Class Polycystina

Anderson, O. R.

Nigrini, C.

Boltovskoy, D.

Takahashi, Kozo
Faculty of Science, Kyushu University

他

出版情報：An illustrated guide to the protozoa : organisms traditionally referred to as protoza, or newly discovered groups, pp.994-1022, 2000. Society of Protozoologists
バージョン：
権利関係：

POLYCYSTINEA

Anderson, O. R., Nigrini, C., Boltovskoy, D., Takahashi, K., and Swanberg, N. R., 2002. Class Polycystina. *In: The Second Illustrated Guide to the Protozoa*, Lee, J.J., Leedale, G.F., and Bradbury, P., (eds.), Society of Protozoologists, Lawrence, KS. 994-1022.

Anderson, O. R., Nigrini, C., Boltovskoy, D., Takahashi, K., and Swanberg, N. R., 2002. Class Polycystina. *In: The Second Illustrated Guide to the Protozoa*, Lee, J.J., Leedale, G.F., and Bradbury, P., (eds.), Society of Protozoologists, Lawrence, KS. 994-1022.

CLASS POLYCYSTINEA

O. ROGER ANDERSON, CATHERINE NIGRINI, DEMETRIO BOLTOVSKOY, KOZO TAKAHASHI, and NEIL R. SWANBERG

The polycystines are solitary or colonial, actinopod-bearing, marine, planktonic protists falling into two main groups: 1) Spumellaria with a spherical, cell body plan (Figs. 1, 2, 4), though the skeletons may have very different symmetries; 2) Nassellaria with a non-spherical cell body plan and skeletons varying from simple spicules to complex helmet-shaped structures (Fig. 3). Sizes vary from about 30 µm to several hundred micrometers for many skeleton-bearing species or to several millimeters for larger gelatinous spumellarian species. Most known species occur in open-ocean environments, but some occur in coastal waters. Radiolarian siliceous skeletons contribute substantially to the microfossil record in marine sediments, providing one of the most continuous records of micro-organismic evolution (e.g. Nigrini, 1970, 1971; Kling, 1978; Sanfilippo and Riedel, 1985; Sanfilippo et al., 1985) extending back to the Cambrian, while many modern species can be clearly traced back at least to the early Mesozoic (e.g. Anderson, 1983a; Riedel and Sanfilippo, 1981).

General Morphology. The spherical body plan of the Spumellaria is particularly evident in the shape of the **central capsule** (nucleus-containing central mass of cytoplasm) which is surrounded by a spheroidal central capsular wall with numerous pores. **Actinopodia** radiate outward from the pores (Figs. 1, 4D). The shape of the surrounding skeletal matter, when present, can be very different, taking quadrangular, trigonal, bilocular, or other geometric shapes

(Figs. 2, 3). The central capsule of Nassellaria is typically a prolate spheroid with a pore plate at the base where several to many relatively robust actinopods extend outward into the surrounding environment. The polycystine central capsule contains reserve substances and major cytoplasmic organelles (nucleus, mitochondria, and other membranous organelles, exclusive of digestive vacuoles). The actinopods radiating from the pores in the central capsular wall produce a frothy or web-like extracapsular cytoplasm (**extracapsulum**) (Fig. 1A) where prey is sequestered within digestive vacuoles.

Skeletal matter is siliceous and is secreted within a thin cytoplasmic sheath or **cytokalymma** (Anderson, 1983a). Some species lack siliceous deposits and are among the largest of the solitary species (Fig. 1A). Algal symbionts, when present, are enclosed within peri-algal vacuoles usually in the extracapsulum (Figs. 1, 4). Colonial species (Fig. 4A-C) contain numerous central capsules, interconnected by a rhizopodial- network, enclosed within a common gelatinous sheath. The colony can be spherical, spheroidal, or filiform forming elongate strands up to one meter or more in length.

Skeletal Morphology. Skeletal morphology is highly varied, often not based on a simple geometric plan, and can be as simple as a porous or latticed sphere or as elaborate as a multi-septate conical shell with pores and latticed wings, etc. (Figs. 2, 3). Some skeletal terminology relevant to use of the keys is presented here. Spicules in Spumellaria are spindle-shaped, curved, multiradiate or of more complex design, but always occurring as scattered, unconnected structures (Figs. 1D, 4E, G, H). The spumellarian skeleton can consist of spherical or spheroidal porous shells singly or in concentric array (Figs. 1B, 2A). Concentric spheres are joined by radial beams (Fig. 2A), which may or may not project outward as spines. Large spines, often in fixed number (2, 4, or 6) and regularly arranged, are known as primary spines. Smaller ones (sometimes bristle- or thorn-shaped) are known as secondary spines and are scattered irregularly about the shell's surface. When there is more than one shell, the outer one is the **cortical shell** and the innermost is the **medullary shell** (Fig. 2A). Skeletal structures may vary substantially across genera. These include spongiose ones, either spherical to spheroidal (Figs. 2D, 5B,C), flattened and square (Figs. 2M, 8J), discoidal (Figs. 2I,J, 8I), or trigonal (Y-shaped, Figs. 2N, 8K,L). In some cases the shell is a biconvex (lenticular) disk enclosing a spherical medullary shell (Fig. 2F,G). The skeleton may include latticed polar caps (Figs. 2H, 6E) or other ornate spongiose or latticed structures. In other genera, the skeleton can be augmented by arches of latticed skeletal matter or girdles which define openings or gates (Figs. 2Q, 7J,K), broad encircling latticed bands, etc., or consist entirely or partially of a spiraling latticed structure (Figs. 2O,P, 7H). A tube-like extension from the surface of the spumellarian skeleton (either entire, latticed, and/or ornamented with spines), or a funnel-like groove in the margin of the spongy disk, is known as a **pylome** (Figs. 2J,K, 11H,K). Sometimes forked or branched rods, **apophyses**, extend outward from the center of the skeleton (Figs. 2A, 5L).

In Nassellaria, the spicule is a complex structure, basically tripodal in design, and often forming the major scaffolding of the skeleton, either as the main skeletal element (Figs. 3A,B, 9C), as a central structure to which other structures are attached (Figs. 3B,C, 9G), or enclosed (hidden) within a porous (simple or segmented) shell (Fig. 3F,N). The shell may consist of only a basal tripod (Fig. 3K); the tripod and associated ring(s) (Fig. 3A,E); a single chamber known as the cephalis (Fig. 3D); or two or more chambers (Fig. 3H,S,T,U) connected serially, designated **cephalis, thorax, abdomen,** and **postabdominal segments.** The final chamber can be either open, without a closing plate (Fig. 3J), or closed by a porous plate (Fig. 3I). The organization of the cephalis varies from a simple helmet- or cap-shaped structure (Fig. 3J) to bilocular (two bilateral lobes, Fig. 3F) or multilocular (more than two lobate protrusions, Fig. 3O-Q) forms. The top of the cephalis can be augmented by a **galea** (cupola) (Fig. 3G) and may have a cylindrical or three-bladed horn (Fig. 3O,T) or lateral cephalic tube (protruding from the side, Fig. 3S). The thorax may have three latticed or solid radial apophyses or "**wings**" projecting from the proximal or middle part of the thoracic wall (Fig. 3D). The rim (**peristome**) of the terminal chamber, either the thorax or abdomen, may bear spine-like protrusions called "**teeth,**" if they are numerous and short (Fig. 3 T), or "**feet,**" if there are three and they are relatively long (Fig. 3C,F,G). The term sagittal ring is used for a circular to D-shaped element that sometimes is the only structure present; or in other cases it reinforces the wall of a latticed shell in the medial sagittal plane (Fig. 3E). This region may be augmented by a sagittal beam.

Reproduction. The reproduction of many species of radiolaria is not known. In those that have been studied (e.g. Anderson, 1983a) reproduction can be by release of biflagellated swarmers, each with a vacuole bearing a large strontium sulfate crystal, or in some cases by fission of the central capsule. It is not known if the swarmers are asexual dissemules or motile gametes.

Distribution and Ecology. Polycystine radiolaria occur in most major oceanic sites with densities of tens to hundreds per cubic meter of seawater. Species bearing algal symbionts often occur in the upper strata of the water column in the well-illuminated portions of the photic zone. Others, preferring a cooler habitat, may extend to great depths at mid-latitudes, but these are often found nearer the surface in high latitudes (Nigrini and Moore, 1979; Boltovskoy, 1981, 1994; Anderson, 1983a; Steineck and Casey, 1990). In extrapolar areas, the layer of maximum radiolarian abundance is usually around 25-50 m for the polycystines, whereas the phaeodarians tend to inhabit deeper strata (Reshetnjak, 1966; Renz, 1976; Kling, 1979; Gowing, 1993; Kling and Boltovskoy [in press]). In polar waters, on the other hand, peak abundances can be located deeper, at 200-300 m (Boltovskoy, 1987; Boltovskoy and Alder, 1992).

Polycystines consume a wide variety of prey, spanning bacteria, algae, and other protists, to copepods, larvacea, and other small zooplankton. Among the species studied, many are omnivorous, taking phytoplankton and zooplankton prey, while others appear to be more algivorous (Anderson, 1983a, 1993; Caron and Swanberg, 1990). Algal symbionts, when present, secrete photosynthetic products that are assimilated by the host as a nutritional source (Anderson, 1983b, 1992).

Taxonomy. Although the first descriptions of radiolarian species date as far back as the beginning of the nineteenth century, the cornerstone of the taxonomy of this group was established in 1887, with Haeckel's impressive work based on collections of the HMS Challenger. In the three volumes of this monograph Haeckel described 3389 polycystine species (617 genera), 80% of them new, mostly on the basis of recent materials. It is now widely recognized, however, that Haeckel's excessively rigid classification system is plagued with synonyms (the estimated number of living polycystine species is probably around 700 to 1000). Its suprageneric categories, moreover, are artificial and unsatisfactory; however, advances in the development of a satisfactory alternative taxonomy have been modest at best, especially for the Spumellaria.

Revisions of Haeckel's spumellarian supra-generic systematics were undertaken by Riedel (1967a,b, 1971) and by French and Russian specialists (Hollande and Enjumet, 1960; Cachon and Cachon, 1972, 1985; Petrushevskaya, 1965, 1967, 1971, 1975, 1981, 1986; Petrushevskaya et al., 1976). In addition, selected groups were subject to detailed morphologic studies, and new classification schemes were suggested (e.g. Zhamoida and Kozlova, 1971; Dumitrica, 1988, 1989). Riedel's proposed system, based on skeletal features alone, is rather similar to Haeckel's and is also the one most widely used at present. By contrast, the revision by the French and Russian workers uses cytoplasmic features, such as the "nucleoaxopodial complex" (*sensu* Petrushevskaya, 1986) for suprageneric divisions, and the skeleton for generic and specific diagnoses. The revision by the French and Russian workers is more elaborate. Its arguments are probably stronger in biologic and phylogenetic terms, and it is based on criteria more closely comparable to those applied to other protista. Its appeal among radiolarian workers, however, has been very limited. The reasons for this are probably multiple, but at least three are more evident: 1) over 90% of radiolarian studies are carried out on the basis of sedimentary material devoid of any soft parts, which precludes applying classification systems centered on protoplasmic details, 2) information on the cytoplasmic morphology is mainly in the biological literature in French or in Russian, especially as applied to taxonomy, and 3) most of the taxonomy was done by English-speaking geologists for whom literature in other languages, particularly Russian, was not readily accessible. Riedel's (1971) spumellarian classification is restricted to 11 (8 extant) families, external skeletal morphology of which is usually quite distinctive; this simplicity is very attractive, especially considering that the French-Russian proposed divisions include orders, superfamilies, families, and subfamilies. The nassellarian classification inherited from earlier workers (Ehrenberg, 1847ab; Müller, 1858a; Haeckel, 1862, 1887; Hertwig, 1879; Popofsky, 1908, 1912, 1913) was profoundly changed both in whole (Riedel, 1967a,b, 1971; Petrushevskaya, 1981, 1986), and in selected groups (Petrushevskaya, 1965; Goll, 1968, 1969; Sanfilippo and Riedel, 1970; Foreman, 1973). Besides cytoplasmic traits (cf. Petrushevskaya, 1986), a feature of primary importance for the classification of this group, but often over-looked, is the internal skeleton.

This consists of a system of internal spines and connecting bars which allow close comparisons between homologous structures in forms differing widely in their external morphology. Analysis of these features is demanding, since it requires dedicated efforts at understanding the complex spatial relationships involved. In addition, observation of this internal skeleton is only feasible with well preserved individuals oriented in the right position, usually on permanent-mount slides. Nevertheless, family-level assignments are generally reasonably stable among publications, and these do take the structure of the internal skeleton into account. Again, the most widespread system is that proposed by Riedel (1971), which includes eight extant families.

In spite of the recognized importance of internal skeletal features, some recent publications on taxonomy of Spumellaria and Nassellaria at the generic and specific levels continue to base identifications solely on external traits of the skeletons. This is true even for new genus and species descriptions. It should be noted in passing, however, that among some larger spongiose Spumellaria (e.g. *Styptosphaera* and *Plegmosphaera*) phenotypic intergradation and variability of the internal structures make separation of the genera difficult, except for extreme extreme cases (Swanberg et al., 1990). The surging interest in ecologically and, especially, paleoecologically-oriented research places special emphasis on morphologically distinguishable indicators that can convey information on recent or past ecological settings. For this work, suprageneric and even generic traits are deemed of little use. Thus, current Linnean binomial denominations often have limited

