	Status	Valid family name (senior synonym)	Type genus	Stem of the genitive single noun form	Highest original rank	Order	Lineage	Superfamily (grammatic correct name)
Theocyrtididae	Haeckel, 1887	syn.	Pterocorythidae	*Theocyrtis*	*Theocyrtid-* (*not Theocyrt-*)	family	N	IV	Pterocorythoidea
Theoperidae	Haeckel, 1882	valid	Theoperidae	*Theopera*	*Theoper-*	tribe	N	IV	Pterocorythoidea
Theophaenidae	Haeckel, 1887	syn.	Theoperidae	*Theophaena*	*Theophaen-*	subfamily	N	IV	Pterocorythoidea
Theophatnidae	Haeckel, 1882	n.n.		*Theophatna*	*Theophatn-*	tribe	N	Ø	
Theophormididae	Haeckel, 1882	valid	Theophormididae	*Theophormis*	*Theophormid-* (*not Theophorm-*)	tribe	N	III	Archipilioidea
Theopiliidae	Haeckel, 1882	valid	Theopiliidae	*Theopilium*	*Theopili-* (*not Theopil-*)	tribe	N	III	Theopilioidea
Therospyrididae	Haeckel, 1882	n.d.	Cephalospyrididae	*Therospyris*	*Therospyrid-* (*not Therospyr-*)	tribe	N	II	Acanthodesmioidea
Tholoniidae	Haeckel, 1887	n.d.	Amphitholidae	*Tholonium*	*Tholoni-* (*not Tholon-*)	family	S	IV	Phorticioidea
Tholospyridae	Tochilina, 1985	syn.	Larcospiridae	*Tholospira*	*Tholospyr-*	family	S	IV	Larcospiroidea
Tholospyrididae	Haeckel, 1887	syn.	Cephalospyrididae	*Tholospyris*	*Tholospyrid-* (*not Tholospyr-*)	family	N	II	Acanthodesmioidea
Tiarospyrididae	Haeckel, 1887	syn.	Cephalospyrididae	*Tiarospyris*	*Tiarospyrid-* (*not Tiarospyr-*)	subfamily	N	II	Acanthodesmioidea
Trematodiscidae	Haeckel, 1862	valid	Trematodiscidae	*Trematodiscus*	*Trematodisc-*	tribe	S	IV	Trematodiscoidea
Triacartidae	Campbell, 1954	syn.	Stichopiliidae	*Triacartus*	*Triacart-*	family	N	III	Stichopilioidea
Triocyrtidae	Haeckel, 1882	i.n.		no species are known	no stem	subfamily	N	Ø	
Triopylidae	Haeckel, 1887	n.d.	Pylodiscidae	*Triopyle*	*Triopyl-*	subfamily	S	IV	Larcospiroidea
Triosphaeridae	Haeckel, 1882	n.n.		no species are known	no stem	subfamily	S	Ø	
Triospyrididae	Haeckel, 1882	n.d.	Cephalospyrididae	*Triospyris*	*Triospyrid-* (*not Triospyr-*)	tribe	N	II	Acanthodesmioidea
Triostephidae	Haeckel, 1882	syn.	Acanthodesmiidae	*Triostephus*	*Triosteph-*	subfamily	N	II	Acanthodesmioidea
Triplagiidae	Haeckel, 1882	syn.	Plagiacanthidae	*Triplagia*	*Triplagi-* (*not Triplag-*)	tribe	N	III	Plagiacanthoidea
Triplecidae	Haeckel, 1882	n.d.	Plagiacanthidae	*Triplecta*	*Triplec-* (*not Triplect-*)	tribe	N	III	Plagiacanthoidea
