Radiolaria and Phaeodaria

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Demetrio Boltovskoy, O. Roger Anderson, and Nancy M. Correa

Abstract

Polycystina (~400–800 living species and several thousand extinct forms) and Phaeodaria (~400–500 living species) are exclusively marine, open-ocean planktonic protists, most of which possess elaborate siliceous skeletons. The cytoplasm is divided into an internal part (endoplasm) separated from the external, more vacuolated one (ectoplasm) by a perforated membrane – the central capsule. The Polycystina protrude long and slender cytoplasmic projections (axopodia) supported internally by a rigid central rod (axoneme); while the Phaeodria have a network of peripheral finely interconnected pseudopodia. A few Polycystina are colonial, but most, as well as all Phaeodaria, are solitary, around 40 μm to almost 2 mm in size. Most polycystine species peak in abundance between 0 and 100 m, whereas phaeodarians tend to live deeper, often below 300 m. Polycystines have a rich fossil record dating from the Cambrian and are important for stratigraphic, paleoecologic, and evolutionary studies. The world-wide biogeography and diversity of radiolarians is chiefly governed by water temperature. Radiolarian prey includes bacteria, algae, protozoa, and microinvertebrates. Many surface-dwelling species of Polycystina possess symbiotic algae and photosynthetic

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cyanobacteria that provide nourishment to the host. Some colonial radiolaria reproduce by binary fission of the central capsules. Sexual reproduction of polycystines or Phaeodaria has not been confirmed, but the release of motile swarmers, likely gametes, has been widely documented. In species with a radial symmetry (Spumellaria) shell-growth is centrifugal, whereas in the Nassellaria the internal cephalic elements and the cephalis appear first. Individual longevity is estimated to range between 2 and 3 weeks and 1–2 months.

Keywords
Radiolaria • Polycystina, Phaeodaria, radiolarians

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Summary Classification

●**Rhizaria**
●●**Cercozoa**
●●●**Thecofilosea**
●●●●**Phaeodaria** (=Tripylea)
●●●●●**Phaeoconchia**
●●●●●**Phaeocystina**
●●●●●**Phaeogromia**
●●●●●**Phaeosphaeria**
●●**Retaria**
●●●**Polycystinea**
●●●●**Collodaria** (skeletonless, or with isolated spicules)

●●●●**Spumellaria**
●●●●**Nassellaria**
●●●●**Archaeospicularia** (extinct)
●●●●**Albaillellaria** (extinct)
●●●●**Latenfistularia** (extinct)
●●●●**Entactiniaria** (extinct)

Introduction

General Characteristics

Polycystines and phaeodarians (Fig. 1) are marine protists, previously assigned to the phylum Actinopoda because they both possess elaborate siliceous skeletons surrounding an organic central capsule with pores, from which axopodia emerge in most members of the phylum. However, the phylum Actinopoda is no longer accepted as a valid taxonomic category, and Polycystinea are assigned to the higher-level group Retaria, and Phaeodaria are now assigned to the higher-level group Thecofilosea (Adl et al. 2012). Axopodia are long and slender cytoplasmic projections that protrude radially from the cell and are supported internally by a rigid central rod composed of a shaft of microtubules. Axopodia support a web-like network of sticky cytoplasmic strands of pseudopodia that aid in the capture of prey. Presently, we know that only polycystines possess typical axopodia, whereas Phaeodaria characteristically produce a network of peripheral finely interconnected pseudopodia that arise from two, specialized protoplasmic strands (parapylae) emerging from two pores in the central capsule. In addition there is a more massive cytoplasmic mass that emanates from an aperature (astropyle) resembling the oral aperture of some testate amoebae. Neither the astropyle nor the accessory openings *parapylae* exhibit structures resembling axopodia or fusules (Anderson 1983). All Phaeodaria are solitary, but Polycystinea include some colonial forms. Single cells vary in size from below 40 μm to almost 2 mm (Phaeodaria are usually larger than Polycystinea), but colonies may exceptionally be as long as 3 m (Swanberg 1979).

Occurrence

Radiolarians are present in all major oceans but absent from some marginal seas, such as the White Sea (Bjørklund and Kruglikova 2003). Different species have different depth preferences; polycystines usually peak in abundance between 0 and 100 m and have secondary peaks at various other depths, whereas phaeodarians tend to live deeper, often below 300 m. Both groups are almost entirely restricted to waters with normal open-ocean salinity levels.

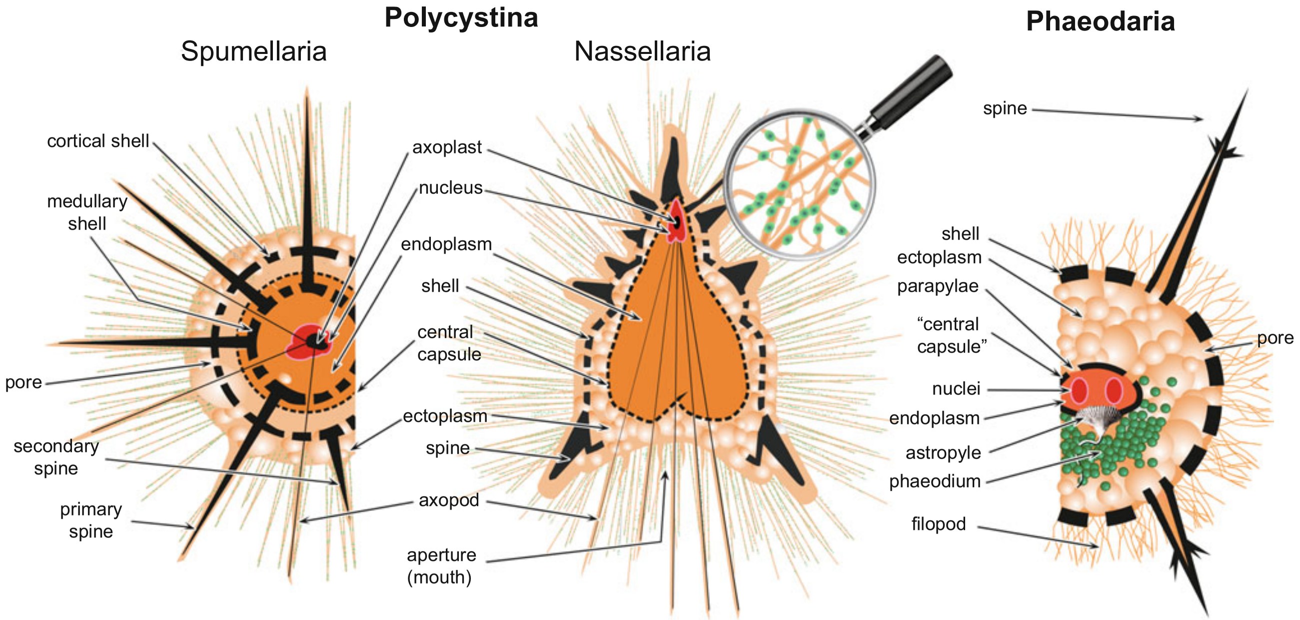


Fig. 1 Schematic diagram of the cellular organization in polycystine radiolarians (Spumellaria and Nassellaria) and phaeodarians. Detail (magnifying glass) shows web-like network of cytoplasmic strands supported by the axopodia and associated symbionts

Literature

The cornerstone of radiolarian studies, including Phaeodaria, is Haeckel's 1887 monograph based on planktonic and sedimentary materials collected by the Challenger Expedition (Haeckel 1887). Kling (1978), Anderson (1983), Petrushevskaya (1986), Anderson et al. (2000), Takahashi and Anderson (2000), De Wever et al. (2001), Afanasieva et al. (2005), Boltovskoy and Pujana (2008), and Nakamura and Suzuki (2015) produced general accounts on radiolarian knowledge. The catalogue assembled by Nigrini and Moore (1979) is still one of the most widely used references for the identification and distribution of the ca. 100 most common recent polycystine species. Other salient references are the works of Petrushevskaya (1967, 1971b) (profusely illustrated descriptions of practically all extant nassellarians and all Antarctic spumellarians); Sanfilippo et al. (1985) (a detailed guide for Cenozoic stratigraphy based on polycystines); Riedel and Foreman (1995) (a catalogue of all the polycystine species described up to 1930); and Boltovskoy et al. (2010) (a compilation of all the distributional data available on Recent polycystines up to 2008).

History of Knowledge

The first description of a living radiolarian is ascribed to Meyen (1834), whereas the first fossil one was recorded by Ehrenberg (1838), who also coined the term "Polycystina". The name "Radiolaria" was first proposed by Müller (1858) to designate planktonic protists with radiating skeletal elements and subsequently used by Haeckel as an informal term encompassing acantharians, polycystines, and phaeodarians (De Wever et al. 2001). The foundation of modern radiolarian studies is Haeckel's (1887) exquisitely illustrated monograph; around the same years several important publications were produced, but interest in the group was limited until the 1950s, when William Riedel and coworkers showed that polycystines could be used for stratigraphic purposes. First stratigraphy, and later paleoecology, fostered radiolarian research, which was particularly active in the 1970s and 1980s (Lazarus 2005; Suzuki and Aita 2011). At present there are about 150–200 specialists that are partially or entirely dedicated to radiolarian studies, over 90% of them with geological-paleontological backgrounds and centered on fossil materials. However, with the advent of modern biological techniques such as electron microscopy and molecular phylogenetic analyses, an increasing number of biologists have begun to elucidate the natural affinities among major groups of radiolaria toward clarifying their taxonomic relations (e.g., Amaral Zettler et al. 1998, 1999; Anderson et al. 1999; Biard et al. 2015; López-García et al. 2002; Polet et al. 2004; Suzuki and Aita 2011).

