

## **Radiolarian Studies by Christian Gottfried Ehrenberg (1795–1876) and Value of his Species as Type Species of Genera**

Noritoshi Suzuki

Institute of Geology and Paleontology, Graduate School of Science, Tohoku University,  
6–3 Aoba Aramaki, Aoba-ku, Sendai 980–8578, Japan  
(e-mail: suzuki.noritoshi@nifty.com)

**Abstract** Since there are a few reports on historical reviews of Ehrenberg’s studies for polycystine radiolarians, his studies are reviewed herein. Christian Gottfried Ehrenberg (1795–1876) published 41 papers concerning polycystine radiolarians. He described 72 genera and 501 species in his life. I list the type species of 134 genera whose type species are selected from Ehrenberg’s species, and summarize taxonomic issues for these genera.

**Key words:** Classification, Ehrenberg, Radiolaria, Type species.

### **Introduction**

Since the first fossil polycystine radiolarians were described from Caltanissetta, Oran and Zante by Ehrenberg (1839), more than 10,000 species have been described over the last 170 years (Suzuki and Aita, submitted). Christian Gottfried Ehrenberg (1795–1876) published 41 papers regarding polycystine radiolarians in the modern sense from 1839 to 1876 (Lazarus and Suzuki, 2009). A total number of 528 polycystine species were found from Recent sea-bottom sediments, Neogene on-land samples and upper Paleogene Barbados samples, and 486 of them are still taxonomically available names (Ogane *et al.*, 2009; Suzuki *et al.*, 2009). Many of Ehrenberg’s species have been used in the subsequent literature as age-diagnostic or paleoceanographic markers. Many of these subsequent papers cited Ehrenberg’s papers with incorrect titles, conflicting pages ranges, inaccurate journal names and even to nonexistent descriptions, presumably due to repeated indirect citation without directly checking the sources, which were until recently not readily obtainable. As described in Lazarus and Suzuki (2009 in this volume) the correct titles, dates and content of Ehrenberg’s publications are now readily available, and are used in this paper throughout.

Ehrenberg’s radiolarian studies largely relied on samples which other scientists and explorers sent to him. His primary research goals were to reveal the diversity of ‘Infusoria’, including polycystine radiolarians, and by comparing assemblages worldwide, to document the geographical distributions of Infusoria, and to attempt, albeit from bottom sediments, to infer their vertical distribution in the water column (e.g. Cole, 1926). His early work focused on description of new species from many localities, which were summarized in his monograph *Mikrogeologie Ehrenberg* (1854c) and its supplement published in 1856. Radiolarian studies by Ehrenberg are thus part of this broader research context.

### Historical review of the radiolarian studies

The first publication regarding polycystine radiolarians (Fig. 1) in the current sense is Ehrenberg (1839). This work was presented earlier orally in the Prussian Academy of Sciences (“Akademie der Wissenschaften”), Berlin, on 20th December, 1838, and was formally distributed as publication in 1839 (Lazarus & Suzuki, 2009). He described four genera and 9 radiolarian species from Caltanissetta (Sicily), Oran (Africa) and Zante of John Island (pullout table in Ehrenberg, 1839). He proposed the “family Polycystina” as a member of the higher (also from Ehrenberg) taxon Polygastrica (p. 128 in Ehrenberg, 1839). Polycystina included *Lithocampe*, *Cornutella*, *Haliomma*. In this paper, a diatom, *Coscinodiscus*, and a silicoflagellate, *Dictyocha*, were regarded as members of Polycystina. The remaining genus, *Flustrella*, was considered to belong to Ehrenberg's higher taxon Polythalamia. Polygastrica was defined by presence of many stomachs in an individual whereas Polythalamia by presence of many chambers which can live individuals in each “chamber”. Although 9 radiolarian species were described, only one specimen, named *Lithocampe radiculata*, was illustrated in this paper.

Ehrenberg (1840) described 274 Polygastrica species, and of these, 10 species belong to Polycystina in the current scheme. In this paper, all the Polycystina which were described at that time were noted. The four new species were newly described from Greece (‘E marga Graeciae’ in the original spelling). In this paper, *Flustrella* was first moved to Polygastrica from Polythalamia because these forms were noted to have a siliceous test (p. 210 in Ehrenberg, 1840). It is noteworthy that Ehrenberg (1840) described “FLUSTRELLA *spiralis*=*Flustrella concentrica* Kr. B. 1838. p. 76. ex parte spirali.” This is interpreted in this paper that the specimen which was identified as *F. concentrica* on page 76 of Ehrenberg (1839) was now transferred to a new species, *F. spiralis*. Ehrenberg (1840) also described *Haliomma ovatum* as a new species. The genus *Haliomma* was first described by Ehrenberg (1839) and included two species *Haliomma crenatum* and *Haliomma medusa*, and consequently, *Haliomma* species could be presumed to belong to Polycystina. However, *Haliomma ovatum* is now considered to be a siliceous sponge spicule. Similar to *H. ovatum*, Ehrenberg (1841) described *Haliomma (?) radians* as a new species from the North Sea (Atlantic) “Nordsee bei Cuxhaven”, but this species belongs to siliceous sponge

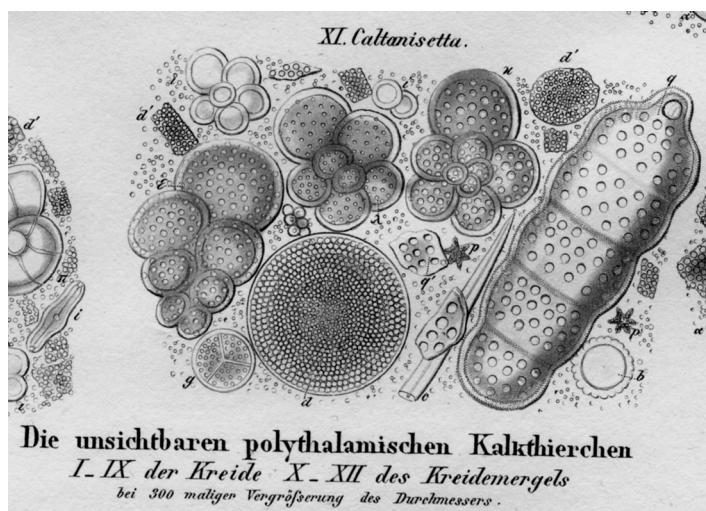


Fig. 1. The first illustrated fossil polycystine radiolarian specimen in the history, from Ehrenberg (1839).

spicules, too. Ehrenberg (1842) introduced 39 new organisms from Aegina but he did not publish any definitions for these species. Two new species: *Lithobotrys cribrosa* and *Cornutella Lithocampe* would presumably be polycystine radiolarians in current taxonomy, but they are apparently nomen nudum. Although Ehrenberg (1842) did not describe new species, he first noted that his organisms were routinely illustrated by him, and at a magnitude of 300X (1842, p. 265).

In the 1844 issues of the Prussian Academy of Sciences Proceedings journal “*Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königlich Preussischen Akademie der Wissenschaften zu Berlin*”, three polycystine radiolarian papers were published, on pages 57–97 (Ehrenberg, 1844a), 182–207 (Ehrenberg, 1844b) and 252–274 (Ehrenberg, 1844c). Ehrenberg (1844a) principally compared the assemblage similarity of micro-organisms (his Infusoria) among North America, Europe and Africa. The faunal similarity of polycystines was compared among Oran (Africa), Caltanissetta and Aegina. Ehrenberg (1844a) also described one new genus (*Lithobotrys*) and 14 new polycystine species from Caltanissetta and Aegina. This paper also introduced the name *Haliomma cornutum* on page 64, but this species has never been formally described. Ehrenberg (1844a) described “*FLUSTRELLA bilobata*=*HALIOMMA Lagena* 1840” on page 81. The meaning of this assignment was not solved solely with his published references but also with the aid of Ehrenberg’s original drawings housed in the Museum, which indicate that the same individuals have two species names. Since ‘*Haliomma lagena*’ is an available name by the description of Ehrenberg (1840), the name ‘*Flustrella bilobata*’ is a primary objective junior synonym of *Haliomma lagena*. Ehrenberg (1844b) is the first report of polycystine radiolarians from the Southern Ocean. The materials were collected between 1841–1843 by captain Ross, and polycystine radiolarians were found from ‘Pancake Ice’ which was obtained at 78°10’S and 162°W. *Lithobotrys* (?) *denticulata* and *Lithocampe antarctica* were newly described in Ehrenberg (1844b). The presence of *Lithocampe australis* was noted in page 187 of Ehrenberg (1844b), but was not formally described in this paper. Ehrenberg (1844c) reported Infusoria from the Bermuda Islands. Three new polycystine radiolarians (*Haliomma* (?) *amphisiphon*, *H.* (?) *nobile* and *Lithocampe aculeata*) were newly described in this paper.