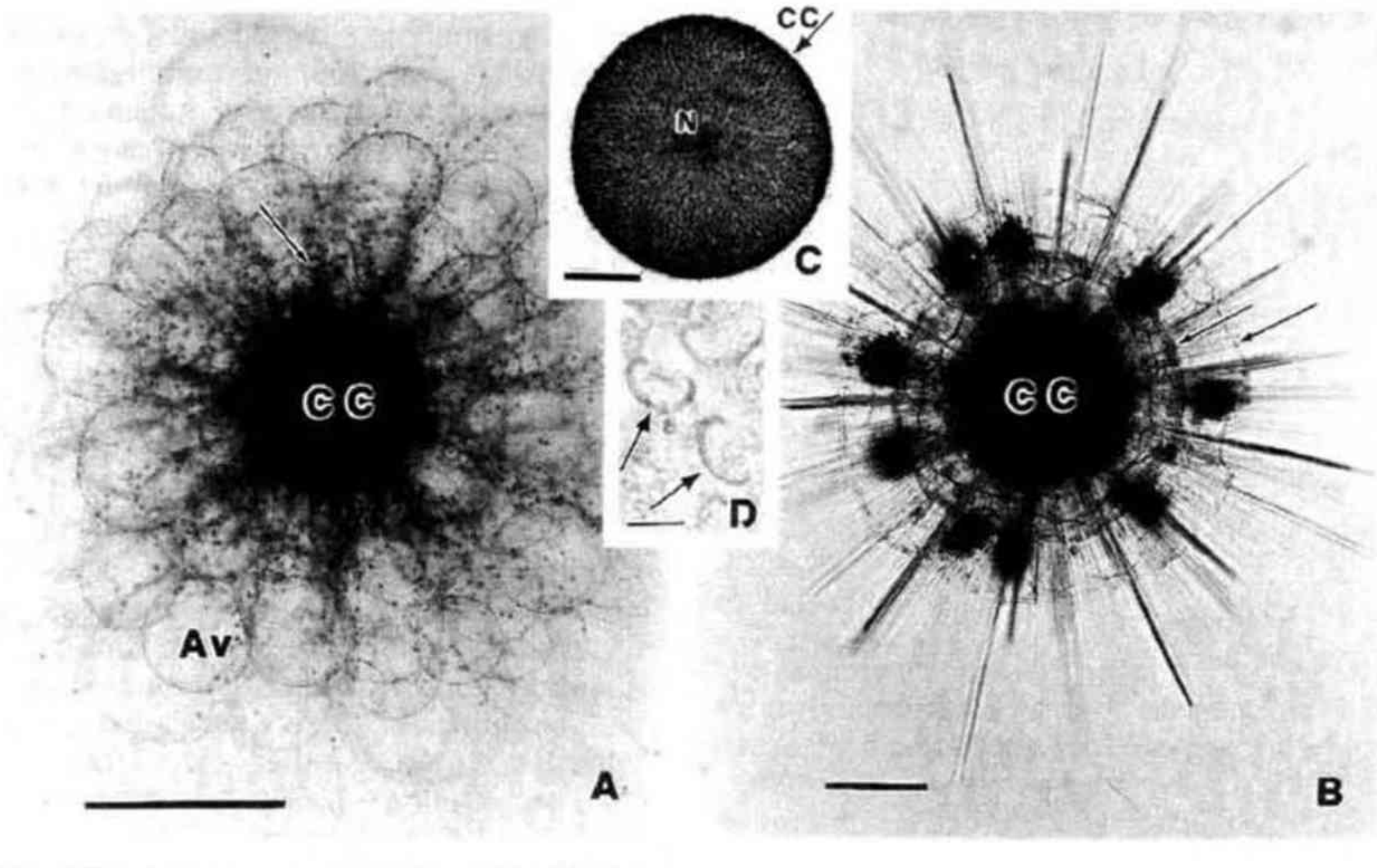

Fig. 1. Light microscopic views of living spumellarian radiolaria. A. *Thalassicolla nucleata* Huxley, 1851 (p. 433), a skeletonless species, with an opaque central capsule (CC) surrounded by an extracapsulum consisting of frothy alveoli (Av) and numerous algal symbionts (arrow). Scale=1 mm. B. A skeleton-bearing species showing two concentric latticed shells (arrows) with radial spines, surrounding the central capsule (CC). Scale=50 µm. C. *Physematium*. Scale =1 mm. D. C-shaped spicules (arrows) on the surface of the central capsular membrane of *P. mulleri*, Meyen, 1834 (p. 163), a large, gelatinous solitary spumellarian with scattered arcuate or variously curved spicules on the surface of a very large central capsule (arrow) enclosing radially arranged internal alveoli surrounding a central nucleus (N). Scale=100 µm. (Adapted from Anderson, 1983a, 1969; Sanfilippo and Riedel, 1970; Foreman, 1973).

value in so far as relationships between taxa are concerned. This is especially so at the generic level, because closely comparable morphotypes are widely recognized under different generic names. Likewise, some very different morphotypes share the same genus. Family-level divisions, on the other hand, while not necessarily correct, are more uniform and stable among publications. The following synopsis to family level for extant species (Riedel, 1971; Kling, 1973, 1978; Anderson, 1983a) is consistent with current perspectives, but is likely to change as more fine structural and evolutionary data are obtained.

Class Polycystina

Ehrenberg, 1838, emend. Riedel, 1967a

Central capsule with numerous actinopodia radiating from pores distributed over the entire surface or at a restricted region at one pole, skeletal matter when present composed of opal, some species with endosymbionts, but all lack a phaeodium.

ORDER SPUMELLARIA

Ehrenberg, 1875

Spherical body plan with actinopodia radiating uniformly from all over the surface of the central capsule.

KEY TO GENERA

The following key is not natural, since our knowledge of polycystine phylogenies is limited. It is a practical guide based on some fairly conspicuous characteristics observable with a light microscope

1. Skeleton lacking, or consisting of scattered spicules, etc...I
1.' Skeleton present II

I. SKELETONLESS OR SPICULAR SPUMELLARIA

1. Skeleton lacking... 2
1'. Spicules or scattered siliceous product present.. 4

2. Colonial .... *Collozoum*
2'. Solitary 3

3. Alveoli neither within or outside central capsule... *Actissa*
3'. Alveoli within central capsule.. *Thalassolampe*
3". Alveoli surrounding central capsule .... *Thalassicolla*

4. Colonial 5
4'. Solitary 6

5. Spicules double tri-radiate (three branches at each end).................................. *Sphaerozoum*
5'. Spicules simple needles or radiate.. *Rhaphidozoum*

6. Alveoli neither within or outside central capsule 7
6'. Alveoli present within or outside central capsule 8

7. Spicules unbranched............*Thalassosphaera*
7'. Spicules branched .... *Thalassoxanthium*

8. Numerous alveoli within transparent central capsule .... *Physematium*
8'. Bubble-like alveoli surrounding central capsule 9

9. Spicules unbranched............. *Thalassoplancta*
9'. Spicules branched .... *Lampoxanthium*

II. SKELETON PRESENT

1. Basic shell symmetry radial (includes spongiose and lattice shelled species).......................... III
1'. Basic shell symmetry not radial (includes tripodal skeletons or those with single or segmented helmet-shaped skeletons)............ IV

III. SKELETON-BEARING SPUMELLARIA

1. Radial symmetry, general shell shape spherical or ellipsoidal, single shell 2
1'. Radial symmetry, general shell shape spherical or ellipsoidal, multiple concentric shells... 13
1". Radial symmetry, general shell shape cylindrical, quadrate, triaxial, or circular/lenticular 36

2. Shell spherical to ellipsoidal without annular constrictions. 3
2'. Shell subspherical with several annular constrictions forming dome-like protuberances........................... *Tholostaurus*

3. Outermost shell composed of a spongy framework 4
3'. Outermost shell composed of a latticed framework 5

4. Spongy sphere without a central cavity............ .... ***Styptosphaera***
4'. Spongy sphere with a central cavity.................. .... ***Plegmosphaera***

5. Pores irregular in size, arrangement, and spacing; shell wall very thin........................... 6
5'. Pores more or less regular in size, arrangement and spacing, shell wall of variable thickness.. 11

6. Surface of shell smooth or lumpy, no spines or tubes.. ***Collosphaera***
6'. Shell surface with internal or external spines or tubes 7

7. Inwardly or outwardly directed tubular protuberances 8
7'. Numerous outwardly directed spines............... .... ***Acrosphaera***

8. Inwardly directed tubes with perforated walls.................................... ***Buccinosphaera***
8'. Outwardly directed tubes................................ 9

9. Tubes poreless...................... ***Siphonosphaera***
9'. Pored tubules.. 10

10. Tube termination smooth .... ***Disolenia***
10'. Tube termination with one or more spines ....***Otosphaera***

11. Shell with prominent primary spines.........12
11'. Shell without prominent primary spines ....***Cenosphaera***

12. Primary spines branched.......... ***Cladococcus***
12'. Primary spines unbranched ....***Acanthosphaera***

13. Multiple shells, outermost shell spongy......14
13'. Multiple shells, outermost shell latticed.....18

14. Innermost (medullary) shell composed of rods which define the edges of a cube, spines radiating from corners of cube.....................15
14'. Innermost (medullary) shell(s) spherical to subspherical.. 16

15. Outer (cortical) shell in close proximity to cubic medullary shell .... ***Centrocubus***
15'. Outer (cortical) shell somewhat separated from cubic medullary shell....... ***Octodendron***

16. Outermost shell without equatorial constriction 17
16'. Outermost shell with equatorial constriction .... ***Spongoliva***

17. Primary spines present....... ***Spongosphaera***
17'. Primary spines absent.......... ***Spongoplegma***

18. Outer shell(s) ellipsoidal with equatorial constriction, with or without polar caps .... ***Didymocyrtis***
18'. Outer shell(s) spherical to ellipsoidal, no equatorial constriction............................. 19

19. Outermost shell composed of a series of girdles 33
19'. Outermost shell not composed of a series of girdles..20

20. Outer shell(s) form a series of concentric spheres/ellipsoids, no spiral structure visible 21
20'. Outer shell(s) partly or totally of a spiral structure 31

21. No primary spines 22
21'. Prominent primary spines........................ 23

22. Two concentric shells: one medullary and one cortical .... ***Carposphaera***
22'. Three concentric shells, two medullary and one cortical............................ ***Thecosphaera***

23. Two primary spines, bipolar...................... 24
23'. More than two primary spines.................... 27

24. Two bipolar spines, not joined distally........25
24'. Two bipolar spines, joined distally so as to form a ring.................................. ***Saturnalis***

25. Two concentric shells, one medullary and one cortical.. 26
25'. Three concentric shells, two medullary and one cortical........................ ***Stylacontarium***

26. Spines similar.......................... ***Stylatractus***
26.' Spines dissimilar............... ***Druppatractus***

27. Four primary spines .... ***Staurolonche***
27'. Six primary spines arranged symmetrically 28
27". Eight or more primary spines................... 29

28. Two concentric shells: one medullary and one cortical...................................... *Hexalonche*
28'. Three concentric shells: two medullary and one cortical.............................. *Hexacontium*

29. With pylome .... *Cromyechinus*
29'. Without pylome 30

30. Two concentric shells, one medullary and one cortical................................... *Astrosphaera*
30'. Three concentric shells, two medullary and one cortical .... *Actinomma*

31. Without pylome.. 32
31'. With pylome................................ *Larcopyle*

32. Spiral tightly wound....................... *Lithelius*
32'. Spiral open................................ *Larcospira*

33. Two systems of concentric girdles............... 34
33'. Three systems of concentric girdles........... 35

34. Four gates bisected by sagittal beam *Octopyle*
34'. Four gates, simple, not bisected.....*Tetrapyle*

35. Six open gates................................ *Hexapyle*
35'. Six closed gates................................ *Pylolena*

36. General shell shape cylindrical.................. 37
36'. Basic shell shape lenticular; overall shape circular to subcircular, quadrate, or trigonal... 38

37. Spongy cylinder with no visible structure but may vary in width .... *Spongocore*
37'. Spongy cylinder, may have some structure, with or without pylome................. *Spongurus*

38. Outer shell lenticular, latticed...*Heliodiscus*
38'. Outer shell spongy, with or without some visible structure 39

39. Shell spongy, but with some chambers or bands visible.. 40
39'. Shell spongy, no visible structure.............. 43

40. Outer meshwork forms two-chambered arm (one of which may bifurcate distally) radiating from central disc.*Amphirhopalum*
40'. No radiating arms, but with more or less concentric or spiral bands around central chamber... 41

41. With external radiating spines.................. 42
41'. Without external radiating spines, but with a pylome...................................*Ommatodiscus*

42. With thin, porous equatorial girdle........... .... *Stylochlamydium*
42'. No equatorial girdle .... *Stylodictya*

43. Lenticular shell without radiating arms......44
43'. Conspicuous arms or dense areas of spongy material radiating from central disc.........46

44 . With pylome .... *Spongopyle*
44'. Without pylome 45

45. With external spines radiating from disc.......... .... *Spongotrochus*
45'. Without external spines radiating from disc .... *Spongodiscus*

46. Outer meshwork forms three radiating arms, sometimes bifurcated distally.........47
46'. Outer meshwork forms four or more radiating "arms" joined by meshwork, outline quadrangular...................................... *Spongaster*

47. Arms disposed bilaterally, two paired arms, one unpaired (forming a Y)........ *Euchitonia*
47'. Arms equally disposed (propeller-like)...... .... *Hymeniastrum*

FAMILY OUTLINE WITH ILLUSTRATIVE GENERA

FAMILY THALASSICOLLIDAE Haeckel, 1862

Solitary Spumellaria without a skeleton, or in some genera containing spicules.

Genus ***Actissa*** Haeckel, 1887

Alveoli neither within nor without the central capsule. Nucleus spherical, sometimes ellipsoidal, not branched (Fig. 4D).

Genus ***Lampoxanthium*** Haeckel, 1887

Numerous large alveoli within the peripheral jelly calymma, not in the central capsule. Spicules branched.

Genus ***Physematium*** Meyen, 1834

Very thin capsular membrane surrounding a spherical nucleus suspended within cytoplasmic strands delineating alveolar spaces radiating toward the peripheral capsular membrane. Spicules smooth and spindle-shaped.

Genus ***Thalassicolla*** Huxley, 1851

Numerous large alveoli surrounding the central capsule within the gelatinous extracapsulum, nucleus spherical (Fig. 1A).

Genus ***Thalassolampe*** Haeckel, 1862

Numerous large alveoli within the central capsule, not in the extracapsulum, nucleus spherical.

Genus ***Thalassoplancta*** Haeckel, 1887

Numerous large alveoli within the extracapsulum, not in the central capsule, with simple, unbranched spicules scattered throughout the extracapsulum (Fig. 4G).

Genus ***Thalassosphaera*** Haeckel, 1862

Alveoli lacking (neither within or surrounding the central capsule), extracapsular-spicules simple.

Genus ***Thalassoxanthium*** Haeckel, 1887

Alveoli absent, branched spicules scattered within the extracapsulum (Fig. 4E).

FAMILY COLLOZOIDAE Haeckel, 1862

Colonial Spumellaria without a skeleton or with scattered spicules in the gelatinous sheath.

Genus ***Collozoum*** Haeckel, 1862

Colonial species lacking spicules and containing numerous central capsules, spherical to irregular in shape depending on the species, enclosed by a gelatinous sheath (Fig. 4A).

Genus ***Rhaphidozoum*** Haeckel, 1862

Colonial species with simple or radiate spicules (most frequently with 4, or more rarely 3, 5, or 6 rays).

Genus ***Sphaerozoum*** Meyen, 1834

Colonial species with scattered, paired-triradiate spines bearing a central shaft and three rays at each pole (Fig. 4G).

FAMILY COLLOSPHAERIDAE Müller, 1858B

Colonial polycystines, each central capsule has a single, thin-walled, spherical or subspherical latticed shell. This is the only group of colonial polycystines with complete latticed shells. Colonies consist of a gelatinous mass in which hundreds to thousands of shells are immersed. The shape of the colony is not species-specific; it may be spherical, ellipsoidal, cylindrical, ribbon-shaped, etc., measuring up to several centimeters in length and a few millimeters in diameter. The siliceous shells are always represented by a single perforated sphere (internal spheres are never present), with or without centrifugal (external) or centripetal (internal) tubular projections and/or spines. Spines (when present) are conical (circular in cross-section) (Fig. 5D-H).

Genus **Acrosphaera** Haeckel, 1881

Central capsules widely spaced and each surrounded by a single latticed shell, the outer surface of which is covered with solid, conical, or radial spines perforated by pores at the base and distributed between the pores of the shell (Fig. 5E).

Genus ***Buccinosphaera*** Haeckel, 1887

Shell surrounding each central capsule appearing as crumpled sphere with shallow depressions from which extend short inwardly directed conical tubules (Fig. 5F).

Genus ***Collosphaera*** Müller, 1855

Each central capsule surrounded by a latticed shell, smooth-surfaced, lying at considerable distance from one another, and varying in shape among species from spherical, crumpled, polygonal, or in the form of a thin net of large and small polygonal meshes (Fig. 5D).

Genus ***Disolenia*** Ehrenberg, 1860

Shell smooth, thin-walled, subspherical, with numerous small irregular pores having no definite arrangement. Pored tubules, 3-8, approximately as long as broad, cylindrical, slightly expanded distally (Fig. 5I).