Practical Importance

During the second half of the twentieth century, studies of polycystines from continuous, well-preserved, mostly Cenozoic sections retrieved by the Deep Sea Drilling

Project (later Ocean Drilling Program, now the Intergrated Ocean Drilling Program) proved the usefulness of these organisms for stratigraphic purposes. By the mid-1970s, a relatively stable tropical zonation had been developed for the Cenozoic (Sanfilippo et al. 1985), and somewhat later several schemes for the polar oceans were proposed (Lazarus 2005). Polycystines are particularly important in Neogene Polar sediments and in red clay bottoms, where carbonate microfossils are largely absent. Polycystine faunas have also been instrumental to the development of paleoenvironmental studies (paleotemperature, paleoceanography, and paleoproductivity), chiefly of open-ocean areas (CLIMAP 1976). Polycystines offer major advantages as material for evolution research: the preservation of almost all species in fossil form, high-resolution chronology, the possibility to sample the entire geographic and chronologic span of the populations, etc. Evolutionary studies of these organisms, in particular speciation and phyletic evolution, have made significant contributions to understanding evolutionary processes in pelagic animals in general. A major limitation in the use of polycystines in all these fields is the problematic species-level taxonomy of the group (Lazarus et al. 2015).

Habitats and Ecology

Geographic Distribution and Biogeography

Horizontal distribution and biogeography. Radiolarians are present in all oceans from the surface to bathypelagic depths, but, with the only known exception of *Lophophaena rioplatensis*, which thrives in the brackish waters of the Río de la Plata estuary at salinities as low as 15.4 PSU (Boltovskoy et al. 2003), they do not tolerate salinities below ca. 30 PSU and are therefore absent from most shelf areas and many inner and marginal seas (e.g., Black Sea, Azov Sea, Caspian Sea, White Sea, Baltic Sea). However, in areas with a narrow shelf where oceanic waters impinge on the shore (e.g. off California, in Norwegian fjords), radiolarians can be collected from the coast. Polycystine densities are usually around 1 cell per liter of water, whereas phaeodarians are normally 15–100 times less abundant (Boltovskoy et al. 1993). Productive, upwelling waters can host 5–10 and up to 70–80 cells/L (Caron and Swanberg 1990). Interestingly, the highest concentrations so far reported (394 cells/L) are those of the monospecific, brackish population of *Lophophaena rioplatensis* in the South American Río de la Plata estuary (Boltovskoy et al. 2003). Polycystine endemicity is generally low, as specific composition changes little with oceanic basin. Even the Arctic and the Antarctic share most of their species (Stepanjants et al. 2004). According to data from 4774 plankton, sediment trap and surface sediment samples compiled by (Boltovskoy et al. 2010), only *Artobotrys borealis* consistently occurs in Arctic and Subarctic waters and has not been recorded in the Antarctic or Subantarctic, but several species are here much more common and abundant than in cold waters of the Southern Hemisphere (*Amphimelissa setosa*, *Artostrobus annulatus*, *Artostrobus jorgenseni*, *Lithomelissa setosa*, *Phormacantha hystrix*, *Plectacantha oikiskos*, *Pseudocubus obeliscus*, *Rhizoplegma boreale*, *Saccospyris conithorax*, and

Siphocampe lineata) (Boltovskoy and Correa 2016a). Species probably restricted to – or at least much more abundant in – the Southern Ocean, include *Actinomma antarcticum*, *Antarctissa denticulata-strelkovi*, *Saccospyris antarctica*, and *Triceraspyris antarctica* (Boltovskoy and Correa 2016a). The other major oceanic climatic belts, defined chiefly by their different water temperature regimes, host dissimilar radiolarian assemblages (Fig. 2), but most of the species occur, albeit sparsely, in more than one area. Within the ranges of normal oceanic conditions (basically salinity), temperature is by far the most important factor in defining polycystine distribution patterns (Boltovskoy and Correa 2016a), followed by nutrients and primary productivity. At ocean basin scales, temperature is also most probably responsible for the fact that polycystine assemblages off the Pacific coasts of Central America differ from the tropical-subtropical ones elsewhere (Fig. 2). In contrast to many open-ocean organisms, whose diversity has been reported to peak at intermediate latitudes (~15–30°N) and drop at the equator (e.g., Foraminifera, Tintinnina, Euphausiacea, and Copepoda), polycystine species numbers are tightly coupled with temperature throughout the entire thermal range of marine waters peaking at the equator (Fig. 3; Boltovskoy and Correa 2016b). In high-latitude assemblages, numerical dominance of a few species is very high, with 1–2 radiolarians often accounting for up to 90% of all the individuals (e.g., *Amphimelissa setosa* in the Atlantic sector of the Arctic and *Antarctissa denticulata-strelkovi* in the Southern Ocean). In warm waters, dominance is much less marked, the most abundant species normally accounting for <5% of the overall inventories in each sample. Throughout the World Ocean, occurrence and abundance of the species are highly correlated: radiolarians recorded in more samples also account for larger proportions of the taxocoenoses analyzed.

Phaeodarian biogeography is still very insufficiently known, but the scarce available evidences suggest that their world-wide patterns are less clearly associated with latitudinal climatic belts. This may be due to the fact that many phaeodarian species are deep-living forms, especially in warm water areas (Nakamura and Suzuki 2015; see below) that inhabit large areas where water temperature is more uniform (Fig. 4).

Vertical distribution. In tropical and subtropical waters polycystines are usually concentrated in the upper 50–100 m (Boltovskoy et al. 2010). Sometimes several discrete maxima are recorded, one at or near the surface and a second one between 50 and 100 m (Kling and Boltovskoy 1995) (Fig. 5). In polar waters, however, peak abundances seem to be associated with deeper and warmer layers, at around 200–400 m and overall polycystine abundances are much lower than in the tropics (Boltovskoy and Alder 1992; Nimmergut and Abelmann 2002; Petrushevskaya 1967) (Fig. 5).

The vertical ranges of most polycystines can be described by the following four patterns: (1) surface (with at least one peak above 100 m), (2) subsurface (around 100 m), (3) intermediate (between 100 and 300 m), and (4) deep (below 300 m) (Fig. 6) (Boltovskoy et al. 2010; Kling 1979; Kling and Boltovskoy 1995). However, worldwide depth zonations cannot be defined in terms of fixed depths because the distribution of radiolarian species is related to water masses which move vertically as well as horizontally. As a result, the same radiolarian species can occupy quite different depth intervals at different locations (Kling 1976). Many cold water radiolarians that

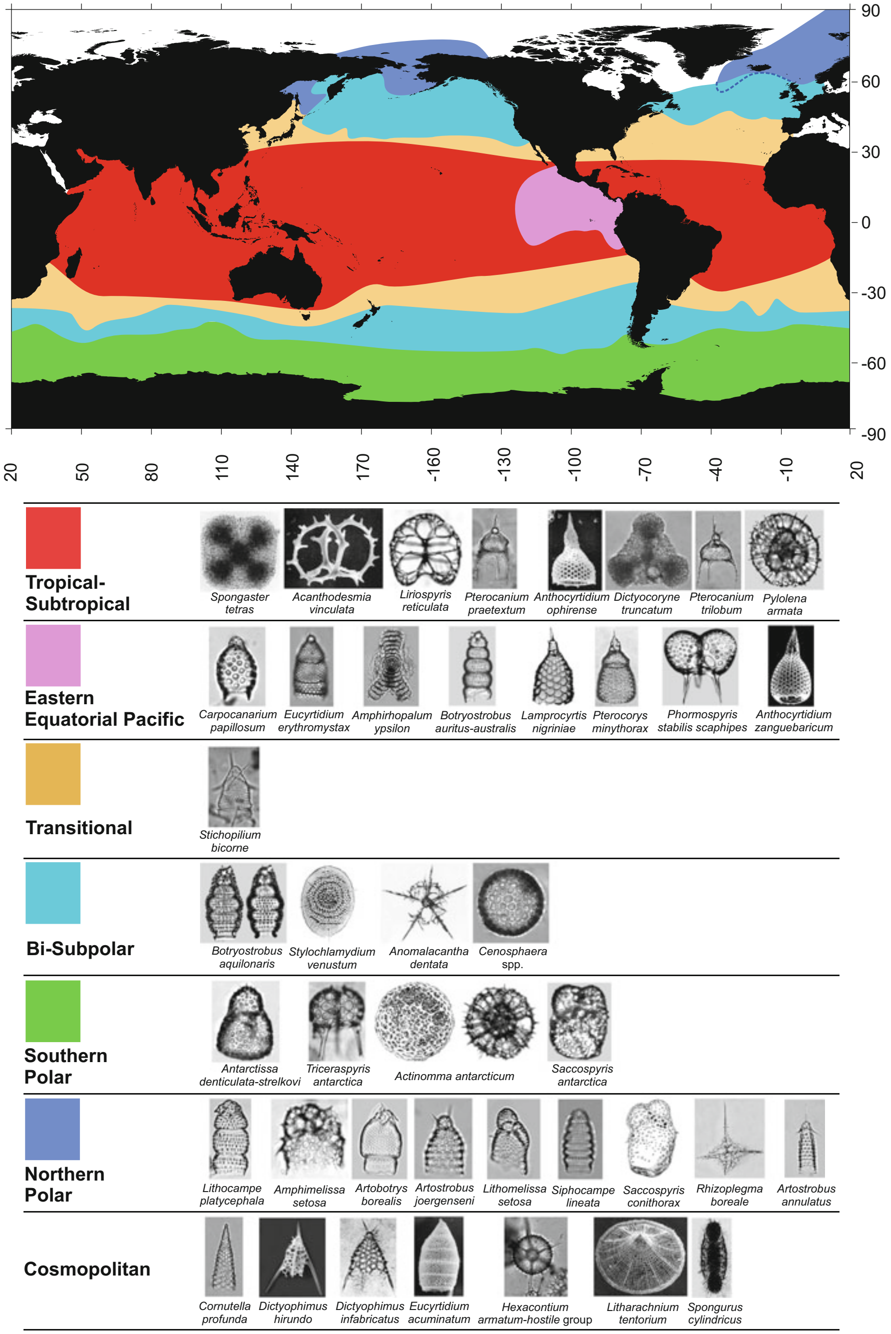


Fig. 2 Biogeographic regions of the World Ocean based on the distribution of polycystines in surface sediments and their most representative species (very few of these are restricted to the provinces indicated) (Simplified from Boltovskoy and Correa (2016a))