Ehrenberg (1845) listed many species of Infusoria from 14 locations, including Charles Darwin’s samples (p. 63–66). This paper also described many new genera and new species of Infusoria, and a species from ‘Westmoreland Virginiae’ was named as *Lithocampe* (?) *stiligera*.

Ehrenberg (1846) was the first paper which focused only polycystine radiolarians. Robert H. Schomburgk donated samples from Barbados to Ehrenberg (Schomburgk, 1847), and Ehrenberg (1846) noted that 140 species were found from Barbados samples. In Ehrenberg (1846), Polycystina was divided into two groups, “Polycystina Solitaria” and “Polycystina Composita”, and they were further subdivided into Halicalyptrina, Lithochytrina and Eucyrtidina in Solitaria while Haliommatina, Spyridina and Lithocyclidina were created within Composita. This paper newly described 26 genera without species (p. 385). Since the definition of these genera was depicted in Ehrenberg (1846), these genera are considered to be formally published in this paper.

His taxonomy was revised, and new taxa were described in Ehrenberg (1847). Ehrenberg (1847) first transferred genera in some species on pages 42–43. The list on these pages is comparable to synonym list in the modern articles, but includes nine nomen nudum species. Ehrenberg (1847) discussed the formation of siliceous tests, added a list of polycystine radiolarians for the previously described samples (e.g. South Pole “Südpols”), and noted 14 new species from Barbados. Of these, 11 species were illustrated. Although these species were not associated with descriptions, they are regarded as taxonomically available names only with illustration on the basis of ICZN 2000. A total of 14 new genera were also newly defined in this paper.

Ehrenberg (1854a) is the first paper to concern the vertical distribution of polycystine radiolarians. He compared the infusorian assemblages between sediments which were recovered from different water depths of 433, 840, 1050, 6480, 8160, 9480, 10800 and 12000 feet (Fuß), from the ocean bottom ('Meersgrund'). In this paper the vertical distribution of 40 polycystine radiolarians were shown. Twenty-eight of 40 species names first appeared in Ehrenberg (1854a), but were not formally described. All of these species were described in Ehrenberg (1854b). The type materials of these new species are recognized as the samples from 6480, 10800, and 12000 feet. '*Flustrella subtilis*' was stated as having been found from the sample 8460 feet on page 242, but the actual specimen was detected from the sample from 6480 feet in our project.

The 'Mikrogeologie' is a milestone for Ehrenberg's studies on Infusoria since all the Infusoria previously published were summarized in this book. Ehrenberg had attached only 12 species (Ehrenberg, 1839, 1847) but Ehrenberg (1854c) showed the illustrations of 70 polycystine radiolarian species, including 23 new species. These illustrations are duplicated with the previously illustrated 12 species, and subsequently the illustrations of 58 species were first published in Ehrenberg (1854c).

After publishing the 'Mikrogeologie', Ehrenberg continued to examine the diversity of infusorians in many regions. Five polycystine radiolarian species were found in an ocean bottom sample which was taken from a water depth of 12,900 feet (Ehrenberg, 1855a), eleven species were found from "Simbirsk" (now Ulyanovsk, a city in Russia on the Volga River) (Ehrenberg, 1855b), one "polycystine" (but now identified as a sponge spicule) from Java (Ehrenberg, 1855c) and seven genera from Chile (Ehrenberg, 1856). Ehrenberg (1855b) noted four new species names, but only one species, *Eucyrtidium simbirscianum*, was formally described in Ehrenberg (1876).

The vertical distributions of polycystine radiolarians were revisited by Ehrenberg (1858). This paper examined seafloor samples from 'Meersgund bei Candia' (possibly modern Crete) and compared these with Ehrenberg (1854c). Ehrenberg (1858) published 13 new species names which were described in Ehrenberg (1859).

A total of 79 polycystine radiolarians were found from the surface sediments (sounding sampling) of the Philippine Sea (18°03'N, 129°11'E) (Ehrenberg, 1861a). Although Ehrenberg (1861a) included 48 nomen nudum species, this paper is of particular importance in providing data with the number of individuals for each species. Vertical distributions of Infusoria were still of interest for Ehrenberg. Ehrenberg (1861b) listed the vertical distributions of 69 polycystine radiolarians from California Ocean, while Ehrenberg (1862a) showed the distributions of four polycystine radiolarians from the Gulf of Mexico, near Florida. Ehrenberg (1861a, 1861b, 1862a) listed many new species, but these papers included neither illustrations nor descriptions. The definition of 22 genera was only depicted in Ehrenberg (1861b).

The significant observation that polycystine radiolarians live in similar oceanographic conditions at the species level was first noted in Ehrenberg (1862b). Ehrenberg (1862b) examined 8 sea-bottom samples which were collected during a preliminary survey for the construction of telegraph lines. He also summarized the vertical distributions of Infusoria based on the water depths of the sea-floor, and he identified seven species which were found in Kamchatka by Bailey (1856). These seven species were *Cadium marinum* Bailey, *Botryocampe inflata* (Bailey), *Carpocanium cornutum* (Bailey), *Cornutella annulata* Bailey, *Eucyrtidium cuspidatum* Bailey, *Eucyrtidium hyperboreum* Bailey and *Eucyrtidium tumidulum* Bailey, which were considered as arctic species. Ehrenberg (1862b) formally described 27 new species and variations. The type localities of these new species are now specified on page 819–820 in Ehrenberg (1861b) for 'Cali-

fornico' (=California Ocean) and page 224–225 in Ehrenberg (1862a) for 'Mexicano' (=Gulf of Mexico, near Florida), and page 276 in Ehrenberg (1862b) for "Groenland" (=Davis strait), respectively.

After 1862, Ehrenberg did not publish papers on polycystine radiolarians until 1873. Ehrenberg (1873a) did not examine any new materials. Instead, he summarized his studies since 1836 and described 249 infusorians, including 109 new polycystine radiolarians from 'Zanguebarica 13200', 'Insulam Milonem 1440', 'Philippine Ocean 19800', 'California Ocean 15600', 'Camorta Nicobarica', 'Florida 9066', 'Atlantic Ocean 9540', and 'Atlantic Ocean 9780'. He counted a total of 287 polycystines that were described by his studies excepting Barbados. The illustrations of some of these species were shown in Ehrenberg (1873b).

Ehrenberg (1873b) is a comprehensive monograph of his studies on marine micro-organisms. The earlier part of Ehrenberg (1873b) summarized the assemblages examined after Ehrenberg (1854c). The examined samples were mainly collected from the sea-floor. The middle part of the paper are summary cross tables (Fig. 5) between geographic zones and water depths of 1924 organisms (605 Polythalamia, 656 Polygastina, 279 Polycystina, 219 Phytolitharia, 56 Geolithia, 39 Zoolitharia, 51 Molluska, 1 Annulata, 2 Entomostraca, 6 Radiata, 1 Anthozoa, and 9 Bryozoa). Ehrenberg (1873b) listed 279 polycystine radiolarian species, but not all of them are taxonomically available species because he marked 44 species without descriptions in these tables. These summary tables are also very useful because the first description and the illustrated papers were given in these tables. This list shows that the highest diversity was recorded in the tropical zone and the diversity increases in deeper waters, although this latter estimation is not based on any direct water column data. The later part of Ehrenberg (1873b) discussed various aspects of his data. Remarks on polycystine radiolarians are given from page 339 to 346. Based on his observations, Ehrenberg (1873b) criticized the observations of living polycystine radiolarians by J. Müller and Haeckel in Messina (e.g. Müller, 1858; Haeckel, 1862). On page 344, Ehrenberg comments that their conclusions were prematurely derived from local phenomena and their claim of rich radiolarians in the surface water is contradicted his compiled data that radiolarians increased in diversity toward deeper waters. Ehrenberg has not used the term "Radiolaria" instead of Polycystina in that Polycystina has a priority (page 345 in Ehrenberg, 1873b). Ehrenberg (1873b) concluded that Polycystina are closely related to Echinodermata based on a similar degree of complexity.

Another of Ehrenberg's monographic works on polycystine radiolarians are his studies of radiolarians from Barbados. Brief notes and illustrations were already published in Ehrenberg (1846, 1847, 1854c), but only a few species were formally described and illustrated in these publications. Ehrenberg (1874) comprehensively described 265 species from Barbados samples. All the genera used in Ehrenberg (1874) were previously published in Ehrenberg (1847, p. 53). According to the final paragraphs of this paper (p. 263), almost all the names in this paper and original drawings were already prepared before publication of his 1846 and 1847 papers. Ehrenberg (1874), however, has no illustrations.