Genus ***Siphonosphaera*** Müller, 1858

Shell surrounding each central capsule spherical, rather thick-walled with somewhat rough or pitted surface and numerous, irregularly scattered, subcircular pores. Wall with 4 to 10 poreless, cylindrical tubules smoothly truncated tangentially or sometimes obliquely (Fig. 5H).

FAMILY ACTINOMMIDAE Haeckel, 1862
emend. Riedel, 1971, Sanfilippo and Riedel, 1980

Solitary species with latticed or spongy spherical, subspherical, or ovoid shells (not discoidal, nor equatorially constricted ellipsoids); with or without medullary shells. Surface of shell is often covered with spines, but not tubes. All actinommids posses either single or multiple, concentric spherical or ovoid shells. When several shells are present, they are connected to each other by radial beams which pierce the cell. (Figs. 2A-D, 7 A-F)

Genus ***Actinomma*** Haeckel, 1860

Without pylome, 3 concentric spheres and 10-20 unbranched spines of either uniform or irregular length (Fig. 7E).

Genus ***Astrosphaera*** Haeckel, 1881

As above, but 2 concentric shells joined by long radial spines (Fig. 7F).

Genus ***Hexacontium*** Haeckel, 1881

Shells composed of 3 spheres bearing 6 radial spines of equal size arranged in 3 mutually perpendicular axes (Fig. 7C).

Genus ***Saturnalis*** Haeckel, 1881

Spherical shell with 2 opposite spines joined by a ring encircling the shell (Fig. 6H).

Genus ***Staurolonche*** Haeckel, 1881

Spheroidal porous shell with 4 unbranched spines Fig. 7A).

FAMILY PHACODISCIDAE Haeckel, 1881
emend. Campbell, 1954

A lenticular, cortical shell, not surrounded by spongy or chambered structures, encloses a much smaller, single or multiple medullary shell. The margin (but less commonly the surfaces) of the cortical shell may bear radial spines. (Figs. 2F,G)

Genus ***Heliodiscus*** Haeckel, 1862

Radial spines unbranched; medullary shell simple Fig. 8B).

FAMILY: COCCODISCIDAE Haeckel, 1862,
emend. Sanfilippo and Riedel, 1980

Discoidal forms consisting of a lenticular cortical shell enclosing a small single or double medullary shell, and surrounded by an equatorial zone of spongy or concentrically-chambered structures. Or forms with ellipsoidal cortical shell, usually equatorially constricted and enclosing a single or double medullary shell. The opposite poles of the shell can bear spongy columns and/or single or multiple latticed caps. Fig. 2H, 6E.

Genus ***Didymocyrtis*** Haeckel, 1860a

Bilocular cortical shell with or without polar spongiose caps (Fig. 6E).

FAMILY: SPONGODISCIDAE Haeckel, 1862
emend. Riedel, 1967b, Petrushevskya and Kozlova, 1972

Discoidal or cylindrical forms with or without a visible central chamber surrounded by concentric or spiral, continuous or interrupted, finely chambered bands, or partially or totally spongy with no visible structure. The surface of some forms may be partly or totally covered with a very thin, porous sieve-plate, which in lenticular forms may extend beyond the central spongy mass forming a delicate equatorial girdle around the periphery of the shell. Major part of the shell can be represented by 2-4 thickenings of the spongy mesh or separate arms radiating from the central disc in the equatorial plane. (Figs. 2I-N, 8J-L)

Genus ***Euchitonia*** Ehrenberg, 1860

Three undivided chambered arms (Y-shaped) with a patagium (spongiose veil) between the arms. Shell bilateral (Fig. 8K).

Genus ***Hymeniastrum*** Ehrenberg, 1847

Like *Euchitonia* but angles between arms equal (Fig. 8L).

Genus ***Spongaster*** Ehrenberg, 1860

Four spongy arms with patagium forming a quadrangular shape (Fig. 8J).

FAMILY PYLONIIDAE Haeckel, 1881
emend. Campbell, 1954

Shell consisting of an ellipsoidal inner chamber or microsphere of complicated construction and with one or two pairs of openings or gates, enclosed by a series of successively larger elliptical latticed girdles in three mutually perpendicular planes; with the major diameter of each girdle being the minor diameter of the next smaller one. Figs. 2Q, 7J)

Genus ***Octopyle*** Haeckel, 1881

Ellipsoidal shell with 2 perfect girdles and 4 gates bisected by sagittal septum (Fig. 7J).

FAMILY THOLONIIDAE Haeckel, 1887

Completely latticed shell, without larger openings, and with two or more annular constrictions or furrows separating dome-shaped protuberances (Fig. 2R).

Genus ***Tholostaurus*** Haeckel, 1887

Central chamber without medullary shell, 4 simple dome-shaped cupolas (Fig. 5A).

FAMILY LITHELIIDAE Haeckel, 1862

Ellipsoidal to spherical or lenticular shell in outer form, and of spiral organization, at least internally; initial chamber of basic pyloniid type (Figs. 2P, 7H).

Genus ***Larcospira*** Haeckel, 1887

Transverse girdle consisting of a simple or double spiral around a principal axis. At least in *L. quadrangula* shell consists of 2 open spirals arising from a common origin (Fig. 7I).

Genus ***Lithelius*** Haeckel, 1860b

Spirally arranged lattice shell with branched or unbranched radial spines (Fig. 7H).

Order **Nassellaria** Ehrenberg, 1875

Body plan typically not spherical; actinopodia arise from a pore plate at one pole of the central capsule, skeleton when present composed of spicules, rings, other geometric shapes or single or multi-segmented latticed chambers. A widely recognized, albeit seldom utilized, feature of primary importance for the classification of the Nassellaria is the internal skeleton. The internal skeleton consists of a complex set of spines and connecting bars enclosed in the cephalis, which allow comparison of homologous structures in forms differing widely in their external morphology.

KEY TO GENERA

The following key is not natural, since our knowledge of polycystine phylogenies is limited. It is a practical guide based on some fairly conspicuous characteristics observable with a light microscope

1. Shell composed of rings, bars and rods, lattice absent or very loose, open.............................. 2
1'. Latticed shell.. V

2. Basal tripod only.. 3
2'. Basal tripod plus sagittal ring......................... 5

3. Branches of basal tripod not connected distally .... *Triplagia*
3'. Branches of basal tripod connected distally......4

4. Distal connections do not form a chamber....... .... *Triplecta*
4'. Distal connections form an irregularly latticed chamber (cephalis)............. *Phormacantha*

5. Simple vertical sagittal ring only. *Zygocircus*
5'. Simple vertical ring with additional rings and/or appendages, open meshwork 6

6. Shell outline bilaterally symmetrical with two lobes clearly defined by a sagittal ring.......... 7
6'. No lobes evident 10

7. Lobes consisting of two crossed rings, verical a vertical meridional; additional horizontal basal ring.............................. *Acanthodesmia*
7'. Lobes defined by open meshwork..................... 8

8. Lobes with large polygonal meshwork................. .... *Lophospyris*
8'. Lobes kidney-shaped with irregular meshwork 9

9. Lobes formed by two plates joined only by sagittal ring .... *Nephrospyris*
9'. Lobes complete, closed.................. *Lithocircus*

10. One complete vertical ring with additional half ring or arch between base and top .... *Neosemantis*
10'. Two parallel polygonal rings of dissimilar size, connected by bars........ *Pseudocubus*

size, connected by bars........ *Pseudocubus*

V. NASSELLARIA WITH LATTICED SHELL

Lattice shell complete, cephalis simple, unilocular, spherical without constrictions or lobes.. VI

1'. Lattice shell complete, cephalis lobed............ 2

2. Cephalis bilocular, lobes defined by a sagittal constriction.. VII

2'. Cephalis multilocular...................................... 3

3. Cephalis trilocular VIII

3'. Cephalis apparently multilocular, composed of cephalis, ante- and post-cephalic lobes (cephalis simple).. IX

VI NASSELLARIA WITH LATTICED SHELL (cephalis unilocular, spherical, without lobes)

1. Simple cephalis distinct from subsequent segments.. 2

1'. Cephalis rudimentary or submerged into thorax 16

2. Simple cephalis without lateral cephalic tube..3

2'. Simple cephalis with lateral cephalic tube; pores in precise horizontal rows.................27

3. Simple cephalis with one additional segment (thorax); rudimentary, poorly defined abdomen may be present.............................. 4

3'. Simple cephalis with more than one additional segment 22

4. Thorax closed; no abdomen .... *Lithopera*

4'. Thorax open 5

5. Cephalis and thorax approximately same width.6

5'. Thorax wider than cephalis............................. 7

6. Without radial apophyses............. *Lophophaen*

6'. With radial apophyses................ *Peromelissa*

7. Thorax cylindrical, ovate or sharply conical...8

7'. Thorax widely conical (like a Chinese peasant hat... 13

8. Thoracic ribs which may become external to form radial apophyses 9

8'. Apophyses form basal thoracic projections..20

9. Three thoracic ribs.................................. 10

9'. Three thoracic ribs, all joined with apical by a delicate meshwork..............*Arachnocorys*

10. Thoracic ribs do not become external........11

10'. Thoracic ribs and a large apical horn, all joined by a delicate meshwork...................12

11. Thoracic wall with regularly arranged sub-circular pores............... *Cycladophora*

11'. Thoracic wall interrupted by large holes... .... *Clathrocanium*

12. Meshwork continuous .... *Callimitra*

12'. Meshwork interrupted by thoracic holes..... .... *Clathrocorys*

13. Three radial apophyses 14

13'. Numerous sinuous ribs .... *Sethophormis*

14. With skirt-like abdominal section......... 15

14'. Without abdominal section.. *Lampromitra*

15. Cephalis with branched horns...................... .... *Eucecryphalus*

15'. Cephalis with unbranched apical horn.......... ....*Theopilium*

16. Cephalis rudimentary 17

16'. Cephalis submerged into thorax 19

17. Thorax narrowly conical......................... 18

17'. Thorax widely conical (like a Chinese peasant hat or dau-li)...... *Litharachnium*

18. Cephalis rudimentary, no thoracic ribs..... .... *Cornutella*

18'. Cephalis rudimentary, numerous thoracic ribs.................................... *Peripyramis*

19. Cephalis completely submerged into thorax .... *Carpocanistrum*

19'. Cephalis partially submerged into thorax.... .... *Antarctissa*

20. Three basal appendages are extensions of thoracic ribs... 21

20'. More than three basal appendages................ .... *Acanthocorys*

21. Appendages project from base of thorax as "feet"..................................... *Pterocanium*

21'. Appendages project distally from wall of thorax as "wings"................ *Dictyophimus*

22. Simple cephalis with two additional segments (thorax,abdomen)...................................... 23

22'. Simple cephalis with more than two additional segments... 24

23. Three external radial apophyses projecting from thorax.................................. *Lipmanella*
23'. No radial apophyses on thorax ....*Clathrocyclas*

24. Basal segment closed, wings on thorax ....*Cyrtopera*
24'. Basal segment open................................. 25

25. Radial apophyses (wings) on thorax ....*Stichopilium*
25'. No radial apophyses on thorax................. 26

26. Complete shell conical in outline ....*Lithostrobus*
26'. Complete shell spindle-shaped in outline ....*Eucyrtidium*

27. Cylindrical lateral cephalic tube 28
27'. Duck-billed lateral cephalic tube, pores quadrate, outline stepped; multisegmented ....*Spirocyrtis*

28. Tube short 29
28'. Tube elongate, lying along thorax................ .... *Phormostichoartus*

29. Three-segmented, but third segment may have minor indentations alternating with single transverse pore rows.... *Siphocampe*
29'. Multisegmented, constrictions well defined, several rows of pores per segment............. .... *Botryostrobus*

VII. NASSELLARIA WITH LATTICED SHELL (cephalis bilocular)

1. Lobed cephalis only 2
1'. Lobed cephalis plus galea and/or false thorax..3

2. Six feet .... *Liriospyris*
2'. Three feet 4

3. Sagittal ring external.............. *Dendrospyris*
3'. Sagittal ring internal.............. *Triceraspyris*

4. Galea present, three feet .... *Tholospyris*
4'. False thorax present............... *Phormospyris*

VIII. NASSELLARIA WITH LATTICED SHELL (cephalis trilocular)

1. Trilocular cephalis with one additional segment (thorax)... 2
1'. Trilocular cephalis with two additiona segments (thorax, abdomen)....................................... 3

2. Thorax ends in distinct poreless peristome with terminal "teeth"....... *Anthocyrtidium*
2'. Thorax without peristome........ *Lamprocyrtis*

3. Paired cephalic lobes lateral to larger unpaired lobe; abdomen wider than thorax.................... 4
3'. Paired cephalic lobes beneath larger unpaired lobe, forming a "neck"; abdomen and thorax of approximately equal width ... *Theocorythium*

4. Abdomen ends in a distinct poreless peristome with terminal "teeth"........... *Lamprocyclas*
4'. No differentiated peristome or terminal "teeth"... *Pterocorys*

IX. NASSELLARIA WITH LATTICED SHELL (cephalis apparently multilocular)

1. Multilocular cephalis, shell monothalamous; one cephalic lobe completely enclosed by the other...................................... *Centrobotrys*

1'. Multilocular cephalis, shell consisting of more than one chamber... 2

2. Multilocular cephalis, shell dithalamous (cephalis, thorax)...................................... 3
2'. Multilocular cephalis (two conspicuous lobes of similar size); shell trithalamous (cephalis, thorax, abdomen).. *Botryocyrtis*

3. Two conspicuous larger lobes of similar size... .... *Saccospyris*
3'. Lobes dissimilar in size................................ 4

4. With cephalic tubes .... *Acrobotrys*
4.' Without cephalic tubes .... *Botryopyle*

FAMILY OUTLINE WITH ILLUSTRATIVE GENERA

FAMILY PLAGONIIDAE Haeckel, 1881 emend. Riedel, 1967b

Simple "tripodal" nassellarian spicule or single latticed chamber (cephalis) lacking post-cephalic chambers. Wide variety of forms developed from elaboration of accessory spines and branches, including latticed chamber surrounding spicule. (Fig. 3A,B)

Genus *Callimitra* Haeckel, 1881

Small, dome-shaped cephalis provided with very long apical (directed upwards), dorsal, and main

