Chapter 9
Phaeodaria: Diverse Marine Cercozoans of World-Wide Distribution

Yasuhide Nakamura and Noritoshi Suzuki

Abstract Phaeodarians are unicellular marine protists characterized by the "central capsule" containing the nucleus, the "phaeodium", or mass of brown particles, and a siliceous skeleton called the "scleracoma". Phaeodaria have long been classified as a member of the Radiolaria; however, this protist group now belongs to the phylum Cercozoa. The ancestor of phaeodarians is thought to have appeared in the upper Triassic Epoch according to the fossil record. They reproduce by cell division and swarmer production. These plankton are heterotrophic, and they presumably feed on organic materials suspended in the water column or capture other plankton. Although this group is widely distributed in the world ocean from the surface to deep waters, they have attracted little attention from marine researchers partly because their abundance has long been underestimated. Recent study, however, revealed that phaeodarians are more numerous than expected, and their high abundance is sometimes reported. Considering their occasional high biomass and the fact that their scleracoma is made chiefly from silica, this plankton group plays an important role in local ecosystems and has a large impact in the silica cycle of the ocean. Knowledge of phaeodarian is indispensable for future oceanography; therefore the hitherto-known information on this marine protist is comprehensively reviewed in this chapter.

Keywords Phaeodaria • Tripylea • Cercozoa • Unicellular • Zooplankton • Protist • Deep sea • Matter cycle • Silica

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9.1 Introduction

9.1.1 What Are "Phaeodarians"?

Phaeodaria are a group of holoplanktonic marine protists. This cercozoan group adapts to marine environments and plays an important role in local ecosystems. Phaeodaria are heterotrophic plankton which chiefly live in pelagic open oceans from the surface to the deep sea. No phaeodarians have been reported from brackish and high-salinity environments up to the present. Their cell size ranges from several hundred micrometers to a few millimeters and depends on the families to a certain extent. The size of the family Tuscaroridae exceeds 3 mm. By contrast, the family Challengeriidae is generally smaller, reaching a few hundred micrometers at the largest (Fig. 9.1). Some phaeodarians bearing spherical skeletons are similar to polycystines and acantharians, but the group in question is essentially different by possessing more porous and fragile skeletons, a peculiar central capsule and a mass of brown particles, phaeodium. Some phaeodarians of the family Challengeriidae resemble marine dinoflagellates (e.g., *Ceratium gravidum*); therefore these two are occasionally mistaken for each other. Such dinoflagellates, however, can be correctly distinguished by the presence of grooves and the absence of phaeodium.

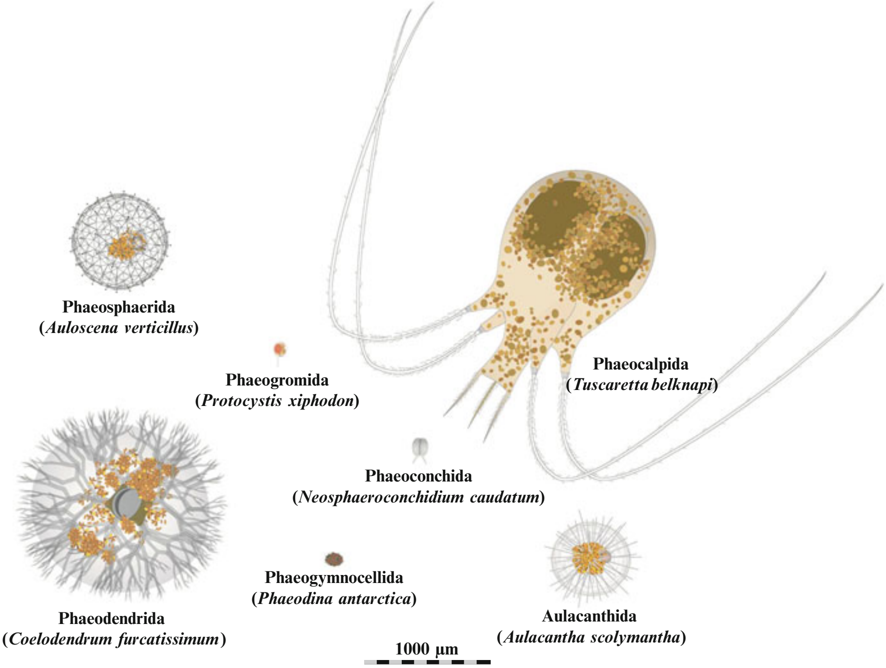

Fig. 9.1 Comparison of cell size between phaeodarian orders

Phaeodarians are often broken by normal sampling methods and are not very abundant in comparison with copepods and ciliates in the euphotic zone, so this protist group has hitherto attracted little attention from plankton researchers as a subject of research. Since the majority of the tremendous taxonomic and ecological studies by Germans ended after World War I, the principal information concerning phaeodarians has been little updated until today. However, our understanding of their taxonomic position and skeletal chemical composition has progressed little by little. They have long been regarded as Radiolaria because of the presence of "ray-like pseudopodia" and a "central capsule" (Calkins 1909), but Phaeodaria are now classified as a subclass of the phylum Cercozoa (Polet et al. 2004; Nikolaev et al. 2004; Yuasa et al. 2005; Howe et al. 2011; Adl et al. 2012; Sierra et al. 2013). This taxonomic revision is important to elucidate the ecological differences between Phaeodaria and "true" Radiolaria (e.g., Suzuki and Aita 2011, Suzuki and Oba, Chap. 15, this volume) and lets us know that we have been unable to estimate the true abundance of phaeodarians with some previous studies, because in such studies, phaeodarians were treated together with the "true" Radiolaria.

Another important point is about the chemical composition of the skeleton (or scleracoma). The phaeodarian skeleton used to be considered as "admixtures of organic matter and silica" or "organic siliceous matter" (e.g., Haeckel 1887). However, it is now confirmed that more than 90 % of their skeleton is actually made up with silica, and organic matter is absent in the structure (Takahashi et al. 1983; Bernstein et al. 1990; Takahashi and Hurd 2007).

9.1.2 History

The first phaeodarian species was described in 1856. Dead specimens of Lirellidae, *Lirella baileyi* Ehrenberg (the original taxonomic name *Cadium marinum* Bailey was replaced by the Ehrenberg name because the former was a junior secondary homonym according to the International Code of Zoological Nomenclature), were collected from surface sediments in the Bering Sea (Bailey 1856), and this species was thought to be a member of Rhizopoda. Living phaeodarians were first illustrated from plankton samples in the Mediterranean Sea (Haeckel 1862). Haeckel (1862) regarded phaeodarians as a member of Radiolaria. Hertwig (1879) clarified their protoplasmic character and named them "Tripylea" after the characteristic three pores on the surface of the central capsule ("Tripyleen" in German is derived from *tri-* Greek three and *pýlē* Greek gate). However, as these structures are not seen in all species, Haeckel (1879) created the taxon name "Phaeodaria" from the presence of "phaeodium."

