Class Phaeodaria

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CLASS PHAEODAREA

by KOZO TAKAHASHI and O. R. ANDERSON

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Phaeodaria are oceanic protists with porous skeletons composed of biogenic opal with organic substances and traces (to 1%) of Mg, Ca, and Cu. They are included in the artificial grouping of radiolaria in the older literature and are found in major oceanic locations, dwelling from the near surface to great depths (4000 to 8000 m) in the water column (e.g. Haeckel, 1887, Anderson, 1983; Takahashi, 1987, 1991). Skeletal sizes vary from approximately 50 µm for some genera to several hundred micrometers for many genera. Some large species are easily visible with the unaided eye. The skeletons of *Aulosphaera* (Fig. 20) and other large, geodesic, spherical genera may be several millimeters in diameter, and other genera such as *Coelographis* (Fig. 3) with long arm-like extensions can be tens of millimeters in over-all dimensions. Due to the porous structure and different chemical composition of the phaeodarian skeleton relative to the polycystines, they are less resistant to dissolution in marine sediments. Hence, the phaeodaria are less represented in the microfossil record (e.g. Takahashi et al., 1983).

Phaeodaria typically lack algal symbionts. Current knowledge of their role in marine food webs is meager although prey has been documented for some species. Phaeodaria appear to be generalists consuming a wide range of particulates including bacteria, *Chlorella*-like cells, other algae, diatoms, scale-bearing algae, tintinnids, crustacea, and "olive-green detrital matter" (Gowing, 1986, 1989; Nöthig and Gowing, 1991; Gowing and Garrison, 1992; Gowing and Wishner, 1986, 1992). *Coelographis* sp., a large phaeodarian with long skeletal styles, collected by SCUBA divers, contained ingested detrital matter, metazoans, flagellates, copepods, and gelatinous organisms (Swanberg et al., 1986). Additional information on phaeodarian ecology in relation to polycystines is presented in Anderson (1983, 1993).

Morphology . Much of the classification is based on the skeletal morphology. Major skeletal types include those with bilateral symmetry (e.g. bivalve shells resembling microscopic clams, Fig. 8), radial symmetry (forming geodesic spheres of

remarkable complexity, Fig. 20), and multi-symmetry with polyhedral or more complex geometric forms (Figs. 13,14,35,47). The central capsular membrane (arrow, Fig. 25) is thick relative to other radiolaria and contains two major kinds of pores, each with a cytoplasmic strand that projects into the surrounding environment: 1) "**astropylum**" or **oral pore** with a large opening and massive cytoplasmic extension (A in Fig. 25) from the central capsular cytoplasm and 2) "**parapylae**" (P in Fig. 25), usually two pores, and smaller in diameter, at the opposite pole (Fig. 25). Digestion of prey can occur in the extracapsulum or within the **intracapsulum** by ingestion through the astropylum. A dense mass of darkly pigmented, undigested debris (**phaeodium**, Fig. 2a,b) is suspended in the **extracapsular cytoplasm**, usually in the vicinity of the oral region at one pole of the central capsule. The vegetative nucleus is large and spherical (only rarely cordiform) and occupies nearly all of the **central capsule** (Fig. 22). During reproduction, the cytoplasm becomes divided into numerous small swarmers, each containing a nucleus with eight chromosomes.

Some genera such as *Phaeodina* (Fig. 1) lack skeletal elements or are surrounded by shells of other protists. Other genera, such as *Aulacantha* (Fig. 2), contain only a loose arrangement of radially directed individual spicules embedded within the extracapsular cytoplasm, but many have more massive skeletal structures (Figs. 10,15,26,38). The skeleton can be bilaterally symmetrical with two halves forming a bivalve resembling a clam (Fig. 3), campanulate (Fig. 29), or nearly spherical (e.g. Figs. 15,16). *Others have hollow tubular skeletal elements forming meshworks (Fig. 24), geodesic spheres* (Fig. 20), and complex frameworks surrounding the central capsule. Skeletal surface structures include spines (Fig. 13) and verticillate extensions, i. e. ray-like extensions with many whorls of lateral spines (Fig. 22). A tubular elongation of the skeletal opening (**peristome**) *near the mouth can be cylindrical (arrow, Fig. 18)* or trumpet-shaped (arrow, Fig. 12) and may be connected to a circular arch (Fig. 11). Massive arm-like extensions of the skeletal framework occur in some genera. These may form paired **styles** (arrow, Fig. 3) supporting a meshwork or lattice mantle. Major projections known as horns (large arrow, Fig. 4), or in other genera, feet (arrow, Fig. 42) may extend from the periphery of the shell, and there may be a ridge-like keel as in *Conchidium* (arrow, Fig. 4). The surface of the mesh may be ornamented by numerous spine-like extensions with swollen or expanded tips (Figs. 3,20,23). The surface of the shell may be smooth (Fig. 26), dimpled (Fig. 37), or ridged (Fig. 4).

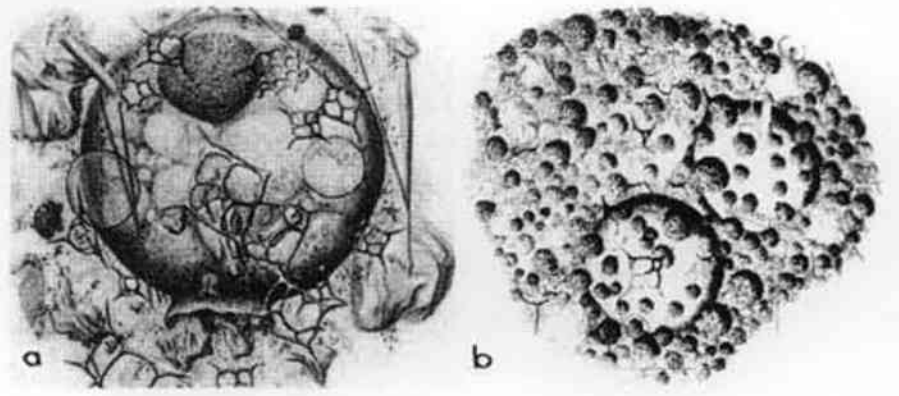


Fig. 1. Families Phaeosphaeridae and Phaeodinidae. 1a. *Phaeopyla spherica* Cachon-Enjumet, 1961. 1b. *Phaeodina valdivia* (Haecker, 1908).