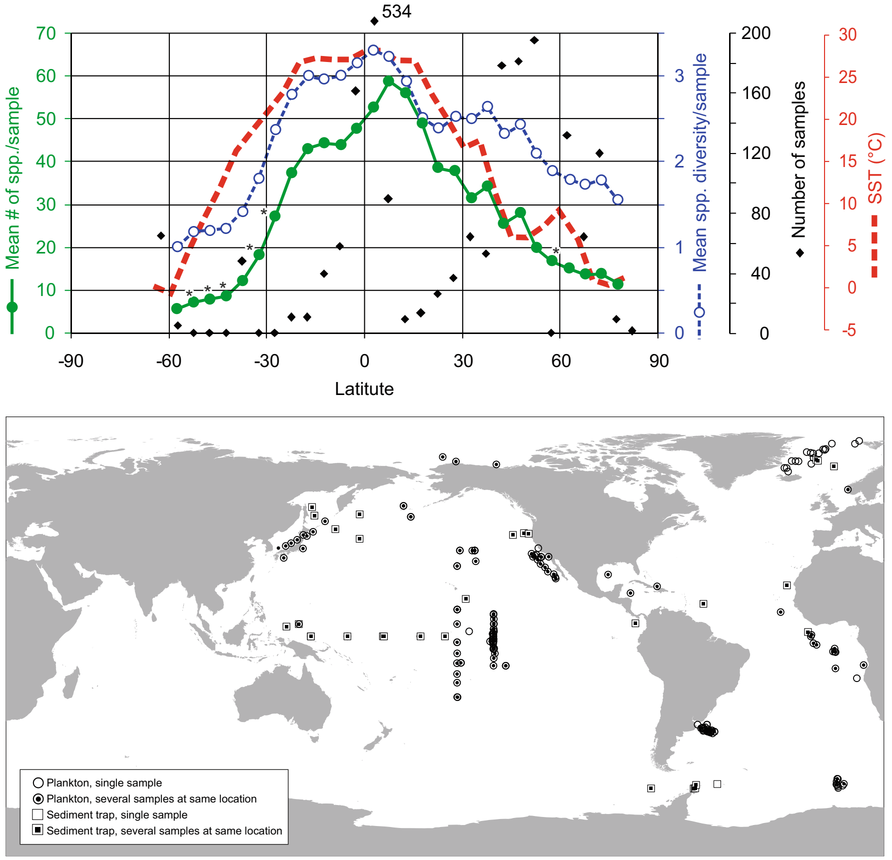


Fig. 3 Numbers of polycystine species, specific diversity (Shannon-Wiener log base 2), and sea surface temperature (SST) in the World Ocean as a function of latitude (pooled data for 5° intervals, 3-point running means, interpolated values are asterisked). Lower panel shows positions of the 2081 water column (plankton and sediment trap) samples used (*diamond symbols* in upper panel). Radiolarian data are based on compilation by Boltovskoy et al. (2010). Temperature curve is representative of mean SST values at the sampling sites involved only (rather than world-wide) (SST data are from Boyer et al. (2013))

inhabit the upper layers at high latitudes submerge with their corresponding water masses and can be found at depth in mid- and low-latitude areas (Boltovskoy 1988; Boltovskoy and Correa 2016b; Casey et al. 1982; Kling 1976).

Vertical changes in radiolarian diversity are more difficult to assess because the living (in situ populations) and dead individuals (i.e., settling shells exported from the upper strata) are seldom adequately differentiated in plankton collections. It is highly probable that protoplasm staining techniques, which are usually applied for these estimates, strongly overestimate the living depth ranges of the species because of the time it takes for the protists' protoplasm to decompose and disappear

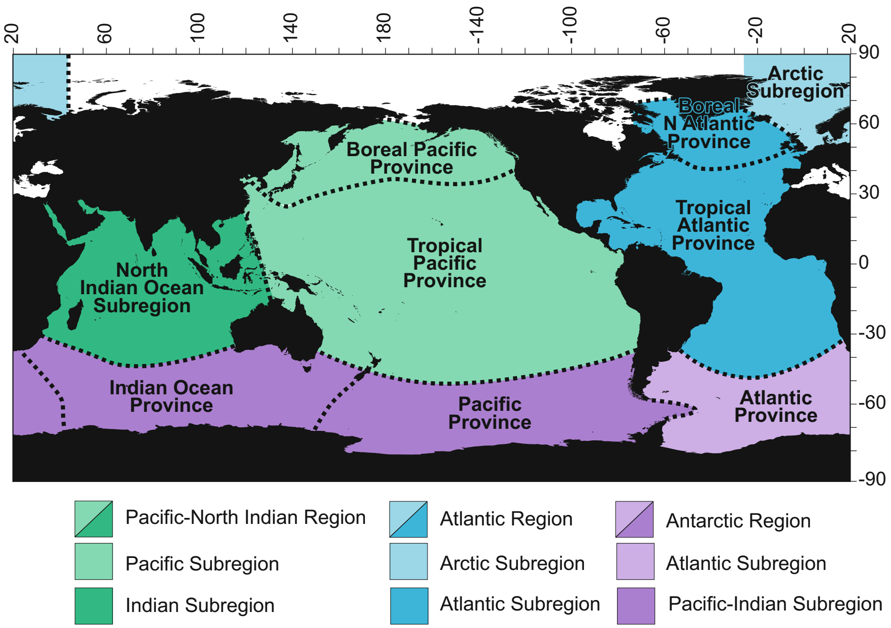


Fig. 4 Biogeographic zonation of the World Ocean based on deep-water Phaeodaria (Redrawn from Reshetnjak (1966))

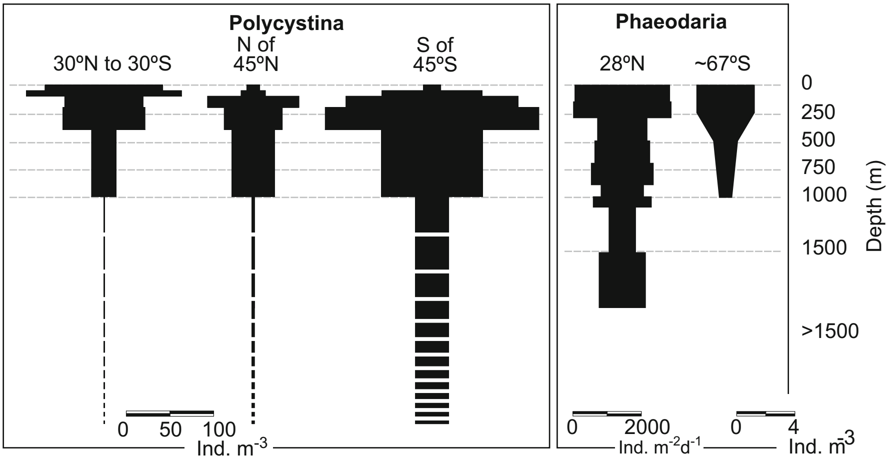


Fig. 5 Vertical profiles of radiolarian abundance in warm water and in cold water areas. Values for Polycystina are based on pooled data from 20 published surveys and our unpublished information from 1145 plankton samples. Values for Phaeodaria are from Gowing (1986) (28°N, North Pacific Central Gyre, sediment trap samples, living specimens only), and from Nothig and Gowing (1991) (Weddell Sea, plankton samples, phaeodarians >0.4 mm only). Notice differences in scales and units

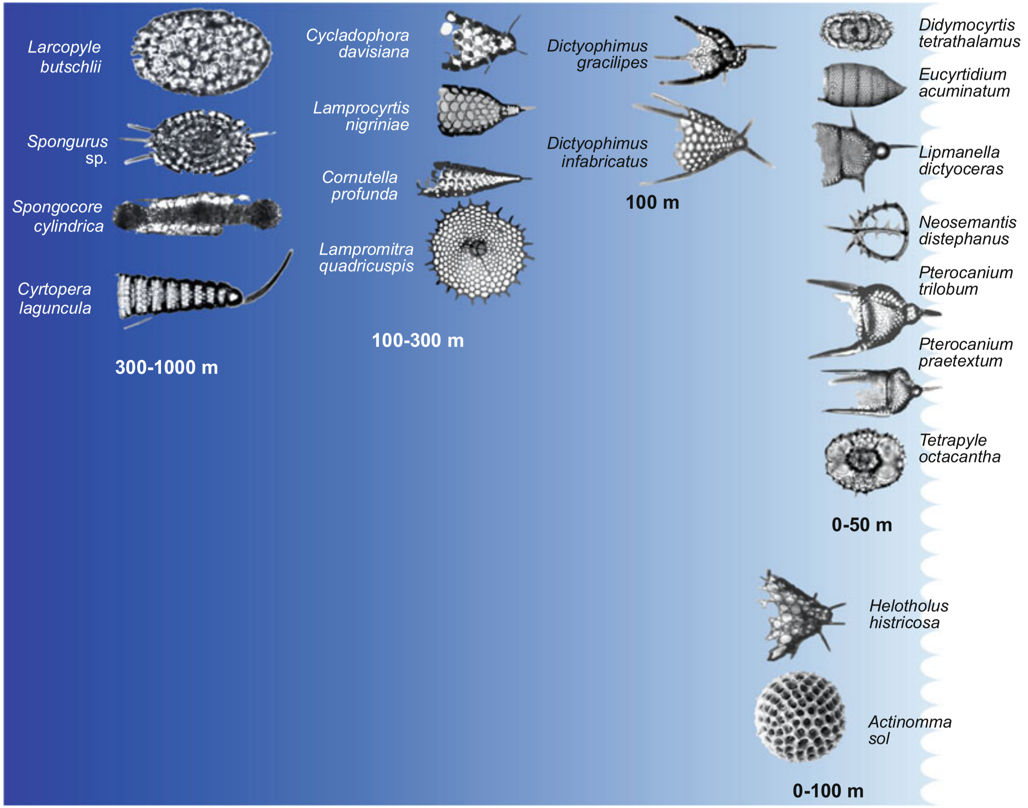
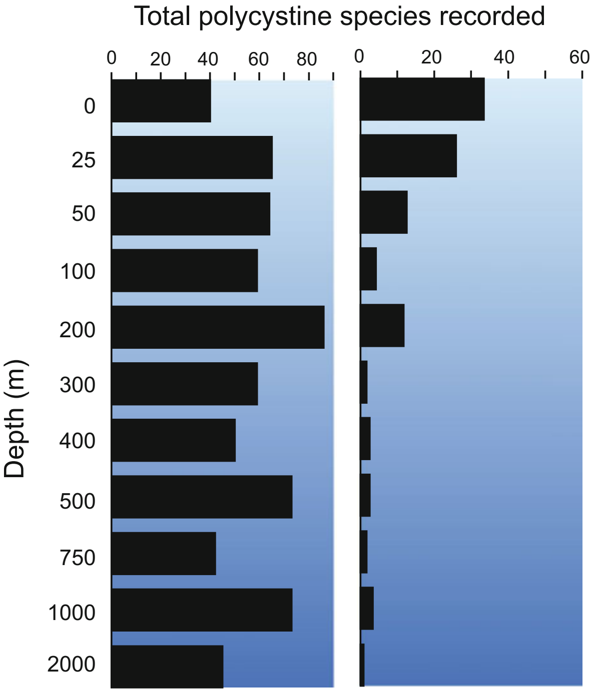