The high morphological diversity of phaeodarians was recognized thanks to the HMS Challenger Expedition (1872–1876). Preliminary reports of the expedition were published as early as 1876, and these documents described the family Challengeriidae as highly diverse deep-sea marine protists. The discovery of this family is one of the distinguishing fruits of this expedition (Murray 1876). Plankton sampling from deep layers revealed that the phaeodarians have high species diversity in the deep seas of the Pacific and the South Atlantic Ocean, and they were assumed to be "deep-sea plankton" (Murray 1876; Haeckel 1887). Their global distribution was further investigated by several expeditions from the late nineteenth to the early twentieth century (e.g., the Valdivia Expedition 1898–1899, the Plankton Expedition in 1889, and the Gauss Expedition 1901–1903). The Valdivia Expedition, or "die Valdivia-Tiefsee-Expedition", carried out scientific programs from the African western coast via the East Antarctic coast to the Indian Ocean between July 1898 and April 1899, and various samples were collected down to 6000 m water depths, particularly in the Southern Ocean. Most of the phaeodarians from these samples were studied by Haecker (1904, 1905, 1906, 1907a, b, 1908a, b). The Plankton Expedition targeted plankton in the North Atlantic Ocean reaching to 60°N from July to November 1899, and collected samples down to 3500 m water depths at 33 stations. These samples made remarkable contributions to the biology of almost all the families (Borgert 1905a, b, 1906, 1907, 1909a, b, c, 1910, 1911, 1913, 1922). The Gauss Expedition, or "die Deutsche Südpolarexpedition", investigated around Antarctica, and its samples were also used for the study of phaeodarians (Schröder 1906, 1913). These investigations clarified the taxonomy and ecology of the greater part of this group. The phaeodarians in the South Atlantic were studied with the samples of the German Meteor expedition, or "die Deutsche Atlantische Expedition", (1925–1927), and the vertical distributions of this protist group at family level were documented as deep as 1500 m water depths (Meyer 1933). Deeper vertical distribution was researched down to 8000 m water depths of the Kuril-Kamchatka Trench by the expedition of R/V *Vityaz* between 1949 and 1979 (Reshetnyak 1955). This is the deepest record of phaeodarian sampling (Reshetnyak 1966).

From the 1950s to the 1970s, the cell structure and cell division process were examined by French and German cytologists (e.g., Cachon-Enjumet 1961; Cachon and Cachon 1973; Grell 1953, 1973), focusing on some phaeodarians possessing a large protoplasm with very significantly observable chromosomes. The abundance of radiolarians including phaeodarians has been investigated as a component of marine plankton since the late 1960s (e.g., Beers and Stewart 1969). According to some dozens of "radiolarian" papers which divide "radiolarians" into polycystines, acantharians and phaeodarians, the vertical flux of phaeodarians was estimated in the western North Pacific (e.g., Bernstein et al. 1990), the eastern North Pacific (e.g., Takahashi 1987; Gowing and Coale 1989), the Sea of Okhotsk (e.g., Okazaki et al. 2003), the Bering Sea (Ikenoue et al. 2012), the tropical Atlantic (e.g., Boltovskoy et al. 1993a, b) and the Southern Ocean (e.g., Abelmann 1992; González 1992).

The classification system of phaeodarians has been modified by some authors (Campbell 1954; Cachon and Cachon 1985; Kling and Boltovskoy 1999; Takahashi and Anderson 2000) since Haeckel (1887) established a framework of the phaeodarian taxonomy. These systems were, however, constructed based only on the morphological criteria. Cachon and Cachon (1973) have insisted that Phaeodaria must be clearly separated from Acantharia and Polycystina because of the peculiar microtubular systems and cytological characters of Phaeodaria. However, researchers have not followed after their opinion (Anderson 1983; De Wever et al. 2001). Molecular studies focusing on protists including phaeodarians started in the first decade of this century (e.g., Polet et al. 2004; Nikolaev et al. 2004), with the result that the taxonomic position of Phaeodaria changed from a member of Retaria to one of Cercozoa, together with Foraminifera and Radiolaria (Polet et al. 2004; Yuasa et al. 2005).

9.2 Classification

9.2.1 Cercozoa

Phaeodaria are now classified as a member of Cercozoa, which are a group of protist including ebridians and chlorarachniophytes, for example. Cercozoa are first recognized as a single supergroup containing some eukaryotes whose taxonomic positions were unknown. The unity of this group was confirmed mainly by molecular analysis of 18S rDNA (Cavalier-Smith 1998). In the current classification system, the phylum Cercozoa taxonomically belongs to the Infrakingdom Rhizaria (Nikolaev et al. 2004; Sierra et al. 2013), and this phylum is divided into 14 groups (Table 9.1). This protist group includes organisms of diverse morphology: filose testate amoebae, zooflagellates, colonial flagellates, protists with axopodia, soft-bodied amoeboflagellates, amoebae with chloroplasts developed from an ingested green alga, testate reticulose amoebae, etc. (Howe et al. 2011).

Table 9.1 Classification system of the phylum Cercozoa (Adl et al. 2012)

Group	Example
Cercomonadidae	*Cercomonas*, *Filomonas*, *Brevimastigomonas*, *Neocercomonas*
Pansomonadida	*Agitata*, *Aurigamonas*
Glissomonadida	*Allantion*, *Bodomorpha*, *Neoheteromita*
Tremula	*T. longifila*
Metromonadea	*Metromomas*, *Metopion*, *Micrometopion*
Granofilosea	*Limnofila*, *Massisteria*, *Mesofila*, *Nanofila*
Thecofilosea	Cryomonadida, Ebriacea, Ventricleftida, *Phaeodaria*
Imbricatea	Spongomonadida, *Nudifila*, Marimonadidia, Silicofilosea
Chlorarachniophyta	*Chlorarachnion*, *Bigelowiella*, *Cryptochlora*, *Lotharella*
Vampyrellida	*Vampyrella*, *Arachnula*, *Gobiella*, *Hyalodiscus*
Phytomyxea	Plasmodiophorida, Phagomyxida
Filoreta	*F. japonica*, *F. marina*, *F. tenera*
Gromia	*G. sphaerica*, *G. oviformis*
Ascetosporea	Haplosporida, Paramyxida, *Claustrosporidium*, Paradiniidae

Cercozoa are attracting a lot of attention because of their ubiquitous distribution, ecological importance and high morphological variation. These protists have a wide range of habitats: in oceans, in freshwater, in soil and even within the roots of terrestrial plants (Bass and Cavalier-Smith 2004; Urich et al. 2008). Environmental DNA research revealed that cercozoan 18S rDNA is abundant in the sea floor sediments of the Arctic and the Southern Ocean (Pawlowski et al. 2011). Considering its high abundance, this group can be a significant player in the matter cycles and the food webs (Howe et al. 2011). Although their genetic unity is strongly supported, their distinctive morphological characters have not been found out yet (Adl et al. 2012).

9.2.2 Outline of Taxonomy

Phaeodaria are a cercozoan group defined by the presence of (1) a "central capsule" perforated by one astropyle and two parapylae; (2) a "phaeodium" in the extracapsular zone; and (3) a hollow siliceous skeleton called a "scleracoma", in most phaeodarians (Howe et al. 2011).

The latest classification system of Phaeodaria was formulated by examining the morphology of specimens, and the group was divided into seven orders and 18 families (Takahashi and Anderson 2000, Table 9.2). The phaeodarians belonging to the orders Aulacanthida (Figs. 9.2a and 9.3-1) and Phaeosphaerida (Figs. 9.4b and 9.3-3) are characterized by the spherical scleracoma of the radial arrangement of numerous hollow needles, spines and tubes. The Phaeogymnocellida phaeodarians are naked or surrounded with shells of other organisms such as diatoms, polycystines and silicoflagellates instead of their own scleracoma (Cachon-Enjumet 1961; Gowing and Coale 1989) (Figs. 9.4a and 9.3-2). The phaeodarians of Phaeocalpida are large in general, and this order contains five families—Tuscaroridae: flask-like form (Figs. 9.5a and 9.3-4a); Castanellidae: castanet-like sphere with round pores (Fig. 9.3-4b); Circoporidae: spherical or polyhedral with radial spines; Porospathidae: spherical with tubular spines and prolonged peristome (Fig. 9.3-4c); and Polypyramidae: polyhedral covered by pyramidal structure with spines. The Phaeogromida species are relatively small, and this order consists of three families—Medusettidae: campanulate (Fig. 9.3-5c–d); Challengeriidae: flask-like (Figs. 9.5b and 9.3-5a–b); and Lirellidae: elliptical with longitudinal grooves. The order Phaeoconchida contains only the family Conchariidae, characterized by clamshell-like scleracoma composed of two valves (Figs. 9.6a and 9.3-6). Phaeodendrida also include only one family, Coelodendridae, whose central capsule is covered with the "inner shell" extending arboroid structures (Figs. 9.6b and 9.3-7).