Ehrenberg (1876) illustrated 85 specimens of 81 polycystine radiolarian species from Barbados, including 14 species (3 nomen nudum species). Ehrenberg (1876) gives an occurrence list of fossil polycystine radiolarians from Barbados samples (coded as 1, 3, 14, 15, 16, 25, 26, 30, 43, 51, 59, 60, 74, 81, 94 and 95) and detailed information for these samples. Ehrenberg (1876) also described occurrences from Nicobarica (p. 116–120), and discussed the systematic classification of his Polycystine from page 151 to 157. Ehrenberg (1876) introduced the division of Spumellaria and Nassellaria on p. 156, and summarized the classification of all genera which were proposed by himself. This summary table excluded any genera which were proposed by other au-



thors (Meyen, 1834; Huxley, 1851; Claparede, 1856; Müller, 1857, 1858; Haeckel, 1860a, 1860b, 1862). Ehrenberg (1876) principally is a comprehensive summary monograph of his fossil studies through his life. Ehrenberg (1876) compiled the worldwide occurrences of more than a thousand micro-organisms with geological ages and regions. A total of 326 polycystine radiolarians were listed as fossils in this paper (p. 65–85) from Barbados, Bermuda, ‘Java, Nicobarien. Scheduba’, the southern States of North America (‘Süd-Staaten North America’), Greece (Griechenland), Italy (Italien), Russia (Rußland), South America (Süd-America), and the southwestern coast of South Africa (‘Oran. Saldanha-Bay. Agulhas-Bank’). Ehrenberg (1876) was probably the first paper to list the geological distributions of polycystine radiolarians, but his results are not usable any longer because the geological time scale used in Ehrenberg (1876) was only divided into Primary, Secondary, Tertiary and Quaternary, and thus all the fossil polycystine radiolarians were classified into the ‘Tertiary’ period.

### Type species using Ehrenberg’s species

Since the concept of type species for a genus did not become common in the 19th century, Ehrenberg himself did not designate any type species for his genera. A total of 131 species, including 6 nomen nudum species, have been selected, mostly by subsequent designation by various later authors, as the type species of 134 genera. These are summarized in Table 1. The inconsistent numbers between species and genus are caused by duplicated designation. Based on the condition of type designation, these species can be categorized into four groups, namely, type species (7 species), monotype (13 species), subsequent monotype (8 species) and subsequent designation (118 species), following ICZN 2000. The definition of each term is cited below:

**Type species (Glossary in ICZN 2000):** *The nominal species that is the name-bearing type of a nominal genus or subgenus.*

**Monotypy (ICZN 2000 Art 68.3):** *When an author establishes a new nominal genus-group taxon for a single taxonomic species and denotes that species by an available name, the nominal species so named is the type species.*

**Subsequent monotypy (ICZN Art 69.3):** *If only one nominal species was first subsequently included in a nominal genus or subgenus established without included species, that nominal species is automatically fixed as the type species, by subsequent monotypy.*

**Subsequent designation (ICZN 2000 Art 69.1):** *If an author established a nominal genus or subgenus but did not fix its type species, the first author who subsequently designates one of the originally included nominal species validly designates the type species of that nominal genus or subgenus (type by subsequent designation), and no later designation is valid.*

As shown Table 1, *Ceratospyrus* Ehrenberg 1846, *Cycladophora* Ehrenberg 1846, *Dic-tyospyris* Ehrenberg 1846, *Haliomma* Ehrenberg 1839, *Lithobotrys* Ehrenberg 1844a, *Lithomelissa* Ehrenberg 1847, *Lithostrobos* Bütschli 1882, *Lychnocanium* Ehrenberg 1846 and *Spon-gosphaera* Ehrenberg 1847 have more than two type species. We don’t solve this issue in our paper because radiolarian communities have been familiar with the current usage, even this is wrong under ICZN 2000, rather than unfamiliar designations of type species. We only note that the following rules in ICZN 2000 are helpful to evaluate better usage of type designation.

Table 1. The Ehrenberg's species which are designated as the type species of polycystine radiolarians.

Genus	Type species	Assigned paper	Type mode
<i>Acanthosphaera</i> Ehrenberg (1862b)	<i>Acanthosphaera haliphormis</i> Ehrenberg (1862b)	Ehrenberg (1862b)	Monotype
<i>Acromelissa</i> Haeckel (1887)	<i>Lithomelissa microptera</i> Ehrenberg (1854c)	Petrushevskaya (1975)	Subsequent designation
<i>Acrosphaera</i> Haeckel (1882)	<i>Polysolenia setosa</i> Ehrenberg (1873a)	Ehrenberg (1862b)	Subsequent designation
<i>Amphicentria</i> Ehrenberg (1862b)	<i>Amphicentria salpa</i> Ehrenberg (1862b)	Ehrenberg (1862b)	Monotype
<i>Amphiptermis</i> Foreman (1973a)	<i>Lithocampe clava</i> Ehrenberg (1874)	Foreman (1973a)	Type species
<i>Antarctissa</i> Petrushevskaya (1967)	<i>Lithobotrys denticulata</i> Ehrenberg (1844b)	Petrushevskaya (1967)	Type species
<i>Anthocyclonella</i> Haeckel (1887)	<i>Anthocyrus mespilus</i> Ehrenberg (1847)	Petrushevskaya and Kozlova (1972)	Subsequent designation
<i>Anthocyrus</i> Ehrenberg (1846)	<i>Anthocyrus mespilus</i> Ehrenberg (1847)	Campbell (1954)	Subsequent designation
<i>Anthocyrus</i> Haeckel (1887)	<i>Anthocyrus ophirensis</i> Ehrenberg (1873a)	Campbell (1954)	Subsequent designation
<i>Anthocyrus</i> Haeckel (1887)	<i>Anthocyrus serrulata</i> Ehrenberg (1874)	Frizzell and Middour (1951)	Subsequent designation
<i>Archiphormis</i> Haeckel (1882)	<i>Halicalypra cancellata</i> Ehrenberg (1854b)	Campbell (1954)	Subsequent designation
<i>Artocyrus</i> Haeckel (1887)	<i>Eucyrtidium profundissimum</i> Ehrenberg (1873a)	Frizzell and Middour (1951)	Subsequent designation
<i>Artoperina</i> Campbell (1951)	<i>Lithormithium loxia</i> Ehrenberg (1854c)	Campbell (1954)	Type species
<i>Artostrobium</i> Haeckel (1887)	<i>Lithocampe aurita</i> Ehrenberg (1844a)	Campbell (1954)	Subsequent designation
<i>Astractinium</i> Haeckel (1887)	<i>Astromma aristotelis</i> Ehrenberg (1847)	Campbell (1954)	Subsequent designation
<i>Astromma</i> Ehrenberg (1846)	<i>Astromma entomocora</i> Ehrenberg (1854c)	Campbell (1954)	Subsequent designation
<i>Botryocampe</i> Ehrenberg (1861b)	<i>Lithobotrys inflatum</i> Bailey (1856)	Ehrenberg (1862b)	Subsequent monotype
<i>Botryocella</i> Haeckel (1887)	<i>Lithobotrys nucula</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Botryocyrtis</i> Ehrenberg (1861b)	<i>Botryocyrtis caput-serpentis</i> Ehrenberg (1873a)	Campbell (1954)	Subsequent designation
<i>Brachiospyris</i> Haeckel (1882)	<i>Ceratospyrus ocellata</i> Ehrenberg (1874)	Frizzell and Middour (1951)	Subsequent designation
<i>Catocyclas</i> Ehrenberg (1847)	<i>Catocyclas turris</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Catocycloma</i> Haeckel (1887)	<i>Eucyrtidium ampullata</i> Ehrenberg (1862a)	Campbell (1954)	Subsequent designation
<i>Carpocanium</i> Ehrenberg (1846)	<i>Lithocampe solitaria</i> Ehrenberg (1839)	Campbell (1954)	Subsequent designation
<i>Cenosphaera</i> Ehrenberg (1854b)	<i>Cenosphaera plutonis</i> Ehrenberg (1854b)	Ehrenberg (1854b)	Subsequent designation
<i>Ceratastrum</i> Haeckel (1882)	<i>Cornutella trochus</i> Ehrenberg (1873a)	Petrushevskaya (1981)	Monotype
<i>Ceratocyrus</i> Bütschli (1882)	<i>Cornutella cucullaris</i> Ehrenberg (1874)	Petrushevskaya (1981)	Subsequent designation
<i>Ceratospyrus</i> Ehrenberg (1846)	<i>Ceratospyrus pentagona</i> Ehrenberg (1873a)	Petrushevskaya (1971)	Subsequent designation
<i>Ceratospyrus</i> Ehrenberg (1846)	<i>Haliomma radicans</i> Ehrenberg (1844a)	Campbell (1954)	Subsequent designation
<i>Chilomma</i> Ehrenberg (1847)	<i>Chilomma saturnus</i> Ehrenberg (1862b)	Ehrenberg (1847)	Subsequent monotype
<i>Cladospyrus</i> Ehrenberg (1846)	<i>Ceratospyrus ramosa</i> Ehrenberg (1874)	Ehrenberg (1862b)	Subsequent monotype
<i>Clathrocanium</i> Ehrenberg (1873a)	<i>Clathrocanium squarrosium</i> Ehrenberg (1873a)	Campbell (1954)	Subsequent designation
<i>Conarachnium</i> Haeckel (1882)	<i>Eucyrtidium trochus</i> Ehrenberg (1873a)	Campbell (1954)	Subsequent designation
<i>Cornutella</i> Ehrenberg (1839)	<i>Cornutella clathrata</i> Ehrenberg (1839)	Campbell (1954)	Subsequent designation
<i>Cornutellium</i> Haeckel (1882)	<i>Cornutella trochus</i> Ehrenberg (1873a)	Ehrenberg (1839)	Monotype
<i>Corythomelissa</i> Campbell (1951)	<i>Cornutella corythium</i> Ehrenberg (1874)	Petrushevskaya and Kozlova (1972)	Subsequent designation
<i>Cryptoprora</i> Ehrenberg (1847)	<i>Cryptoprora fundicola</i> [nomen nudum] Ehrenberg (1873b)	Campbell (1954)	Type species
		Campbell (1954)	Subsequent designation