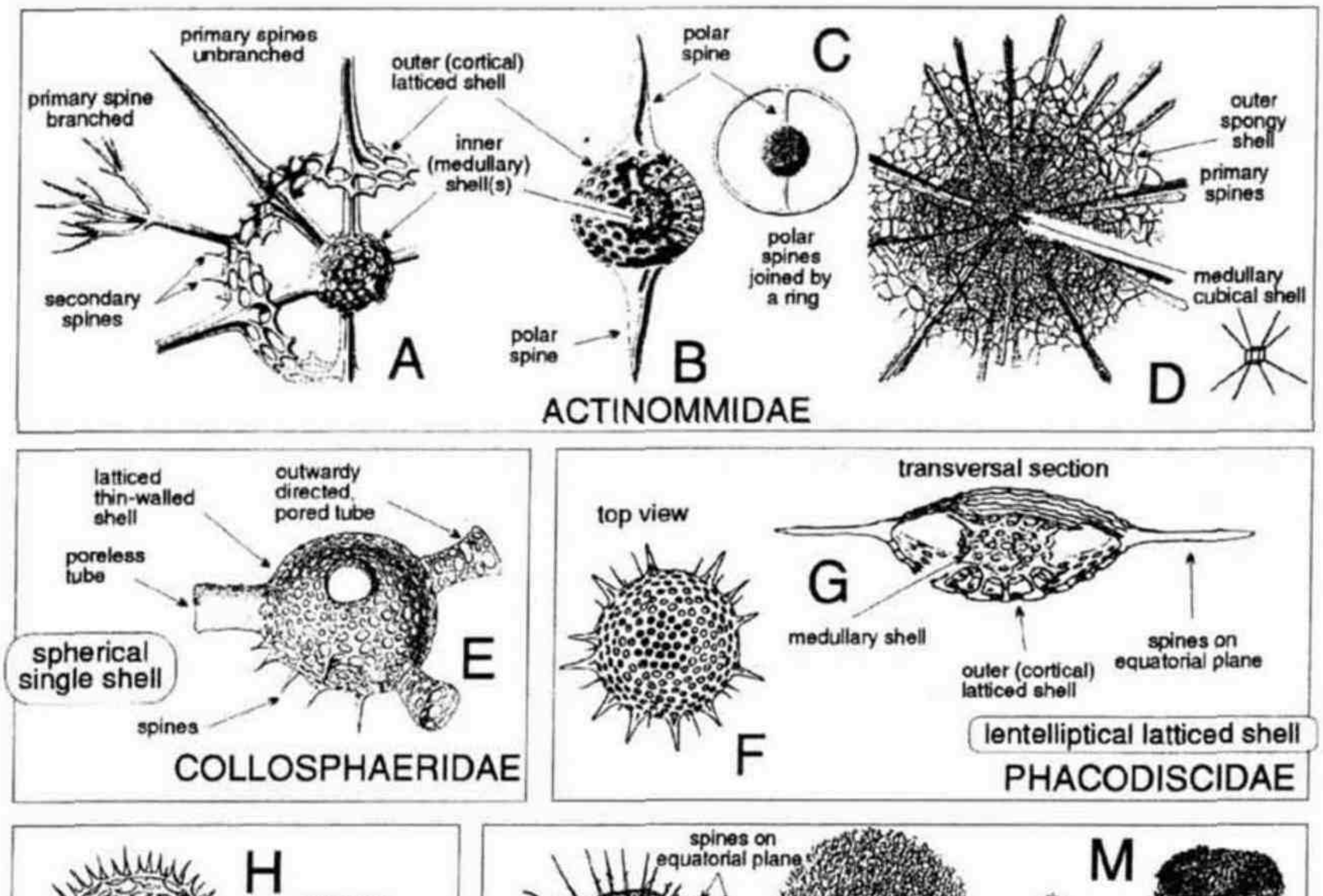

Fig. 2. Structural elements of the spumellarian skeleton and their nomenclature. A-D. Actinommidae Haeckel, 1862, *sensu* Riedel (1967b). E. Collosphaeridae Müller, 1858a,b. F,G. Phacodiscidae Haeckel, 1881. H. Coccodiscidae Haeckel, 1862. I-N. Spongodiscidae Haeckel, 1862, *sensu* Riedel, 1967b. O,P. Litheliidae Haeckel, 1862. Q. Pyloniidae Haeckel, 1881. R. Tholoniidae Haeckel, 1887. Sources. A-E, H, Q, R, modified from Haeckel (1887); F, G, M, modified from Boltovoskoy (1981); I, K, P, Petrushevskaya (1967); J, Dreyer (1889); L, modified from Riedel (1958); N, Nigrini and Moore (1979); and O, Takahashi (1991).

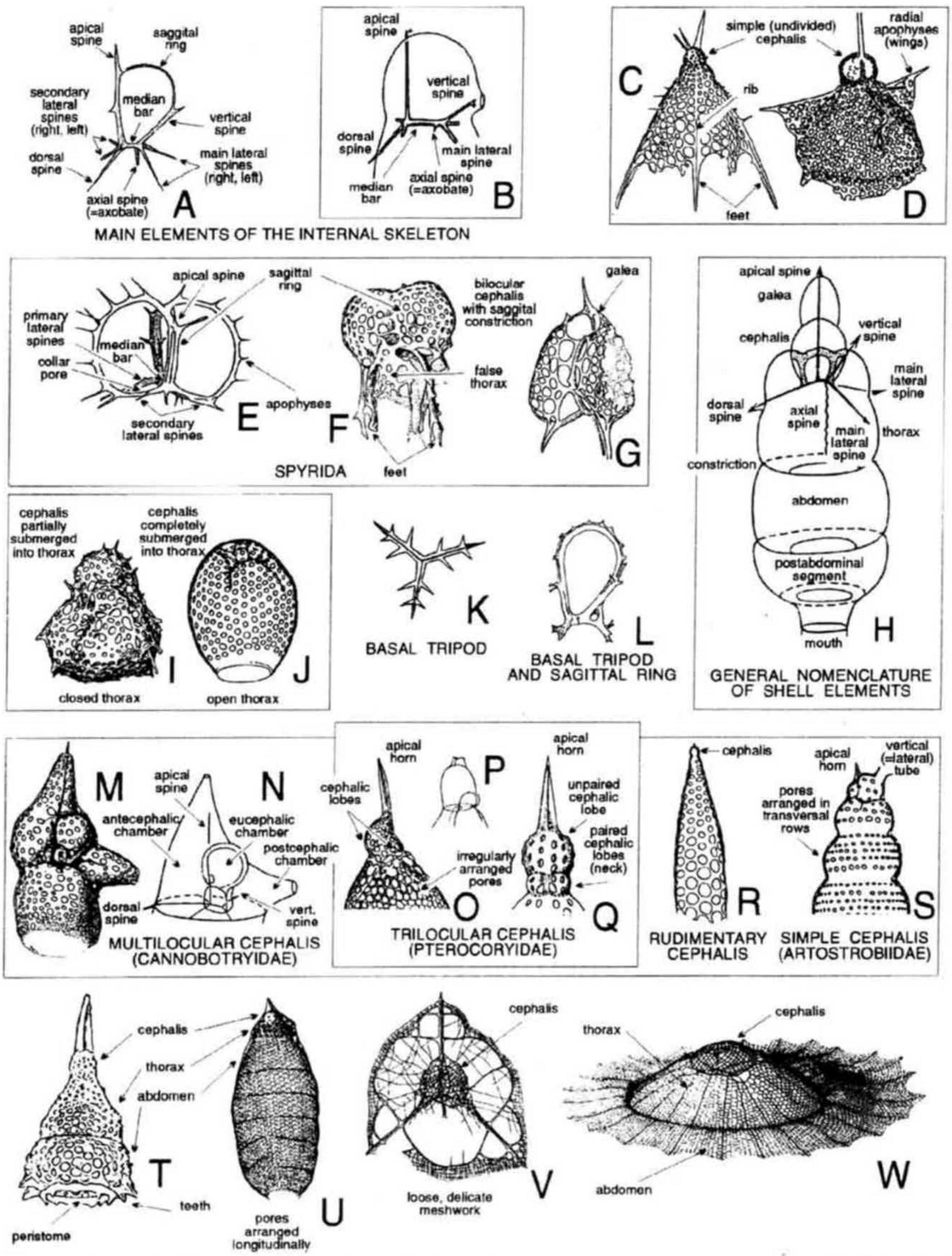

Fig. 3. Diversity and skeletal elements of Nassellaria. Sources. A, H, N, Petrushevskaya (1981); B, Riedel (1958); C-E, G, I, J, L, M, O, S, U, V, Petrushevskaya (1971); F, R, Petrushevskaya (1967); K, W, Haeckel (1887); P, Riedel (1957); Q, Nigrini (1967); T, Hays (1965).

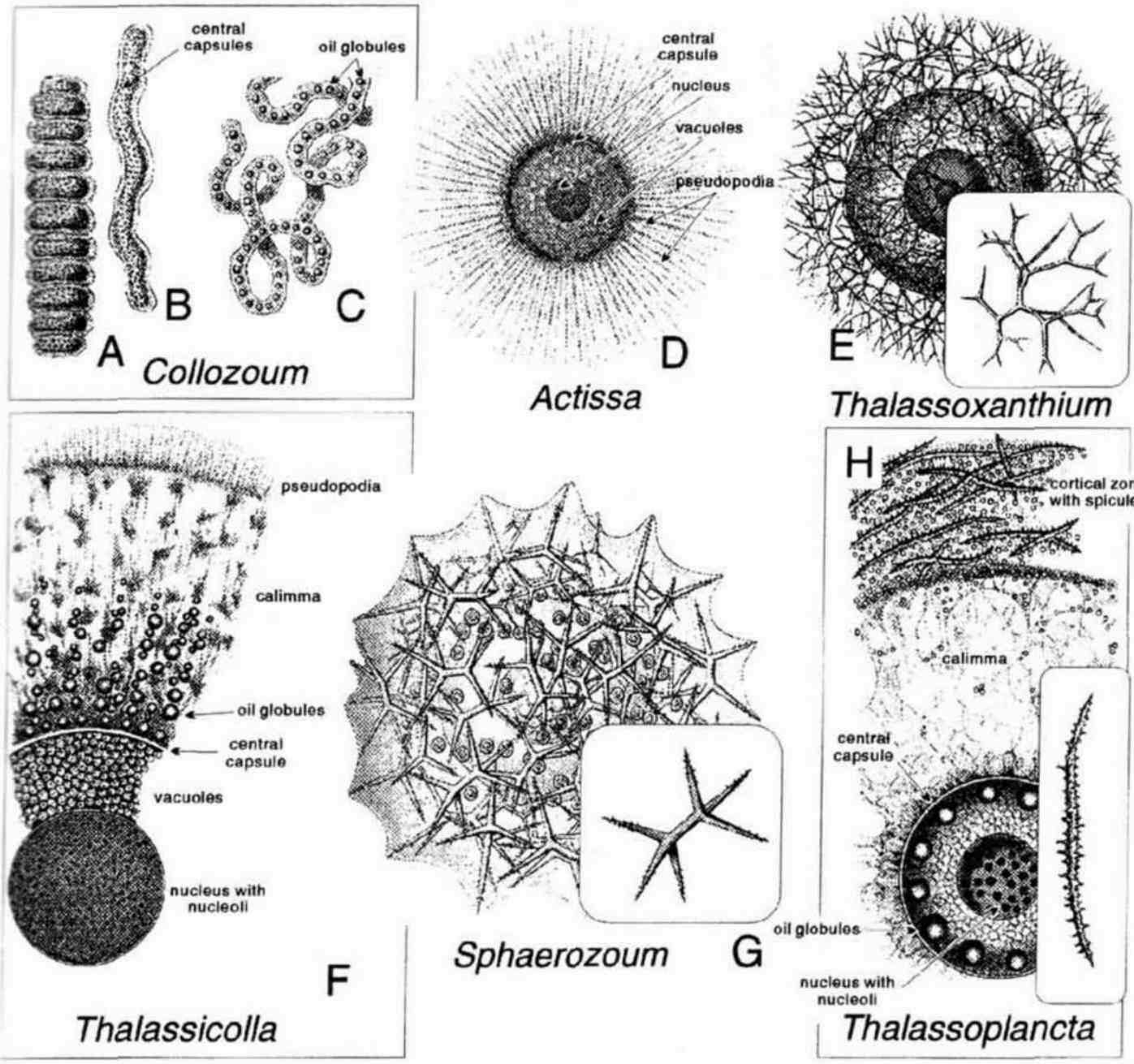

Fig. 4. Skeletonless and spiculated Spumellaria. A-C. *Collozoum* sp. Haeckel, 1862 (p 522), D. *Actissa* sp. Haeckel, 1887 (p 12), E. *Thalassoxanthium* sp. Haeckel, 1881 (p 470), F. *Thalassicolla* sp. Huxley, 1851 (p 433), G. *Sphaerozoum* sp. Meyen, 1834 (p 163), and G. *Thalassoplancta* sp. Haeckel, 1887 (p 29). (All adapted from Haeckel, 1887)

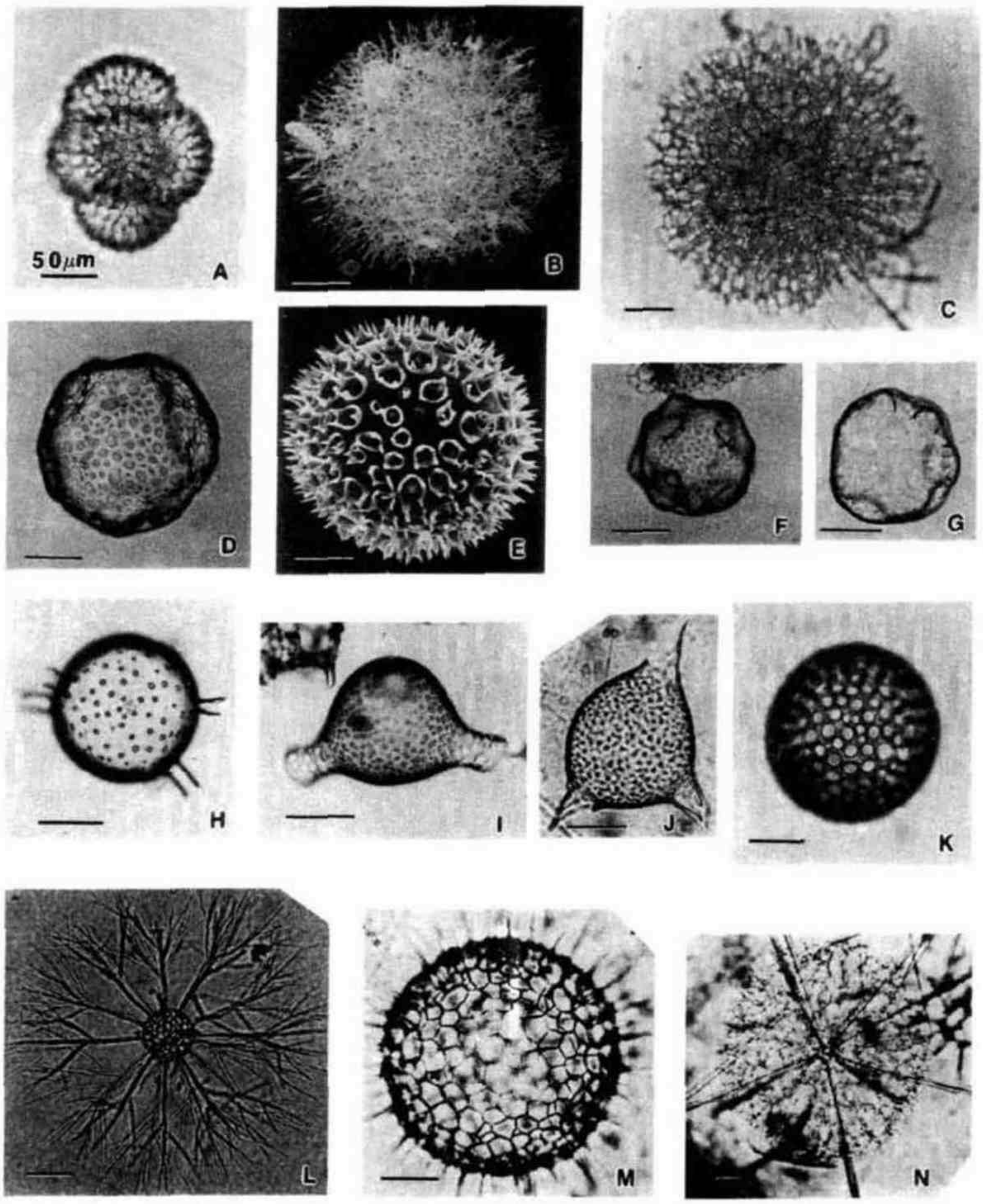

Fig. 5. Spumellaria. A. *Tholostaurus* sp. Haeckel, 1887 (p 670) (x225). B. *Styptosphaera spongiacea* Haeckel, 1881 (p 455 in Haeckel, 1887) (x210). C. *Plegmosphaera* sp. Haeckel, 1881 (p 455) (x180). D. *Collosphaera tuberosa* Müller, 1855 (p 238 in Haeckel, 1887) (x225). E. *Acrosphaera murrayana* Haeckel, 1881 (p 471in Haeckel, 1887) (x230). F. *Buccinosphaera invaginata* Haeckel, 1887 (p 99) (x215). G. *Buccinosphaera invaginata* (x215). H. *Siphonosphaera polysiphonia* Müller, 1858b (p 59 in Haeckel, 1887) (x233). I. *Disolenia quadrata* Ehrenberg, 1860 (p 831in Ehrenberg, 1872) (x250). J. *Otosphaera polymorpha* Haeckel, 1887 (p 116) (x210). K. *Cenosphaera* sp. Ehrenberg, 1854 (p 237) (x200). L. *Cladococcus scoparius* Müller, 1857 (p 485 in Haeckel, 1887) (x160). M. *Acanthosphaera tunis* Ehrenberg, 1858 (p 12 in Haeckel, 1887) (x210). N. *Centrocubus octostylus* Haeckel, 1887 (p 277) (x104). (A,C) D. Boltovskoy; (D,F) J. Caulet; (K—J) Morley; (G-I) Nigrini (1967, 1971); (B,E,J,L-N) Takahashi (1991).