Phaeodaria consist of valid ~120 genera and ~500 species (e.g., Campbell 1954; Takahashi and Anderson 2000, Suzuki unpublished synonym database). When we exclude *nomina dubia* with indiscriminable illustrations or without illustrations and the taxa which have never been reported since the first description, a total of ~200

Table 9.2 Classification system of the subclass Phaeodaria (Takahashi and Anderson 2000)

Order	Family	Representative species	Figs.
Aulacanthida	Aulacanthidae	*Aulacantha scolymantha*	9.2a and 9.3-1
	Astracanthidae		
Phaeogymnocellida	Phaeodinidae	*Phaeodina antarctica*	9.4a and 9.3-2
	Phaeosphaeridae		
	Atlanticellidae		
Phaeosphaerida	Aulosphaeridae	*Auloscena verticillus*	9.4b and 9.3-3
	Cannosphaeridae		
	Sagosphaeridae		
Phaeocalpida	Tuscaroridae	*Tuscaretta belknapi*	9.5a and 9.3-4
	Castanellidae		
	Circoporidae		
	Porospathidae		
	Polypyramidae		
Phaeogromida	Challengeriidae	*Protocystis xiphodon*	9.5b and 9.3-5
	Medusettidae		
	Lirellidae		
Phaeoconchida	Conchariidae	*Neosphaeroconchidium caudatum*	9.6a and 9.3-6
Phaeodendrida	Coelodendridae	*Coelodendrum furcatissimum*	9.6b and 9.3-7

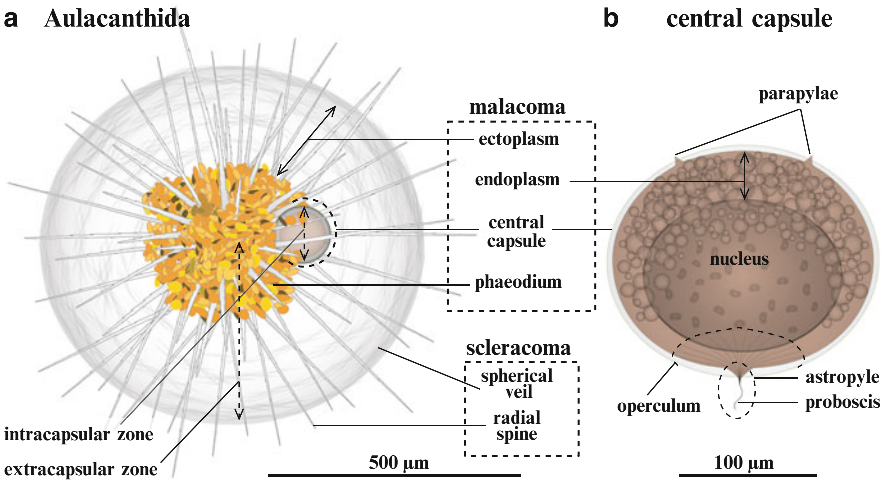

Fig. 9.2 Schematic illustrations of *Aulacantha scolymantha* Haeckel (Aulacanthidae, Aulacanthida): (**a**) overall structure; (**b**) central capsule

species belonging to ~80 genera practically exist (Fig. 9.7). Although molecular analysis allowed development of cercozoan studies, the DNA sequences of phaeodarians have never been analyzed in order to discuss their intra-group phylogenetic relationship.

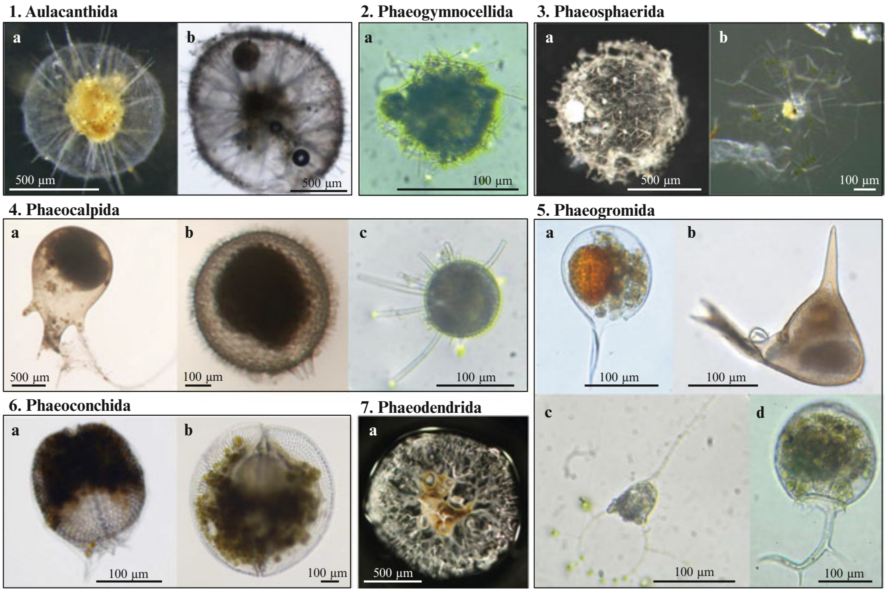

Fig. 9.3 1-a: *Aulacantha scolymantha* Haeckel (Aulacanthidae). 1-b: *Aulographis japonica* Nakamura Tuji and Suzuki (Aulacanthidae). 2-a: *Phaeodina* sp. (Phaeodinidae). 3-a: *Auloscena verticillus* Haeckel (Aulosphaeridae). 3-b: *Coelacantha ornata* Borgert (Cannosphaeridae). 4-a: *Tuscaretta belknapi* (Murray) (Tuscaroridae). 4-b: *Castanella sloggetti* Haeckel (Castanellidae). 4-c: *Porospathis holostoma* (Cleve) (Porospathidae). 5-a: *Protocystis xiphodon* (Haeckel) (Challengeriidae). 5-b: *Protocystis vicina* Reshetnyak (Challengeriidae). 5-c: *Medusetta parthenopaea* Borgert (Medusettidae). 5-d: *Euphysetta lucani* Borgert (Medusettidae). 6-a: *Neosphaeroconchidium caudatum* (Haeckel) (Conchariidae). 6-b: *Conchopsis compressa* Haeckel (Conchariidae). 7-a: *Coelodendrum furcatissimum* Haeckel (Coelodendridae)

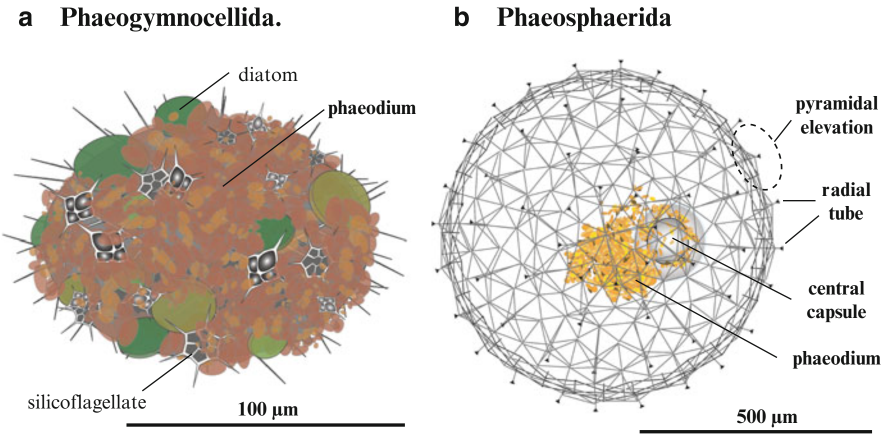

Fig. 9.4 Schematic illustrations of (**a**) *Phaeodina antarctica* (Schroeder) (Phaeodinidae, Phaeogymnocellida) and (**b**) *Auloscena verticillus* Haeckel (Aulosphaeridae, Phaeosphaerida)