Genus	Type species	Assigned paper	Type mode
<i>Cycladophora</i> Ehrenberg (1846)	<i>Cycladophora</i> (?) <i>davisiana</i> Ehrenberg (1862b)	Lombardi and Lazarus (1988)	Subsequent designation
<i>Cycladophora</i> Ehrenberg (1846)	<i>Cycladophora stitigera</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Dendrospyrus</i> Haeckel (1882)	<i>Dendrospyrus stylophora</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Dictyostrum</i> Ehrenberg (1861b)	<i>Dictyostrum angulatum</i> Ehrenberg (1873a)	Strelkov and Reshetnyak (1959)	Subsequent designation
<i>Dictyocephalus</i> Ehrenberg (1861b)	<i>Cornutella obtusa</i> Ehrenberg (1844a)	Ehrenberg (1861b)	Monotype
<i>Dictyocoryne</i> Ehrenberg (1861b)	<i>Dictyocoryne profunda</i> Ehrenberg (1873a)	Campbell (1954)	Subsequent designation
<i>Dictyocryphalus</i> Haeckel (1887)	<i>Cornutella obtusa</i> Ehrenberg (1844a)	Loeblich and Tappan (1961)	Subsequent designation
<i>Dictyomitrella</i> Haeckel (1887)	<i>Eucyrtidium articulatum</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Dictyophimus</i> Ehrenberg (1846)	<i>Dictyophimus cristatae</i> Ehrenberg (1854b)	Riedel and Sanfilippo (1970)	Subsequent designation
<i>Dictyopodium</i> Ehrenberg (1847)	<i>Dictyopodium euryplophus</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Dictyospyrella</i> Haeckel (1887)	<i>Dictyospyris tristoma</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Dictyospyris</i> Ehrenberg (1846)	<i>Dictyospyris ceratospyris</i> [nomen nudum] Ehrenberg (1873b)	Campbell (1954)	Subsequent designation
<i>Dictyospyris</i> Ehrenberg (1846)	<i>Dictyospyris trilobata</i> Ehrenberg (1854c)	Sanfilippo et al. (1973)	Subsequent designation
<i>Dictyospyrissa</i> Haeckel (1887)	<i>Dictyospyris fenestra</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Dipospyris</i> Haeckel (1887)	<i>Dictyospyris ceratospyris</i> [nomen nudum] Ehrenberg (1873b)	Campbell (1954)	Subsequent designation
<i>Disolenia</i> Ehrenberg (1861b)	<i>Disolenia follis</i> [nomen nudum] Ehrenberg (1873b)	Campbell (1954)	Subsequent designation
<i>Druppatractona</i> Haeckel (1887)	<i>Stylospiraera laevis</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Euchitonina</i> Ehrenberg (1861b)	<i>Euchitonina furcata</i> Ehrenberg (1873a)	Campbell (1954)	Subsequent designation
<i>Eucyrtidium</i> Ehrenberg (1846)	<i>Lithocampe acuminata</i> Ehrenberg (1844a)	Campbell (1954)	Subsequent designation
<i>Eucyrtis</i> Haeckel (1882)	<i>Lithocampe acuminata</i> Ehrenberg (1844a)	Frizzell and Middour (1951)	Subsequent designation
<i>Flustrella</i> Ehrenberg (1839)	<i>Flustrella concentrica</i> Ehrenberg (1839)	Frizzell and Middour (1951)	Subsequent designation
<i>Giraffospyris</i> Haeckel (1882)	<i>Ceratospyris heptaceros</i> Ehrenberg (1874)	Ehrenberg (1839)	Monotype
<i>Glycobotrys</i> Campbell (1951)	<i>Lithobotrys geminata</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Halicadypha</i> Ehrenberg (1846)	<i>Halicadypha virginica</i> Ehrenberg (1854c)	Campbell (1954)	Type species
<i>Haliomma</i> Ehrenberg (1839)	<i>Haliomma aequorea</i> Ehrenberg (1844a)	Campbell (1954)	Subsequent designation
<i>Haliomma</i> Ehrenberg (1839)	<i>Haliomma beroes</i> Ehrenberg (1854b)	Strelkov and Reshetnyak (1959)	Subsequent designation
<i>Haliomma</i> Ehrenberg (1839)	<i>Haliomma medusa</i> Ehrenberg (1839)	Ehrenberg (1839)	Monotype
<i>Haliophormis</i> Ehrenberg (1846)	<i>Haliophormis calva</i> [nomen nudum] Ehrenberg (1854b)	Campbell (1954)	Subsequent designation
<i>Hexaspyridium</i> Haeckel (1887)	<i>Ceratospyris setigera</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Hexasyllus</i> Haeckel (1882)	<i>Acanthosphaera setosa</i> Ehrenberg (1873a)	Petrushevskaya (1981)	Subsequent designation
<i>Histiastrom</i> Ehrenberg (1846)	<i>Histiastrom quaternarium</i> Ehrenberg (1874)	Kozur and Mostler (1979)	Subsequent designation
<i>Hymenastromma</i> Haeckel (1887)	<i>Histiastrom ternarium</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Hymenastrom</i> Ehrenberg (1846)	<i>Hymenastrom pythagorae</i> Ehrenberg (1854c)	Campbell (1954)	Subsequent designation
<i>Lamprodiscus</i> Ehrenberg (1861b)	<i>Lamprodiscum monoceros</i> Ehrenberg (1873a)	Strelkov and Reshetnyak (1959)	Subsequent designation
<i>Litharachnidium</i> Haeckel (1887)	<i>Carpocanium arachmodiscus</i> Ehrenberg (1862b)	Campbell (1954)	Subsequent designation
<i>Litharachnidium</i> Haeckel (1861b)	<i>Carpocanium arachmodiscus</i> Ehrenberg (1862b)	Petrushevskaya (1981)	Subsequent designation
<i>Lithobotrys</i> Ehrenberg (1844a)	<i>Lithobotrys geminata</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
		Petrushevskaya (1981)	Subsequent designation



Table 1. Continued.