Fig. 6 Vertical distribution of polycystine species, as exemplified by some forms abundant in the northern subtropical Pacific (Based on data from Kling and Boltovskoy (1995))

Fig. 7 Total number of polycystine species recorded per sample (*left*) and number of new species added to the inventory of the overlying waters (*right*) in a set of vertical plankton tows performed in the eastern subtropical Pacific. The absence of significant vertical diversity changes (*left panel*) is attributed to the presence at depth of dead, sedimenting skeletons of species whose living ranges are restricted to the upper layers (Adapted from Kling and Boltovskoy (1995))



(Bernhard 1988). The widespread occurrence of large numbers of healthy diatoms, dinoflagellates, and Cyanobacteria at depth >4000 m (Agusti et al. 2015) confirms the assumption that radiolarian sedimentation velocities are fast enough to yield large proportions of stained individuals well below their living depth range. Thus, raw data often show little species richness variation with depth (Fig. 7, left panel). On the other hand, when raw numbers are reinterpreted taking this artifact into account, highest diversities are clearly associated with the uppermost levels (Fig. 7, right panel).

Unlike most other sarcodines, phaeodarians are typically deep-water organisms usually peaking in both abundance and diversity below 200 m (Nakamura and Suzuki 2015), although high concentrations near the surface are not uncommon (Fig. 5). A detailed depth zonation for the area of the Kurile-Kamchatka trench was produced by Reshetnjak (1955, 1966). She concluded that only two (of the 103 species recorded) inhabit the upper 50 m; approximately 30 more have restricted vertical ranges at various depths, while over 50% of the taxa were retrieved from the broad depth interval of 50 to 2000–8000 m. These vertical patterns at a given locale, however, may change significantly because of the dynamics of deep ocean circulation, with species exhibiting quite variable depth ranges over oceanic distances. Vertical profiles in the North Pacific (Kling 1966, 1976) illustrate that species dwelling in near surface water (25 m depth) at high latitudes, are distributed gradually toward lower depths in decreasing latitudes, and dwell at depths

>300 m closer to the equator. Thus, as with the polycystines, depth distributions of phaeodarians on regional scales are not describable in terms of fixed ranges.

Equatorward submergence may account for so-called bipolar distributional patterns characteristic of many radiolarians. High-latitude species could pass under equatorial waters via the Intermediate Water or the Deep Water, to reappear near the surface in the opposite polar or subpolar seas where the adequately colder water temperatures support their growth (Aita et al. 2009; Stepanjants et al. 2006). In the Pacific Ocean, the Intermediate Water circulates in anti-cyclonic gyres that mimic the surface circulation (Reid 1965), thus providing continuity for the water masses and their biological contents. Such bipolar patterns have been described for a number of zooplanktonic species in both the Atlantic (Darling et al. 2000; Pierrot-Bults 1974) and the Pacific Ocean (Alvariño 1965), whereby the north and south polar or subpolar near-surface populations are joined at depths of 800–1000 m across the equator. The fact that these apparently disjoint populations interbreed through their deep-water, tropical and subtropical representatives has been suggested for some protists (Darling et al. 2000).

Radiolarian studies based on sedimentary materials. Because their skeletons preserve in the geological record, studies of extant polycystines have been chiefly based on sedimentary – rather than on planktonic – samples (phaeodarian skeletons very seldom preserve in the sediments). Sediment samples present some advantages but also several important shortcomings (Fig. 8) (Boltovskoy 1994). Whereas polycystine abundances seldom exceed 5 cells per liter in the plankton (Caron and Swanberg 1990), one gram of surface sediments can contain thousands to hundreds of thousands of radiolarian skeletons. Plankton samples yield a snapshot-type image of the composition of the assemblages, which does not necessarily adequately reflect long-term trends. The daily, seasonal, and interannual variability involved is

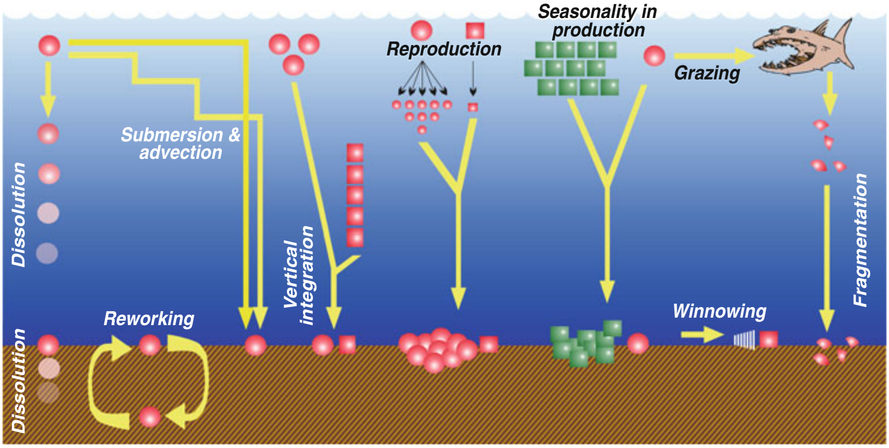


Fig. 8 Schematic diagram of the mechanisms that can distort the sedimentary imprint of the planktonic pattern of fossilizable microplankton in general, and of polycystine radiolarians in particular

smoothed out in the sedimentary record, which may be a welcome trait when general patterns are sought. Further, sedimentary materials are more readily available from the various repositories around the globe than plankton samples. On the other hand, interpretation of the geographic distribution of extant radiolarians on the basis of sediment samples presents several important drawbacks. On their way to the sea-floor and after settling, radiolarian remains dissolve and are grazed upon by various consumers thus breaking their skeletons into unidentifiable fragments. Because more delicate shells are destroyed more readily than the more robust ones, specific skeletal compositions on the bottom and at mid-depths can differ significantly from the living assemblage in the upper water-column. Bottom materials can be reworked after deposition (as a result of which non-Recent deposits, sometimes characteristic of quite dissimilar oceanographic settings, are brought up to the surface layer, or winnowed by bottom currents dislodging settled skeletons and carrying them thousands of kilometers away). Sediments integrate the imprint of near-surface faunas (which are generally associated with surficial environmental traits, as well as with currents and water masses), with the meso- and bathypelagic species whose geographic distribution is uncoupled with upper-water oceanography. The sedimentary distributions of cold-water species tend to show conspicuous equatorward extensions as compared with their planktonic patterns. This distortion is most probably due to the fact that extended survival of the cold water taxa that are expatriated towards lower latitudes is facilitated by submersion (Boltovskoy 1988, 1994; Boltovskoy and Correa 2016a); as a consequence, sediment-derived species-specific ranges may wrongly suggest an enhanced tolerance to gradients in the ecological factors.

Characterization and Recognition

Cell Ultrastructure

Cellular Organization. In broad view, three categories of pseudopod-producing protoctista (including amoebae, Foraminifera and Radiolaria) have been described based on cellular ultrastructure (Anderson 1983): (1) Diffuse, e.g., the naked amoebae without enclosing shells or thecae and a flowing, changeable cell shape, (2) Transitional, including the testate amoebae and foraminifera with a surrounding theca or shell that demarcates a more condensed cytoplasm internally from the web-like, pseudopodial array externally, and (3) Zonal, exemplified by the polycystine Radiolaria with a distinctive porous capsule wall that separates the central, sometimes lobate, intracapsular cytoplasm from the outer, extracapsular, layer of cytoplasm where prey is captured and digested. Interestingly, the Phaeodaria are categorized as transitional since they have a “capsule” with at least one large opening through which the endoplasm protrudes into the ectoplasm, similar to that of testate amoebae. Molecular genetic evidence indicates that Phaeodaria are closely related to testate amoebae within the group Cercozoa (Yuasa et al. 2006) (see below). The chemical composition of the siliceous skeleton and the test-like capsular wall of Phaeodaria also are similar to that of testate amoebae.