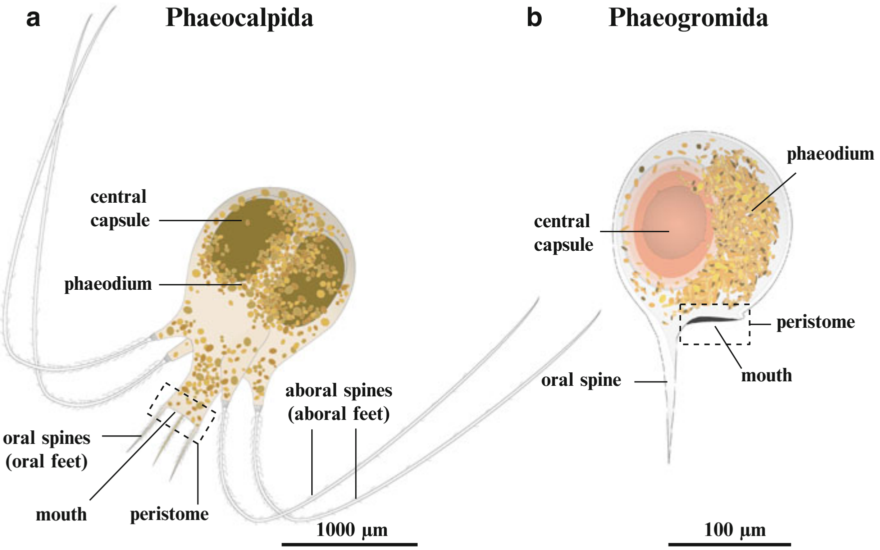

Fig. 9.5 Schematic illustrations of (**a**) *Tuscaretta belknapi* (Murray) (Tuscaroridae, Phaeocalpida) and (**b**) *Protocystis xiphodon* (Haeckel) (Challengeriidae, Phaeogromida)

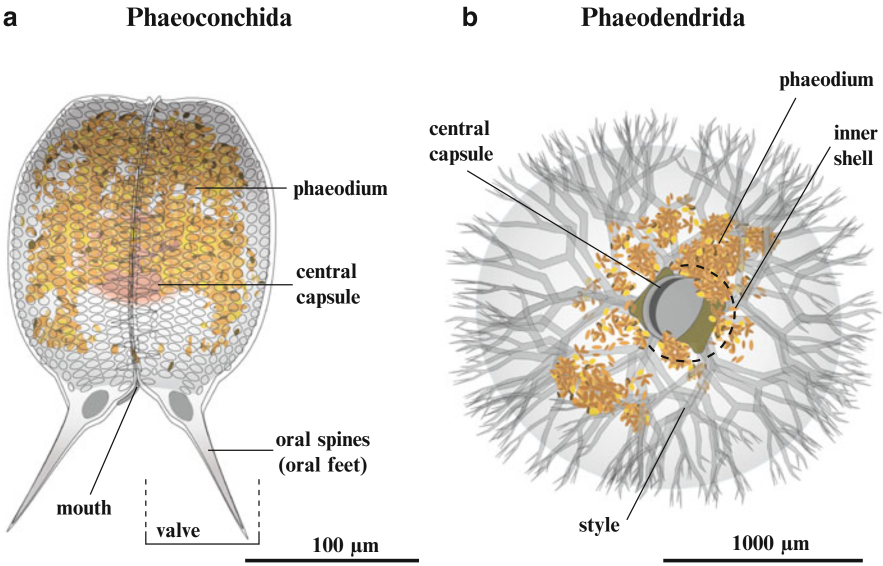

Fig. 9.6 Schematic illustrations of (**a**) *Neosphaeroconchidium caudatum* (Haeckel) (Conchariidae, Phaeoconchida) and (**b**) *Coelodendrum furcatissimum* Haeckel (Coelodendridae, Phaeodendrida)

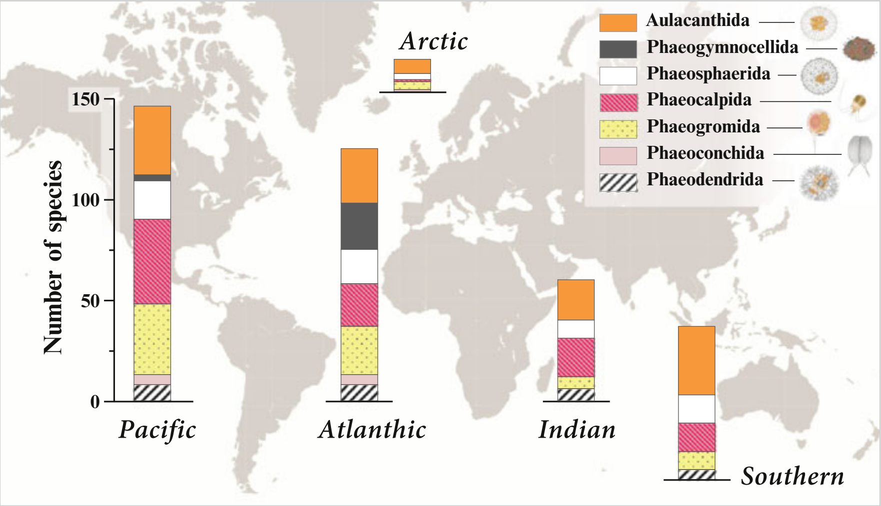

Fig. 9.7 Numbers of phaeodarian species reported from each oceanic region based on the documents published between 1966 and 2014. The composition of the orders is also indicated. Note that the "Pacific" region includes the data from the Bering Sea, the Sea of Okhotsk, the Gulf of California and the Sea of Japan; the "Atlantic" region also contains the data from the Mediterranean Sea

9.3 Cell Structure

Morphological terms concerning the structure of phaeodarians are indicated in Figs. 9.2 and 9.4–6 in accordance with major reviews of this group (Campbell 1954; Cachon-Enjumet 1961; Tibbs 1976; Kling and Boltovskoy 1999; Takahashi and Anderson 2000). Their body is mainly composed of two parts: the scleracoma (hard skeletal parts) and the malacoma (protoplasmic soft part) (Fig. 9.2).

9.3.1 Malacoma

The malacoma is a collective name for soft parts that contain the phaeodium and the protoplasm such as the central capsule and the ectoplasm. The central capsule is a spherical protoplasmic body which has the endoplasm and one or two large spherical nuclei containing a significant number of chromosomes. The endoplasm contains mitochondria, digestive vacuoles, endoplasmic reticulum and several Golgi bodies (Swanberg et al. 1986) (Fig. 9.2). The central capsule is divided from the extracapsular zone by the membranous double capsular wall. The outer wall is relatively thicker than that of radiolarians, whereas the inner wall is thinner, and these two walls are intimately connected with each other (Cachon-Enjumet 1961). This double-walled structure is one of key characteristics in Phaeodaria, which is thought to be derived from "theca", a structure characterizing the class Theofiliosea (Howe et al. 2011). The central capsule also has three characteristic pore-like structures on its surface, namely, one astropyle (or astropylum) and two parapylae (Cachon and Cachon 1973). These structures are thought to exist for communication between the ecto- and endoplasm. The astropyle is supposed to be a cytopharynx that forms a cone-like structure having cytopharynic screens of microtubules and determines the oral pole of phaeodarians (Cachon-Enjumet 1961). This pore-like structure is surrounded by a conical area called an “operculum” and usually has a tubular extension, a “proboscis”. The parapylae are orifices penetrated by the endoplasmic axopodia, which is characterized by large bundles of microtubules with a club-shaped root.

The ectoplasm is sticky and usually covered by the scleracoma. No straight stiff pseudopodia relevant to axopodia of Radiolaria have been observed in any Phaeodaria (Cachon and Cachon 1973). Some species belonging to the family Challengeriidae have two endoplasmic pseudopodia.