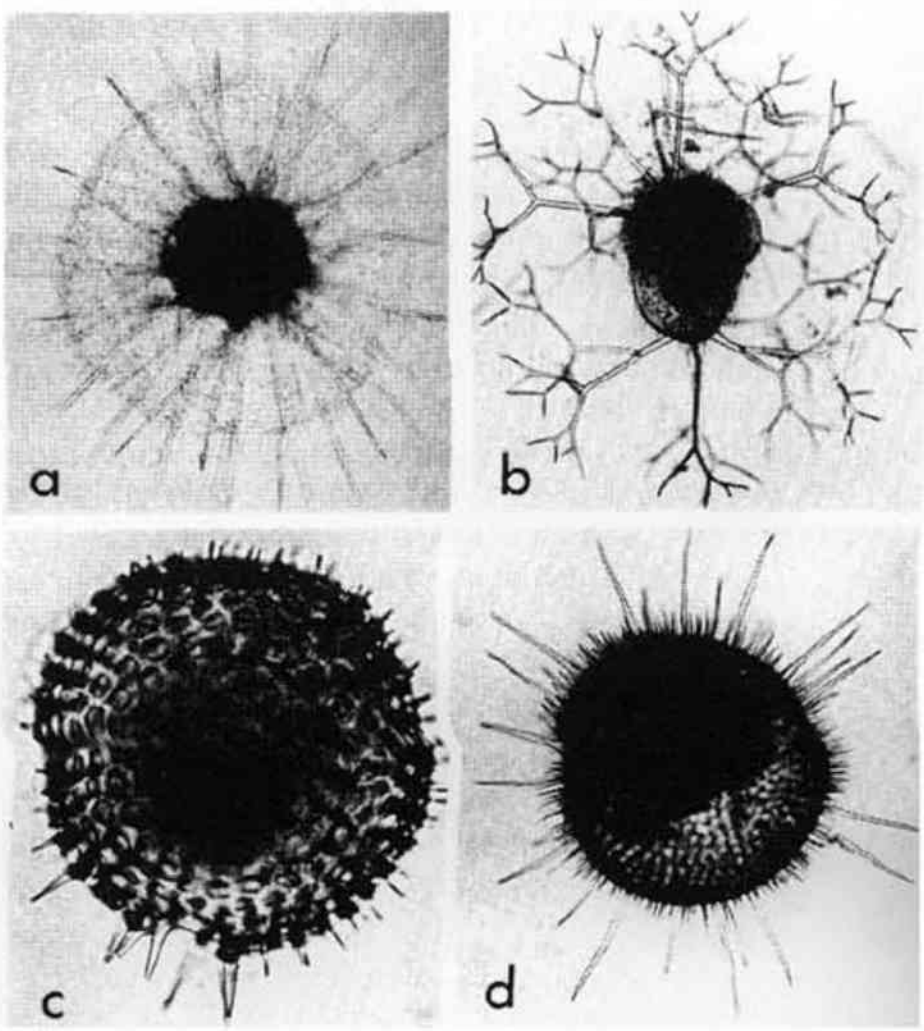


Fig. 2. Families Aulacanthidae, Coelodendridae, Castenellidae. 2a. *Aulacantha scolymantha* Haeckel, 1982. 2b. *Coelodendrum ramosissimum* Haeckel 1962. 2c. *Castanella wivillei* Haeckel, 1887. 2d. *Castanissa valdiviae* Haecher, 1907 (all alive).

Taxonomy. The taxonomy of the Phaeodaria needs extensive modern revision as is generally true for the "radiolaria." Much of our current taxonomy is based on the extensive systematics

published by Haeckel (1887), but it is clearly artificial. A synopsis of current thought on taxonomy at the level of Family is presented here (Anderson, 1983, Cachon and Cachon, 1985, Takahashi, 1991) though it may change substantially with increasing evidence from fine structural and perhaps molecular taxonomic research.

The following key to some major living genera is not a natural grouping, but a practical guide to some commonly observed genera collected in plankton samples.

KEY TO MAJOR LIVING GENERA

1. Skeleton lacking or composed of radiating loose spicules I
1'. Skeleton entire, robust or composed of rods in framework..... II

I. GENERA WITHOUT SKELETONS

1. No skeleton, loosely aggregated scales and spicules collected from other protists..... 2
1'. Radially arranged needle-like spicules, not connected ..... ***Aulacantha***

2. Phaeodium extra- and intracapsular, with thick capsular membrane..... ***Phaeopyla***
2'. Phaeodium extracapsular only..... ***Phaeodina***

II. GENERA WITH SKELETONS

1. With bivalves 2
1'. Without bivalves 6

2. With long paired styles, rhinocanna (nasal tube), and outer lattice-mantle. ***Coelographis***
2'. Without styles 3

3. With two horns, one on each valve at aboral hinge, lenticular, with keel ..... ***Conchidium***
3'. Without horns..... 4

4. Spherical bivalves 5
4'. Lenticular bivalves, and keel..... ***Conchopsis***
4". Lattice with circular pores and no hollow spines ..... ***Conchellium***

5. With conical process (galea) and three or more branched spines..... ***Coelodenrum***
5'. Lattice with rectangular pores.. ***Conchophacus***

6. With tubular arch and trumpet-shaped peristome ..... ***Borgertella***
6'. Without tubular arch 7

7. Radial symmetry (spheres)..... 8
7'. Bilateral symmetry (ovate, lenticular, campanulate) 17
7". Multilateral symmetry (polyhedral), smooth shell..... 24

8. With aperture 9
8'. Without aperture 13

9. Porcellaneous shell, radial spines at center of stellate circles..... ***Haeckeliana***
9'. Non-porcellaneous, with lattice work 10
9". Trizonal meshwork (triangular pores), and tubular peristome..... ***Porospathis***

10. With main radial spines..... 11
10'. Without main radial spines, teeth on peristome..... ***Castanella***

11. Main radial spines branched, teeth on peristome ..... ***Castanea***
11'. Main radial spines unbranched 12

12. With teeth on peristome..... ***Castanissa***
12'. Without peristomal teeth..... ***Castanidium***

13. Large shells composed of tangential tubules, triangular or regular simple mesh, lacking pyramidal elevations.....14
13'. Large partial skeletons, many radial tubules touching central capsule 15

14. With radial tubes.....***Aulosphaera***
14'. Without radial tubes.....***Aularia***

15. Lateral, verticillate branches on radial tubes ..... ***Aulospathis***
15'. Lacking lateral branches on radial tubes 16

16. Terminal branches simple..... ***Aulographis***
16'. Terminal branches forked..... ***Auloceros***

17. Ovate or lenticular shells 18
17'. Campanulate shells 23

18. With pharynx 19
18'. Without pharynx..... 20

19. With one or more oral teeth ..... ***Pharyngella***
19'. Lacking oral teeth or marginal spine..... ***Entocannula***

20. With marginal spines..... 21
20'. Without marginal spines 23

21. Shell surface basically smooth 22
21'. Shell surface alveolate..... ***Challengeranium***

22. With partial alveolate surface..... ***Challengerosium***
22'. Without alveoli..... ***Challengeron***

23. Smooth surface with oral teeth.... ***Protocystis***
23'. Ridged or furrowed surface, without oral teeth 25

24. Four equidistant articulate feet..... ***Medusetta***
24'. One large and three rudimentary articulate feet ..... ***Euphysetta***

25. Octahedral shell..... ***Circoporus***
25'. Icosahedral shell ..... ***Circogonia***

CLASS PHAEODAREA Haeckel, 1879

Skeleton composed of biogenic opal with porous, sometimes hollow, structures; thick capsular wall with openings, a large astropyle and usually two smaller parapylae: one kind of axopodium associated with the parapylae and a different kind with the astropyle.

ORDER PHAEOGYMNOCELLIDA
CACHON & CACHON, 1985

Skeleton absent or forming only a cup-shaped structure covering oral pole.

FAMILY PHAEOSPHAERIDAE
Cachon-Enjumet, 1961

Skeleton lacking; peripheral cytoplasm contains shells of other protists (diatoms, silicoflagellates, dinoflagellates, etc.) and enclosed by much phaeodium. Intracapsular phaeodium present. (Fig. 1)

Genus ***Phaeopyla*** Cachon-Enjumet, 1961

Phaeodium extra- and intracapsular. Capsular membrane thick. Astropylum large, simple, widely open (Fig. 1a).

Genus ***Phaeodactylis*** Cachon-Enjumet, 1961

Phaeodium extracapsular only. Capsular membrane thick. Astropylum bordered with various long, finger-like appendages.

Genus ***Phaeosphaera*** Cachon-Enjumet, 1961

With characters of the family, intracapsular phaeodium present.

FAMILY PHAEODINIDAE Cachon-Enjumet, 1961

Skeleton lacking; central capsule surrounded by cytoplasm containing shells of other protists and numerous phaeodium-globules. No intracapsular phaeodium. (Fig. 1b)

Genus ***Phaeodina*** (Haecker)
Cachon-Enjumet, 1961

With characters of the family. Generally with 2 central capsules (Fig.1b).

FAMILY ATLANTICELLIDAE Cachon-Enjumet, 1961

Skeleton and phaeodium usually absent, but when skeleton is present, it forms a cup-shaped structure covering the oral pore. Capsule always globular, usually with 3 openings. Nucleus usually adjacent to astropylum.

Genus ***Gymnocella*** Cachon-Enjumet, 1961

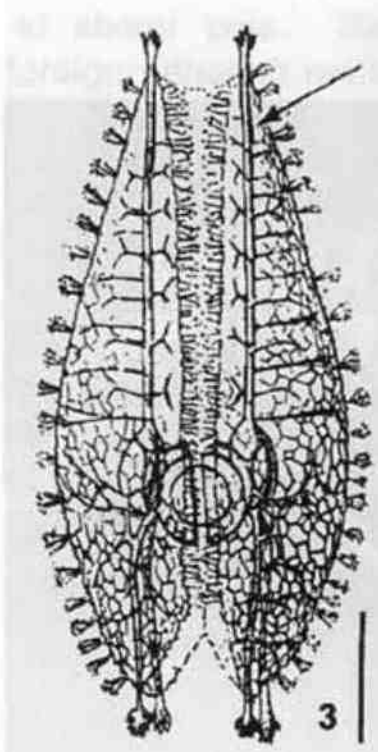
No cytoplasmic strand; parapylae in aboral hemisphere. Neither skeleton nor phaeodium.