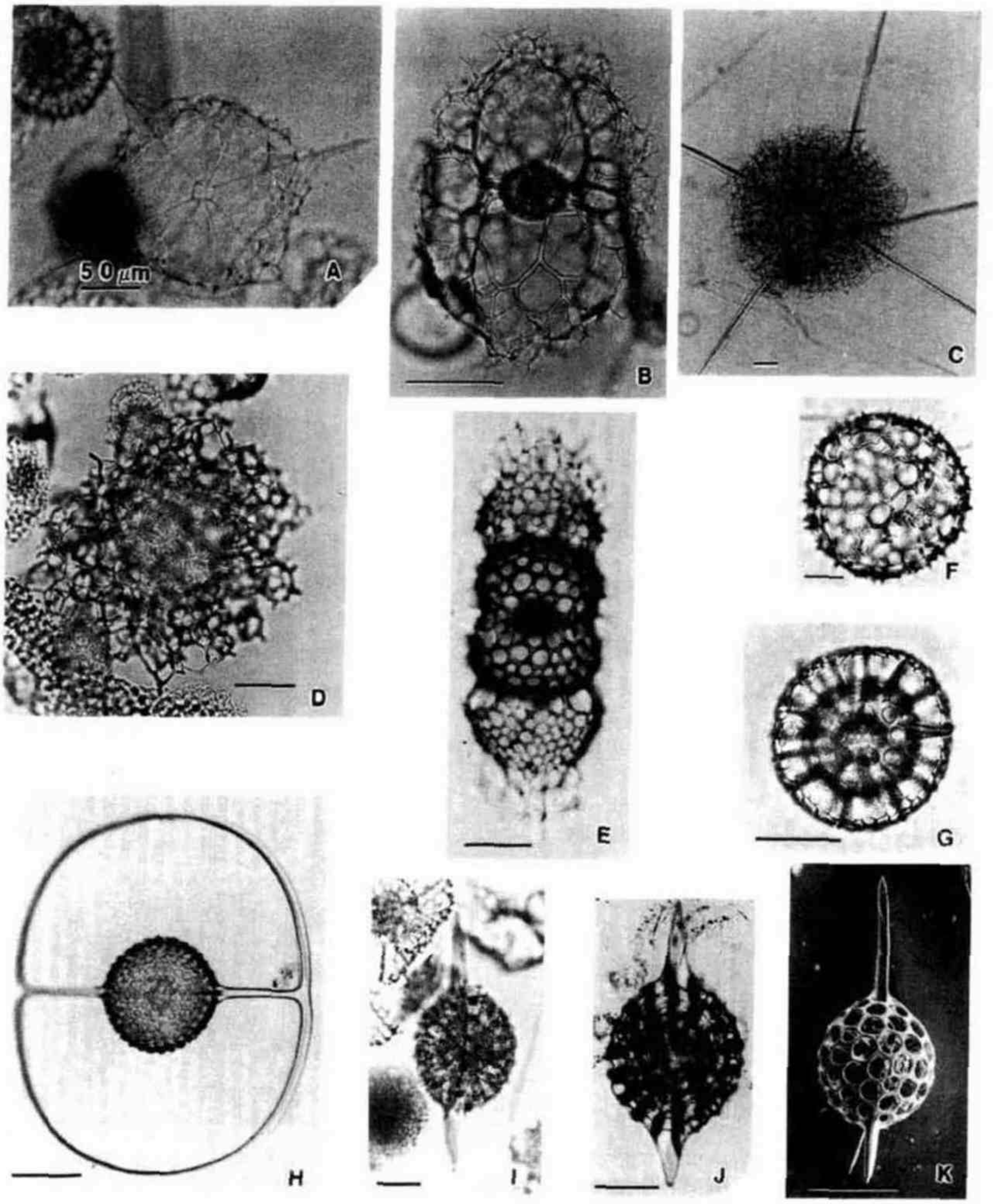

Fig. 6. Spumellaria. A. *Octodendron* sp. Haeckel, 1887 (p 279) (x200). B. *Spongoliva* sp. Haeckel, 1887, (p 351) (x360). C. *Spongosphaera* sp. Ehrenberg, 1847b (p 54) (x85). D. *Spongoplegma* sp. Haeckel, 1881 (p 455) (x225). E. *Didymocyrtis tetrathalamus* Haeckel, 1881 (p 816 in Haeckel, 1887) (x250). F. *Carposphaera* sp. Haeckel, 1881 (p 451) (x160). G. *Thecosphaera* sp. Haeckel, 1881 (p 452) (x320). H. *Saturnalis circularis* Haeckel, 1881 (p 450 in Haeckel, 1887) (x233). I. *Stylacontarium* sp. Popofsky, 1912 (p 90) (x160). J. *Stylatractus* sp. Haeckel, 1887 (p 328) (x233). K. *Druppatractus* sp. Haeckel, 1887 (p 324) (x325). (A) Boltovskoy (1987); (B,D,E) C. Nigrini; (F,G,I) D. Boltovskoy; (H) Nigrini (1967); (J, courtesy of J. Moore); (K, courtesy of J. Caulet).

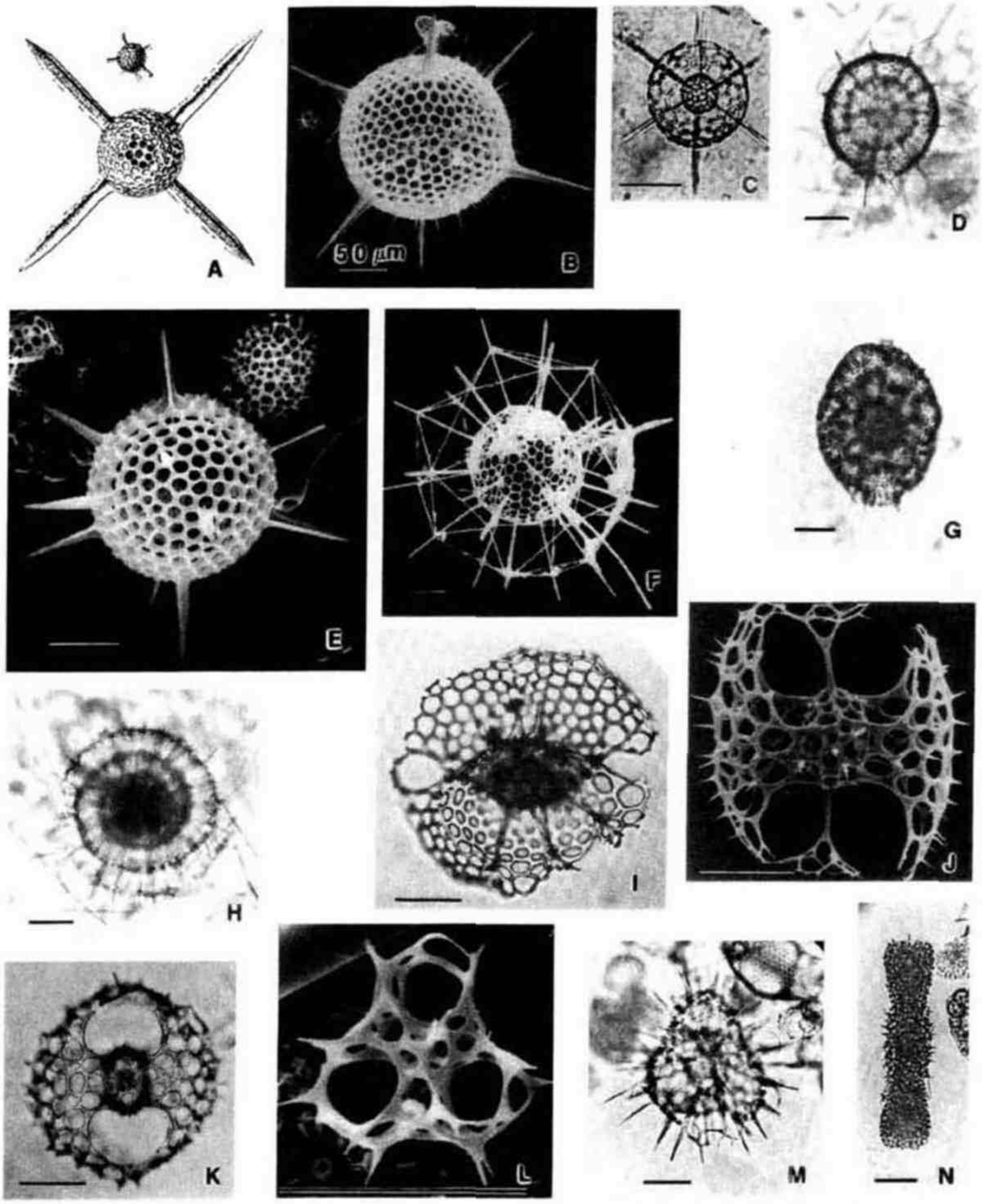

Fig. 7. Spumellaria. A. *Staurolonche pertusa* Haeckel, 1881 (p 451 in Haeckel, 1887) (mag. unknown). B. *Hexalonche amphisiphon* Haeckel, 1881 (p 451 in Haeckel, 1887) (x180). C. *Hexacontium axotrias* Haeckel, 1881 (p 452 in Haeckel, 1887) (x210). D. *Cromyechinus* sp. Haeckel, 1881 (p 453) (x160). E. *Actinomma* sp. Haeckel, 1860a (p 815) (X250). F. *Astrosphaera hexagonalis* Haeckel, 1887 (p 250) (x120). G. *Larcopyle* sp. Dreyer, 1889 (p 124) (x160). H. *Lithelius* sp. Haeckel, 1860b (p 843) (x160). I. *Larcospira quadrangula* Haeckel, 1887 (p 695) (x233). J. *Octopyle stenozona* Haeckel, 1881 (p 463, Haeckel, 1887) (x330). K. *Tetrapyle octachantha* Müller 1858a (p 154) (x230). L. *Hexapyle* sp. Haeckel, 1881 (p 463) (X960). M. *Pylolena* sp. Haeckel, 1887 (p 567) (x160). N. *Spongocore* sp. Haeckel, 1887 (p 345) (x160). (A) Haeckel (1887); (B,C,J) Takahashi (1991); (D,G,H,M,N) D. Boltovskoy; (E, K) J. Caulet; and (I) Nigrini (1970).

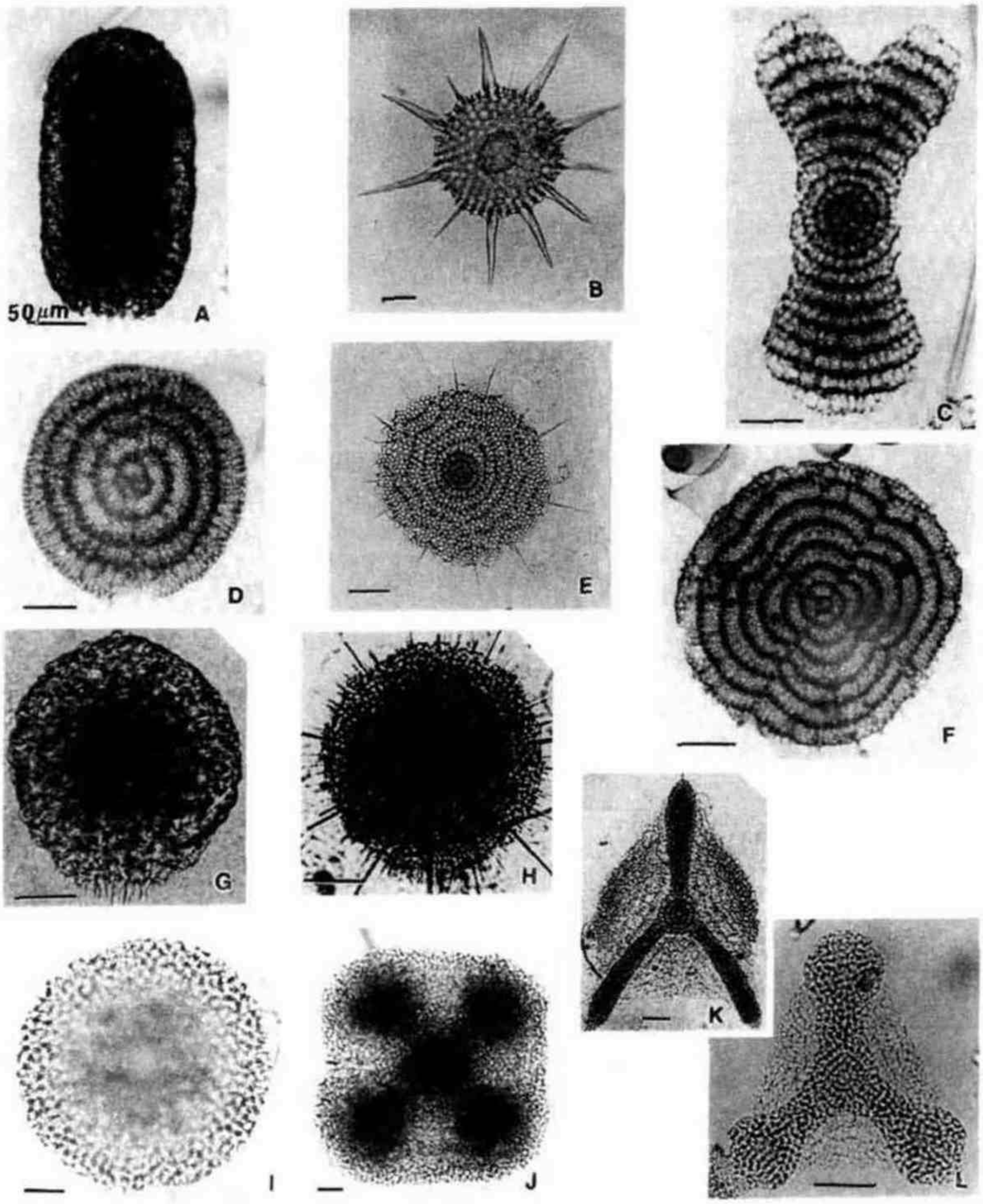

Fig. 8. Spumellaria. A. *Spongurus* sp. Haeckel, 1860b (p 844) (x200). B. *Heliodiscus asteriscus* Haeckel, 1862 (p 436 in Haeckel, 1887) (x136). C. *Amphirhopalum ypsilon* Haeckel, 1881 (p 460, Haeckel, 1887) (x233). D. *Ommatodiscus* sp. Stohr, 1880 (p 115) (x190). E. *Stylochlamydium* sp. Haeckel, 1881 (p 460) (x160). F. *Stylodictya* sp. Ehrenberg, 1847a (chart to p 385) (x200). G. *Spongopyle osculosa* Dreyer, 1889 (p 118) (x210). H. *Spongotrochus glacialis* Haeckel, 1860b (p 844, Popofsky, 1908) (x210). I. *Spongodiscus* sp. Ehrenberg, 1854 (p 237) (x160). J. *Spongaster tetras* Ehrenberg, 1860 (p 833) (x106). K. *Euchitonia elegans* Ehrenberg, 1860 (p 831in Ehrenberg, 1872) (x105). L. *Hymeniastrum euclidis* Ehrenberg, 1847a (chart to p 385 in Haeckel, 1887) (x225). (A) J. Morley; (B,C) C. Nigrini; (D) J. Caulet; (E,I,J,L) D. Boltovskoy; (G,H,K) Takahashi (1991).