Another important structure characterizing the group Phaeodaria is the phaeodium, a mass of brown aggregated particles which does not exist in radiolarians (Gowing 1986, 1989; Gowing and Bentham 1994). The phaeodium are usually suspended in the extracapsular zone near to the astropyle and sometimes in the intracapsular zone (Figs. 9.2 and 9.4-6). These particles are thought to be an assemblage of food and waste vacuoles (Haecker 1908b; Cachon-Enjumet 1961; Gowing 1986, 1989, 1993; Gowing and Silver 1985; Gowing and Bentham 1994). This structure seems to be necessary for the life of phaeodarians because the phaeodium is inherited by daughter cells after the cell division (Haecker 1908b).

The terms “intracapsular zone” and “extracapsular zone” are different from “endoplasm” and “ectoplasm”. The endoplasm and the ectoplasm signify the cytoplasm positioned inside or outside of the central capsular wall, respectively. On the other hand, the intracapsular and extracapsular zones indicate the space within and without the wall. For instance, the phaeodium exists in the extracapsular zone, but does not belong to the ectoplasm.

9.3.2 Scleracoma

The scleracoma is a collective name for hard siliceous skeletal parts surrounding and supporting the malacoma, such as the test, spherical veil, spines and tubes (Figs. 9.2 and 9.4-6). This structure is generally porous and substantially different from the radiolarian skeleton. In terms of the chemical components, the scleracoma consists chiefly of silica, but it also contains various metal elements: Al and Si (>1.0 % of the wet weight of the scleracoma), Mg (1.0–0.1 %), Ca, Fe, Mg, Ti and Ag (0.01–0.1 %), V and Ba (0.001–0.01 %) (Reshetnyak 1966).

The appearance of scleracoma is characteristically different among the orders and the families. The scleracoma of the orders Aulacanthida and Phaeosphaerida is generally spherical and composed of the radial arrangement of numerous hollow needles, spines and tubes. Aulacanthida (Figs. 9.2a and 9.3-1) have spheres of meshwork called a “spherical veil”, whereas Phaeosphaerida (Figs. 9.4b and 9.3-3) form more geometric spheres made of numerous “tubes”. Phaeocalpida, Phaeogromida and Phaeoconchida have scleracoma forming a relatively firm test. The form of their tests can be flask-like (e.g., Tuscaroridae, Figs. 9.5a and 9.3-4a; Challengeriidae, Figs. 9.5b and 9.3-5a–b), chestnut-like (Castanellidae, Fig. 9.3-4b), campanulate (e.g., Medusettidae, Fig. 9.3-5c–d), clamshell-like (Conchariidae, Figs. 9.6a and 9.3-6) and polyhedral (e.g., Circoporidae). The scleracoma of the order Phaeodendrida is very characteristic. Their central capsule is covered with the “inner shell” extending arboroid, hollow “styles” branching into numerous spines (Figs. 9.6b and 9.3-7). Most of the species belonging to the order Phaeogymnocellida lack the scleracoma, and they are encircled by shells of other organisms such as diatoms, polycystines and silicoflagellates (Cachon-Enjumet 1961; Gowing and Coale 1989) (Figs. 9.4a and 9.3-2). This order seems to select the materials encircling its malacoma: *Miracella ovulum* Borgert (Atlanthicellidae) aggregates silicoflagellates *Dictyocha* and polycystines, while *Phaeodina valdiviae* Haecker (Phaeodinidae) is surrounded with centric diatoms only (Gowing and Coale 1989).

The internal structure of the test-type scleracoma differs among the families. Challengeriidae have a double-walled platy test with an hourglass-like cross-section surface, whereas the tests of Medusettidae have a porous cross-section surface. The tests of Lirellidae and Castanellidae consist of very fine spongy structures. Conchariidae usually have numerous pores on its surface (Takahashi and Hurd 2007).

9.4 Mode of Life

Phaeodarians seem to lack a swimming organ, and this protist is incapable of swimming against the current. They float in the water column presumably by maintaining the neutral buoyancy (Swanberg et al. 1986).

Almost all the phaeodarians are considered to be solitary plankton, but some species belonging to the families Coelodendridae and Tuscaroridae form colonies (Kling and Boltovskoy 1999). The genus *Coelographis* (Coelodendridae) is observed to be sometimes connected to each other by their styles (Swanberg et al. 1986). *Tuscaretta globosa* Borgert and *Tuscaridium cygneum* (Tuscaroridae) are attached on the surface of an intricate “latticed sphere” composed of siliceous rods (Haecker 1908a, Fig. 9.8). The colony of *Tuscaridium cygneum* (Murray) consists of 8–16 individuals, and they hook on the surface of the latticed sphere of 1.2–2.0 cm in diameter (Takahashi 1987, Ling and Haddock 1997).

Little is known about the ecology of phaeodarians, but some interesting features have been reported. Like other deep water marine organisms, *Tuscaridium cygneum* produces a bioluminescent glow probably for distraction to visual predators (Ling and Haddock 1997). Several individuals of *Aulacantha scolymantha* (Aulacanthidae), sampled from the shallows of the northern Mediterranean, showed molt-like behavior. They reconstructed new spherical veils and threw off the original ones which were damaged through the sampling process after the 24 h incubation (Fig. 9.9). This behavior was also seen for a scleracoma-less species of the family Phaeodinidae.

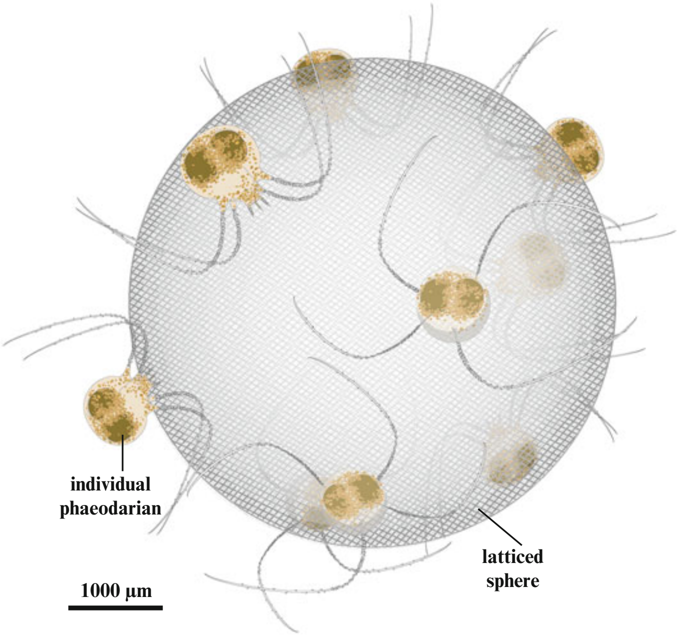

Fig. 9.8 Colony of *Tuscaretta globosa* Borgert (Tuscaroridae), referred from Haecker (1908a)

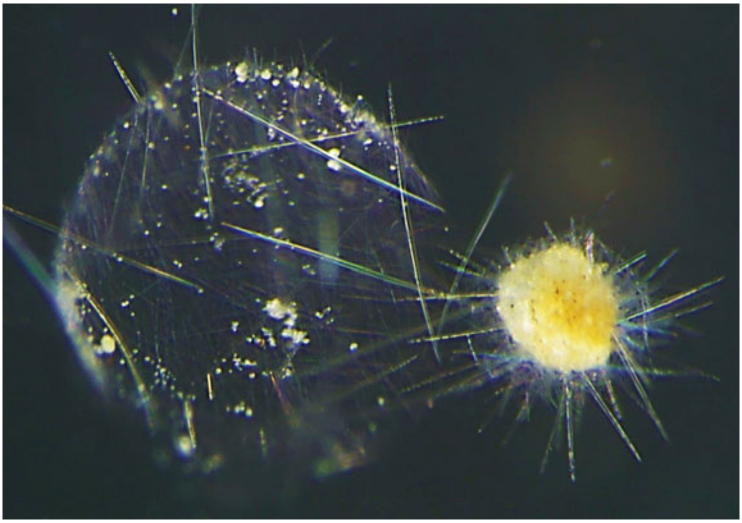

Fig. 9.9 Molt-like behavior of *Aulacantha scolymantha* (Aulacanthidae) sampled in the northern Mediterranean, off the coast of Villefranche-sur-Mer. This individual reconstructed a new spherical veil and got out of the original one damaged through the sampling process after 24 h incubation

9.5 Reproduction

Phaeodarians are thought to reproduce by cell division and by swarmer production (Grell 1973; Hollande 1981; Cachon and Cachon 1985), but the complete life cycle has never been replicated in the laboratory.