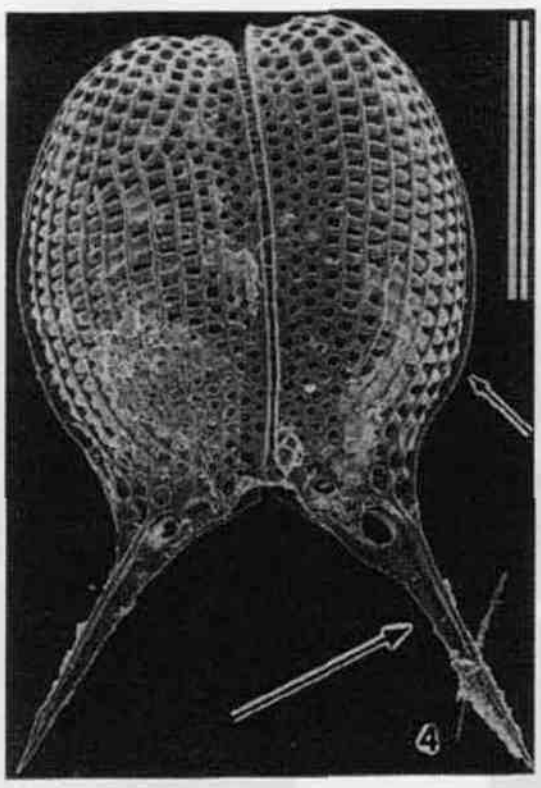
Genus ***Halocella*** Borgert, 1907

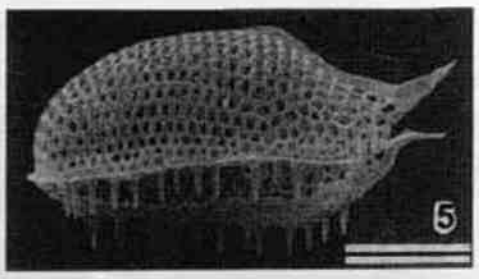
Skeleton formed of spongy basket-like piece and 2 small wing-like rods.

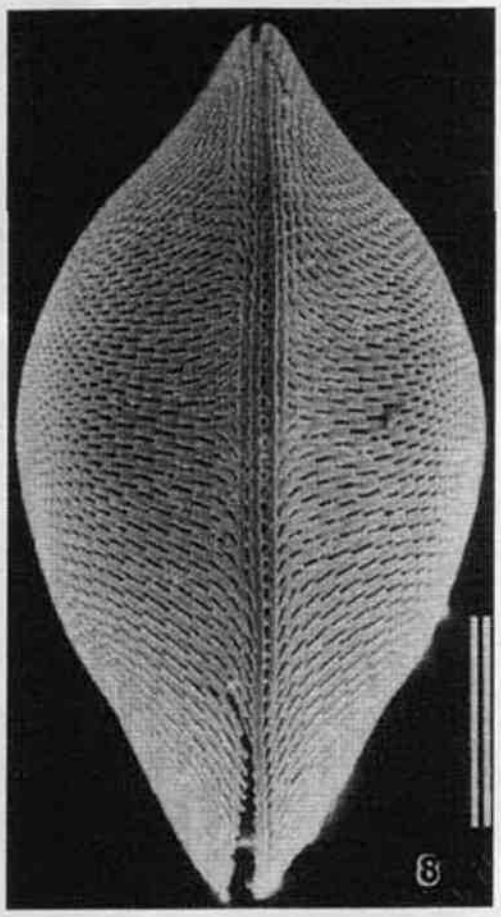
Genus ***Lobocella*** Borgert, 1907

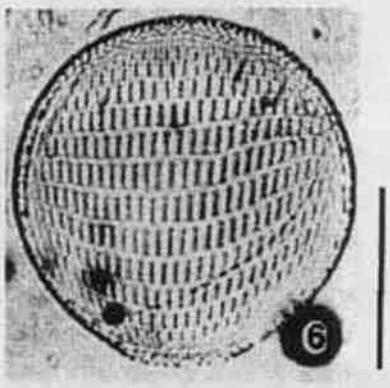
Saccular central capsule with finger-like processes.