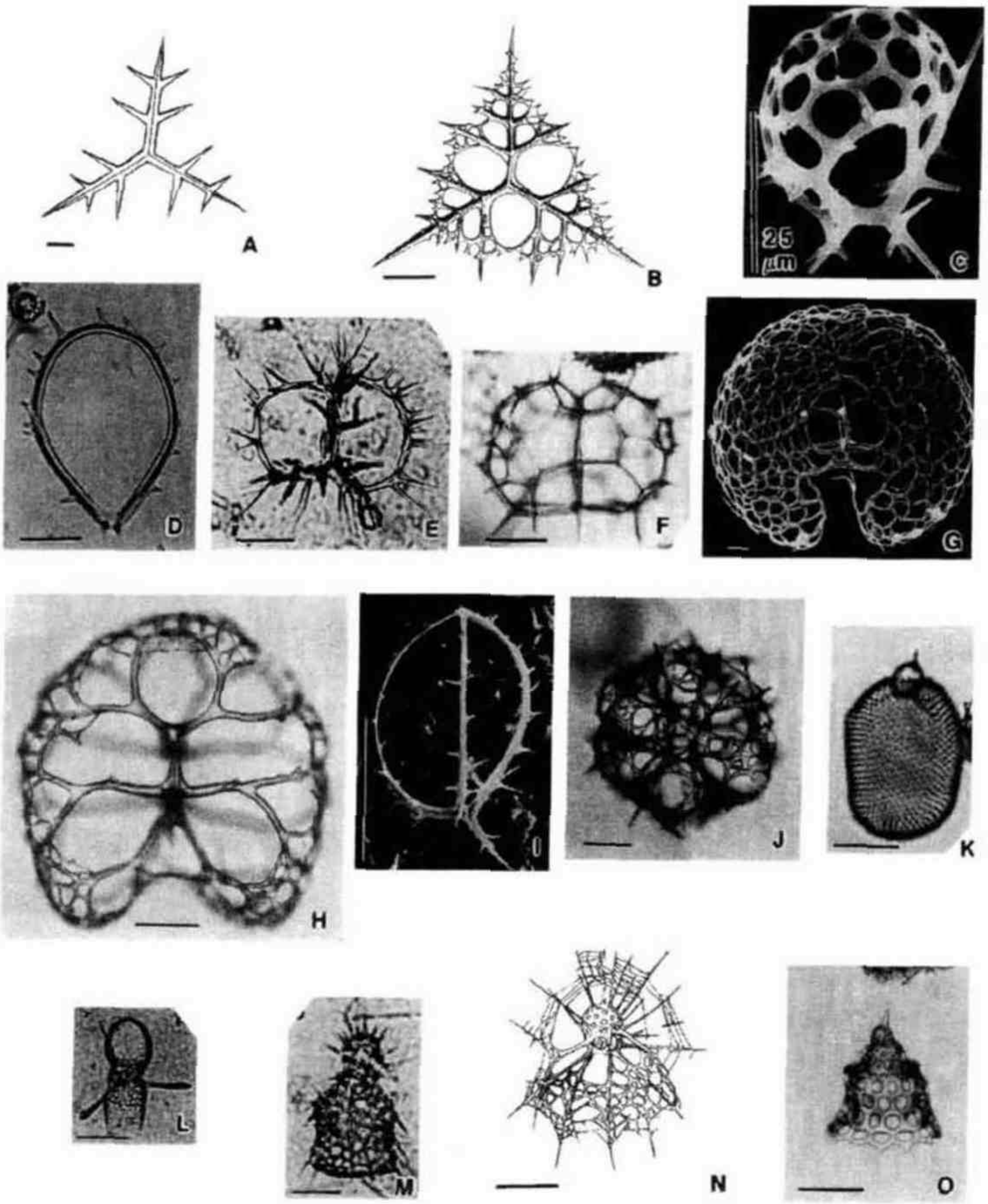

Fig. 9. Nassellaria. A. *Triplagia primordialis* Haeckel, 1881 (p 423 in Haeckel, 1887) (x100). B. *Triplecta triactis* Haeckel, 1881 (p 424 in Haeckel, 1887) (x180). C. *Phormacantha hystrix* Jörgensen, 1905 (p 132, Jörgensen 1900) (x1200). D. *Zygocircus productus* Butschli, 1882 (p 496) (x210). E. *Acanthodesmia vinculata* Müller, 1857 (x210). F. *Lophospyris pentagona* Haeckel, 1887 (p 1080 in Ehrenberg, 1872) (x233). G. *Nephrospyris renilla* Haeckel, 1887 (p 1100) (x80). H. *Lithocircus reticulata* Müller, 1857 (p 484, Ehrenberg, 1872) (x233). I. *Neosemantis distephanus* Popofsky, 1913 (p 298) (x520). J. *Pseudocubus warreni* Haeckel, 1887 (p 1010 in Goll, 1980) (x200). K. *Lithopera bacca* Ehrenberg, 1847a (chart to p 385 in Ehrenberg, 1872) (x233). L. *Lophophaena cylindrica* Ehrenberg, 1847b (p 54, Cleve, 1900) (x210). M. *Peromelissa phalacra* Haeckel, 1881 (p 433 in Haeckel, 1887) (x210). N. *Arachnocorys circumtexta* Haeckel, 1860b (p 837 in Haeckel, 1862) (x240). O. *Cycladophora davisiana* Ehrenberg, 1847a (chart to p 385 in Ehrenberg, 1861) (x230). Sources. (A,B) Haeckel (1887); (B,E,G,I,L,M) Takahashi (1991); (D,O) J. Caulet; (F,H,K) Nigrini (1967); (J) Nigrini and Caulet (1992); (N) Petrushevskaya (1971).

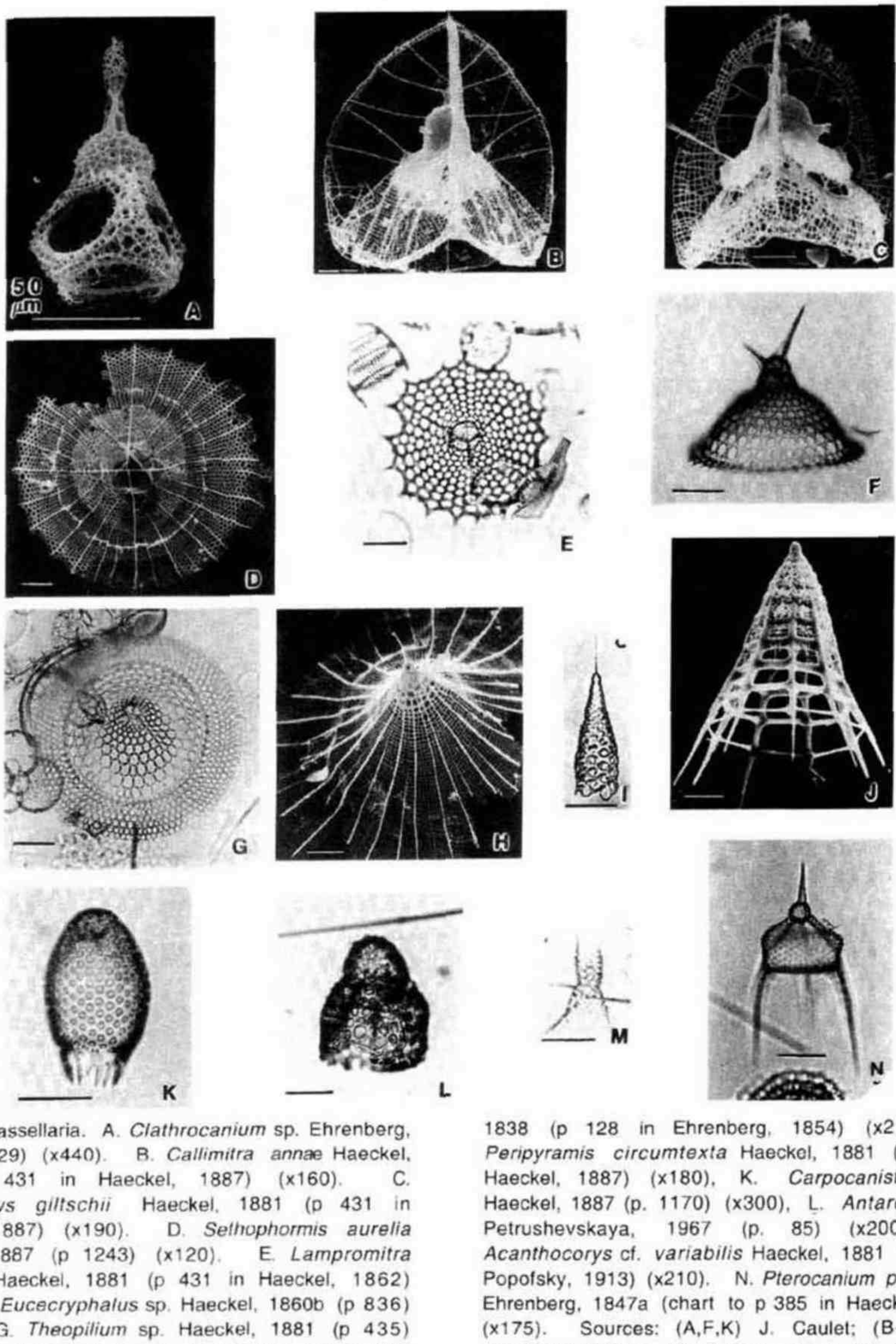

Fig. 10. Nassellaria. A. *Clathrocanium* sp. Ehrenberg, 1860 (p 829) (x440). B. *Callimitra annae* Haeckel, 1881 (p 431 in Haeckel, 1887) (x160). C. *Clathrocorys giltschii* Haeckel, 1881 (p 431 in Haeckel, 1887) (x190). D. *Sethophormis aurelia* Haeckel, 1887 (p 1243) (x120). E. *Lampromitra schultzei* Haeckel, 1881 (p 431 in Haeckel, 1862) (x180). F. *Eucecryphalus* sp. Haeckel, 1860b (p 836) (x200). G. *Theopilium* sp. Haeckel, 1881 (p 435) (x160). H. *Litharachnium tentorium* Haeckel, 1860b (p 835) (x150). I. *Cornutella profunda* Ehrenberg, 1838 (p 128 in Ehrenberg, 1854) (x210). J. *Peripyramis circumtexta* Haeckel, 1881 (p 428 in Haeckel, 1887) (x180), K. *Carpocanistrum* sp. Haeckel, 1887 (p. 1170) (x300), L. *Antarctissa* sp. Petrushevskaya, 1967 (p. 85) (x200). M. *Acanthocorys* cf. *variabilis* Haeckel, 1881 (p 432 in Popofsky, 1913) (x210). N. *Pterocanium praetextum* Ehrenberg, 1847a (chart to p 385 in Haeckel. 1872) (x175). Sources: (A,F,K) J. Caulet; (B-D,H-J,M) Takahashi (1991); (E) D. Boltovskoy; (L) J. Morley; (N) Nigrini (1970).