9.5.1 Cell Division

Binary division of three genera, *Aulacantha* (Aulacanthidae), *Aulosphaera* (Aulosphaeridae) and *Coelodendrum* (Coelodendridae), was well documented (Cachon-Enjumet 1961). It is confirmed that the division is accompanied by morphological change of chromosomes. Its interpretation has, however, been the subject of controversy whether the division is mitotic (Borgert 1901, 1909d; Bělař 1926; Cachon-Enjumet 1961) or a simple genomic segregation (Grell 1953; Grell and Ruthmann 1964). The most likely process of the nuclear division of *Aulacantha scolymantha* is summarized herein according to Borgert (1909d), Cachon-Enjumet (1961) and Grell (1973).

Metaphase The chromosomes do not align at the equator plane of a spindle unlike the normal binary division. They form a contorted "mother plate" within which they are oriented parallel to the direction of movement and not perpendicular to it. At the end of this process, the nuclear membrane vanishes.

Anaphase The mother plate divides into two daughter plates. The daughter plates are at first still contorted, and then they form plane parallel discs.

Telophase The daughter plates reach a certain distance from each other. The nuclear membrane is reconstructed. The daughter nucleus has a radial structure because of the chromosomes directed toward the outside. The endoplasm splits into two parts. The capsular walls envelop the two masses of the endoplasm covering the daughter nuclei.

Cytokinesis The ectoplasm, phaeodium and scleracoma are completely separated. The original cell becomes two daughter cells.

9.5.2 Swarmer Production

The swarmer production (or sporogenesis) of two species has been reported previously: *Coelodendrum ramosissimum* (Coelodendridae) and *Aulacantha scolymantha* (Aulacanthidae). The capsular membrane and the phaeodium vanish first, and several “plasmatic spheres” of different size appear within the scleracoma. Then, these plasmatic spheres, containing numerous interphasic secondary nuclei, fall apart into small cells. The cells form two long flagella and become swarmers. They swim out from the scleracoma in the end. Each swarmer possesses crystalline inclusions, therefore they are called "crystal swarmers" (Grell 1973; Cachon and Cachon 1985). Two types of swarmers have been observed: isospores and anisospores. Some researchers suggest that the "anisospores" of *A. scolymantha* are actually parasitic dinoflagellates (Chatton 1934; Hollande and Enjumet 1953). Although the sexuality of phaeodarians is still unknown, the swarmers are thought to be gametes (Borgert 1909d).

9.6 Trophic Interactions

9.6.1 Feeding

Phaeodarians are supposed to be heterotrophic feeders and omnivorous generalists (Gowing 1986, 1989; Swanberg et al. 1986; Gowing and Bentham 1994; Nakamura et al. 2013). As this group cannot swim against the current, most of them seem to float in the water column and to obtain the food coming close to them. They feed generally on particles and cells associated with fecal pellets and aggregates (Gowing 1989; Nöthig and Gowing 1991). *Coelographis* sp. (Coelodendridae) presumably prey on living organisms over a wide range of size. This phaeodarian catches large metazoans such as copepods and salps by the styles, and captures microflagellates by the spathillae (Swanberg et al. 1986).

The captured food is taken into the extracapsular zone, then accumulated within the food vacuoles forming the phaeodium. The food vacuoles of some families (Aulacanthidae, Phaeodinidae, Atlanticellidae, Cannosphaeridae, Lirellidae, Porospathidae, Challengeriidae, Medusettidae and Conchariidae) contain various organic materials: algal cells (diatoms, dinoflagellates, chrysophytes, prasinophytes, *Chlorella*-like cells and algal cysts), microheterotrophs, bacteria, loricae and nematocysts of metazoans, coccoliths, trichocysts, cuticles, amorphous material and siliceous skeletal fragments (Gowing 1986, 1989, 1993; Gowing and Bentham 1994). Vacuoles are present not only in the extracapsular zone but also in the intracapsular zone. The vacuoles filled with partially digested organic matter are observed within the central capsule, suggesting that a part of the food is carried into the intracapsular zone through the astropyle, presumed cytopharynx (Cachon and Cachon 1973; Swanberg et al. 1986).

Phaeodarians inhabit variable depths, so it is presumed that the compositions of the food vacuoles change depending on the depth. The composition of the vacuoles in each depth is similar to that of sinking organic aggregates in the oligotrophic North Pacific, suggesting that phaeodarians selectively feed on organic aggregates rather than bacteria, which is more abundant in the area (Gowing and Bentham 1994).

Scleracoma of some phaeodarians occasionally contains partially ingested diatom frustules, therefore they may directly feed on phytoplankton, depending on the environment (González 1992).

9.6.2 Predators and Symbiosis

Some zooplankton are known to consume phaeodarians but details are not well clarified yet (Raymont 1983; Hopkins 1985; Hopkins and Torres 1989). Only one species has so far been reported as a predator of phaeodarians: a non-selective particle feeding salp, *Salpa thompsoni*, in the western Weddell Sea and near the Antarctic Peninsula (Gowing 1989).

Phaeodarians are often infected with dinoflagellates: *Syndinium borgerti* (host: *Aulacantha scolymantha*, Aulacanthidae), *Syndinium* sp. (host: *Coelodendrum* sp., Coelodendridae), *Atlanticellodinium tregouboffi* (host: *Planktonetta atlantica*, Medusettidae) (Hollande and Enjumet 1955; Cachon and Cachon 1987; Hollande 1974; Théodoridès 1989). These parasitic dinoflagellates are considered to multiply in the central capsule of the host phaeodarian, resulting in the death of the host. Some of these dinoflagellates are apparently similar to the phaeodarian swarmers (Grell 1973). It is also reported that numerous bacteria (50–100 x 10^3 cells g^{-1} of wet phaeodarians) are attached to *Castanidium longispium* (Castanellidae) (Jones 1958). Although many radiolarians have symbiotic microalgae, phaeodarians have been thought to lack symbionts.

9.7 Distribution

9.7.1 Global Distribution

Phaeodarians are largely distributed in the water mass below 150 m in the tropical and subtropical regions, but they also occur in the surface layer of high-latitude regions, such as the Sea of Okhotsk and the Southern Ocean (Nöthig and Gowing 1991; González 1992). Bipolar distributions are recognized for nine species (e.g., *Aulastrum spinosum*, *Sagenoscena irmigeriana* and *Aulacantha laevissima*) (Reshetnyak 1966). Their species diversity is the highest in the Pacific region (approximately 150 species) and the lowest in the Arctic region (approximately 15 species) (Fig. 9.7). These numbers may, however, not reflect the true species diversity, because the species compositions of phaeodarians were thoroughly examined in limited sampling sites.

The composition of phaeodarians at order level is different between the oceanic regions. The species number of the order Phaeodendrida is almost the same in every oceanic region except the Arctic, even though the numbers of other orders differ greatly. The order Phaeogymnocellida also shows a marked difference, they have been found mainly in the Atlantic region. The large part of this order was described in the Mediterranean Sea, with the result that their proportion is relatively high in the Atlantic region (Fig. 9.7).

The zoogeographic zonation of phaeodarians can be divided into three regions, namely (1) the Pacific and North Indian deep water region; (2) the Atlantic deep water region; and (3) the Antarctic deep water region, according to Reshetnyak (1966) (Table 9.3). The Pacific and North Indian deep water region is further subdivided into three sub-regions: the boreal North Pacific, the tropical Pacific and the North Indian. The Atlantic deep water region is also subdivided into three sub-regions: the Arctic, the boreal North Atlantic and the tropical Atlantic. The Antarctic deep water region contains three sectors: the Atlantic, the Indian and the Pacific. This zonation is made based on the degrees of endemism of the phaeodarian assemblages. Since the information concerning their distribution was limited in the time of Reshetnyak (1966), it is necessity to verify these zoogeographic data by examining the reports published after this paper.