Genus	Type species	Assigned paper	Type mode
<i>Lithobotrys</i> Ehrenberg (1844a)	<i>Lithobotrys quadriloba</i> Ehrenberg (1844a)	Campbell (1954)	Subsequent designation
<i>Lithocampe</i> Ehrenberg (1839)	<i>Lithocampe radricula</i> Ehrenberg (1839)	Campbell (1954)	Subsequent designation
<i>Lithochytrix</i> Ehrenberg (1846)	<i>Lithochytrix vesperitilo</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Lithocorythium</i> Ehrenberg (1847)	<i>Lithocorythium galea</i> Ehrenberg (1844a)	Petrushevskaya (1981)	Subsequent designation
<i>Lithocyelia</i> Ehrenberg (1846)	<i>Lithocyelia ocellus</i> Ehrenberg (1854c)	Campbell (1954)	Subsequent designation
<i>Lithomelissa</i> Ehrenberg (1847)	<i>Lithomelissa</i> (?) <i>tartari</i> Ehrenberg (1854b)	Campbell (1954)	Subsequent designation
<i>Lithomelissa</i> Ehrenberg (1847)	<i>Lithomelissa microptera</i> Ehrenberg (1854c)	Petrushevskaya and Kozlova (1979)	Subsequent designation
<i>Lithomitra</i> Bütschli (1882)	<i>Eucyrtidium pachyderma</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Lithopora</i> Ehrenberg (1846)	<i>Eucyrtidium acephalum</i> Ehrenberg (1874)	Petrushevskaya and Kozlova (1979)	Subsequent designation
<i>Lithornithium</i> Ehrenberg (1847)	<i>Lithopora bacca</i> Ehrenberg (1873a)	Campbell (1954)	Subsequent designation
<i>Lithostrobilus</i> Bütschli (1882)	<i>Lithocampe hirundo</i> Ehrenberg (1840)	Campbell (1954)	Subsequent designation
<i>Lithoconus</i> Haeckel (1887)	<i>Eucyrtidium argus</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Lophocyrtis</i> Haeckel (1887)	<i>Eucyrtidium picus</i> Ehrenberg (1874)	Strelkov and Reshetnyak (1959)	Subsequent designation
<i>Lophophaena</i> Ehrenberg (1847)	<i>Eucyrtidium antilope</i> Ehrenberg (1872)	Frizzell and Middour (1951)	Subsequent designation
<i>Lophophaenoma</i> Haeckel (1887)	<i>Eucyrtidium stephanophorum</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Lychnocanium</i> Ehrenberg (1846)	<i>Lophophaena galea</i> Ehrenberg (1854b)	Campbell (1954)	Subsequent designation
<i>Mazosphaera</i> Ehrenberg (1861b)	<i>Lophophaena radians</i> Ehrenberg (1874)	Petrushevskaya and Kozlova (1979)	Subsequent designation
<i>Microlecitus</i> Isse (1890)	<i>Lychnocanium falciiferum</i> Ehrenberg (1854c)	Campbell (1954)	Subsequent designation
<i>Octalacorys</i> Haeckel (1887)	<i>Lychnocanium lucerna</i> Ehrenberg (1847)	Ehrenberg (1847)	Subsequent monotype
<i>Ommatocampe</i> Ehrenberg (1861b)	<i>Mazosphaera laevis</i> Ehrenberg (1873a)	Campbell (1954)	Subsequent designation
<i>Ommatogramma</i> Ehrenberg (1861b)	<i>Cornutella cassis</i> Ehrenberg (1844a)	Isse (1890)	Monotype
<i>Ommatospyrus</i> Ehrenberg (1861b)	<i>Podocyrus aculeata</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Patagospyrus</i> Haeckel (1882)	<i>Ommatocampe polyarthra</i> Ehrenberg (1873a)	Campbell (1954)	Subsequent designation
<i>Pentalacorys</i> Haeckel (1882)	<i>Ommatogramma navicularis</i> Ehrenberg (1873a)	Campbell (1954)	Subsequent designation
<i>Perichlamydidium</i> Ehrenberg (1846)	<i>Ommatospyrus apicata</i> Ehrenberg (1873a)	Campbell (1954)	Subsequent designation
<i>Periphaena</i> Ehrenberg (1874)	<i>Petalospyrus confuens</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Petalospyrivella</i> Haeckel (1887)	<i>Astronomia pentactis</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Petalospyrus</i> Ehrenberg (1846)	<i>Podocyrus pentacanthus</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Podocyrus</i> Ehrenberg (1846)	<i>Flusnella praetexta</i> Ehrenberg (1844a)	Campbell (1954)	Subsequent designation
<i>Polysolemia</i> Ehrenberg (1861b)	<i>Periphaena decora</i> Ehrenberg (1874)	Ehrenberg (1874)	Monotype
<i>Psilomelissa</i> Haeckel (1882)	<i>Petalospyrus platycantha</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Pteractis</i> Ehrenberg (1873a)	<i>Podocyrus foveolata</i> Ehrenberg (1854c)	Campbell (1954)	Subsequent designation
	<i>Podocyrus papalis</i> Ehrenberg (1847)	Campbell (1954)	Subsequent designation
	<i>Polysolemia setosa</i> Ehrenberg (1873a)	Campbell (1954)	Subsequent designation
	<i>Dicycephalus galeatus</i> Ehrenberg (1873a)	Campbell (1954)	Subsequent designation
	<i>Pteractis elegans</i> Ehrenberg (1873a)	Ehrenberg (1873a)	Monotype

Genus	Type species	Assigned paper	Type mode
<i>Pterocanium</i> Ehrenberg (1846)	<i>Pterocanium proserpinæ</i> Ehrenberg (1858)	Campbell (1954)	Subsequent designation
<i>Pterocodon</i> Ehrenberg (1847)	<i>Pterocodon campana</i> Ehrenberg (1847)	Ehrenberg (1847)	Monotype
<i>Pterocyrtidium</i> Bittschli (1882)	<i>Pterocanium barbadense</i> Ehrenberg (1874)	Petrushkevskaya and Kozlova (1972)	Subsequent designation
<i>Pylospheera</i> Ehrenberg (1858)	<i>Pylospheera mediterranea</i> Ehrenberg (1858)	Ehrenberg (1858)	Monotype
<i>Rhabdolithis</i> Ehrenberg (1847)	<i>Rhabdolithis pipa</i> Ehrenberg (1854c)	Sanfilippo and Riedel (1973)	Subsequent designation
<i>Rhopalastrum</i> Ehrenberg (1846)	<i>Haliomma lagena</i> Ehrenberg (1840)	Strelkov and Reshetnyak (1959)	Subsequent designation
<i>Rhopalocanium</i> Ehrenberg (1846)	<i>Rhopalocanium ornatum</i> Ehrenberg (1847)	Campbell (1954)	Subsequent designation
<i>Rhopalodictyum</i> Ehrenberg (1861b)	<i>Rhopalodictyum abyssorum</i> Ehrenberg (1873a)	Campbell (1954)	Subsequent designation
<i>Schizomma</i> Ehrenberg (1861b)	<i>Schizomma quadrilobum</i> Ehrenberg (1862b)	Ehrenberg (1862b)	Subsequent monotype
<i>Sestropyramis</i> Haeckel (1887)	<i>Cornutella scalaris</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Sethoconus</i> Haeckel (1887)	<i>Eucyrtidium trochus</i> Ehrenberg (1873a)	Petrushkevskaya and Kozlova (1972)	Subsequent designation
<i>Sethodisculus</i> Haeckel (1887)	<i>Haliomma radians</i> Ehrenberg (1841)	Campbell (1954)	Subsequent designation
<i>Sethopyramis</i> Haeckel (1882)	<i>Haliomma radiatum</i> Ehrenberg (1854c)	Kozur and Mostler (1979)	Subsequent designation
<i>Solenosphaera</i> Haeckel (1887)	<i>Cornutella scalaris</i> Ehrenberg (1874)	Petrushkevskaya and Kozlova (1972)	Subsequent designation
<i>Spirillina</i> Ehrenberg (1858)	<i>Disolenia foliis</i> [nomen nudum] Ehrenberg (1873b)	Riedel (1971)	Subsequent designation
<i>Spongaster</i> Ehrenberg (1862a)	<i>Spirillina imperforata</i> Ehrenberg (1858)	Ehrenberg (1858)	Monotype
<i>Spongatractus</i> Haeckel (1887)	<i>Spongaster tetras</i> Ehrenberg (1862b)	Ehrenberg (1862b)	Subsequent monotype
<i>Spongospheera</i> Ehrenberg (1854b)	<i>Spongospheera pachystyla</i> Ehrenberg (1874)	Sanfilippo and Riedel (1973)	Subsequent designation
<i>Spongospheera</i> Ehrenberg (1847)	<i>Spongodiscus resurgens</i> Ehrenberg (1854b)	Frizzell and Middour (1951)	Subsequent designation
<i>Stauronchidium</i> Haeckel (1887)	<i>Spongospheera polyacantha</i> Müller (1858)	Campbell (1954)	Subsequent designation
<i>Stephanastrum</i> Ehrenberg (1846)	<i>Spongospheera pacifystyla</i> Ehrenberg (1874)	Müller (1858)	Subsequent monotype
<i>Stylactis</i> Ehrenberg (1873a)	<i>Spongospheera perspicuum</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Stylocyelia</i> Ehrenberg (1847)	<i>Staphanastrum rhombus</i> Ehrenberg (1847)	Campbell (1954)	Subsequent designation
<i>Stylocyelia</i> Ehrenberg (1846)	<i>Stylactis pacifica</i> Ehrenberg (1873a)	Ehrenberg (1873a)	Subsequent monotype
<i>Stylosphaera</i> Ehrenberg (1846)	<i>Stylocyelia dimidiata</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Theocoonium</i> Haeckel (1887)	<i>Stylocyelia gracilis</i> Ehrenberg (1854c)	Campbell (1954)	Subsequent designation
<i>Theocotylissa</i> Haeckel (1882)	<i>Stylosphaera hispida</i> Ehrenberg (1854b)	Campbell (1954)	Subsequent designation
<i>Theocotylissa</i> Foreman (1973a)	<i>Eucyrtidium turgidulum</i> Ehrenberg (1873a)	Frizzell and Middour (1951)	Subsequent designation
<i>Theocytis</i> Haeckel (1887)	<i>Eucyrtidium turgidulum</i> Ehrenberg (1873a)	Frizzell and Middour (1951)	Subsequent designation
<i>Tholodiscus</i> Petrushevskaya and Kozlova (1972)	<i>Eucyrtidium ficus</i> Ehrenberg (1874)	Foreman (1973a)	Type species
<i>Thrysoyrtium</i> Haeckel (1887)	<i>Eucyrtidium barbadense</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
<i>Xiphatractylis</i> Haeckel (1887)	<i>Eucyrtidium ocellata</i> Ehrenberg (1874)	Petrushkevskaya and Kozlova (1972)	Type species
	<i>Thrysoyrtis rhizodon</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
	<i>Ceratospyrus furcata</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation
	<i>Stylosphaera spinulosa</i> Ehrenberg (1874)	Campbell (1954)	Subsequent designation