Polycystine Radiolaria. The polycystine Radiolaria include the Spumellaria and Nassellaria (See Systematics). The Spumellaria have a spherical body plan with a centrally located nucleus surrounded by radially arranged lobes of cytoplasm, enclosed by a porous capsular wall (Figs. 1 and 9a, b), (Anderson 1980, 1983; Hollande et al. 1971). Axopodia emanate through pores (fusules) in the capsular wall and protrude radially (Cachon and Cachon 1976a, b). The axopodia support a web-like network of cytoplasmic strands that are sticky and aid in the capture of prey. The external cytoplasm encloses or coats the siliceous skeleton, when present. The Nassellaria have a monoaxial body plan (Anderson 1977), typically an elongated, ovoid, central capsule with a porous plate at the base where the axopodia emerge through closely spaced fusules (Fig. 9c, d). Shafts of microtubules in the axopodia emerge from a conical array of microtubules (podoconus) within the intracapsular cytoplasm (arrow, Fig. 10). Skeletons vary from simple tripods to elaborate, helmet-shaped structures, often with spines or other ornamentation (e.g., Figs. 9c, d and 11). The extracapsular cytoplasm coats the siliceous skeleton, when present, and extends outward as a halo of axopodia and their associated network of rhizopodia, including fine, tapered extensions known as filopodia that are present in Nassellaria and Spumellaria (Fig. 1). In polycystines, digested prey products are transported in small vesicles through the fusules into the intracapsular cytoplasm (Anderson 1977).

Phaeodaria. The ultrastructure of Phaeodaria is distinctly different from the polycystines. The "capsular wall" surrounding the denser endoplasm lacks fusules. There is one large opening (astropyle) containing an emergent massive strand of cytoplasm and two smaller openings (parapylae) with finer strands of cytoplasm (Fig. 9e, f). A large, often darkly colored, mass of partially digested food (phaeodium) is typically located external to the capsule near the astropyle (Figs. 1 and 9e). The continuous, massive strand of cytoplasm in the astropyle provides a pathway for digested prey matter to be carried into the endoplasm as occurs with some testate amoebae and foraminifera (Anderson 1983; Swanberg et al. 1986).

The Skeleton

The skeleton of polycystine Radiolaria, when present, is composed of amorphous silica and is deposited outside of the cytoplasm, but within an enclosing cytoplasmic sheath called the cytokalymma (Anderson 1983). The cytokalymma is a dynamic, living sheath that molds the shape of the silica deposited within it as silicification takes place during skeletal growth. Thus, the species-specific shape of the skeleton is determined by cellular dynamics and undoubtedly is under genetic control. Skeletal morphology is remarkably diverse (Anderson et al. 2000), but species specific.

The two major divisions of the Polycystinea, Spumellaria and Nassellaria, differ in the symmetry of their skeletons. Most spumellarians have a radial or spherical

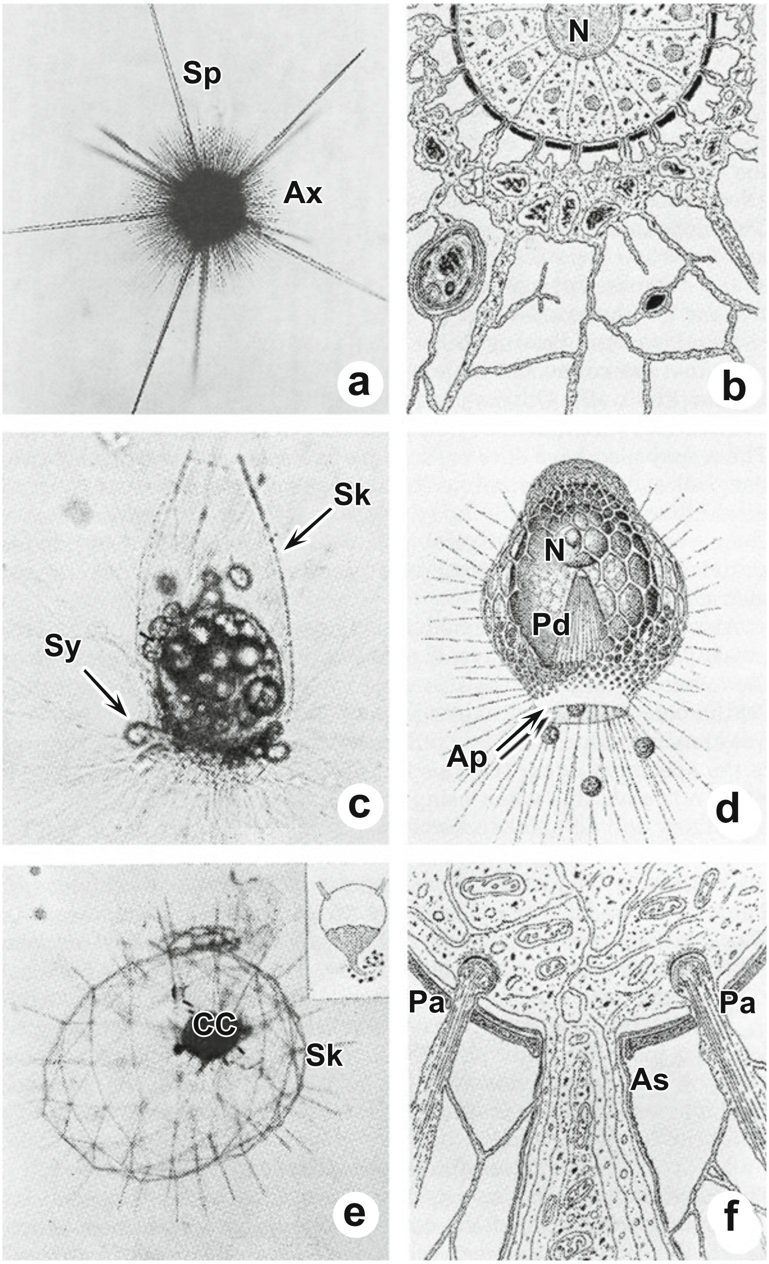


Fig. 9 Comparative morphology and cellular organization of Spumellaria (**a**, **b**), Nassellaria (**c**, **d**), and Phaeodaria (**e**, **f**). (**a**) A living spumellarian with radiating siliceous spines (Sp) and a halo of axopodia (Ax) surrounding the cell. (**b**) A diagram of the cellular organization of a spumellarian showing the centrally located nucleus (N) surrounded by radial lobes of cytoplasm that extend as cytoplasmic strands through pores (fusules) in the dense capsular wall and produce an extracapsular

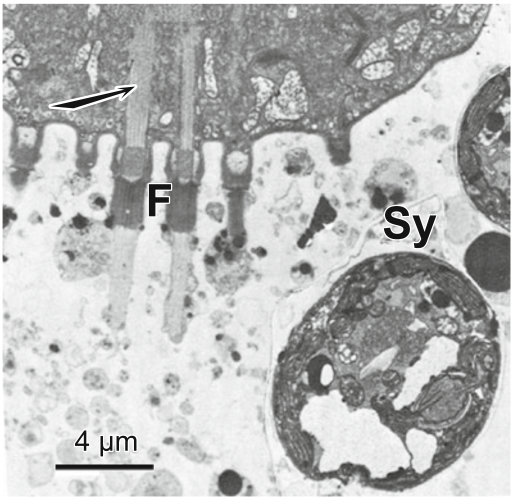


Fig. 10 A transmission electron micrograph of the lower portion of a Nassellarian central capsule showing the shafts of microtubules in the conical podoconus (*Arrow*) that extend from the intracapsular cytoplasm through the pore-like fusules (F) in the capsular wall and protrude outward as axopodia surrounding the cell. Algal symbionts (Sy) are scattered in the peripheral axopodial array (Adapted from Anderson (1983))

symmetry, whereas in nassellarians the body plan usually includes an anteroposterior axis. Figure 11 shows a characteristic, spherical spumellarian whose skeleton comprises several concentric shells. Growth in spumellarians starts with the first, innermost shell and proceeds centrifugally. Nassellarian shells often comprise several sections aligned along an axis. Shell growth starts with the inner, often tripodal, skeleton located inside the first section, or cephalis, and proceeds along the axis to form the thorax, the abdomen, and the postabdominal segments (when present). The wealth of skeletal shapes and morphologies is, however, very ample, including simple spines arranged as a tripod, porous, helmet-shaped skeletons, porous spherical shells, single or multiple concentric geodesic shells composed of rod-like elements joined at nodes in a framework (with or without radially arranged spines), spongiose shells of varied shapes ranging from flattened discs to spheres, and a myriad of other forms, some with ideal geometric shapes (e.g., regular icosahedrons,

◄

Fig. 9 (continued) layer of cytoplasm within a network of rhizopodia. (**c**) A living small nassellarian showing the siliceous skeleton (Sk) forming a conical porous shell (cephalis) surrounding the ovate central capsule. Algal symbionts (Sy) are distributed within the extracapsular rhizopodial network. (**d**) A diagram of the nassellarian cephalis, and a cut-away view of the central capsule showing the nucleus (N) and conical array of microtubules, forming the podoconus (Pd), that extend out of the central capsule as axopodia through the aperture (Ap) at the base of the cephalis. See also Fig. 9. (**e**) A living phaeodarian showing the geodesic siliceous skeletal framework (Sk) surrounding a network of rhizopodia that emerge from a dense central capsule (CC) and the morphology of the central capsule (inset) with a major cytoplasmic strand (astropyle) emerging at the base and two smaller cytoplasmic strands (parapylae) emerging at the opposite pole. (**f**) A diagram of a section of the base of a phaeodarian central capsule showing the emergence of the massive astropyle (As) and smaller parapylae (Pa) projecting outward through openings in the capsular wall (Adapted from Anderson (1983) and J. Cachon et al. (1990))