9.7.2 *Vertical Distribution*

Phaeodarians have long been regarded as "deep-sea plankton" since Haeckel (1887). This is partly true because a large part of phaeodarian species live in 1000–4000 m water depth (Reshetnyak 1955), but it is not the case for every species. *Aulacantha scolymantha* (Aulacanthidae) and *Phaeodina* spp. (Phaeodinidae) are abundant in

Table 9.3 Global zoogeographic zonation of phaeodarians (Reshetnyak 1966)

Region	Number of endemic genus	Sub-region	Number of endemic species and subspecies
Pacific and North Indian deep water	10 (e.g., *Auloplegma, Sagoplegma*)	Boreal North Pacific	13 (e.g., *Aulacantha pacifica, Castanissa megastoma*)
		Tropical Pacific	143 (e.g., *Cannobelos calymnata, Aulactinium actinastrum*)
	2 (e.g., *Aulaphacus, Cirorrhegma*)	North Indian	43
Atlantic deep water	0	Arctic	9 (e.g., *Aulosphaera multifurca, Haeckeliana labradoriana*)
	6 (e.g., *Porcupinia, Coelodasea*)	Boreal North Atlantic	9 (e.g., *Aulocoryne zetesios, Cannosphaera antarctica*)
		Tropical Atlantic	160 (e.g., *Cannobelos thalassoplancta, Astracantha heteracanthoides*)
Antarctic deep water	3 (e.g., *Aulodictyum, Conchasma*)	Atlantic sector	4 (e.g., *Sagenoarium anthophorum, Protocystis micropelectus*)
		Indian sector	23 (e.g., *Phaeodina antarctica, Sagoscena pellorium*)
		Pacific sector	7 (e.g., *Aulactinium actinosphaerium, Castanidium antarcticum*)

the warm surface layer of the Mediterranean Sea (e.g., Cachon-Enjumet 1961). The species diversity of phaeodarians increases with the depth, reaching the highest (approximately 50 species) in the deepest layer (6000–8000 m) in the Kuril-Kamchatka Trench (Reshetnyak 1955, 1966). A similar tendency is also reported in the Gulf of California (Zasko and Rusanov 2005). The cell size of deep-living phaeodarians tends to be larger than that of the same or related species dwelling in shallower zones (Haecker 1908a; Reshetnyak 1966; Zasko and Rusanov 2005).

Their vertical distribution is probably species specific. Several species belonging to the family Castanellidae show clearly different vertical distributions (Kling 1976). Challengeriid species were also collected from variable depth intervals in the North Pacific (Okazaki et al. 2004). The vertical distribution of phaeodarians at species level can be categorized into two types: eurybathic (widely distributed from the epipelagic to the hadal zone) and stenobathic (living in limited depth layers). The eurybathic species have wider horizontal distribution than the stenobathic phaeodarians (Zasko 2003; Zasko and Rusanov 2005). The stenobathic species in the Kuril-Kamchatka Trench are subdivided into the following five categories: surface (0–50 m), subsurface (50–200 m), middle bathyal (200–1000 m), bathypelagic (1000–2000 m) and superabyssal (4000–8000 m) (Reshetnyak 1955, 1966).

9.8 Interactions with the Environment

9.8.1 Restricting Factors of Phaeodarian Distribution

The distribution of phaeodarians is partly influenced by the water temperature. Five challengeriid species are sampled from cold waters of less than 5 °C, whereas two different species are collected in the water masses of higher temperature (Meyer 1933) (Table 9.4). Their temperature-dependent distribution is seen in the Sea of Japan too. *Aulographis japonica* (Aulacanthidae) is found only in the water mass of low temperature (approximately 1 °C) (Nakamura et al. 2013). Their vertical distribution pattern is also influenced by the amount of food. As phaeodarians are generalist feeders and presumably feed upon organic aggregates in general, they prefer to be suspended in the zones where plenty of plankton or POM sinking from

Table 9.4 The range of water temperature at the sampling stations of the species belonging to the family Challengariidae (Meyer 1933)

	Water temperature (°C)	
Species	Lowest	Highest
Protocystis micropelecus	2.5	3
Protocystis gravida	3	4
Protocystis swirei	−1	5
Protocystis triangularis	0.5	5
Protocystis thomsoni	2	5
Challengeron willemoesii	5	12
Protocytis varians	5	18

the upper layers. Phaeodarians are abundant in the surface layer of the Weddell Sea, where krill fecal pellets, on which they feed, are more plentiful (González 1992). Another possible restricting factor of their distribution is silica. Certain species change their living depths probably in relation to the concentration of dissolved silica in order to easily build their scleracoma (Bjørklund 1974; Okazaki et al. 2004). These restricting factors could account for the observed patchy distribution of this protist group (Bernstein et al. 1990).

9.8.2 Biomass

The abundance of phaeodarians does not increase with the depth, unlike the species diversity which grows with the depth. Their abundance reaches the maximum in the lower epipelagic or mesopelagic zone of the Antarctic (Morley and Stepien 1984; Abelmann 1992), the North Pacific (Steinberg et al. 2008) and the Sea of Japan (Nakamura et al. 2013). However, the reported abundance of phaeodarians is presumably underestimated because their scleracoma is fragile, and it could easily be broken during net sampling. Most of the coelodendrid phaeodarians have never been caught by normal plankton-net sampling. Aulosphaeridae and Cannosphaeridae are commonly captured in the subtropical shallow waters, but they are often crumpled up. The species of the Order Phaeogymnocellida have been erroneously regarded as “marine snow” or “sinking aggregates” due to the absence of scleracoma or to their body surrounded by siliceous dead remains of diatoms, polycystines and silicoflagellates. These phaeodarians can be identified by dyeing their nuclei using DAPI (Gowing 1989; Gowing and Coale 1989).

Careful examination of phaeodarian abundances revealed that these protists are more numerous than expected, and their high abundance is occasionally reported. Their vertical flux is much higher than that of polycystines in the Panama Basin (Takahashi and Honjo 1983) and on the California coast (Gowing and Coale 1989). The biomass of the families Aulosphaeridae, Sagosphaeridae, Aulacanthidae and Coelodentridae occupies 2.7–13.7 % of the total metazoan biomass in the 150–1000 m layer of the western North Pacific (Steinberg et al. 2008). The dominance of the family Aulacanthidae is also reported in the Sea of Japan. The proportion of *Aulographis japonica* with respect to the total zooplankton biomass is 22.3 % in the 250–3000 m layer, which is the second largest, following that of copepods (Nakamura et al. 2013). Considering their high biomass, especially in deep waters, this protist group would play an important role in the local food webs.

9.8.3 Seasonality

The seasonality of phaeodarian vertical flux seems to depend on the oceanic region. The total phaeodarian flux shows a regular seasonal cycle and peaks in spring and fall–winter at 3198 m depth of the Bering Sea (Ikenoue et al. 2012). The peaks of their flux were seen in summer and spring at 853 m depth in the equatorial eastern

Atlantic (Boltovskoy et al. 1993b). These data are, however, the sum total of their flux, and the flux seasonality of each species possibly differs. Two congeneric species of the family Medusettidae (*Euphysetta staurocodon* and *E. elegans*) show the flux peak in different seasons in the eastern North Pacific (Takahashi 1987).

9.8.4 Importance in the Matter Cycle

The high biomass of phaeodarians suggests that they have a significant influence on the matter cycles of the world ocean. The cell size of some phaeodarians (e.g., Aulacanthidae) is generally larger than that of other heterotrophic siliceous protists such as polycystines (Takahashi and Honjo 1983). Therefore, even though phaeodarians are less abundant than other plankton in number, their contribution to the silica flux could become larger. The large part of silica flux usually comes from diatoms in the western North Pacific, but heterotrophic siliceous protists show higher contributions in several stations because of large phaeodarians (Bernstein et al. 1990). In addition, phaeodarians accumulate ingested organic matter within the phaeodium, and the volume of silica gathered in this part becomes as much as that of their scleracoma (Gowing and Coale 1989). The vertical flux of scleracoma-less phaeodarians is estimated to be almost equal to that of scleracoma-bearing phaeodarians in the eastern North Pacific (Gowing and Coale 1989).