**Doubtfully included species (ICZN 2000 Art 67.2.5):** *A nominal species is deemed not to be originally included if it was doubtfully or conditionally included.*

**Type fixation overlooked (ICZN 2000 Art 70.2):** *If it is found that an earlier type species fixation has been overlooked, the overlooked fixation is to be accepted and any later fixations are invalid.*

Under ICZN Art 67.2.5 and Art 70.2, *Cycladophora* (?) *davisiana* Ehrenberg 1862b (type species of the genus *Cycladophora*. Subsequent designation by Lombardi and Lazarus, 1988) and *Lithomelissa* (?) *tartari* Ehrenberg 1854b (the type species of the genus *Lithomelissa*, subsequent designation by Campbell, 1954) need consideration. Nomen nudum species are also designated as type species, e.g. of *Cryptoprora* Ehrenberg 1847, *Dictyospyris* Ehrenberg 1846, *Dipospyris* Haeckel 1887, *Disolenia* Ehrenberg 1861b, *Haliphormis* Ehrenberg 1846 and *Solenosphaera* Haeckel 1887. Except for *Dictyospyris*, no genus has replaced [none of these genera has been provided with a valid] type species. This issue also needs discussion by the radiolarian community.

A total 12 species are designated as the type species of more than two genera, but it is acceptable by the following rule in ICZN 2000.

**Nominal species that are already type species (ICZN 2000, Art 67.11):** *The fact that a nominal species is the type species of a nominal genus or subgenus does not prevent it from being the type species of another. In such a case, the genus-group names are objective synonyms of one another.*

Based on the ICZN 2000 Art 67.11, the following combinations are objective synonyms. The underlined genus is the junior objective synonym when we rigidly follow ICZN 2000.

*Anthocyrtis* Ehrenberg 1846 and *Anthocyrtella* Haeckel 1887 (type species: *Anthocyrtis mespilus* Ehrenberg 1847),

*Conarachnium* Haeckel 1882 and *Sethoconus* Haeckel 1887 (type species: *Eucyrtidium trochus* Ehrenberg 1873a),

*Dictyocephalus* Ehrenberg 1861b and *Dictyocryphalus* Haeckel 1887 (type species: *Cornutella obtusa* Ehrenberg 1844a),

*Eucyrtidium* Ehrenberg 1846 and *Eucyrtis* Haeckel 1882 (type species: *Lithocampe acuminata* Ehrenberg 1844a),

*Litharachnium* Haeckel 1861b and *Litharachnidium* Haeckel 1887 (type species: *Carpocanium arachnodiscus* Ehrenberg 1862b),

*Lithomelissa* Ehrenberg 1847 and *Acromelissa* Haeckel 1887 (type species: *Lithomelissa microptera* Ehrenberg 1854b),

*Polysolenia* Haeckel 1882 and *Acrosphaera* Haeckel 1882 (type species: *Polysolenia setosa* Ehrenberg 1873a),

*Sethopyramis* Haeckel 1882 and *Sestropyramis* Haeckel 1887 (type species: *Cornutella scalaris* Ehrenberg 1874),

*Spongosphaera* Ehrenberg 1847 and *Spongatractus* Haeckel 1887 (type species: *Spongosphaera pachystyla* Ehrenberg 1874), and

*Theocorys* Haeckel 1882 and *Theocoronium* Haeckel 1887 (type species: *Eucyrtidium turgidulum* Ehrenberg 1873a),

Furthermore, the genera *Conarachnium*, *Eucyrtis*, *Spongosphaera* and *Theocorys* have other type species (*Sethoconus rayianus* Haeckel 1887 for *Conarachnium* by subsequent designation of Caulet, 1971; *Eucyrtis conoidea* Rüst 1885 for *Eucyrtis* by subsequent designation of Foreman, 1973b; *Spongosphaera polyacantha* Müller 1858 by subsequent monotype; and *Theocorys morchellula* Rüst 1885 by subsequent designation of Campbell 1954 and *Theocorys veneris* Haeckel 1887 by subsequent designation of Strelkov and Reshetnyak 1959 for *Theocorys*). Type species issues have been resolved for only a few of these genera (e.g. *Spongosphaera* and *Eucyrtidium*). Although we don't fix these taxonomic issues in our paper, proper type species should be selected in consideration of not only the precise application of ICZN 2000 but also consensus in the radiolarian community.

### Concluding remarks

Ehrenberg described a total of 72 genera and 501 species, excluding 31 *nomen nudum* species in his life. He described 544 species in Ehrenberg (1873a, 1874), but it includes species that were described by other authors. The precise number of the species described by Ehrenberg is variably estimated in papers (530 new species in Tanimura *et al.*, 2006; about 500 species at p. clxxiv in Haeckel, 1887), which is probably due to presence of *nomen nudum*. Ehrenberg's contribution to the study of polycystine radiolarians also include proposals for a higher classification (e.g. Ehrenberg, 1847, 1876) and the first reports to stress their geographical and geological distributions (e.g. Ehrenberg, 1874, 1876). Ehrenberg also commented the taxonomic position of Polycystina and probable physiological functions, but these comments were strongly criticized in other studies (e.g. Haeckel, 1862, 1887). Haeckel (1887, page clxxiii to clxxv) summarized his view of problems in Ehrenberg's studies:

1. Ehrenberg ignored any contrary observations and remarks, specifically those regarding living radiolarians.
2. Ehrenberg often changed the taxonomic of position of Polycystina between Echinoderma, Bryozoa and Oscillaria.
3. Ehrenberg believed that Polycystina were multi-cellular animals and that the pores of the siliceous test were comparable to cells, disregarding the extensive detailed observations of living radiolarians by Haeckel, Huxley and Müller.
4. Ehrenberg's diagnoses for genera were inadequate.

Although Haeckel (1887) criticized Ehrenberg using rather emotional words (e.g. *strange, remained entirely ignorant, the invincible obstinacy, his preconceived opinion*, etc.), Haeckel recognized the accuracy of Ehrenberg's sketches (p. clxxv in Haeckel, 1887). Since the species published by Ehrenberg have been extensively used up to the modern day, they are still important taxonomic concepts. His simple sketches are often insufficient for modern taxonomic work, and subsequently re-examination of the original specimens of Ehrenberg's species is necessary.

### References

- Bailey, J. W., 1856. Notice of microscopic forms found in the soundings of the Sea of Kamchatka-with a plate. *Amer. J. Sci. Arts Ser. 2*, **22** (64): 1–6.