Triplozonaridae	Haeckel, 1887	i.n.		no species are known	no stem	subfamily	S	Ø	
Tripocalpididae	Haeckel, 1882	n.d.	Pseudodictyophimidae Suzuki, n. fam.	*Tripocalpis*	*Tripocalpid-* (*not Tripocalp-*)	tribe	N	III	Plagiacanthoidea
Tripocyrtididae	Haeckel, 1887	syn.	Sethoperidae	*Tripocyrtis*	*Tripocyrtid-* (*not Tripocyrt-*)	family	N	IV	Sethoperoidea
Tripodisciidae	Haeckel, 1882	valid	Tripodisciidae	*Tripodiscium*	*Tripodisci-* (*not Tripodisc-*)	below tribe	N	III	Plagiacanthoidea
Tripospyrididae	Campbell, 1954	n.d.	Cephalospyrididae	*Tripospyris*	*Tripospyrid-* (*not Tripospyr-*)	family	N	II	Acanthodesmioidea
Trissocyclidae	Haeckel, 1882	syn.	Acanthodesmiidae	*Trissocyclus*	*Trissocycl-* (*not Trisocycli-*)	tribe	N	II	Acanthodesmioidea
Trissopiliidae	Haeckel, 1882	n.d.	Archipiliidae	*Trissopilium*	*Trissopili-*	tribe	N	III	Archipilioidea
Trochodiscidae	Haeckel, 1887	n.d.	Lithocycliidae	*Trochodiscus*	*Trochodisc-*	subfamily	S	I	Lithocyclioidea
Tubosphaeridae n. fam.	Suzuki in Suzuki *et al.* (this paper)	valid	Tubosphaeridae n. fam.	*Tubosphaera*	*Tubosphaer-*	family	S	?	Stylosphaeroidea
Tympaniidae	Haeckel, 1887	syn.	Acanthodesmiidae	*Tympanium*	*Tympani-* (*not Tympan-*)	family	N	II	Acanthodesmioidea
Ximolzidae nom. nov.	Dumitrica in Suzuki *et al.* (this paper)	valid	Ximolzidae nom. nov.	*Ximolzas*	*Ximolz-*	subfamily	N	III	Plagiacanthoidea
Xitomitridae	O'Dogherty *et al.*, 2017	valid	Xitomitridae	*Xitomitra*	*Xitomitr-*	family	N	I	Eucyrtidioidea
Zamolxidae	Dumitrica, 1982b	hom.	Ximolzidae nom. nov.	*Zamolxis*	*Zamolx-*	subfamily	N	III	Plagiacanthoidea
Zonariidae	Haeckel, 1887	valid	Zonariidae	*Zonarium*	*Zonari-*	family	S	IV	Larcospiroidea
Zonodiscidae	Haeckel, 1887	n.d.	Ethmosphaeridae	*Zonodiscus*	*Zonodisc-*	subfamily	S	II	Cladococcoidea
Zygartidae	Haeckel, 1882	n.d.	Panartidae	*Zygartus*	*Zygart-*	family	S	I	Lithocyclioidea
Zygocampidae	Haeckel, 1887	n.d.	Panartidae	*Zygocampe*	*Zygocamp-*	subfamily	S	I	Lithocyclioidea
Zygocyrtidae	Haeckel, 1862	i.n.		no species are known	no stem	tribe	N	Ø	
Zygospyrididae	Haeckel, 1887	n.d.	Cephalospyrididae	*Zygospyris*	*Zygospyrid-* (*not Zygospyr-*)	family	N	II	Acanthodesmioidea
Zygostephanidae	Haeckel, 1882	n.d.	Cephalospyrididae	*Zygostephanus*	*Zygostephan-*	tribe	N	II	Acanthodesmioidea