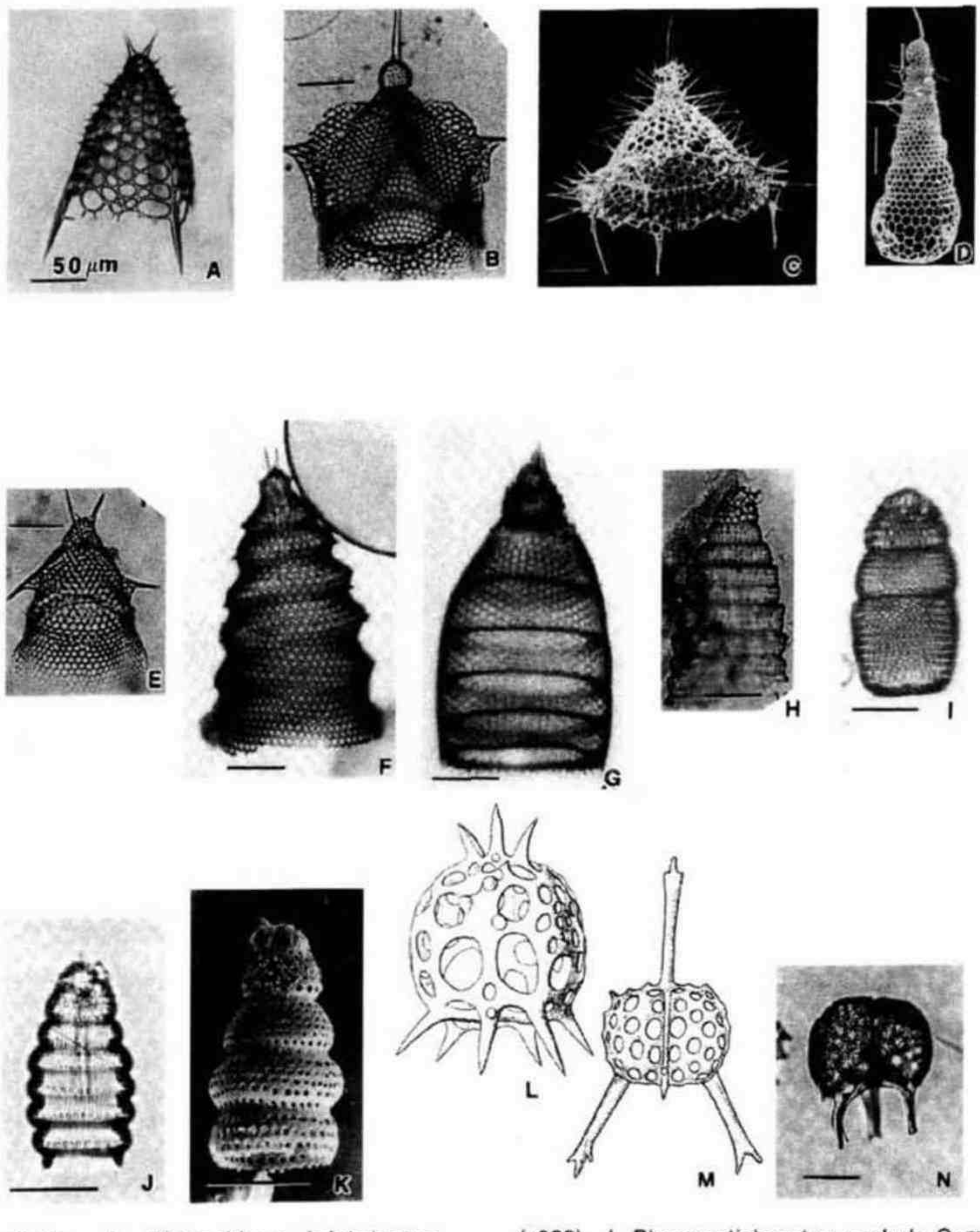

Fig. 11. Nassellaria. A. *Dictyophimus infabricatus* Ehrenberg, 1847a, (chart to p 383 in Nigrini, 1968) (x200). B. *Lipmanella virchowii* Loeblich & Tappan, 1961 (p 226 in Haeckel, 1862) (x210). C. *Clathrocyclas cassiopejae* Haeckel, 1881 (p 439 in Haeckel, 1887) (x150). D. *Cyrtopera laguncula* Haeckel, 1881 (p 434 in Haeckel, 1887) (x190). E. *Stichopilium bicorne* Haeckel, 1881 (p 439 in Haeckel, 1887) (x210). F. *Lithostrobus* cf *hexagonalis* Bütschli, 1882 (p 529 in Haeckel, 1887) (x200). G. *Eucyrtidium hexagonatum* Ehrenberg, 1847a (chart to p 385 in Haeckel, 1887) (x250). H. *Spirocyrtis scalaris* Haeckel, 1881 (p 438 in Haeckel, 1887) (x220). I. *Phormostichoartus corbula* Campbell, 1951 (p. 530, Harting, 1863) (x250). J. *Siphocampe nodosaria* Haeckel, 1881 (p 438 in Haeckel, 1887) (x320). K. *Botryostrobus auritus/australis* Haeckel, 1887 (p 1475 in Ehrenberg, 1844ab) (x400). L. *Liriospyris hexapoda* Haeckel, 1881 (p 441) (mag. unknown). M. *Dendrospyris* sp. Haeckel, 1881 (p 443 in Haeckel, 1887) (mag. unknown). N. *Triceraspyris* sp. Haeckel, 1881 (p 441) (x200). Sources. (A) Nigrini and Caulet (1992); (B-E) Takahashi (1991); (F, K) J. Caulet; (G) Nigrini (1967); (H) Nigrini (1977); (I) C. Nigrini; (J) D. Boltovskoy; (L) Haeckel (1887); (M) Petrushevskaya (1981); (N) J. Morley.

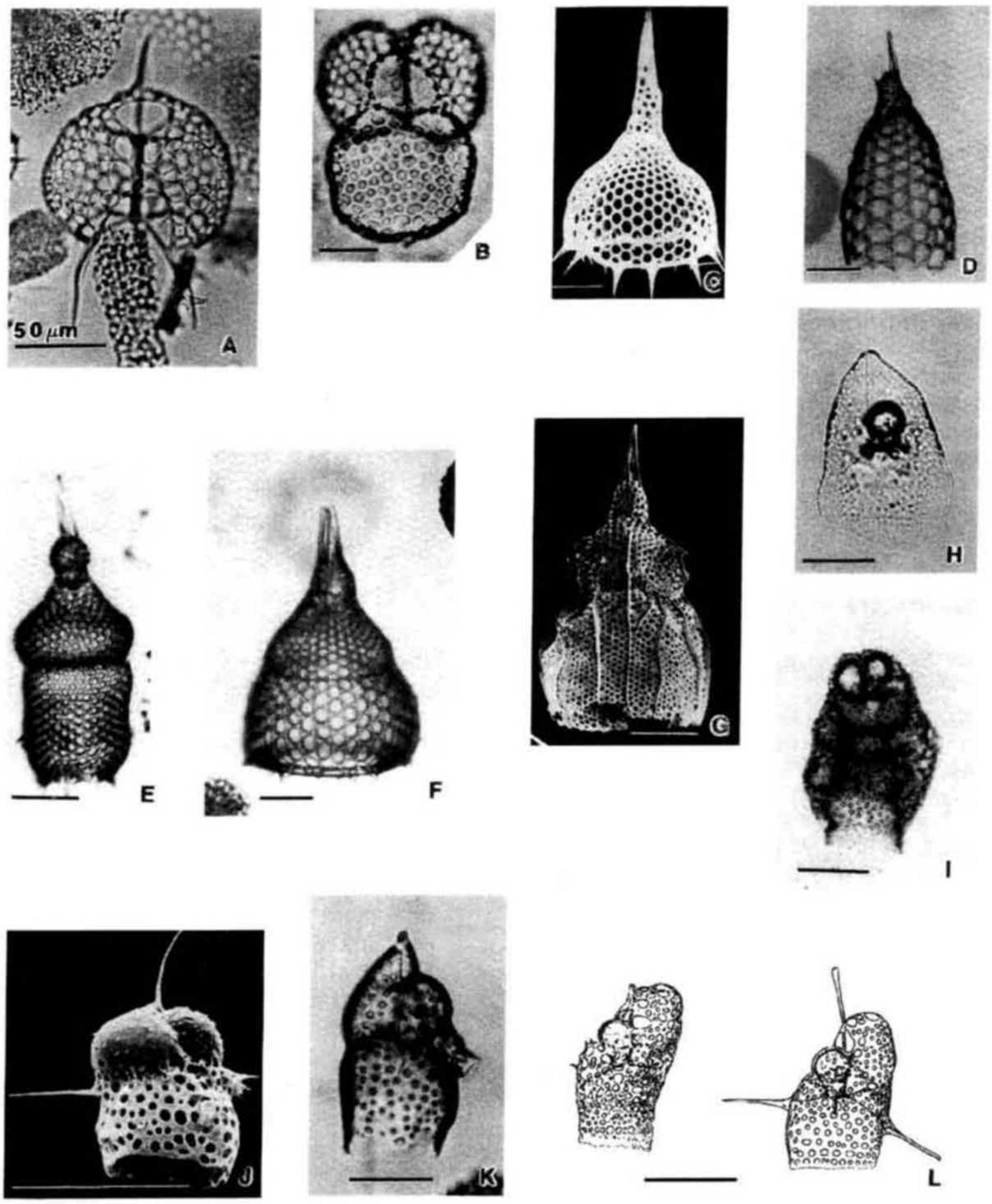

Fig. 12. Nassellaria. A. *Tholospyris* sp. Haeckel, 1881 (p 441) (x320). B. *Phormospyris stabilis* Haeckel, 1881 (p 442 in Goll, 1976) (x210). C. *Anthocyrtidium ophirense* Haeckel, 1881 (p 430 in Ehrenberg, 1872) (x200). D. *Lamprocyrtis nigriniae* Kling, 1973 (p 638 in Caulet, 1971) (x200). E. *Theocorythium trachelium* Haeckel, 1887 (p 1416 in Ehrenberg, 1872) (x233). F. *Lamprocyclas maritalis* Haeckel, 1881 (p 434 in Haeckel, 1887) (x200). G. *Pterocorys hertwigii* Haeckel, 1881 (p 435 in Haeckel, 1887) (x240). H. *Centrobotrys thermophila* Petrushevskya, 1965 (p 113) (x250). I. *Botryocyrtis scutum* Ehrenberg, 1860 (p 829 in Harting, 1863) (x250). J. *Saccospyris preantarctica* Haecker, 1907 (p 124 in Petrushevskya, 1975) (x630). K. *Acrobotrys* sp. (p 440 in Haeckel, 1881) (x300). L. *Botryopyle dictyocephalus* Haeckel, 1881 (p 440 in Haeckel, 1887) (x360). Sources: (A) D. Boltovskoy; (B,C,J) Takahashi (1991); (D) Nigrini and Caulet (1992); (E,I) Nigrini (1967); (F, G, K) J. Caulet; (H) C. Nigrini; (L) Petrushevskaya (1971).

lateral spines (directed down and sideways) interconnected by a delicate meshwork which forms 3 basal plates and 3 lateral plates (Fig. 10B).

Genus ***Clathrocanium*** Ehrenberg, 1860

Cephalis with a large, 3-bladed apical horn which may have lateral thread-like, anastomosing projections. The dorsal and 2 main lateral spines, directed down and sideways, are joined by narrow lattice plates which form a small thorax (Fig. 10A).

Genus ***Clathrocorys*** Haeckel, 1881

Terminal mouth of thorax as above and 3 radial ribs enclosed in the wall of the thorax that bears 3 large lateral holes between the 3 ribs. No frontal horn (Fig. 10C).

Genus ***Phormacantha*** Jörgensen, 1905

Primary spines with 3 arches and a strong ventral sagittal spine (Fig. 9C).

Genus ***Sethophormis*** Haeckel, 1887

Terminal mouth wide open. Radial ribs smooth, enclosed in the wall of the thorax. Shell flat, campanulate, or nearly discoidal. Cephalis without a horn (Fig. 10D).

Genus ***Triplagia*** Haeckel, 1881

Three radial spines simple or branched, radiating from a point (Fig. 9A).

Genus ***Triplecta*** Haeckel, 1881

Three regularly arranged spines in one plane, which anastomose to form a loose wickerwork (Fig. 9B).

Genus ***Zygocircus*** Bütschli, 1882

Pear-shaped or D-shaped, spiny, 3-bladed sagittal ring (Fig. 9D).

FAMILY ACANTHODESMIIDAE Haeckel, 1862

Skeleton represented by a well-developed D-shaped sagittal ring (median bar and anastomosed vertical and apical spines), either free or embedded into the latticed cephalic wall, in which case the cephalis is usually bilaterally lobed. Sometimes with thorax, abdomen always absent. The typical heteropolar nassellarian symmetry is often inconspicuous in the Spyridae (Fig. 3E, 9E).

Genus ***Acanthodesmia*** Müller, 1857

Four open lateral gates, partly latticed (Fig. 9E).

Genus ***Dendrospyris*** Haeckel, 1881

Shell composed of cephalis without apical cupola or dome or thorax. Feet branched like a tree, single apical horn (Fig. 11M).

Genus ***Liriospyris*** Haeckel, 1881

Shell as above, but with 6 basal feet and 3 apical horns (Fig. 11L).

Genus ***Lophospyris*** Haeckel, 1881.

Shell with 7 to 12 or more basal feet; spines unbranched, meshes polygonal or within polygonal frames (Fig. 9F).

Genus ***Tholospyris*** Haeckel 1881

Cephalis with an apical cupola and horn, without thorax. Three basal feet (Fig. 12A).

FAMILY THEOPERIDAE Haeckel, 1881
emend. Riedel, 1967B

Small spherical or nearly spherical cephalis (smallest anterior chamber), often poreless or sparsely perforate and with apical spine, and one or more post-cephalic chambers. Cephalis contains a reduced internal spicule homologous with that of the plagoniids. Generally, cap- or helmet-shaped nassellarians or tending toward conical in overall plan (Fig. 9K)

Genus ***Eucyrtidium*** Ehrenberg, 1847
emend. Nigrini, 1967

Ovate or spindle-shaped shell with solid apical horn, multisegmented, with constricted mouth (Fig. 11G).

Genus ***Lithopera*** Ehrenberg, 1847

Shell 2-segmented with cephalis partly submerged into an oval thorax with a closed mouth. Three divergent ribs initially enclosed in the cavity of the thorax (Fig. 9K).

Genus ***Peripyramis*** Haeckel, 1881

Pyramidal shell with simple lattice and an outer net-like mantle, without apical horn; shell mouth open (Fig. 10J).

FAMILY CARPOCANIIDAE Haeckel, 1881
emend. Riedel, 1967b

Cephalis small and included in large second segment (thorax), nearly indistinguishable from latter, and reduced to a few bars that are homologous with nassellarian spicule in other groups. Abdomen absent or rudimentary (Fig. 10K).

Genus ***Carpocanistrum*** Haeckel, 1887

Shell subspherical to oval, cephalis completely submerged in thorax. Poreless peristome with or without terminal teeth (Fig. 10K).

FAMILY PTEROCORYTHIDAE Haeckel, 1881
emend. Riedel 1967b, emend. Moore, 1972

Cephalis large, elongate, divided into three lobes by two lateral furrows directed obliquely and downward from the apical spine to the base of the cephalis. The upper unpaired lobe is located above the two smaller paired ones; these basal paired lobes are not always conspicuous. Many pterocorythids are two or three-segmented, lacking postabdominal segments (Fig. 12C, G)

Genus ***Anthocyrtidium*** Haeckel, 1881

Two-segmented shell with apical horn, poreless peristome, mouth open, constricted, bearing terminal and subterminal teeth outside the mouth opening (Fig. 12C).

Genus ***Lamprocyclas*** Haeckel, 1881

Trilocular cephalis with 2 additional segments (thorax and abdomen). Shell mouth open, with terminal teeth. Peristome differentiated (Fig. 12F).

Genus ***Lamprocyrtis*** Kling, 1973

Lamprocyrtis hannai. Cephalis elongate, with a large 3-bladed apical horn. Thorax campanulate, thick-walled, with subregular, circular pores. Abdomen truncate-conical, with large, subregular, circular pores and usually with terminal and/or subterminal teeth (Fig. 12D).

Lamprocyrtis nigriniae. Cephalis elongated, usually open proximally, with a large 3-bladed horn. Thorax campanulate, thin-walled, with large, subregular, circular pores increasing in size distally; peristome absent or weakly developed. No abdomen.

Genus ***Pterocorys*** Haeckel, 1881

Shell with 3 segments, mouth open, with 3 solid thoracic ribs which may project as thorns or wings. No differentiated peristome or terminal feet (Fig. 12G).

Genus ***Theocorythium*** Haeckel, 1887

Shell with 2-part cephalis: (1) upper sphere and (2) 1 or 2 lobes directly beneath or slightly lateral to the upper sphere. Single apical horn. Abdomen subcylindrical with numerous terminal teeth and sometimes with subterminal teeth scattered irregularly over the distal half of the abdomen. Cephalic lobes form a "neck" structure between the upper cephalis and thorax, a feature peculiar to this genus (Fig. 12E).

FAMILY ARTOSTROBIIDAE Riedel 1967a
emend. Foreman, 1973

Cephalis spherical with a lateral tubule, homologous with vertical spine, and one or more post-cephalic chambers. Pores usually in transverse rows encircling the chambers (Fig. 11H, K).

Genus ***Botryostrobus*** Haeckel, 1887
emend. Nigrini, 1977

Shell with more than 4 segments, vertical tube cylindrical, basal mouth open (Fig. 11K).

Genus ***Phormostichoartus***
Campbell, 1951, emend. Nigrini, 1977

Shell with 4 segments, cylindrical; mouth slightly constricted with well-developed peristome; vertical tube well developed, cylindrical lying along the thorax; no apical horn (Fig. 11I).

Genus ***Spirocyrtis*** Haeckel, 1882
emend. Nigrini, 1977

Shell with more than 4 segments, expanding distally; intersegmental constrictions sharply rounded to angular; vertical tube flared (duck-billed); apical horn or tube present (Fig. 11H).

FAMILY CANNOBOTRYIDAE Haeckel, 1881
emend. Riedel, 1967b

Cephalis, multilobed (sometimes appearing as irregular bulges), unpaired and asymmetrical; one lobe homologous with cephalis of theoperids (Fig. 12K).