- Bütschli, O., 1882. Beiträge zur Kenntnis des Radiolarienskelette, insbesondere der der Cyrtida. *Zeit. Wiss. Zool.*, **36**: 485–540.
- Campbell, A. S., 1951. New genera and subgenera of Radiolaria. *Jour. Paleont.*, **25**: 527–530.
- Campbell, A. S., 1954. Radiolaria. In R. C. Moore (ed.) Treatise on Invertebrate Paleontology, Part D Protista 3. Protozoa (Chiefly Radiolaria and Tintinnina). Geological Society of America and University of Kansas Press, Kansas, p. D1–D163.
- Caulet, J. P., 1971. Contribution à l'étude de quelques Radiolaires Nassellaires des boues de la Méditerranée et du Pacifique. *Cah. Micropaléont.*, Ser. 2, **10**: 1–10.
- Claparede, E., 1856. Über die Lebenserscheinungen und insbesondere Bewegungserscheinungen der Acanthometren. *Monat. Königl. Preuß. Akad. Wiss. Berlin*, **1855**: 647–676.
- Cole, F. J., 1926. The history of protozoology. Univ. London Press, Ltd., London. 64 pp.
- Ehrenberg, C. G., 1839. Über die Bildung der Kreidefelsen und des Kreidemergels durch unsichtbare Organismen. *Abh. Königl. Akad. Wiss. Berlin*, **1838**: 59–147.
- Ehrenberg, C. G., 1840. Hierauf 274 Blätter von ihm selbst ausgeführter Zeichnungen von eben so vielen Arten in dem 1838 erschienenen grösseren Infusorienwerke noch nicht abgebildeter Infusorien. *Ber. Königl. Preuß. Akad. Wiss. Berlin*, **1840**: 197–219.
- Ehrenberg, C. G., 1841. Über noch jetzt zahlreich lebende Thierarten der Kreidebildung und den Organismus der Polythalamien. *Abh. Königl. Akad. Wiss. Berlin*, **1839**: 81–174.
- Ehrenberg, C. G., 1842. Über einen plastischen Kreidemergel von Ägina aus mikroskopischen Organismen und über die Möglichkeit, durch mikroskopische Untersuchung des Materials den Ursprung gewisser alter ächtgriechischer Kunstdenkmäler aus gebrannter Erde (Terracotten) mit bisher unbekannter Sicherheit zu bestimmen. *Ber. Königl. Preuß. Akad. Wiss. Berlin*, **1842**: 263–268.
- Ehrenberg, C. G., 1844a. Über 2 neue Lager von Gebirgsmassen aus Infusorien als Meeres-Absatz in Nord-Amerika und eine Vergleichung derselben mit den organischen Kreide-Gebilden in Europa und Afrika. *Ber. Königl. Preuß. Akad. Wiss. Berlin*, **1844**: 57–97.
- Ehrenberg, C. G., 1844b. Einige vorläufige Resultate seiner Untersuchungen der ihm von der Südpolreise des Captain Ross, so wie von den Herren Schayer und Darwin zugekommenen Materialien über das Verhalten des kleinsten Lebens in den Ozeanen und den grössten bisher zugänglichen Tiefen des Weltmeeres. *Ber. Königl. Preuß. Akad. Wiss. Berlin*, **1844**: 182–207.
- Ehrenberg, C. G., 1844c. Untersuchungen über die kleinsten Lebensformen im Quellenlande des Euphrats und Araxes, so wie über eine an neuen Formen sehr reiche marine Tripelbildung von den Bermuda-Inseln. *Ber. Königl. Preuß. Akad. Wiss. Berlin*, **1844**: 253–275.
- Ehrenberg, C. G., 1845. Neue Untersuchungen über das kleinste Leben als geologisches Moment. *Ber. Königl. Preuß. Akad. Wiss. Berlin*, **1845**: 53–87.
- Ehrenberg, C. G., 1846. Über eine halibolithische, von Herrn R. Schomburgk entdeckte, vorherrschend aus mikroskopischen Polycystinen gebildete, Gebirgsmasse von Barbados. *Ber. Königl. Preuß. Akad. Wiss. Berlin*, **1846**: 382–385.
- Ehrenberg, C. G., 1847. Über die mikroskopischen kieselschaligen Polycystinen als mächtige Gebirgsmasse von Barbados und über das Verhältniss der aus mehr als 300 neuen Arten bestehenden ganz eigenthümlichen Formengruppe jener Felsmasse zu den jetzt lebenden Thieren und zur Kreidebildung. Eine neue Anregung zur Erforschung des Erdlebens. *Ber. Königl. Preuß. Akad. Wiss. Berlin*, **1847**: 40–60.
- Ehrenberg, C. G., 1854a. Über das organische Leben des Meeresgrundes in bis 10800 und 12000 Fuss Tiefe. *Ber. Königl. Preuß. Akad. Wiss. Berlin*, **1854**: 54–75.
- Ehrenberg, C. G., 1854b. Systematische Charakteristik der neuen mikroskopischen Organismen des tiefen atlantischen Oceans. *Ber. Königl. Preuß. Akad. Wiss. Berlin*, **1854**: 236–250.
- Ehrenberg, C. G., 1854c. Mikrogeologie. Voss, Leipzig, 374 pp.
- Ehrenberg, C. G., 1855a. Über die weitere Entwicklung der Kenntniss des Grünsandes als grüner Polythalamien-Steinkerne, über braunrothe und corallothe Steinkerne der Polythalamien-Kreide in Nord-Amerika, und über den Meeresgrund aus 12,900 Fuss Tiefe. *Ber. Königl. Preuß. Akad. Wiss. Berlin*, **1855**: 172–178.
- Ehrenberg, C. G., 1855b. Über ein europäisches marines Polygastern-Lager und über verlarvte Polythalamien in den marinen Polygastern Tripeln von Virginien und Simbirsk. *Ber. Königl. Preuß. Akad. Wiss. Berlin*, **1855**: 292–305.
- Ehrenberg, C. G., 1855c. III. Nähere Bestimmung der Mischung des frischen Auswurfs des Schlamm-Vulkans von Poowadadi auf Java. *Ber. Königl. Preuß. Akad. Wiss. Berlin*, **1855**: 570–576.
- Ehrenberg, C. G., 1856. Über 2 neue südamerikanische Gebirgsmassen aus mikroskopischen Organismen, eine aus Meeresorganismen in Chile und eine als mit gefritteten Süßwasserorganismen gemischten vulkanischen essbaren



- Tuff aus Honduras in Centro-Amerika. *Monat. Königl. Preuß. Akad. Wiss. Berlin*, **1856**: 425–431.
- Ehrenberg, C. G., 1858. Über die organischen Lebensformen in unerwartet grossen Tiefen des Mittelmeeres. *Monat. Königl. Preuß. Akad. Wiss. Berlin*, **1857**: 538–570.
- Ehrenberg, C. G., 1859. Kurze Charakteristik der 9 neuen Genera und der 105 neuen Species des ägäischen Meeres und des Tiefgrundes des Mittel-Meeres. *Monat. Königl. Preuß. Akad. Wiss. Berlin*, **1858**: 10–40.
- Ehrenberg, C. G., 1861a. Über die organischen und unorganischen Mischungsverhältnisse des Meeresgrundes in 19800 Fuss Tiefe nach Lieut. Brookes Messung. *Monat. Königl. Preuß. Akad. Wiss. Berlin*, **1860**: 765–774.
- Ehrenberg, C. G., 1861b. Über den Tiefgrund des stillen Oceans zwischen Californien und den Sandwich-Inseln aus bis 15600' Tiefe nach Lieut. Brooke. *Monat. Königl. Preuß. Akad. Wiss. Berlin*, **1860**: 819–833.
- Ehrenberg, C. G., 1862a. Beitrag zur Übersicht der Elemente des tiefen Meeresgrundes im Mexikanischen Golfstrom bei Florida. *Monat. Königl. Preuß. Akad. Wiss. Berlin*, **1861**: 222–240.
- Ehrenberg, C. G., 1862b. Über die Tiefgrund-Verhältnisse des Oceans am Eingange der Davisstrasse und bei Island. *Monat. Königl. Preuß. Akad. Wiss. Berlin*, **1861**: 275–315.
- Ehrenberg, C. G., 1873a. Mikrogeologische Studien als Zusammenfassung seiner Beobachtungen des kleinsten Lebens der Meeres-Tiefgründe aller Zonen und dessen geologischen Einfluss. *Monat. Königl. Preuß. Akad. Wiss. Berlin*, **1872**: 265–322.
- Ehrenberg, C. G., 1873b. Mikrogeologische Studien über das kleinste Leben der Meeres-Tiefgründe aller Zonen und dessen geologischen Einfluss. *Abh. Königl. Akad. Wiss. Berlin*, **1872**: 131–399.
- Ehrenberg, C. G., 1874. Grössere Felsproben des Polycystinen-Mergels von Barbados mit weiteren Erläuterungen. *Monat. Königl. Preuß. Akad. Wiss. Berlin*, **1873**: 213–262.
- Ehrenberg, C. G., 1876. Fortsetzung der mikrogeologischen Studien als Gesamt-Übersicht der mikroskopischen Paläontologie gleichartig analysirter Gebirgsarten der Erde, mit specieller Rücksicht auf den Polycystinen-Mergel von Barbados. *Abh. Königl. Akad. Wiss. Berlin*, **1875**: 1–226.
- Foreman, H. P., 1973a. Radiolaria of Leg 10 with systematics and ranges for the families Amphipyndacidae, Artostrobidae, and Theoperidae. In J. T. Worzel & W. Bryant (eds.) Init. Rep. DSDP, 10, U.S. Government Printing Office, p. 407–474.
- Foreman, H. P., 1973b. Radiolaria from DSDP Leg 20. In B. C. Haezen & I. D. MacGregor (eds.) Init. Rep. DSDP, 20, U.S. Government Printing Office, p. 249–305.
- Frizzell, D. L. & E. S. Middour, 1951. Paleocene Radiolaria from southeastern Missouri. *Bull., Univ. Missouri, Sch. Min. Meta., Tech. Ser.*, **77**: 1–41.
- Haeckel, E., 1860a. Über neue, lebende Radiolarien des Mittelmeeres und legte die dazu gehörigen Abbildungen. *Monat. Königl. Preuß. Akad. Wiss. Berlin*, **1860**: 794–817.
- Haeckel, E., 1860b. Fernere Abbildungen und Diagnosen neuer Gattungen und Arten von lebenden Radiolarien des Mittelmeeres. *Monat. Königl. Preuß. Akad. Wiss. Berlin*, **1860**: 835–845.
- Haeckel, E., 1862. Die Radiolarien (Rhizopoda Radiolaria). Eine Monographie. Tafel 1. Reimer, Berlin, 572 pp.
- Haeckel, E., 1882. Entwurf eines Radiolarien-Systems auf Grund von Studien der Challenger-Radiolarien. *Jena. Zeit. Naturwiss. Med. -Naturwiss. Gesell. Jena*, **15**: 418–472.
- Haeckel, E., 1887. Report on the Radiolaria collected by H.M.S. Challenger during the years 1873–1876. *Rep. Sci. Res. Voyage H.M.S. Challenger 1873–1876, Zool.*, **18**: 1–1803.
- Huxley, T. H., 1851. Zoological notes and observations made on board H.M.S. Rattlesnake. *An. Mag. Natur. Hist., Ser. 2*, **8**: 433–443.
- ICZN, 2000. International Code of Zoological Nomenclature. Fourth Edition. The International Trust for Zoological Nomenclature. London, 306 pp.
- Issel, A., 1890. Il calcifiro fossilifero di Rovergo in val di Trebbia. *Ann. Mus. Civ. Stor. Nat. Genova Ser. 2*, **9**: 91–119.
- Kozur, H. & H. Mostler, 1979. Beiträge zur Erforschung der mesozoischen Radiolarien. Teil III: Die Oberfamilien Actinommacea HAECKEL 1862 emend., Artiscacea HAECKEL 1882, Multiarcusellacea nov. der Spumellaria und triassische Nassellaria. *Geol.-Paläont. Mitt. Innsbruck*, **9**: 1–132.
- Lazarus, D. & N. Suzuki, 2009. Introduction to the reexamination of the Haeckel and Ehrenberg radiolarian collections. In Y. Tanimura & Y. Aita (eds.), Joint Haeckel and Ehrenberg Project, Reexamination of the Haeckel and Ehrenberg Microfossil Collections as a Historical and Scientific Legacy, National Museum of Nature and Science Monographs, **40**: 000–000
- Loeblich, A. R. J. & H. Tappan, 1961. Remarks on the systematics of the Sarkodina (Protozoa), renamed homonyms and new and validated genera. *Proc. Biol. Soc. Washington*, **74**: 213–234.
- Lombardi, G. & D. B. Lazarus, 1988. Neogene cycladophorid radiolarians from North Atlantic, Antarctic, and North Pa-