APPENDIX 3. — Suprageneric classification of Polycystinea proposed in the present study.

Order SPUMELLARIA Ehrenberg, 1876
- Phylogenetical Molecular LINEAGE I (Sandin *et al.* 2021)
  - Superfamily Hexacromyoidea Haeckel, 1882 n. stat.
- Clade A (Sandin *et al.* 2021)
    - Family Hexacaryidae Haeckel, 1882 n. stat.
- Clade B (Sandin *et al.* 2021)
    - Family Hexacromyidae Haeckel, 1882 n. stat.
- Clade C (Sandin *et al.* 2021)
    - Family Hollandosphaeridae Deflandre, 1973
- Clade D (Sandin *et al.* 2021)
  - Superfamily Spongosphaeroidea Haeckel, 1862
    - Family Spongosphaeridae Haeckel, 1862
- Clade E1 (Sandin *et al.* 2021)
  - Superfamily Lithocyclioidea Ehrenberg, 1846
    - Family Astracturidae Haeckel, 1882
    - Family Lithocycliidae Ehrenberg, 1846
    - Family Panartidae Haeckel, 1887
    - Family Phacodiscidae Haeckel, 1882
  - Superfamily Spongodiscoidea Haeckel, 1862 *sensu* Suzuki emend. herein
- Clade E2 (Sandin *et al.* 2021)
    - Family Spongodiscidae Haeckel, 1862 *sensu* Suzuki emend. herein
- Clade E3 (Sandin *et al.* 2021)
    - Family Euchitoniidae Stöhr, 1880 *sensu* Suzuki emend. herein
- Clade indet.
    - Family Spongobrachiidae Haeckel, 1882 *sensu* Suzuki emend. herein

- Phylogenetical Molecular LINEAGE II (Sandin *et al.* 2021)
  - Superfamily Cladococcoidea Haeckel, 1862 n. stat.
- Clade F1 (Sandin *et al.* 2021)
    - Family Ethmosphaeridae Haeckel, 1862
- Clade F2 (Sandin *et al.* 2021)
    - Family Cladococcidae Haeckel, 1862

- Phylogenetical Molecular LINEAGE IV (Sandin *et al.* 2021)
- Clade J1-J2 (Sandin *et al.* 2021)
  - Superfamily Trematodiscoidea Haeckel, 1862 *sensu* Suzuki emend. herein
    - Family Trematodiscidae Haeckel, 1862 *sensu* Suzuki emend. herein
- Clade K (Sandin *et al.* 2021)
  - Superfamily Haliommoidea Ehrenberg, 1846
    - Family Actinommidae Haeckel, 1862 *sensu* Suzuki emend. herein
    - Family Haliommidae Ehrenberg, 1846 *sensu* Suzuki emend. herein
    - Family Heliodiscidae Haeckel, 1882 *sensu* De Wever *et al.* (2001)
  - Superfamily Lithelioidea Haeckel, 1862 *sensu* Matsuzaki *et al.* (2015)
- Clade indet.
    - Family Conocaryommidae Lipman, 1969
- Clade L1 (Sandin *et al.* 2021)
    - Family Litheliidae Haeckel, 1862 *sensu* Suzuki emend. herein
    - Family Phaseliformidae Pessagno, 1972
    - Family Pyramispongiidae Kozur & Mostler, 1978 *sensu* O'Dogherty (1994)
    - Family Sponguridae Haeckel, 1862
- Clade L2 (Sandin *et al.* 2021)

Appendix 3. — Continuation.