The mini pellets are mass of digested organic matter ejected by plankton, and this substance is thought to play an important role in matter cycle (Gowing and Silver 1985). Phaeodarians could occasionally be a major producer of mini pellets (Gowing and Coale 1989; Nöthig and Bodungen 1989; Buck et al. 1990; González 1992). They transform organic particles into mini pellets sinking into deeper layers in the North Pacific (Gowing and Bentham 1994). The number of mini pellets (4.89×10^5 pieces m^{-3}) is reported to be extraordinarily larger than that of krill feces (8.7 pieces m^{-3}) in the Weddell Sea, and these pellets are important as a nutrition source for marine organisms (González 1992).

9.9 Fossil Records

Phaeodarian scleracoma is so fragile that their fossils are rarely found. Even in the area where they are abundant in the water column, the sediments on the sea floor seldom contain their remains except in the Norwegian Sea (Stadum and Ling 1969). In spite of the large number of “radiolarian” studies (e.g., Suzuki and Aita 2011), phaeodarian fossils are limitedly reported: the Rhaetian (uppermost Triassic) of Japan (Hori et al. 2009); the Upper Cretaceous of Sakhalin (Bragina 2003), Japan (Takahashi 2004), and the Southwest Pacific subsurface sediments (Dumitrica and Hollis 2004); the upper Paleocene of Denmark (Dumitrica and Van Eetvelde 2009);

the upper Eocene (Petrushevskaya and Reshetnyak 1980; Vitukhin 1993); the Miocene of Romania (Dumitrica 1964, 1965) and Kamchatka (Runeva 1974); and the Miocene to the Quaternary of the sea floor sediments in the South Atlantic (Ling 1991) (Fig. 9.10). The family Conchariidae was once reported from the lower Cambrian in China (Hao and Shu 1987; Shu and Chen 1989), but these fossils were later confirmed as parts of extinct metazoans, lobopodians (Chen et al. 1995, Zhang and Aldridge 2007).

The large part of the fossil phaeodarians is occupied by members of the families Challengeriidae and Medusettidae. Only a few reports concern other families. The oldest fossil phaeodarian specimens were sampled in Rhaetian strata (208.5–201.3 million years ago): *Medusetta japonica* and *Triassiphaeodina niyodoensis* (Medusettidae) (Hori et al. 2009, Fig. 9.10). It is noteworthy that the genus *Medusetta* is an extant genus. This Rhaetian sample comes from a deep water sedimentary rock in association with pelagic polycystines, suggesting that these phaeodarians were members of the deep-sea pelagic fauna. The second oldest fossil records jumps to the Cenomanian (the lowest Upper Cretaceous), 100 million years later from the Rhaetian, from the Bykov Formation in southern Sakhalin (Bragina 2003, Fig. 9.10). This report is of particular importance because this is the oldest record of the Challengeriidae. Other genera of this family have been discovered as fossils from the upper Campanian–lower Maastrichtian (Takahashi 2004; Dumitrica

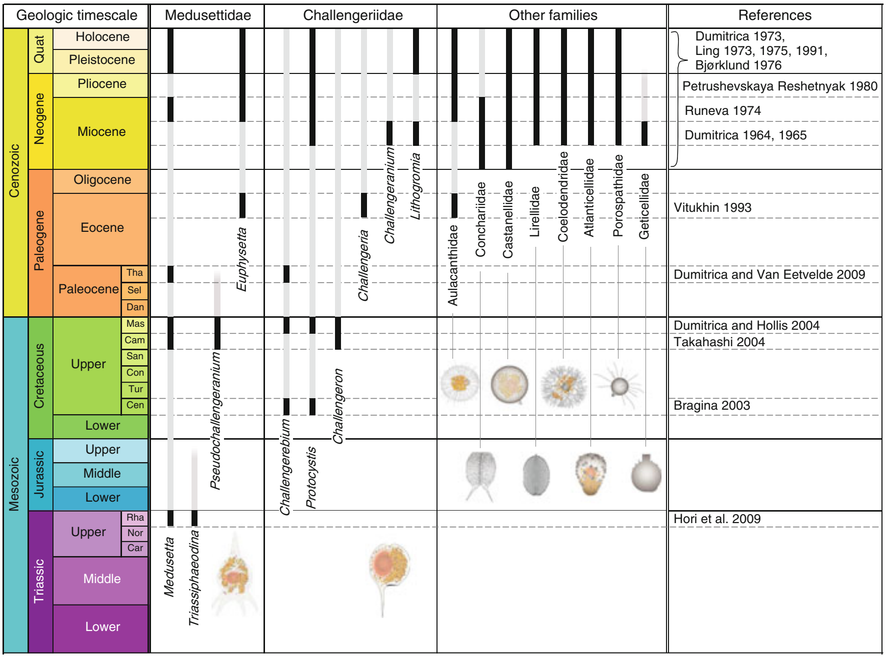

Fig. 9.10 Geologic range of phaeodarians. *Black vertical bar* indicates the age with fossil evidence, whereas the *gray one* shows the age without fossil evidence. Note that all the fossil reports published until 2014 are included in this figure

and Hollis 2004) to the Holocene (Dumitrica 1973), probably because of the intermittent records. Only a few records are reliable concerning other families (Fig. 9.10). The remains of the radial spine probably belonging to the family Aulacanthidae (or morphologically similar families) are found from the upper Eocene (Vitukhin 1993). The oldest records of the families Conchariidae and Castanellidae are noted from the lower Miocene (Dumitrica 1973). From the middle Miocene, the oldest fossils of the following families are sampled: Lirellidae, Coelodendridae, Atlanticellidae and Porospathidae (Dumitrica 1973, Ling 1991). Dumitrica (1965) described a fossil genus *Geticella*, which was decided to belong to the extinct family Geticellidae, from the middle Miocene in Romania. A total of ten genera of the families Challengeriidae and Medusettidae have so far been reported as fossils since the Rhaetian (Fig. 9.10), but extinct genera are only two: *Triassiphaeodina* from the Rhaetian (Hori et al. 2009) and *Pseudochallengeranium* from the upper Campanian–lower Maastrichtian (Dumitrica and Van Eetvelde 2009). The fact that most phaeodarian genera have remained until today suggests that their evolutionary rate is relatively slow for the genus level. The extant genera survived through many global oceanic crises, such as oceanic anoxic events at the Toarcian (Lower Jurassic) and the Cretaceous as well as the Cretaceous–Paleogene mass extinction.

Delicate and fragile fossils are generally found from the Lagerstätte, the strata with extremely well-preserved fossils such as Burgess Shale and Ediacara Hills (see Suzuki and Oba, this volume). The phaeodarians of the Rhaetian, the Maastrichtian and the upper Paleocene are found from nodules or soft sediments, a kind of Lagerstätte (Dumitrica and Hollis 2004; Dumitrica and Van Eetvelde 2009; Hori et al. 2009). These phaeodarians may be preserved under the following conditions (Dumitrica and Van Eetvelde 2009): (1) the mineralogical replacement of the original phaeodarian silica to celestobarite ($BaSrSO_4$), a complete solid solution series between barite ($BaSO_4$) and celestite ($SrSO_4$); (2) exclusive of clays in nodules and concretions; and (3) protection of the siliceous scleracoma from the effects of compaction and destructive pore-fluids percolating through the host sediments. However, other factor could be attributed to the fossilization of phaeodarians because the upper Campanian–lower Maastrichtian phaeodarians are obtained from a “normal” siliceous mudstone sample after chemically sever treatment with hydrofluoric acid (Takahashi 2004).

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