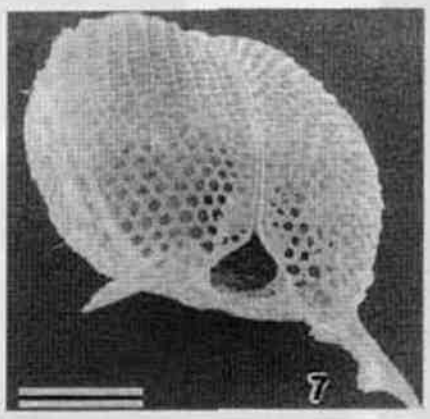


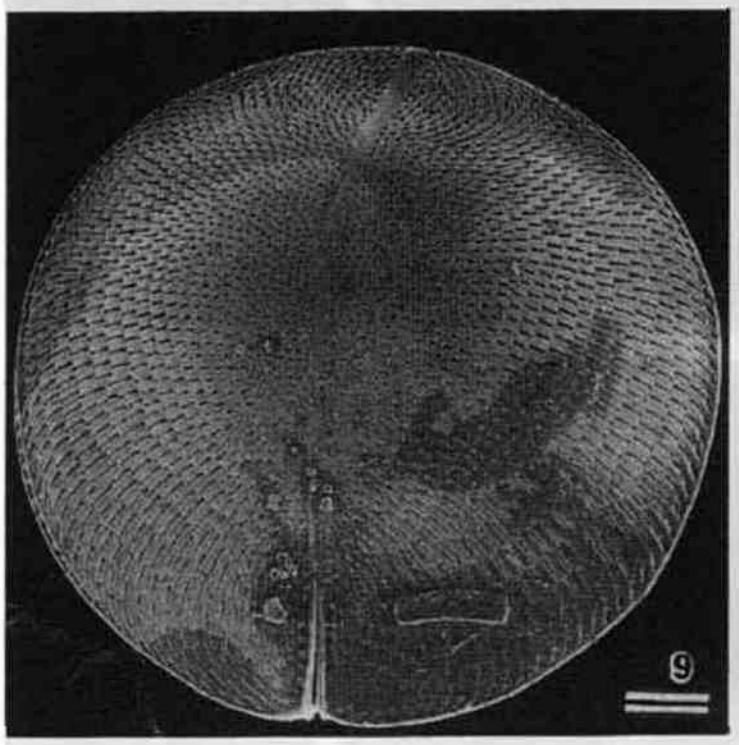


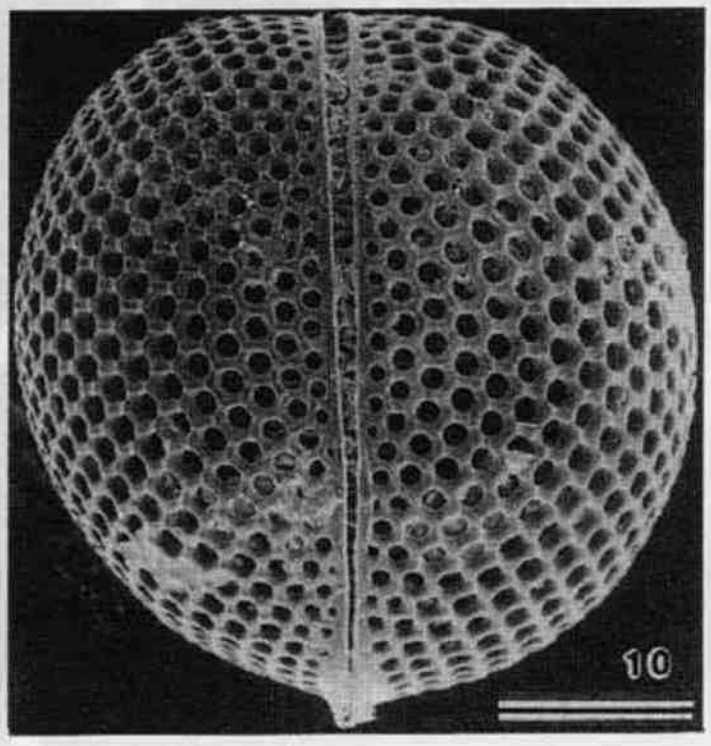




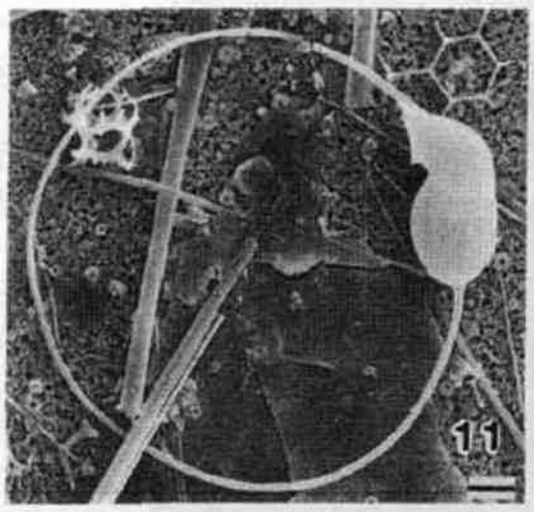


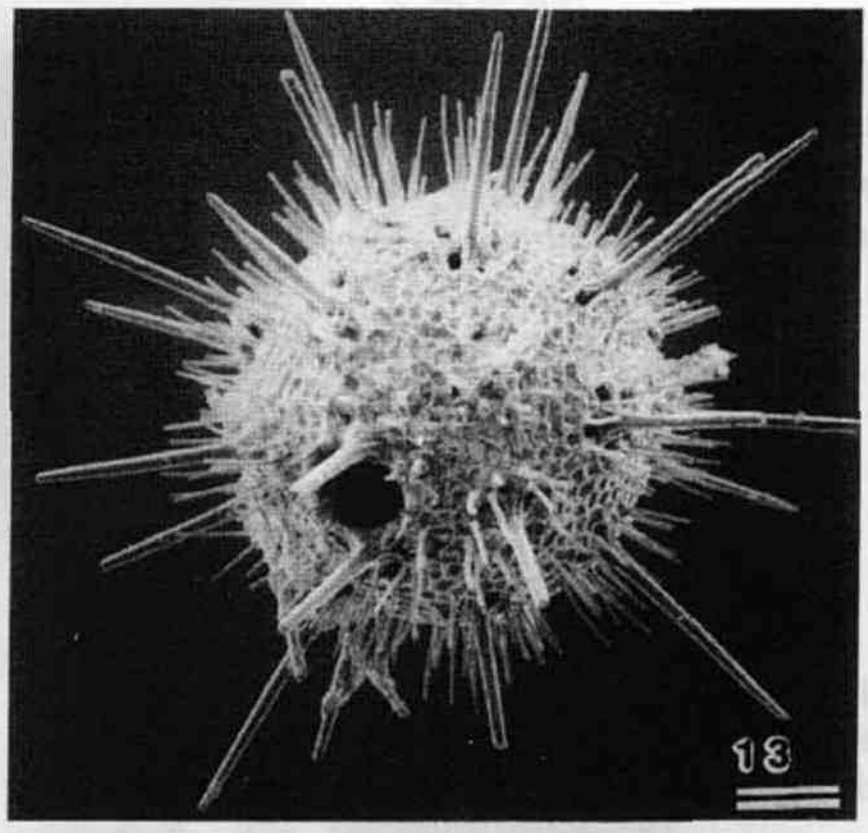


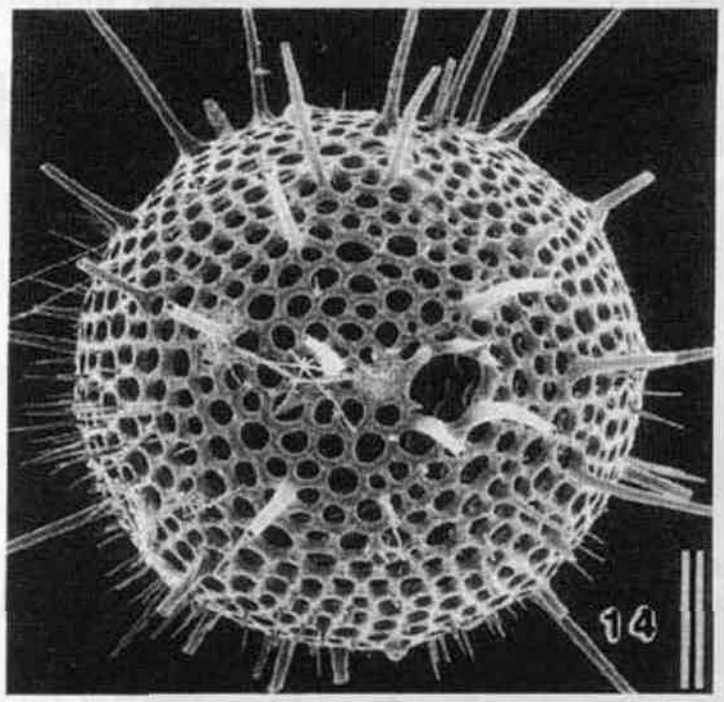


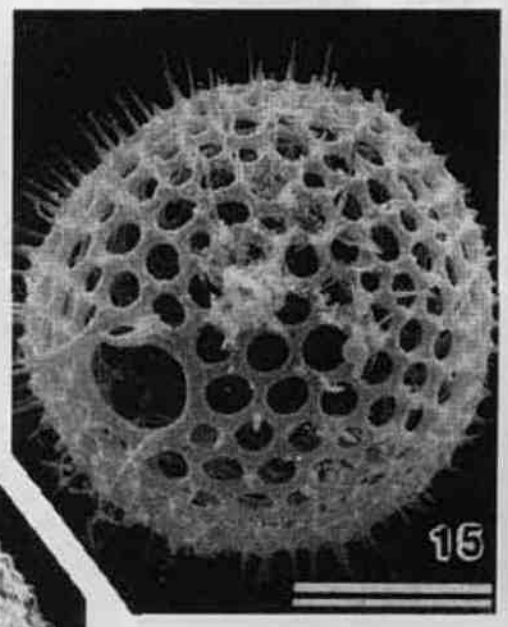


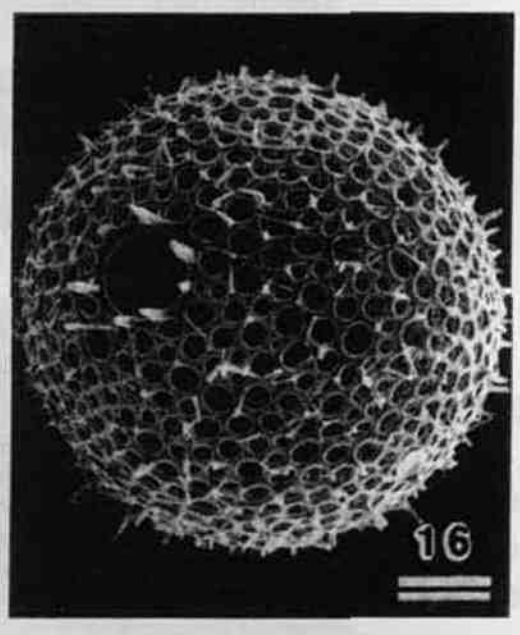
Families Coelodendridae and Concharidae. All scale bars are 100 µm except for Fig. 3, which is 1 mm, and Fig. 10, which is 50 µm. 3. *Coelographis regina* Haeckel, 1887, showing styles (arrow) (line drawing from Haeckel, 1887). 4,7. *Conchidium caudatum* (Haeckel, 1887), with keel (arrow) and horns (large arrow). 5. *Conchidium argiope* Haeckel, 1887. 6. *Conchophacus diatomeus* Haeckel, 1887. 8,9. *Conchopsis compressa* Haeckel, 1887. 10. *Conchellium capsula* Borgert, 1907.