Superfamily Spongopyloidea Dreyer, 1889 n. stat., *sensu* Suzuki emend. herein
Family Spongopylidae Dreyer, 1889 *sensu* Suzuki emend. herein
Family Cristallosphaeridae Popofsky, 1912
Clade indet.
Family Prunopylidae Poche, 1913
Superfamily Phorticioidea Haeckel, 1882 n. stat.
Clade M1 (Sandin *et al.* 2021)
Family Amphitholidae Haeckel, 1887 n. stat., *sensu* De Wever *et al.* (2001)
Clade M2 (Sandin *et al.* 2021)
Family Circodiscidae Dumitrica, 1989 n. stat.
Family Cryptolarnaciidae Dumitrica, 1989 n. stat.
Family Histiastridae Dumitrica, 1989 n. stat.
Family Phorticiidae Haeckel, 1882 *sensu* Dumitrica (1989)
Superfamily Larcospiroidea Haeckel, 1887 n. stat., *sensu* Dumitrica (1989)
Family Dipylissidae Dumitrica, 1989 n. stat.
Family Larcospiridae Haeckel, 1887 n. stat.
Family Palaeotetrapylidae Dumitrica, 1989 n. stat.
Clade M3 (Sandin *et al.* 2021)
Family Pylodiscidae Haeckel, 1887 *sensu* Dumitrica (1989)
Clade M4 (Sandin *et al.* 2021)
Family Zonariidae Haeckel, 1887 *sensu* Dumitrica (1989)

Phylogenetical Molecular LINEAGE indet.
Superfamily Pseudoaulophacoidea Riedel, 1967 (Riedel 1967a) *sensu* De Wever *et al.* (2001)
Family Patulibracchiidae Pessagno, 1971 (Pessagno 1971a) *sensu* De Wever *et al.* (2001)
Family Pseudoaulophacidae Riedel, 1967a (Riedel 1967a) *sensu* De Wever *et al.* (2001)
Family Suttoniidae Schaaf, 1976 *sensu* Dumitrica (2019)

Phylogenetical Molecular LINEAGE indet.
Superfamily Stylosphaeroidea Haeckel, 1887 *sensu* Dumitrica (1984)
Family Entapiidae Dumitrica *in* De Wever, Dumitrica, Caulet Nigrini & Caridroit, 2001
Family Stylatractidae Schröder, 1909 n. stat., *sensu* Suzuki, emend. herein
Family Stylosphaeridae Haeckel, 1887 *sensu* Dumitrica (1985)
Family Tubosphaeridae Suzuki, n. fam.
Incertae familiae spumellarians
Orphaned spumellarians family ranks

Order ENTACTINARIA Kozur & Mostler, 1982
Phylogenetical Molecular LINEAGE III Sandin *et al.* (2021)
Clade G (Sandin *et al.* 2021)
Superfamily Rhizosphaeroidea Haeckel, 1882 n. stat.
Family Rhizosphaeridae Haeckel, 1882 *sensu* Dumitrica (2017b)
Superfamily Centrocuboidea Hollande & Enjumet, 1960 *sensu* Dumitrica (2001)
Clade H (Sandin *et al.* 2021)
Family Centrocubidae Hollande & Enjumet, 1960 *sensu* De Wever *et al.* (2001)
Clade I (Sandin *et al.* 2021)
Family Excentroconchidae Hollande & Enjumet, 1960 *sensu* Dumitrica (2014a)
Family Quinquecapsulariidae Dumitrica, 1995
Family Spongodrymidae Haeckel, 1887 n. stat.
Clade indet.
Superfamily Centrolonchoidea Campbell, 1954 n. stat.
Family Centrolonchidae Campbell, 1954 *sensu* Hollande & Enjumet (1960)

Appendix 3. — Continuation.

Clade indet.
Superfamily Heliosaturnaloidea Kozur & Mostler, 1972 n. stat.
Family Axoprunidae Dumitrica, 1985
Family Saturnulidae Suzuki, n. fam.

Phylogenetical Molecular LINEAGE indet.
Superfamily Thalassothamnoidea Haecker, 1906
Family Thalassothamnidae Haecker, 1906

Order NASSELLARIA Ehrenberg, 1876
Phylogenetical Molecular LINEAGE I Sandin *et al.* (2019)
Clade A (Sandin *et al.* 2019)
Superfamily Amphipyndacoidea Riedel, 1967 (Riedel 1967a)
Family Amphipyndacidae Riedel, 1967 (Riedel 1967a)
Superfamily Archaeodictyomitroidea Pessagno, 1976
Family Archaeodictyomitridae Pessagno, 1976
Superfamily Eucyrtidioidea Ehrenberg, 1846 *sensu* Suzuki emend. herein
Family Eucyrtidiidae Ehrenberg, 1846 *sensu* Suzuki emend. herein
Family Lithostrobidae Petrushevskaya, 1975
Family Xitomitridae O'Dogherty, Goričan & Gawlick, 2017 (O'Dogherty *et al.* 2017)