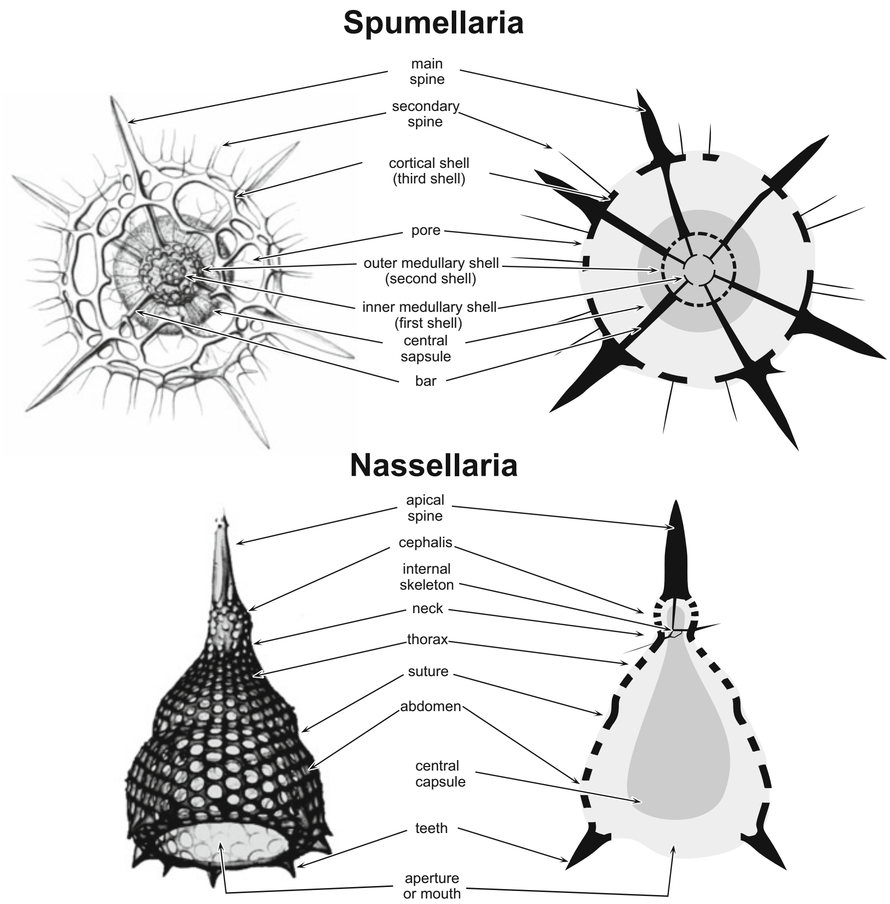
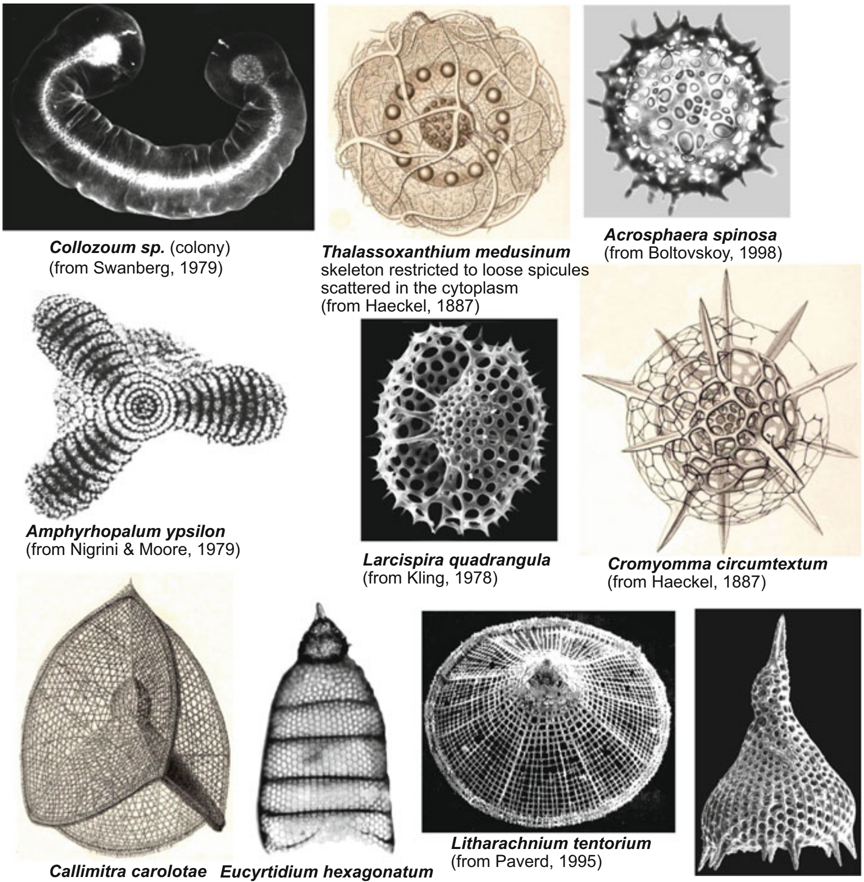


Fig. 11 Scheme of the skeletal elements of the shell of a typical Spumellaria and Nassellaria (Adapted from Boltovskoy and Correa (2014))

dodecahedrons, and octahedrons; Fig. 12) not found in any other living organism (Afanasieva 2006, 2007; Anderson 1983).

The skeleton of Phaeodaria is also composed of amorphous silica but may contain more organic matter than polycystines. The skeletal framework in some species is composed of hollow tubes (e.g., Fig. 9e), not solid rods as in the polycystines. Other species of Phaeodaria have ornate spicules scattered in the external cytoplasm or shells that are either bivalved, resembling small clams or vase-like to pouch-shaped with ornate protuberances around the opening (Fig. 13). Other species have only much branched antler-like spines protruding from a central shell (Fig. 13) (Takahashi and Anderson 2000). However, overall, porous microstructures and basic tubular ultrastructures appear to be common in most of the taxa examined in plankton and sedimentary trap samples from several open ocean locations (Takahashi and Hurd 2007).



***Collozoum* sp.** (colony)
(from Swanberg, 1979)

Thalassoxanthium medusinum
skeleton restricted to loose spicules
scattered in the cytoplasm
(from Haeckel, 1887)

Acrosphaera spinosa
(from Boltovskoy, 1998)

Amphyrhopalum ypsilon
(from Nigrini & Moore, 1979)

Larcispira quadrangula
(from Kling, 1978)

Cromyomma circumtextum
(from Haeckel, 1887)

Callimitra carolotae
(from Haeckel, 1887)

Eucyrtidium hexagonatum
(from Boltovskoy, 1998)

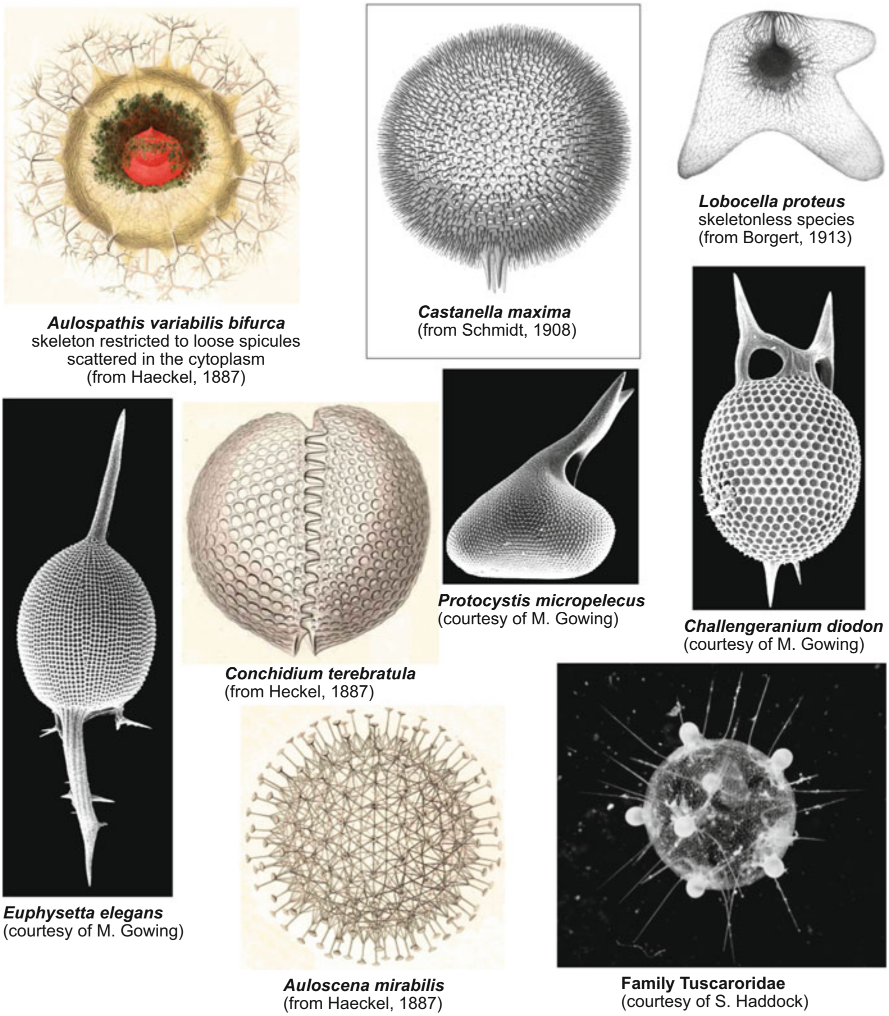
Litharachnium tentorium
(from Paverd, 1995)

Anthocyrtidium ophirense
(from Boltovskoy, 1998)

Fig. 12 Representative examples of polycystine species (figures are not to scale)

Feeding, Symbionts, Necrotrophs, and Predators

Feeding. Considerably more is known about the feeding behavior of polycystine Radiolaria compared to Phaeodaria, although our knowledge is still rather limited. Polycystines consume a wide variety of prey including bacteria, algae, protozoa, and microinvertebrates such as copepods and small larvae of marine arthropods. In a rather extensive study of prey observed in SCUBA-collected radiolaria from epipelagic plankton, Swanberg and Caron (1991) noted that a relatively small proportion of captured radiolaria possessed prey (46%), but there was a wide variety of prey consumed including diatoms, tintinnids, and more frequently copepods and their nauplii, or mollusc larvae. Smaller radiolarian species prey largely on bacteria and algae, whereas larger radiolaria also consume small invertebrates (Anderson 1983, 1996; Caron and Swanberg 1990).