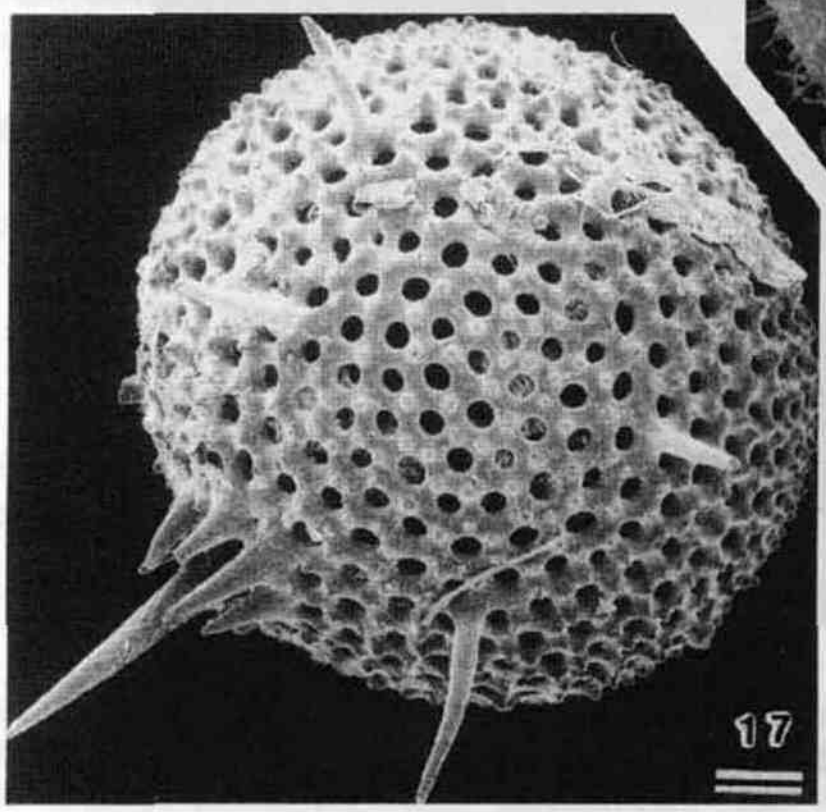


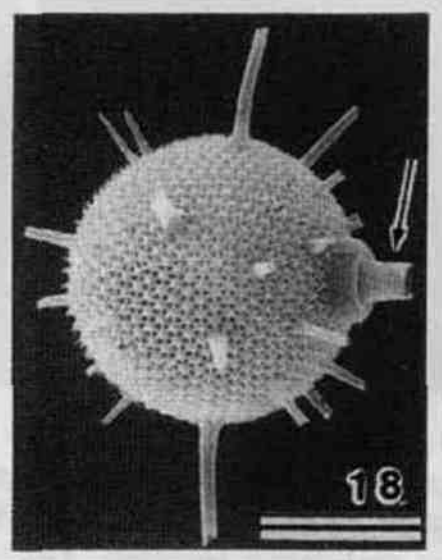


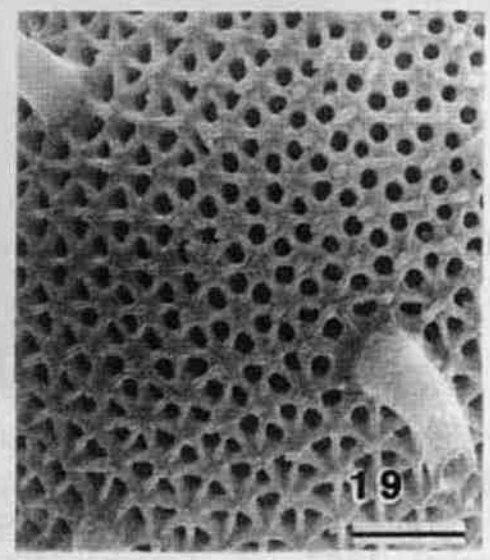












Families Lirellidae, Castanellidae, and Porospathidae. Scale bars=10 μm for Figs. 11,12,19 and 100 μm for Figs. 13—18. 11,12. *Borgertella caudata* (Wallich, 1869), with trumpet-shaped peristome (arrow). 13. *Haeckeliana porcellana* Murray, 1885. 14. *Castanidium longispinum* Haecker, 1908. 15. *Castanella macropora* (Schmidt, 1908). 16. *Castanella aculeata* Schmidt, 1907. 17. *Castanissa circumvallata* Schmidt, 1907. 18,19. *Porospathis holostoma* (Cleve, 1899), with tubular peristome (arrow).

Genus ***Miracella*** Borgert, 1911

Parapylae at aboral pole. Skeleton absent or formed by foreign adhering matter.

Genus ***Planktonetta*** Borgert, 1902
emend. Cachon-Enjumet, 1961

Skeleton cup-shaped shell with articulate arms. Parapylae (2 or more) near astropylae (1 or more). Large central capsule with single, large vacuole.

ORDER PHAEOCYSTIDA Haeckel, 1887

Skeleton simple, composed of numerous hollow, thin and tangential needles at periphery or composed only of radial spines with proximal ends near the central capsule, or combinations of radial and tangential needles (Fig. 2).

FAMILY AULACANTHIDAE Haeckel, 1887

Skeleton simple, composed of numerous hollow, thin, and tangential needles at periphery, or composed only of radial spines with proximal ends near the central capsule; or combinations of radial and tangential needles (Fig. 2a).

Genus ***Aulacantha*** Haeckel, 1860

Tangential needles numerous, make an external interwoven veil; radial spines denticulate (Fig. 2a).

FAMILY: ASTRACANTHIDAE Haeckel, 1887

Skeleton of radial, hollow spines with proximal ends united at center, forming a hollow space, surrounding two enclosed central capsules.

Genus ***Astracantha*** Haecker, 1908

Spines with small, regularly disposed thorns.

Genus ***Castanella*** Haeckel, 1879

Dentate (toothed) mouth, without radial spines (Figs. 2c,15).

Genus ***Castanissa*** Haeckel, 1879

Large unbranched radial main spines scattered between short bristles; with dentate mouth.

ORDER PHAEOSPHAERIDA Haeckel, 1887

Shell, one or more, composed of hollow or solid rods enclosing the central capsule.

FAMILY AULOSPHAERIDAE Haeckel, 1887

Shell generally latticed, or sometimes spongy, composed of hollow rods that form a cortical network with triangular or polygonal meshes supporting radial by-spines (spines arising at the nodes of the meshwork) (Fig. 20).

Genus ***Aulosphaera*** Haeckel, 1887

Lattice shell with triangular meshes; smooth cylindrical, radial tubes, a verticil of 3 divergent terminal branches (Fig. 20).

Genus ***Aularia*** Haeckel, 1887

Like *Aulosphaera*, but shell surface smooth, lacks radial tubules (Fig. 25).

Genus ***Aulotractus*** Haeckel, 1887

Single shell elongate, ellipsoidal to spindle-shaped; radial tubules at nodal points.

FAMILY: CANNOSPHAERIDAE Haeckel, 1887

Two concentric shells united by numerous strands; external shell latticed with polygonal meshes and internal one massive with a pylum. Radial spines arise from nodal points of cortical network.

Genus ***Coelocantha*** Hertwig, 1879

Internal shell latticed, with 60 to 90 radial spines; external shell pentagonal meshed; from each nodal point emerges a smooth radial spine bearing a verticil of 3 by-spines.

FAMILY SAGOSPHAERIDAE Haeckel, 1887

Skeleton spherical with lattice work containing subregular triangular meshes and filiform solid rods. Internal shell, when present, has no pylum.

Genus ***Sagenoarium*** Borgert, 1891

Double lattice shell with numerous pyramidal elevations without axial rods and with radial spines.

Genus ***Sagenoscena*** Haeckel, 1887

Pyramidal tents or elevations formed by rodlets united at the apex, arising from the surface of the lattice work, with internal axial rods, in some species prolonged into a crowned radial spine.

Genus ***Sagoscena*** Haeckel, 1887

Pyramidal tents, arising from the surface of the lattice work, without internal axial rods.

ORDER PHAEOCALPIDA Haeckel, 1887

Spherical, polyhedral, or ovate shells, some with porcellanous quality.

FAMILY CASTANELLIDAE Haeckel, 1887

Shell spherical with round pores. Radial spines, arising from nodes of the lattice shell, cover the surface. Shell has a large mouth (Fig. 15).