Phylogenetical Molecular LINEAGE II Sandin *et al.* (2019)
Clade B (Sandin *et al.* 2019)
Superfamily Plectopyramidoidea Haecker, 1908 n. stat.
Family Plectopyramididae Haecker, 1908
? Family Lampromitridae Haeckel, 1882 *sensu* Suzuki emend. herein
Family Incertae
Clade C (Sandin *et al.* 2019)
Superfamily Carpocanioidea Haeckel, 1882 n. stat.
Family Carpocaniidae Haeckel, 1882 *sensu* Sugiyama (1998)
Family Diacanthocapsidae O'Dogherty, 1994
Clade D (Sandin *et al.* 2019)
Superfamily Artostrobioidea Riedel, 1967 (Riedel 1967a)
Family Artostrobiidae Riedel, 1967 (Riedel 1967a) *sensu* Sugiyama (1998)
Family Rhopalosyringiidae Empson-Morin, 1981
Clade E (Sandin *et al.* 2019)
Superfamily Acanthodesmioidea Haeckel, 1862
Family Acanthodesmiidae Haeckel, 1862
Family Cephalospyrididae Haeckel, 1882 n. stat.
Family Paradictyidae Haeckel, 1882 n. stat., *sensu* Petrushevskaya (1981)
Family Stephaniidae Haeckel, 1882

Phylogenetical Molecular LINEAGE III Sandin *et al.* (2019)
Clade X (Sandin *et al.* 2019)
Superfamily Archipilioidea Haeckel, 1882 *sensu* Sandin, Not & Suzuki *in* Sandin *et al.* (2019)
Family Archipiliidae Haeckel, 1882 *sensu* Sandin *et al.* (2019)
Family Theophormididae Haeckel, 1882 *sensu* Suzuki emend. herein
Clade F (Sandin *et al.* 2019)
Superfamily Theopilioidea Haeckel, 1882 n. stat., *sensu* Suzuki emend. herein
Family Anthocyrtididae Haeckel, 1882 *sensu* Caulet emend. herein
Family Theopiliidae Haeckel, 1882 *sensu* Caulet emend. herein
Superfamily Stichopilioidea Haeckel, 1882 n. stat.
Family Stichopiliidae Haeckel, 1882 *sensu* Petrushevskaya (1986)

APPENDIX 3. — Continuation.

Clade G (Sandin *et al.* 2019)
Superfamily Plagiacanthoidea Hertwig, 1879
Family Ceratocyrtidae Petrushevskaya, 1981 n. stat., *sensu* Caulet emend. herein
Family Dictyocryphalidae Suzuki, n. fam.
Family Dimelissidae Petrushevskaya, 1981 n. stat., *sensu* Caulet emend. herein
Family Phaenocalpididae Haeckel, 1887 *sensu* Caulet emend. herein
Family Plagiacanthidae Hertwig, 1879 *sensu* Dumitrica (2004)
Family Pseudodictyophimidae Suzuki, n. fam.
Family Tripodisciidae Haeckel, 1882 n. stat.
Family Ximolzidae Dumitrica, nom. nov.
Superfamily Pylobotrydoidea Haeckel, 1882 n. stat.
Family Pylobotrydidae Haeckel, 1882 *sensu* Sugiyama (1998)