Aulospathis variabilis bifurca
skeleton restricted to loose spicules scattered in the cytoplasm
(from Haeckel, 1887)

Castanella maxima
(from Schmidt, 1908)

Lobocella proteus
skeletonless species
(from Borgert, 1913)

Protocystis micropelecus
(courtesy of M. Gowing)

Challengeranium diodon
(courtesy of M. Gowing)

Euphysetta elegans
(courtesy of M. Gowing)

Conchidium terebratula
(from Heckel, 1887)

Auloscena mirabilis
(from Haeckel, 1887)

Family Tuscaroridae
(courtesy of S. Haddock)

Fig. 13 Representative examples of phaeodarian species (figures are not to scale)

The algal and protozoan prey become snared on the sticky surface of the axopodial array and is engulfed by invagination of the surface membrane to form an intracytoplasmic food vacuole. The food vacuole is converted to a digestive vacuole by secretion of digestive enzymes (Anderson 1996). A much more elaborate mechanism of predation occurs when small arthropods, such as copepods, are consumed (Anderson 1978). The prey becomes entangled within the axopodia and associated rhizopodial network. Eventually, it is surrounded by the rhizopodia that penetrate through weak zones of the prey exoskeleton. Once inside of the host body, the rhizopodia engulf large segments of prey tissue, enclosing them within digestive vacuoles that are carried by cytoplasmic streaming out of the host into the radiolarian cytoplasm near the central capsule. Small vesicles containing the digestive products are transported through the fusules into the intracapsular cytoplasm where food reserves are stored and major metabolic activities take place. Vacuoles containing undigested, waste material are eventually ejected from the axopodial array by cytoplasmic streaming (Anderson 1983). Among the limited evidence of phaeodarian predation, Swanberg et al. (1986) reported that a mesopelagic, coelographic phaeodarian contained microflagellate and metazoan prey. Copepods and salps also were snared when introduced in the laboratory cultures.

Symbionts. A wide variety of symbionts are sequestered within vacuoles (symbiosomes) including algae and photosynthetic cyanobacteria (Bråte et al. 2012; Probert et al. 2014; Yuasa et al. 2012). Algal symbionts include dinoflagellates (golden yellow), prasinophytes (yellow green), and prymnesiophytes (tawny brown) (Anderson 1978; M. Cachon and Caram 1979; Hollande and Carré 1974). Algal symbionts are highly productive photosynthetically, fixing more carbon than primary producers in an equivalent volume of the surrounding seawater of the Sargasso Sea (Caron et al. 1995). A similar assessment was reported in earlier studies by Khmeleva (1967) in the Red Sea and Gulf of Aden. The symbionts associated with radiolaria, however, account for only a small fraction of the total primary production of the entire water column in the Sargasso Sea studies. The symbionts may provide substantial nourishment to the host. Cytochemical and ^{14}C isotopic tracer studies have shown that the symbionts release organic nutrients that are assimilated by the host and that the host occasionally digests some of them by secretion of enzymes within the normally benign symbiosome vacuoles (Anderson 1983).

Necrotrophs. Dinoflagellate necrotrophs (e.g., *Meriodinium brandti*) infect some species of spumellaria, including colonial radiolaria. *M. brandti* invades the nucleus where it forms a plasmodium (Anderson 1983; Hollande 1974 ; Hollande and Enjumet 1953). Eventually, the *Meriodinium* nuclei divide profusely leading to necrosis of the radiolarian nucleus. The parasite nuclei become segregated from the plasmodial mass to form swarmers with undulipodia and typical dinoflagellate morphology including an epicone and hypocone. They escape from the host to initiate another infective cycle. In other species of *Meriodinium*, the initial proliferation in the nucleus is followed by release of plasmodial fragments that invade the intracapsular cytoplasm and eventually release motile infective swarmers with characteristic dinoflagellate features. The large, skeletonless radiolarian, *Thalassicolla* sp., is parasitized by *Solenodinium fallax*. This dinoflagellate invades the nucleus, forms a plasmodium, and produces tubular inclusions that subsequently emerge from the disintegrating nucleus and protrude into the surrounding intracapsular cytoplasm. The tubules eventually give rise to numerous infective swarmers with typical dinoflagellate morphology. Necrotrophs also have been reported in Phaeodaria, including *Syndinium nucleophaga* (Cachon-Enjumet 1961; Hovasse 1923).

Predators. Our knowledge of radiolarian predators is very limited, but based on digestive tract samples from diverse geographic locations, radiolaria have been detected in tunicates (e.g., salps), crustacea such as copepods, euphausids, and in certain penaeidae, among others. There is some evidence that planktonic foraminifera prey occasionally on radiolaria. Amphipods have been reported invading and ingesting cells of colonial radiolaria (Swanberg 1979). However, much more detailed analyses of the digestive tract contents of freshly collected predators is needed to verify predatory pressures on radiolaria.

Reproduction, Growth and Longevity

Reproduction. Reproduction in Polycystinea and Phaeodaria has been observed in laboratory cultures. Collodarian Radiolaria (e.g., some colonial Radiolaria) reproduce by binary fission of the central capsules. Sexual reproduction of Polycystinea or Phaeodaria has not been confirmed, but numerous instances of the release of motile swarmers, likely gametes, bearing two undulipodia have been documented (Anderson 1983; Kimoto et al. 2011). Among polycystines, impending reproduction is signaled by contraction of the extracapsular cytoplasm and jettisoning of symbionts and waste matter. The nucleus undergoes repeated division, eventually filling the intracapsular cytoplasm. Each nucleus becomes segregated from the cytoplasmic mass as swarmers that escape through ruptures in the capsule wall. The fate of the swarmers is unknown. Syngamy (swarmer fusion) has not been observed (Anderson 1983; Cachon et al. 1973). Each swarmer contains a vacuolar-bound strontium sulfate (celestite) crystal (Anderson 1983; Hollande and Martoja 1974) enclosed by an organic envelope that appears to control the ultimate shape of the crystal (Anderson et al. 1990). In the phaeodarian *Coelodendrum ramosissimum*, reproduction begins with the disappearance of the phaeodium, followed by degeneration of the capsule and the appearance of small plasmodial spheres in the ectoplasm. Each of the spheres produces hundreds of polynucleated amoeboids that eventually form swarmers with two undulipodia (Borgert 1900, 1909; Cachon-Enjumet 1964).

Growth and Longevity. During the course of maturation, some skeletal-bearing species exhibit a “stair-step” pattern of growth, undergoing one to several days of silica deposition and increase in size followed by plateaus for several days before the next growth phase (Anderson et al. 1989). However, no predictable periodicity of silica deposition has been observed within a given species, and the stair-step curves are highly variable. Further research is needed to document patterns of growth among a wide variety of polycystines. Among the Polycystinea, two processes of skeletal growth and maturation appear to account for all examples of skeletal morphology: (1) Rim growth, commonly found in porous shells, with round to nearly round pores. The pores are formed by deposition of silica on the rims of larger pores that become increasingly smaller in diameter during maturation. (2) Bridge growth, producing geodesic frameworks and latticed shells that are formed by repeated production of rod like elements that grow from one node to another across an opening in the framework, thus producing a skeleton with increasingly more complex design, and in some cases increasingly smaller openings (Anderson 1983). Species with concentric spherical shells construct the innermost, small, primary shell first, typically by bridge growth. Spines elongate from the primary shell and provide scaffolding for the construction of successive larger surrounding shells, also by bridge growth. Some spongiose skeletal species deposit a small spherical, porous shell initially, followed by very fine bridge growth producing a surrounding meshwork of silica with the characteristic morphology of the species. The skeleton provides protection for the delicate cytoplasmic structures and also supports the axopodia and network of pseudopodial strands radiating from the central cell body, thus permitting efficient capture of prey, including invertebrates such as copepods that may be larger than the radiolarian (Anderson 1978).

Our knowledge of the longevity of radiolaria is limited. Evidence from laboratory maintenance cultures of radiolaria, and inferential data based on environmental observations of the periodic appearance of juvenile and adult stages of radiolarian species, indicates that they live for several weeks to several months before reproducing. Additional research is needed on comparative analyses of life spans of different species and also on the effects of environmental variables on longevity, such as abundance of prey, temperature, and other seasonal and biogeographic factors (Anderson 1983; Casey et al. 1970).