Genus ***Castanea*** Haecker, 1906

Large solid shell; main radial spines branched; small smooth mouth, spines on peristome.

FAMILY CIRCOPORIDAE Haeckel, 1887

Shell spherical or polyhedral (generally large mouth) with either porcellanous structure (nearly polygonal network with crests), or tabulate (surface flattened and smooth at places, like a slate tablet). Hollow radial spines encircled at base by circle of radial pores (Fig. 46).

Genus ***Circoporus*** Haeckel, 1879

Spherical shell with 6 radial spines (Fig. 46).

Genus ***Circospathis*** Haeckel, 1879

Tetradecahedral shell with 9 radial spines.

Genus ***Haeckeliana*** Haeckel, 1887

Dimpled spherical shell without polygonal plates; unbranched radial spines often numerous but variable in number (Fig. 13).

FAMILY TUSCARORIDAE Haeckel, 1887

Shell spherical, ovate or spindle-shaped with a porcellanous surface, smooth or spiny, but not tabulate or paneled (with flattened tile-like segments). Few tubular spines regularly arranged around a large pore or around circle of small pores.

Genus ***Tuscarora*** Murray, 1879

Three equidistant radial legs.

Genus ***Tuscarilla*** Haeckel, 1887

Four crossed teeth.

Genus ***Tuscaretta*** Haeckel, 1887

Two oral teeth.

FAMILY POROSPATHIDAE Borgert, 1900

Shell spherical or ovate with a smooth or tabulate surface containing irregularly disposed tubular spines. Peristome prolonged as a tubule. (Fig. 18)

Genus ***Porospathis*** Haeckel, 1879

Single genus with characteristics of the family (Fig. 18).

FAMILY POLYPYRAMIDAE Reschetnjak, 1966

Shell spherical or polyhedric, loosely polygonal pores, covered by pyramids formed by 4-5 beams (rod-like segments) and from which arise radial spines.

Genus ***Polypyramis*** Reschetnjak, 1966

One genus, one species with characteristics of the family.

ORDER PHAEOGROMIDA Haeckel, 1887

Shell ovate, lenticular or cape-shaped, sometimes with spines.

FAMILY CHALLENGERIDAE Murray, 1885

Shell ovate or lenticular with fine pores composing hexagonal meshes. The peristome is prolonged as a tubular pharynx surrounded by spines. Shell may be covered by marginal or aboral spines (Fig. 34).

Genus ***Challengeria*** Murray, 1876

Shell with oral teeth, without marginal spines.

Genus ***Challengeron*** Murray, 1879

Like *Challengeria*, but has spines on sharp marginal edge of shell (Fig. 34).

FAMILY MEDUSETTIDAE Haeckel, 1887

Ovate, hemispherical or cape-shaped (ovate with a broad basal opening) shell of alveolated structure, with by-spines, and with or without apical spine. Peristome surrounded by cylindrical, hollow, articulated spines (Fig. 42).

Genus ***Euphysetta*** Haeckel, 1887

With apical spine; 1 long and 3 small teeth-spines.

Genus ***Gazelletta*** Haeckel, 1887

Shell hemispherical, no apical spine; 6 "feet" (very long) that are radiate without terminal branches.

Genus ***Medusetta*** Haeckel, 1887

Four branched feet, apex usually with horn (Figs. 42-43).

FAMILY LIRELLIDAE Loeblich & Tappan, 1961

Small, elliptical shell with longitudinal striae: apex with or without apical spine, or with an elliptical ring connecting apex and exterior of aperture. One of the most abundant families of deep-water dwellers (Fig. 40).

Genus ***Borgertella*** Dumitrica, 1973

Shell with 2 main parts: egg-shaped chamber closed at the aboral end and armed with a hollow spine, and a long, more or less curved, trumpet-like peristome. Inner cavity of 2 parts separated by a diaphragm and communicating only through a narrow tube entering the peristomal cavity (Fig. 11).

Genus ***Lirella*** Ehrenberg, 1872

Ovate or lenticular shell (not bivalved) without pharynx, ridged or furrowed surface, without oral teeth (Fig. 40).

ORDER PHAEOCONCHIDA Haeckel, 1887

Shell composed of 2 thick-walled valves resembling the 2 halves of a clam shell.

FAMILY CONCHARIDAE Haeckel, 1887

Shell composed of 2 thick-walled latticed valves, spherical or lenticular, perforated by many pores; valves with smooth or dentate edges and oral split between valves; horn on aboral hinge (Fig. 5).

Genus ***Conchidium*** Haeckel, 1887

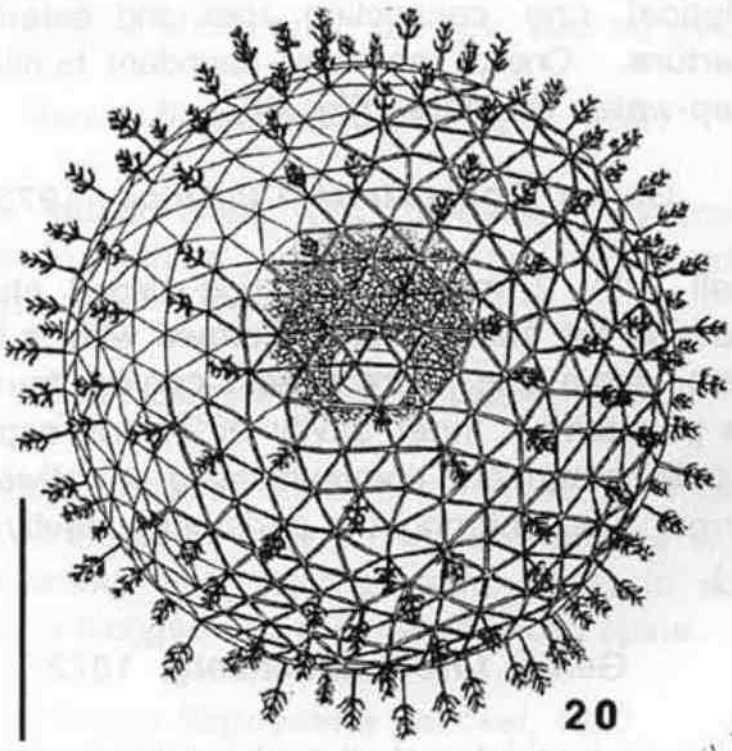
Bivalve shell without styles, but with 2 horns, one on each valve at aboral hinge, lenticular, with keel (Figs. 4 ,5)

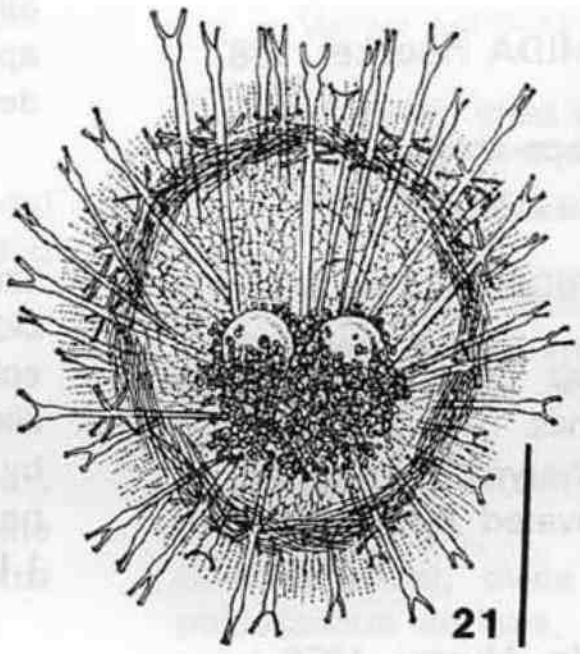
ORDER PHAEODENDRIDA Haeckel, 1887

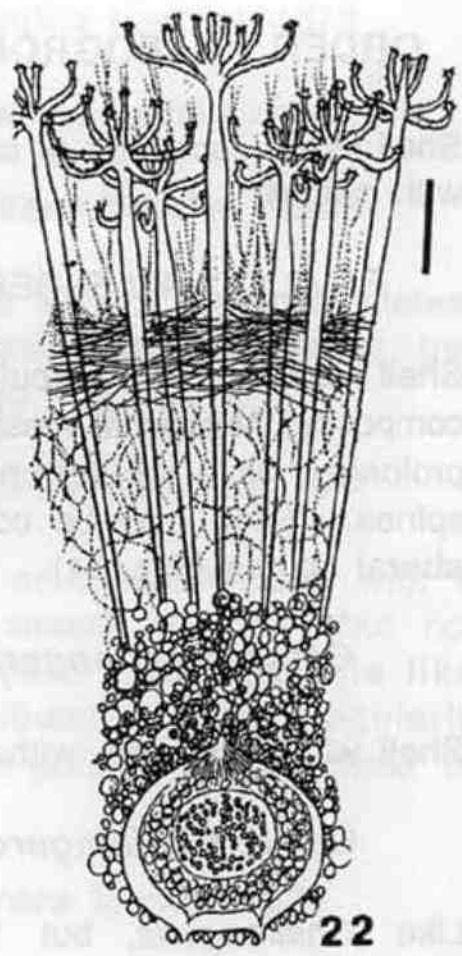
Shell with 2 hemispherical, thin-walled valves.