Phylogenetical Molecular LINEAGE IV Sandin *et al.* (2019)
Clade H (Sandin *et al.* 2019)
Superfamily Cycladophoroidea Suzuki *in* Sandin, Pillet, Biard, Poirier, Bigeard, Romac, Suzuki & Not, 2019 n. stat. (Sandin *et al.* 2019)
Family Cycladophoridae Suzuki *in* Sandin, Pillet, Biard, Poirier, Bigeard, Romac, Suzuki & Not, 2019 (Sandin *et al.* 2019)
Superfamily Sethoperoidea Haeckel, 1882 n. stat.
Family Sethoperidae Haeckel, 1882 *sensu* Suzuki emend. herein
Clade I (Sandin *et al.* 2019)
Superfamily Lithochytridoidea Ehrenberg, 1846 n. stat.
Family Bekomidae Dumitrica *in* De Wever, Dumitrica, Caulet, Nigrini & Caridroit, 2001 (De Wever *et al.* 2001)
Family Lithochytrididae Ehrenberg, 1846 *sensu* Suzuki *in* Matsuzaki *et al.* (2015)
Clade J (Sandin *et al.* 2019)
Superfamily Pterocorythoidea Haeckel, 1882 *sensu* Suzuki emend. herein
Family Lophocyrtiidae Sanfilippo & Caulet *in* De Wever, Dumitrica, Caulet, Nigrini & Caridroit, 2001 (De Wever *et al.* 2001)
Family Pterocorythidae Haeckel, 1882
Family Theocotylidae Petrushevskaya, 1981
Family Theoperidae Haeckel, 1882 *sensu* Suzuki emend. herein
Incertae familiae nassellarians
Orphaned nassellarians family ranks

Order COLLODARIA Haeckel, 1882
"Collonial collodarians" Lineage (Biard *et al.* 2015)
Superfamily Sphaerozoidea Müller, 1859 (Müller 1859a)
Family Collophidiidae Biard & Suzuki *in* Biard, Pillet, Decelle, Poirier, Suzuki & Not, 2015 (Biard *et al.* 2015)
Family Collosphaeridae Müller, 1859 (Müller 1859a)
Family Sphaerozoidae Müller, 1859 (Müller 1859a)
"Solitary collodarians" Lineage (Biard *et al.* 2015)
Superfamily Thalassicolloidea Müller, 1859 (Müller 1859a)
Family Thalassicollidae Müller, 1859 (Müller 1859a)
Family Thalassosphaeridae Haeckel, 1862
Lineage indet. (Nakamura *et al.* 2020)
Superfamily Oroscenoidea Haeckel, 1887 n. stat.
Family Oroscenidae Haeckel, 1887 n. stat.
Doubtful Radiolaria, non-Polycystinea, but initially described as Polycystinea

Appendix 4. — Integrated morpho- and molecular systematic classification of Cenozoic radiolarians (Polycystinea) with indication of the stratigraphic occurrence for the families, which are issued of the revision of genera and species presented in this special thematic volume. This table also shows those family groups having representation in the modern plankton (71 families), as well as those crossing the Cretaceous/Tertiary (**K/T**) boundary. In the K/T column, the "**0**" indicates those families "virtually" crossing (17) and the "**1**" those having a continuous record (24). These discontinuities observed in the stratigraphic ranges were already noticed by O'Dogherty *et al.* (2011). They correspond to long gaps between two genera "apparently" belonging to the same family (based on the initial spicule), but without representatives throughout the stratigraphic record that separate them (continuation on the next page).