Systematics

Polycystinea. Haeckel (1887) produced one of the earliest comprehensive systems of radiolarian classification describing over 3000 polycystine species, ~2400 of which were new to science. Haeckel's work is still a necessary reference guide, but it does not satisfactorily represent natural relationships because groupings are only based on morphologic similarities, and because the rigidity of these geometry-based diagnoses often ignores the ample intraspecific variability of the radiolarians (Lazarus et al. 2015). Efforts to improve upon the classification schemes inherited from earlier workers have mainly followed two different approaches: cytological data and evolutionary studies. Several authors (Cachon and Cachon 1972a, b; Hollande and Enjumet 1960; Petrushevskaya 1981; Petrushevskaya et al. 1976) proposed revisions which rely heavily on cytoplasmic features, in particular the “nucleoaxopodial complex” (Petrushevskaya 1981). Although these schemes are probably sounder in biological terms, their application to fossil and subfossil materials lacking the protoplasm is problematic, which is one of the reasons for their very limited acceptance among radiolarian workers. Analyses of evolutionary lineages in geological sequences were used as a basis to assess the taxonomic value of key skeletal traits; it was concluded that many of them (e.g., number of segments, number of supplementary concentric spheres, number of feet, number of rays and of equatorial spines in discoidal Spumellaria, and presence and nature of thoracic wings) have little or no suprageneric value. In contrast, several others (especially cephalic structure, but also pore arrangement, shell terminations in Nassellaria, etc.), traditionally considered as of minor value, are conservative through time, reveal evolutionary lineages and, therefore, are relevant for higher-rank divisions (Riedel and Sanfilippo 1986). These results are at least partly in disagreement with the conclusions of the major review by De Wever et al. (2001), who based their classification scheme on the notion that “the farther the skeletal elements are from the first shell, or initial skeleton, the less important they are for higher level systematics." Riedel (1967, 1971); Petrushevskaya (1971a); (Petrushevskaya 1986); Goll (1968); (Goll 1969); Sanfilippo and Riedel (1970); Dumitrica (1989); De Wever et al. (2001) based on skeletal features alone worked out alternative classifications, either for the entire group or for selected parts of it. Of these, Riedel's (1967, 1971) suprageneric system has become the most widely accepted for extant and Cenozoic radiolarians and is the one adopted herewith with slight modifications. Classification of pre-Cenozoic polycystines follows De Wever et al. (2001).

Phaeodaria. The classification of this group proposed by Haeckel (1862, 1887) has been used by subsequent students with but minor additions. Generic assignments have been followed with few modifications, with the exception of some occasional revisions (Korsun 2011; Nakamura et al. 2015; Nakamura and Suzuki 2015; Reshetnjak 1966), but inconsistent usage (particularly among the family Challengeridae) persists into modern times (Kling and Boltovskoy 1999). The morphology of each family is so distinctive that there has been essentially no controversy as to their taxonomic identity, although lack of discrepancy is probably more a reflection of reduced interest and absence of new research, than of the quality of the information available.

Outline Classification

The classification outlined below incorporates the major higher-order categories defined on the basis of molecular phylogenetic studies, particularly the results of Adl et al. (2012). The classification outline proposed by these authors deliberately omits formal taxonomic categories; for the sake of clarity, we have included them (in parentheses, after the taxon name), as used in traditional classification systems. Adl's divisions within Polycystinea and Phaeodaria are practically identical to those of traditional taxonomy, which seems to be justified by the very scarce information available so far (Ishitani et al. 2012a, b). On the other hand, molecular results obtained with other planktonic protists (e.g., Foraminifera) (Darling and Wade 2008; De Vargas et al. 2004; Seears et al. 2012) suggest that many existing morphospecies include several genetically different organisms with more or less distinct distributional patterns. The few data on Polycystinea published in the last years support this assumption, suggesting that taxonomic assignments based on morphologic features often conflict with genetic molecular studies (Biard et al. 2015; Sierra et al. 2013) and that genetically defined units can differ both morphologically and distributionally (Ishitani et al. 2012b, 2014). It should be stressed that these results do not necessarily imply that traditional, morphological classifications are wrong and those based on molecular data are correct. While molecular studies are undoubtedly a very powerful tool for evolutionary and taxonomic investigations, as any other technique they have important limitations (Decelle et al. 2014). Among other limitations, the use of a single gene to decipher phylogenetic relationships may bias the results, and use of more than one gene often improves the analyses. However, the usefulness of molecular analyses as an additional tool is beyond doubt, not only for addressing taxonomic and phylogenetic issues, including conflicting identifications based on skeletal features (Yuasa et al. 2009), but also for addressing distributional, evolutionary and ecologic problems.

Rhizaria

- Cercozoa
  - Thecofilosea
    - **Phaeodaria** (=Tripylea) (Superorder) Siliceous skeleton, when present, may consist of scattered spicules or a well-developed meshwork, but skeletal rods are usually hollow and skeletal material is provided with an organic matrix. Skeletons rarely preserve in sediments. The central capsule normally with one large and two smaller pores. Around 400–500 extant species.
      - **Phaeoconchia** (Order) Skeleton formed by two symmetrical valves that can be large and conspicuous (family Concharidae) or small, internal, surrounded by an elaborate meshwork of tubes and spines (family Coelodendridae) (living representatives only, two families).
      - **Phaeocystina** (Order) Skeleton absent or formed by loose elements around the central capsule (living representatives only, four families).
      - **Phaeogromia** (Order) Skeleton, when present, represented by a globular or ovoidal solid structure with one large opening, often with one or more large radial spines. Very heterogeneous group (a few shelled forms known since the Eocene, 8 families).
      - **Phaeosphaeria** (Order) Skeleton usually represented by a large sphere with triangular meshes (living representatives only, 3 families).
- Retaria
  - Acantharia (Subclass)
  - **Polycystinea** (Subclass/Superorder) Usually endowed with a siliceous skeleton with solid bars. Cytoplasm divided into two regions: an inner endoplasm and an outer ectoplasm or calymma, separated by a perforated organic membrane, the central capsule. Probably around 400–800 extant species and several thousands of fossil forms.
    - **Collodaria** (Order) Solitary or colonial polycystines without a siliceous skeleton or provided with simple or branched spicules scattered in the calymma. (Eocene?-Holocene, four families, all with extant representatives).
    - **Spumellaria** (Order) Solitary or colonial (one family only: Collosphaeridae). Shell well developed, with radial symmetry or one derived from it (spiral, discoidal or lenticular biconvex, triaxonic, quadrangular, etc.) or asymmetric. Central capsule with many small pores (Paleozoic-Holocene, 37 families, eight with extant representatives).
    - **Nassellaria** (Order) Solitary. Shell represented by several fused spicules only, by a D-shaped ring and associated spines, or by more elaborate mono- or multilocular latticed skeletons. The symmetry of the shell is characterized by the fact that the two extremes of its major axis define two morphologically different poles (Devonian- Holocene, 54 families, seven with extant representatives).
    - **Archaeospicularia**, **Albaillellaria**, **Latenfistularia**, **Entactiniaria** (Orders) Fossil polycystines (Cambrian-Triassic, 37 families).

Evolutionary History

Polycystines possess some exceptional traits for their use in evolutionary studies: they appear very early – in the Lower Cambrian (Nazarov 1973; Obut and Iwata 2000), they preserve well in the geological record, they are highly diversified, and they are often very abundant. However, their potential is seriously hindered by the generally poor state of their taxonomy, which affects not only the species concept but also the definition of supraspecific categories and the taxonomic and evolutionary value of most morphologic traits. Thus, with the exception of a few well-researched Cenozoic lineages, our understanding of the evolution of the polycystines is still in an embryonic stage. Modern molecular phylogenetic research, in addition to clarifying the taxonomy of polycystines, has provided additional sources of evidence to trace their origins and divergences during the evolution of this group in relation to other taxa in the tree of life (Ishitani et al. 2012a; Sierra et al. 2013).

Although some authors have presented debatable evidence of links with benthic ancestors (Petrushevskaya 1986), the origin of radiolarians is uncertain. Until the Permian, their diversification was moderate, but in the Triassic, many new families appeared and from there on the number of extinctions was roughly balanced with that of new forms. For the Paleozoic, over 600 polycystine species (80 genera) have been described, suggesting a speciation rate of about 1–2 species per million years (Vishnevskaya and Kostyuchenko 2000). For the Mesozoic, this rate soars to over 10 species per million years; the total number of Mesozoic species described is around 2500 (Vishnevskaya and Kostyuchenko 2000), including the first multi-segmented nassellarians, the appearance of twisted spines in spumellarians, etc. In agreement with most other organisms, polycystines show a strong diversity drop around the Cretaceous-Tertiary boundary, recovering in the Eocene (Sanfilippo et al. 1985; Vishnevskaya and Agarkov 1998). In the Cenozoic, the number of polycystine species varies around 400–800. The skeletons of these species are conspicuously lighter than those of most pre-Cenozoic forms, presumably due to the competition for dissolved silica with the diatoms (Lazarus et al. 2009). The longevity of most Cenozoic species ranges around 1–5 Ma (before going extinct or changing sufficiently to be identified as a different species) (Sanfilippo et al. 1985). Thus, despite the fact that polycystines represent potentially useful evolutionary and stratigraphic tools, taxonomic inconsistencies and the scarcity of specialists hinder their extensive use in these fields.

Maintenance and Cultivation

Continuous, reproducing cultures of radiolaria have not been established in the laboratory, probably due to the particular environmental requirements of the earliest growth stages. However, juvenile radiolaria that are collected by gentle drift tows using nets, or captured in hand-held small jars by SCUBA divers, can be maintained in laboratory culture (Anderson 1992). Individual radiolaria are retrieved from the sample using pipettes fitted with a rubber bulb and a tip with a large opening. The radiolarian is gently deposited in glass culture dishes or small vials containing seawater, freshly collected from the sampling site. Symbiont-bearing species are illuminated by fluorescent lights and temperature is maintained by surrounding the dishes with recirculating water from a constant temperature bath set at a temperature equivalent to the sampling site. Algal cultures established in the laboratory, including planktonic diatoms, dinoflagellates, and other small protists, provide a source of protistan prey. Small droplets are introduced into the culture vessels, but only sparingly and at intervals of several days to avoid fouling the culture dishes with overgrowth. Small crustacea or young nauplii of brine shrimp (*Artemia*) reared in the laboratory are suitable additional prey for larger species. In some cases, the freshly collected, unfiltered, seawater from the sample site contains sufficient prey to sustain growth of illuminated radiolarian cultures if the seawater is replaced with freshly collected seawater every several days. No additional prey are required, especially if the cultures are illuminated. The larger radiolaria can be observed using a high-power dissecting microscope. Inverted microscopes with long-distance objective lenses can be used for more detailed visualization of smaller floating radiolaria, preferentially maintained in small culture vials with optically clear flat bottoms.

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