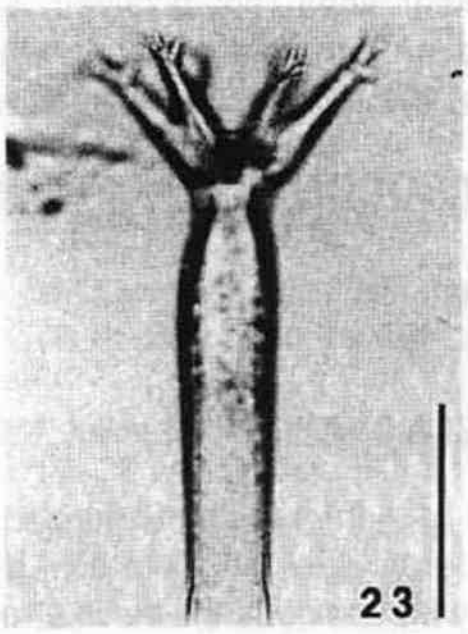
FAMILY COELODENDRIDAE Haeckel, 1887

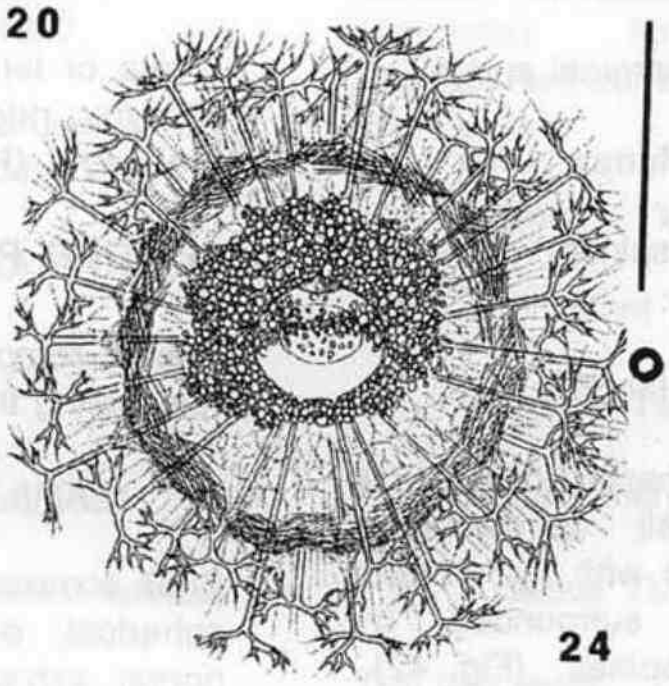
Shell composed of two thin-walled hemispherical valves (a dorsal and a ventral one) with many pores. Each valve with a conical process (galea)

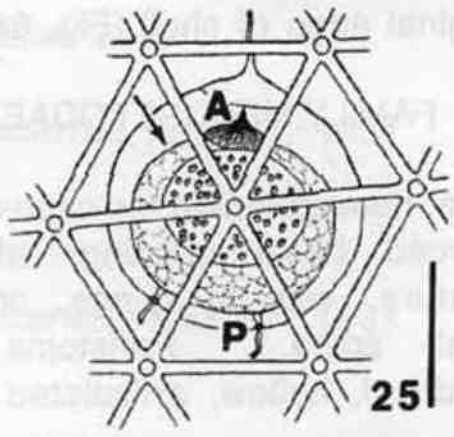


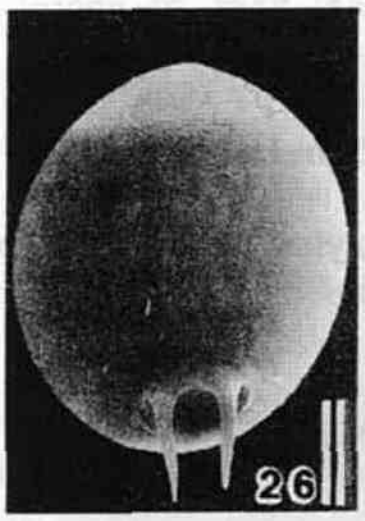


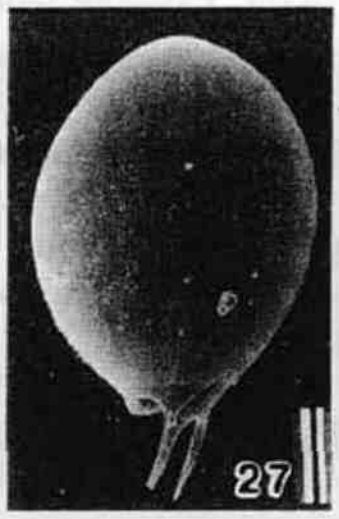


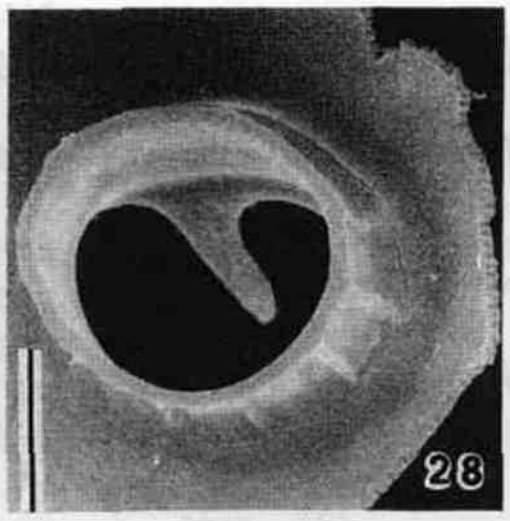


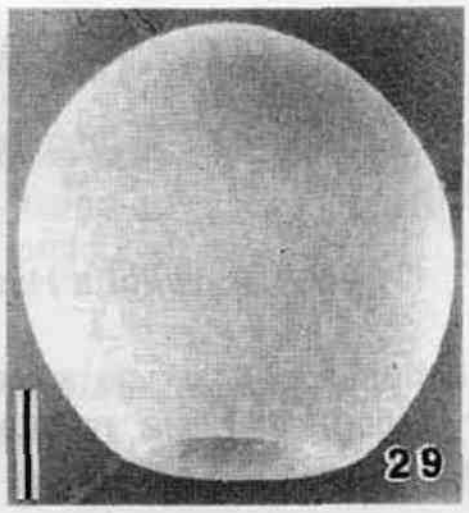












Families Aulacanthidae, Aulosphaeridae, and Challengeriidae. Scale bars=1 mm for Figs. 20-24, 100 µm for Figs. 25-27, 29, and 50 µm for Fig. 28. 20. *Aulosphaera dendrophora* Haeckel, 1887 (line drawing from Haeckel, 1887). 21. *Aulospathis bifurca* Haeckel, 1887 (line drawing from Haeckel, 1887). 22. *Aulographis candelabrum* Haeckel, 1887 (line drawing from Haeckel, 1887). 23. *Auloceros spathillaster* Haeckel, 1887. 24. *Auloceros elegans* Haeckel, 1887 (line drawing from Haeckel, 1887). 25. *Aularia ternaria* Haeckel, 1887 (line drawing from Haeckel, 1887). 26-27. *Pharyngella gastrula* Haeckel, 1887 with inside view (Fig. 28) showing detail of a pharynx. 29. *Entocannula infundibulum* Haeckel, 1887.

from which three or more divergent, branched hollow spines arise whose branches may anastomose and form a spongy mantle (Fig. 3). Many genera.