Order	Lineage	Clade	Superfamily	Family (according to ICZN)	K/T	Stratigraphic occurrence	Living
SPUMELLARIA	I	A	Hexacromyoidea	Hexacaryidae	0	Late Paleocene-Living	1
		B		Hexacromyidae		Late Paleocene-Living	1
		C		Hollandosphaeridae		Holocene-Living	1
		D	Spongosphaeroidea	Spongosphaeridae		early Middle Miocene-Living	1
		E1	Lithocyclioidea	Astracturidae		late Middle Eocene-Early Oligocene	
				Lithocycliidae		Late Paleocene-Living	1
				Panartidae		Early Oligocene-Living	1
				Phacodiscidae		Early Eocene-Living	1
		E2	Spongodiscoidea	Spongodiscidae	0	Early Eocene-Living	1
		E3		Euchitoniidae		early Middle Miocene-Living	1
		indet.		Spongobrachiidae		early Middle Miocene-Living	1
	II	F1	Cladococcoidea	Ethmosphaeridae		Late Oligocene-Living	1
		F2		Cladococcidae	0	early Middle Miocene-Living	1
ENTACTINARIA	III	G	Rhizosphaeroidea	Rhizosphaeridae	0	Early Paleocene-Living	1
		H	Centrocuboidea	Centrocubidae	0	early Middle Miocene-Living	1
				Excentroconchidae		early Early Miocene-Living	1
		I		Quinquecapsulariidae	0	Late Miocene-Living	1
		E		Spongodrymidae		Middle Pleistocene-Living	1
		indet.	Centrolonchoidea	Centrolonchidae		late Late Miocene-Living	1
			Heliosaturnaloidea	Axoprunidae	1	Early Paleocene-Living	1
				Saturnulidae n. fam.	1	Early Toarcian-Early Paleocene	
	indet.		Thalassothamnoidea	Thalassothamnidae	0	Holocene-Living	1
SPUMELLARIA	IV	J1-J2	Trematodiscoidea	Trematodiscidae		Middle Paleocene-Living	1
		K	Haliommoidea	Actinommidae	1	Middle Paleocene-Living	1
				Haliommidae		Late Paleocene-Living	1
				Heliodiscidae	0	Early Eocene-Living	1
		indet.	Lithelioidea	Conocaryommidae	0	Early Eocene-Late Eocene	
		L1		Litheliidae	0	Early Paleocene-Living	1
				Phaseliformidae	1	Early Hauterivian-Early Paleocene	
				Pyramispongiidae	1	Late Tithonian-Late Paleocene	
				Sponguridae	1	Late Campanian-Living	1
		L2	Spongopyloidea	Spongopylidae	1	Late Eocene-Living	1
				Prunopylidae		Early Oligocene-Holocene	
				Cristallosphaeridae		Late Eocene-Living	1
		M1	Phorticioidea	Amphitholidae		Holocene-Living	1
		M2		Circodiscidae		Middle Paleocene-Living	1
				Cryptolarnaciidae	0	Late Paleocene-Late Eocene	
				Histiastridae	1	Late Campanian-Living	1
				Phorticiidae		late Middle Eocene-Living	1
			Larcospiroidea	Dipylissidae		late Late Miocene-Holocene	
				Larcospiridae		late Middle Eocene-Living	1
				Palaeotetrapylidae		Early Paleocene	
		M3		Pylodiscidae		Late Miocene-Living	1
		M4		Zonariidae		late Late Miocene-Living	1
	indet.		Pseudoaulophacoidea	Patulibracchiidae	1	Early Paleocene-Early Pliocene	
				Pseudoaulophacidae	0	early Early Miocene-Early Pliocene	
				Suttoniidae		Early Paleocene-Holocene	
			Stylosphaeroidea	Entapiidae		Middle Paleocene-early Middle Eocene	
				Stylatractidae	1	Late Campanian-Holocene	
				Stylosphaeridae	1	Late Campanian-Living	1
				Tubosphaeridae n. fam.		late Middle Eocene-Living	1
			incertae placement	incertae familiae	1	Late Campanian-Holocene	

Appendix 4 (continuation). — The family names are tied to the revised dataset by a permanent link to ninety-seven PDF files (see the appendix 2 in the revision article of genera [O'Dogherty *et al.* in press]). Each family file includes those genera considered as valid with a list of the species and their objective synonyms; the stratigraphic occurrences assigned in the original papers are also documented. The reader can quickly navigate visually, or jump to a given genus, by clicking on the bookmarks in the left navigation pane. An objective evaluation of each species with respect to its taxonomic status (junior/senior synonyms) is beyond the scope of this revision. Nonetheless, each genera file gathers the group of species subjectively assigned after several working sessions through the different stages of this project.