- cific deep-sea sediments. *Micropaleontology*, **34**: 97–135.
- Meyen, F. J. F., 1834. Beiträge zur Zoologie: gesammelt auf einer Reise um die Erde. Fünfte Abhandlung von F.J.F. Meyen. Über das Leuchten des Meeres und Beschreibung einiger Polypen und anderer niederer Thiere. *Nova Acta Physico-Medica. Academiae Caesariae Leopoldino-Carolinae. Naturae Curiosorum* (Verhandlungen der Kaiserlichen Leopoldinisch-Carolinischen Akademie der Naturforscher), **16** (supplement 1): 125–216.
- Müller, J., 1857. Über die Thalassicollen, Polycystinen und Acanthometren des Mittelmeeres. *Monat. Königl. Preuß. Akad. Wiss. Berlin*, **1857**: 474–503.
- Müller, J., 1858. Über die Thalassicollen, Polycystinen und Acanthometren des Mittelmeeres. *Abh. Königl. Akad. Wiss. Berlin*, **1858**: 1–62.
- Ogane, K., N. Suzuki, Y. Aita, T. Sakai & D. Lazarus, 2009. Ehrenberg's radiolarian collections from Barbados. In Y. Tanimura & Y. Aita (eds.), Joint Haeckel and Ehrenberg Project, Reexamination of the Haeckel and Ehrenberg Microfossil Collections as a Historical and Scientific Legacy, National Museum of Nature and Science Monographs, **40**: 97–106.
- Petrushevskaya, M. G., 1967. Radiolaryii otriyadov Spumellaria i Nassellaria Antarkicheskoi oblasti (po materialam Sovetskoi Antarkicheskikh Ekspeditsii). *Issl. Faun. Morey*, **4**: 5–186.
- Petrushevskaya, M. G., 1971. Radiolaryii Nassellaria v planktone Mirovogo okeana. *Tr. Zool. Inst., Akad. Nauk, SSSR*, **9**(17): 1–294.
- Petrushevskaya, M. G., 1975. Cenozoic radiolarians of the Antarctic, Leg 29, DSDP. In J. P. Kennet & R. E. Houtz (eds.) Init. Rep. DSDP, 29, U.S. Government Printing Office, p. 541–675.
- Petrushevskaya, M. G., 1981. Radiolaryii Otryada Nassellaria Mirovogo Okeana. *Akad. Nauk SSSR, Zool. Inst.*, **128**: 1–405.
- Petrushevskaya, M. G. & G.E. Kozlova, 1972. Radiolaria: Leg 14, Deep Sea Drilling Project. In D. E. Hays *et al.* (eds.) Init. Rep. DSDP, 14, U.S. Government Printing Office, p. 459–648.
- Petrushevskaya, M. G. & G. E. Kozlova, 1979. Opisanie rodove i vidov radiolaryiy. *Issl. Faun. Morey*, **23**: 86–157.
- Riedel, W. R., 1971. Systematic classification of Polycystine Radiolaria. In B. M. Funnel and W. R. Riedel (eds.) *The Micropaleontology of Oceans*, Cambridge University Press, London, p. 649–661.
- Riedel, W. R. & A. Sanfilippo, 1970. Radiolaria, Leg. 4 Deep Sea Drilling Project. In R. G. Bader *et al.* (eds.) Init. Rep. DSDP, 4, U.S. Government Printing Office, p. 503–575.
- Rüst, D., 1885. Beiträge zur Kenntniss der fossilen Radiolarien aus Gesteinen des Jura. *Palaeontographica*, **31**: 273–321.
- Sanfilippo, A., L. H. Burckle, E. Martini & W. R. Riedel, 1973. Radiolarians, diatoms, silicoflagellates and calcareous nannofossils in the Mediterranean Neogene. *Micropaleontology*, **19**: 209–234.
- Sanfilippo, A. & W. R. Riedel, 1973. Cenozoic Radiolaria (exclusive of theoperids, artostrobiids and amphipyndacids) from the Gulf of Mexico, Deep Sea Drilling Project Leg 10. In J. L. Worzel *et al.* (eds.) Init. Rep. DSDP, 10, U.S. Government Printing Office, p. 475–611.
- Schomburgk, R. H., 1847. The History of Barbados. Cass Library of West Indian Studiesno, 19, 722 pp. (reprint version in 2005).
- Strelkov, A. A. & V. V. Reshetnyak, 1959. Novaya zhiznennaya forma u radiolaryiy. *Zool. Zhur.*, **38**: 355–361.
- Suzuki, N. & Y. Aita, submitted. Achievement and unsolved issues on radiolarian studies (Part 1): Taxonomy and cytology.
- Suzuki, N., K. Ogane, Y. Aita, T. Sakai & D. Lazarus, 2009. Reexamination of Ehrenberg's Neogene radiolarian collections and its impact on taxonomic stability. In Y. Tanimura & Y. Aita (eds.), Joint Haeckel and Ehrenberg Project, Reexamination of the Haeckel and Ehrenberg Microfossil Collections as a Historical and Scientific Legacy, National Museum of Nature and Science Monographs, **40**: 87–96.
- Tanimura, Y., A. Tuji, T. Sakai, Y. Aita, N. Suzuki, K. Ogane, J. Young, D. M. Williams, D. Lazarus, O. Breidebach & T. Bach, 2006. Joint Haeckel and Ehrenberg Project. A Taxonomic Reexamination of the Haeckel and Ehrenberg Microfossil Collections as a Historical and Scientific Legacy. Research Report of the Museum Director General's Support Program in 2004–2006, The National Science Museum, Tokyo, 23 pp.