Genus ***Coelodendrum*** Haeckel, 1860

Spherical bivalves with conical process (galea) and 3 or more branched spines (Fig. 2b).

Genus ***Coelographis*** Haeckel, 1887

Bivalved shell with long paired styles, rhinocanna (nasal tube) and outer lattice-mantle (Fig. 3).

FAMILY CHALLENGERIDAE Murray, 1885

Shell ovate or lenticular with fine pores composing hexagonal meshes. The peristome is prolonged as a tubular pharynx surrounded by spines. Shell may be covered by marginal or aboral spines. (Fig. 34)

FAMILY MEDUSETTIDAE Haeckel, 1887

Ovate, hemispherical, or cape-shaped (ovate with a broad basal opening) shell of alveolated structure, with by-spines, and with or without apical spine. Peristome surrounded by cylindrical, hollow, articulated spines. (Fig. 42)

ORDER PHAEOCONCHIDA Haeckel, 1887

Shell composed of two thick-walled valves resembling the two halves of a clam shell.

FAMILY CONCHARIDAE Haeckel, 1887

Shell composed of two thick-walled latticed valves, spherical or lenticular, perforated by many pores; valves with smooth or dentate edges and oral split between valves; horn on aboral hinge. (Fig. 5)

ORDER PHAEODENDRIDA Haeckel, 1887

Shell with two hemispherical, thin-walled valves.

FAMILY COELODENDRIDAE Haeckel, 1887

Shell composed of two thin-walled hemispherical valves, dorsal and ventral, each with many pores. Each valve with a conical process (galea) from which three or more divergent, branched hollow spines arise, the branches of which may anastomose and form a spongy mantle. (Figs. 2, 3)

Literature Cited

Anderson, O. R. 1983. *Radiolaria*.. Springer-Verlag, NY.

Anderson, O. R. 1993. The trophic role of planktonic foraminifera and radiolaria. *Mar. Microbial Food Webs*, 7:31-51.

Borgert, A. 1982. Vorbericht über einige Phaeodarien- (Trijpyleen-) Familien der Plankton-Expedition. *Ergebn. der Plankton-Expedition.*, 1A:176-184.

Borgert, A. 1900. Untersuchungen über die Fortzpflanzung der Tripyleen Radiolarien, speziell von *Aulacantha scolymantha. Teil I -- Zool. Jahrb.*, 14:203-276.

Borgert, A. 1902. Mittheilungen über die Tripyleen-Ausbeute der Plankton-Expedition. I. Neue Medusettidae, Circoporidae, und Tuscaroridae. *Zool. Jahrb.*, 2:566-577.

Borgert, A. 1907. Die Tripyleen Radiolarien der Plankton-Expedition. Concharidae. *Ergebnisse der Plankton Expedition*, 3, L.h.(5):195-232.

Cachon, J. & Cachon, M. 1985. III. Class Phaeodarea. *In*: Lee, J. J., Hutner, S. H. & Bovee, E. C. (eds.), *An Illustrated Guide to the Protozoa.* Society of Protozoologists, Lawrence, KS. pp 295-302

Cachon-Enjumet, M. 1961. Contribution à l'études Radiolaires Phaeodariés. *Arch. Zool. Exp. Gén.*, 100:152-273.

Cleve, P. T. 1899. Plankton collected by the Swedish Expedition to Spitzbergen in 1898. *K. Svenska Vetensk.-Akad., Handl.*, 32(3):1-51.

Ehrenberg, C. G. 1872. Nachtrag zur Übersicht der organischen Atmospharilen. *Kgh. Akad. Wiss. Berlin, Jahrg. 1871.* p 233

Gowing, M. M. 1986. Trophic biology of phaeodarian radiolarians and flux of living radiolarians in the upper 2000 m of the North Pacific central gyre. *Deep-Sea Res.*, 33:655-674.

Gowing, M. M. 1989. Abundance and feeding ecology of Antarctic phaeodarian radiolarians. *Mar. Biol.*, 103:107-118.

Gowing, M. M. & Coale, S. L. 1989. Fluxes of living radiolarians and their skeletons along a northeast Pacific transect from coastal upwelling to open ocean waters. *Deep-Sea Res.*, 36:561-576.

Gowing, M. M. & Garrison, D. L. 1992. Abundance and feeding ecology of larger protozooplankton in the ice edge zone of the Weddel and Scotia Seas during the austral winter. *Deep-Sea Res.*, 39:893-919.

Gowing, M. M. & Silver, M. W. 1985. Minipellets: a new and abundant size class of marine fecal pellets. *J. Mar. Res.*, 43:395-418.

Gowing, M. M. & Wishner, K. E. 1986. Trophic relationships of deep-sea calanoid copepods from the benthic boundary layer of the Santa Catalina Basin, California. *Deep-Sea Res.*, 33:939-961.

Gowing, M. M. & Wishner, K. E. 1992. Feeding ecology of benthopelagic zooplankton on an eastern tropical Pacific seamount. *Mar. Biol.*, 112:451-467.

Haeckel, E. 1862. *Die Radiolarien (Rhizopoda, Radiolaria). Eine Monographie.* Georg Reimer, Berlin. 586 pp

Haeckel, E. 1887. Report on Radiolaria collected by H. M. S. Challenger during the years 1873-1876. *In*: Thompson, C.W. & Murray, J. (eds.), *The Voyage of the H. M. S. Challenger.* Her Majesty's Stationery Office, London, V. 18:1-1803.

Haecker, V. 1906. Über Kenntis der Challengeriden; vierte Mitteilung über die Tripyleen-Ausbeute der deutschen Tiefsee-Expedition. *Arch. Protistenkd.*, 7(2):259-306.

Haecker, V. 1907. Zur Kenntis der Castanellide und Porospathiden. *Arch. Protistenkd.*, 8:52-65.

Haecker, V. 1908. Tiefsee Radiolarien Speziel Teil. L1, Aulacanthidae-Concharidae. *Deutsch. Tiefsee-Exped., Wiss. Ergeben.*, 14:1-336.

Murray, J. 1885. The Radiolaria. *In*: Tizard, T. H., Moseley, H. N., Buchanan, J. Y. & Murray, J. (eds.), *Narrative of the Cruise of the H.M.S. Challenger with a General Account of the Scientific Results of the Expedition. Rept. Voy. Challenger, Narrative*, 1(pt. 1):219-227.

Nöthig, E.-M. & Gowing, M. M. 1991. Late winter abundance and distribution of phaeodarian radiolarians, other large protozooplankton and copepod nauplii in the Weddell Sea, Antarctica. *Mar. Biol.*, 111:473-484.

Reschetnjak, B. B. 1966. Deep Sea Phaeodarian Radiolaria of the North-west Pacific. *Fauna SSSR. New Series*, 94:1-208.

Schmidt, W. J. 1907. Einige neue Castanellide-Arten. *Zool. Anz.*, 32:297-307.

Schmidt, W. J. 1908. Die Tripyleen Radiolarien der Plankton-Expedition. Castanellidae. *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung*, Bd. III, L.h. 6:234-279.

Swanberg, N. R., Bennett, P., Lindsey, J. L. & Anderson, O. R. 1986. The biology of a coelodendrid: a mesopelagic phaeodarian radiolarian. *Deep-Sea Res.*, 33:15-25.

Takahashi, K. 1987. Radiolarian flux and seasonality: Climatic and *El Niño* Response in the Subarctic Pacific, 1982-1984. *Global Geochemical Cycles*, 1:213-231.

Takahashi, K. 1991. Radiolaria: flux, ecology, and taxonomy in the Pacific and Atlantic. *In*: Honjo, S. (ed.), *Ocean Biocoenosis*, Series No. 3. Woods Hole Oceanographic Institution Press. 303 pp

Takahashi, K., Hurd, D. C. & Honjo, S. 1983. Phaeodarian skeletons: their role in silica transport to the deep sea. *Science*, 222(4624):616-618.

Wallich, G. C. 1869. On some undescribed testaceous rhizopods from the North Atlantic deposits. *Monthly Microsc. Jour.*, 1:104-110.