Order	**Lineage**	**Clade**	**Superfamily**	**Family (according to ICZN)**	**K/T**	**Stratigraphic occurrence**	**Living**
NASSELLARIA	I	A	Amphipyndacoidea	Amphipyndacidae	1	Early Berriasian-early Middle Miocene	
			Archaeodictyomitroidea	Archaeodictyomitridae	1	Early Berriasian-late Middle Eocene	
			Eucyrtidioidea	Eucyrtidiidae	1	Early Paleocene-Living	1
				Lithostrobidae	1	Early Turonian-late Late Miocene	
				Xitomitridae	1	Early Aalenian-late Middle Eocene	
	II	B	Plectopyramidoidea	Plectopyramididae	1	Late Anisian-Living	1
				Lampromitridae ?		Early Pliocene-Living	1
				incertae familiae		Early Eocene-early Late Miocene	
		C	Carpocanioidea	Carpocaniidae	1	Early Eocene-Living	1
				Diacanthocapsidae	1	Early Campanian-early Middle Eocene	
		D	Artostrobioidea	Artostrobiidae	1	Early Toarcian-Living	1
				Rhopalosyringiidae	1	Early Bajocian-Living	1
		E	Acanthodesmioidea	Acanthodesmiidae		Middle Paleocene-Living	1
				Cephalospyrididae		Middle Paleocene-Living	1
				Paradictyidae		Late Paleocene-Living	1
				Stephaniidae		early Middle Eocene-Living	1
	III	X	Archipilioidea	Archipiliidae		Late Oligocene-Living	1
				Theophormididae		Middle Paleocene-Living	1
		F	Theopilioidea	Anthocyrtididae	1	Early Berriasian-Late Oligocene	
				Theopiliidae		early Early Miocene-Living	1
			Stichopilioidea	Stichopiliidae		Late Oligocene-Living	1
		G	Plagiacanthoidea	Ceratocyrtidae		Late Paleocene-Living	1
				Dictyocryphalidae n. fam.		early Middle Eocene-Living	1
				Dimelissidae		late Middle Eocene-Living	1
				Phaenocalpididae		Middle Paleocene-Living	1
				Plagiacanthidae	0	late Middle Eocene-Living	1
				Pseudodictyophimidae n. fam.		Late Eocene-Living	1
				Tripodisciidae		Living	1
				Ximolzidae nom. nov.	1	Early Coniacian-Living	1
			Pylobotrydoidea	Pylobotrydidae	0	late Middle Eocene-Living	1
	IV	H	Cycladophoroidea	Cycladophoridae		Late Eocene-Living	1
			Sethoperoidea	Sethoperidae	0	Late Eocene-Living	1
		I	Lithochytridoidea	Bekomidae		Middle Paleocene-Living	1
				Lithochytrididae	0	Early Paleocene-Living	1
		J	Pterocorythoidea	Lophocyrtiidae		Late Paleocene-early Middle Miocene	
				Pterocorythidae		Late Paleocene-Living	1
				Theocotylidae		Middle Paleocene-early Middle Miocene	
				Theoperidae		Early Paleocene-early Middle Miocene	
		indet.		incertae familiae		Middle Paleocene-Late Paleocene	
COLLODARIA	solitary		Sphaerozoidea	Collophidiidae		Living	1
				Collosphaeridae		early Early Miocene-Living	
				Sphaerozoidae		Living	1
	colonial		Thalassicolloidea	Thalassicollidae		Living	1
				Thalassosphaeridae		Living	1
	indet.		Oroscenoidea	Oroscenidae	0	Late Eocene-Living	1