Genus **Acrobotrys** Haeckel, 1881

Cephalis has tubules, thorax open (Fig. 12K).

Genus ***Botryopyle*** Haeckel, 1882

Lacks cephalic tubules, thorax is open (Fig. 12L).

Genus ***Saccospyris*** Haecker, 1907

Without apical horn, has corona of minute serrations around basal shell mouth (Fig. 12J).

ACKNOWLEDGEMENTS

We are very pleased to acknowledge the very generous contribution of drawings and photographs from Drs. J. Caulet, J. Moore, J. Morley, M. Petrushevskaya, and T. Takahashi. Some of the line drawings are adapted from Haeckel (1887).

LITERATURE CITED

Anderson, O. R. 1983a. *Radiolaria.* Springer-Verlag, New York. 355 pp

Anderson, O. R. 1983b. The radiolarian symbiosis. *In:* Goff, L. (ed.), *Algal Symbiosis: A Continuum of Interaction Strategies.* Cambridge Univ. Press, Cambridge. pp 69-89

Anderson, O. R. 1992. Radiolarian algal symbioses. *In:* Reissèr, W. (ed.), *Algae and Symbioses: Plants, Animals, Fungi, Viruses, Interactions Explored.* Biopress Ltd., Bristol, England. pp. 93-109

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

Boltovskoy, D. 1981. Radiolaria. *In:* Boltovskoy, D. (ed.), *Atlas del Zooplankton del Atlantico Sudoccidental. Public. esp. del INIDEP.* Mar del Plata, Argentina.

Boltovskoy, D. 1987. Sedimentary record of radiolarian biogeography in the equatorial to Antarctic western Pacific Ocean. *Micropaleontology,* 33:267-281.

Boltovskoy, D. 1994. The sedimentary record of pelagic biogeography. *Progress in Oceanography* (in press).

Boltovskoy, D. & Alder, V. A. 1992. Paleoecological implications of radiolarian distribution and standing stocks versus accumulation rates in the Weddell Sea. *The Antarctic Environment: a Perspective on Global Change, Antarctic Research Series,* American Geophysical Union, 56:377-384.

Bütschli, O. 1882. Beitrage zur Kenntnis der Radiolarienskelette, insbesondere der der Cyrtida. *Z. Wiss. Zool.,* 36:485-540.

Cachon, J. & Cachon, M. 1972. Le système axopodial des radiolaires sphaeroidés. II. Les Periaxoplastidiés, III - Cryptoaxoplastidiés (anaxoplastidiés), IV - Les fusules et le système rhèoplasmique. *Arch. Protistenkd.,* 114:291-307.

Cachon, J. & Cachon, M. 1985. II. Class Polycystinea. *In:* Lee, J. J., Hutner, S. H., & Bovee, E. C. (eds.), *An Illustrated Guide to the Protozoa.* Society of Protozoologists, Lawrence, Kansas. pp 283-295

Campbell, A. S. 1951. New genera and subgenera of Radiolaria. *J. Paleontol.,* 25(4):527-530.

Caron, D. A. & Swanberg, N. R. 1990. The ecology of planktonic sarcodines. *Aquatic Sciences.* CRC Press, Boca Raton, 3:147-180.

Caulet, J. P. 1971. Contribution à l'étude de quelques Radiolaires Nassellaires des boues de la Mediterrané et du Pacifique (Study of some nassellarian Radiolaria from Mediterranean and Pacific sediments). *Cahiers de micropaleontologie Serie 2. Archives originales Centre de Documentation C.N.R.S. No. 498,* 10:1-10.

Cleve, P. T. 1900. Notes on some Atlantic plankton-organisms. *Kongliga Svenska Vetenskapsakademiens handlingar,* 34(1):1-22.

Dreyer, F. 1889. Morphologischen Radiolarien studien. 1. Die Pylombildungen in vergleichend-anatomischer und entwicklungs geschichtlicher Beziehung bei Radiolarien und bei Protisten uberhaupt nebst System und Beschreibung neuer und der bis jetzt bekannten pylomatischen Spumellarien. *Jena. Z. Naturwiss.,* 23:1-138.

Dumitrica, P. 1988. New families and subfamilies of Pyloniacea (Radiolaria). *Rev. Micropaleontol.,* 31:178-195.

Dumitrica, P. 1989. Internal skeletal structures of the superfamily Pyloniacea (Radiolaria), a basis of a new systematics. *Rev. Esp. Micropaleontol.,* 21:207-264.

Ehrenberg, C. G. 1838. Über die Bildung der Kreidefelsen und des Kreidemergels durch unsichtbare Organismen. *K. Akad. Wiss. Berlin, Abh.,* 1838:59-147.

Ehrenberg, C. G. 1844a. Über 2 neue Lager von Gebirgsmassen aus Infusorien als Meeres-Absatz in Nord-Amerika und eine Vergleichung derselben mit den organischen Kreide-Gebilden in Europa und Afrika. *K. Akad. Wiss. Berlin, Abh.*, 1844:57-97.

Ehrenberg, C. G. 1844b. Einige vorlaufige Resultate seiner Untersuchungen der ihm von der Sudpolreise des Captain Ross, so wie von den Herren Schayer und Darwin zugekommenen Materialien uber das Verhalten des kleinsten Lebens in den Oceanen und den grossten bisher zuganglichen Tiefen des Weltmeeres. *K. Akad. Wiss. Berlin, Abh.*, 1844:182-207.

Ehrenberg, C. G. 1847a. Über eine halibiolithische, von Herrn R. Schomburgk entdeckte, vorherrschend aus mikroskopischen Polycystinen gebildete, Gebirgsmasse von Barbados. *K. Akad. Wiss. Berlin, Abh.*, 1846:382-385.

Ehrenberg, C. G. 1847b. Über die mikroskopischen kieselschaligen Polycystinen als machtige Gebirgsmasse von Barbados und über das Verhaltniss deraus mehr als 300 neuen Arten bestehenden ganz eigenthumlichen Formengruppe jener Felsmasse zu den jetzt lebenden Thieren und zur Kreidebildung. Eine neue Anregung zur Erforschung des Erdlebens. *K. Akad. Wiss. Berlin, Abh.*, 1847:40-60.

Ehrenberg, C. G. 1854. Die systematische Charakteristik der neuen mikroskopischen Organismen des tiefen atlantischen Oceans. *K. Akad. Wiss. Berlin, Abh.*, 1854:236-250.

Ehrenberg, C. G. 1858. Kurze Characteristik der 9 neuen Genera und der 105 neuen Species des agaischen Meeres und des Tiefgrundes des Mittel-Meeres. *K. Akad. Wiss. Berlin, Abh.*, 1858:10-40.

Ehrenberg, C. G. 1860. Über den Tiefgrund des stillen Oceans Inseln aus bis 15600' Tiefe nach Lieutenant Brooke. *K. Akad. Wiss. Berlin, Abh..*, 1860:819-833.

Ehrenberg, C. G. 1861. Über die Tiefgrund Verhaltnisse des Oceans am Eingange der Davisstrasse und bei Island. *K. Akad. Wiss. Berlin, Abh.*, 1861:275-315.

Ehrenberg, C. G. 1872. Mikrogeologische Studien als Zusammenfassung seiner Beobachtungen des kleinsten Lebens der Meeres-Tiefgrunde aller Zonen und dessen geologischen Einfluss. *K. Akad. Wiss. Berlin, Abh.*, 1872:265-322.

Ehrenberg, C. G. 1875. Fortsetzung der mikrogeologischen Studien als Gesammt-Uebersicht der mikroskopischen Palaeontologio. *K. Akad. Wiss. Berlin, Abh.*, 1875. 226 pp

Foreman, H. P. 1973. Radiolaria of Leg 10 with systematics and ranges for the families Amphipyndacidae, Artostrobiidae, and Theoperidae. *In:* Worzel, J. L., Bryant, W., et al. (eds.), *Initial Reports of the Deep Sea Drilling Project, vol. 10.* Washington, D.C.: U. S. Government Printing Office, 407-474.

Goll, R. M. 1968. Classification and phylogeny of Trissocyclidae (Radiolaria) in the Pacific and Caribbean Basins. Pt I. *J. Paleontol.*, 42:1409-1432.

Goll, R. M. 1969. Classification and phylogeny of Trissocyclidae (Radiolaria) in the Pacific and Caribbean Basins. Pt II. *J. Paleontol.*, 43:322-339.

Goll, R. M. 1976. Morphological intergradation between modern populations of *Lophospyris* and *Phormospyris* (Trissocyclidae, Radiolaria). *Micropaleontology*, 22(4):379-418.

Goll, R. M. 1980. Pliocene-Pleistocene Radiolaria from the East Pacific Rise and the Galapagos spreading center, Deep Sea Drilling Project Leg 54. *In:* Rosendahl, B. R., Hekinian, R., et al., (eds.) *Initial Reports of the Deep Sea Drilling Project, vol.54.* Washington, D.C.: U. S. Government Printing Office, 1980, 54:425-454.

Gowing, M., M. 1993. Seasonal radiolarian flux at the VERTEX North Pacific time-series site. *Deep-sea Res.*, 40:517-545.

Haeckel, E. 1860a Über neue, lebende Radiolarien des Mittelmeeres und die dazu gehorigen Abbildungen (Some new living Radiolaria from the Mediterranean Sea and their illustration). *K. Akad. Wiss. Berlin, Abh.*, 1860:794-817.

Haeckel, E. 1860b. Fernere Abbildungen und Diagnosen neuer Gattungen und Arten von lebenden Radiolarien des Mittelmeeres (Supplementary illustrations and diagnosis of new genera and species of living radiolarian of the Mediterranean Sea). *K. Akad. Wiss. Berlin, Abh.*, 1860:835-845.

Haeckel, E. 1862. *Die Radiolarien (Rhizopoda Radiaria). Eine Monographie.* Reimer, Berlin. 572 pp

Haeckel, E. 1881. Entwurf eines Radiolarien-Systems auf Grund von Studien der Challenger-Radiolarien (Basis for a radiolarian classification from the study of Radiolaria of the Challenger collection). *Jena. Z. Naturwiss.*, 15:418-472.

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, pp 1-1803.

Haecker, V. 1907. Altertümliche sphärellarien und cyrtellarien aus grossen Meerestiefen. *Arch. Protistenkd.*, 10:114-126.

Harting, P. 1863. Bijdrage tot de kennis der mikroskopische fauna en flora van de Banda-Zee (Contribution to the knowledge of microscopic fauna and flora from the Banda Sea). *Verh. K. Akad. Wet. Lett., Amsterdam*, 10(1):1-34.

Hays, J. D. 1965. Radiolarians and late Tertiary and quaternary history of Antarctic seas. *Biol. Ant. Seas II, Ant. Res. Ser. 5*, Amer. Geophys. Union. pp 125-184

Hertwig, R. 1879. *Der Organismus der Radiolarien.* G. Fischer, Jena. pp. 149 pp

Hollande, A. & Enjumet, M. 1960. Cytologie, évolution et systématique des Sphaeroidés (Radiolaires). *Arch. Mus. Nat. Hist. Natur., Paris, Ser. 7*, 7:1-134.

Huxley, T. H. 1851. Zoological notes and observations made on board H.M.S. Rattlesnake. III. Upon *Thalassicolla*, a new zoophyte. *Annals and Magazine of Natural History, ser. 2*, 8(48):433-442.

Jörgensen, E. 1900. Protophyten und Protozoen im Plankton aus der norwegischen Westküste. *Bergens Museums Aarbog (1899)*, 2 (6):112.

Jörgensen, E. 1905. The protist plankton and the diatoms in bottom samples. *Bergens Museums Skrifter, Bergen, 1905.* pp 49-151

Kling, S. A. 1973. Radiolaria from the eastern North Pacific, Deep Sea Drilling Project Leg 18. *In:* Kulm, L. D., Von Huene, R., et al., (eds.), *Initial Reports of the Deep Sea Drilling Project.* vol. 18. Washington, D.C.: U. S. Government Printing Office. pp 617-671

Kling, S. A. 1978. Radiolaria. *In:* Haq, B. U. & Boersma, A. (eds.), *Introduction to Marine Micropaleontology.* Elsevier, NY. pp 203-244

Kling, S. A. 1979. Vertical distribution of polycystine radiolarians in the central North Pacific. *Mar. Micropaleontol.*, 4:295-318.

Kling, S. A. & Boltovskoy, D. Radiolarian vertical distribution patterns across the southern California Current. *Deep-Sea Res.* (In press)

Loeblich, A. R. & Tappan, H. 1961. Remarks on the systematics of the Sarkodina (Protozoa), renamed homonyms and new validated genera. *Proc. Biol. Soc. Wash.*, 74:213-234.

Meyen, F. J .F. 1834. Über das Leuchten des Meeres und Beschreibung einiger Polypen und anderer niederer Tiere (On starfish and a description of some polyps and other inferior animals). Beitrage zur Zoologie, gesammelt auf einer Reise um die Erde, vol. 16. *Nova acta Academiae Caesareae Leopoldino Carolinae germanicae naturae curiosorum.* pp 125-216

Moore, T. C., Jr. 1972. Mid-Tertiary evolution of the radiolarian genus *Calocycletta*. *Micropaleontology*, 18(2):144-152.

Müller, J. 1855. Über *Sphaerozoum* und *Thalassicolla*. *K. Akad. Wiss. Berlin, Abh.*, 1855:229-253.

Müller, J. 1857. Über die Thalassicollen, Polycystinen und Acanthometren des Mittelmeeres (The Thalassicolla, Polycystina, and Acanthometra from the Mediterranean Sea). *K. Akad. Wiss. Berlin, Abh.*, 1856:474-503.

Müller, J. 1858a. Einige neue bei St. Tropez am Mittelmeer beobachtete Polycystinen und Acanthometren. *K. Akad. Wiss. Berlin, Abh..*, 1858:154-155.

Müller, J. 1858b. Über die Thalassicollen, Polycystinen und Acanthometren des Mittelmeeres. *K. Akad. Wiss. Berlin, Abh.*, 1858:1-62.

Nigrini, C. A. 1967. Radiolaria in pelagic sediments from the Indian and Atlantic oceans. *Bull. Scripps Inst. Oceanogr. Univ. Calif.*, 11:1-125.

Nigrini, C. A. 1968. Radiolaria from eastern tropical Pacific sediments. *Micropaleontology*, 14(1):51-63.

Nigrini, C. A. 1970. Radiolarian assemblages in the North Pacific and their applications to a study of Quaternary sediments in core V20-130. *In:* Hays, J. D. (ed.) *Geological Investigations of the North Pacific.* Geol. Soc. Amer. Mem., 126:139-183.

Nigrini, C. A. 1971. Radiolarian zones in the Quaternary of the Equatorial Pacific Ocean. *In:* Funnell, B. M. & Riedel, W. R. (eds.), *Micropaleontology of Oceans.* Cambridge University Press, Cambridge. pp 443-461

Nigrini, C. A. 1977. Tropical Cenozoic Artostrobiidae (Radiolaria). *Micropaleontology*, 23:241-269.

Nigrini, C. A. & Caulet, J. P. 1992. Late Neocene radiolarian assemblages characteristic of Indo-Pacific areas of upwelling. *Micropaleontology*, 38:139-164.

Nigrini, C. A. & Moore, T. C., Jr. 1979. *A Guide to Modern Radiolaria.* Cushman Foundation for Foraminiferal Research, Sp. Publ. No. 16, Washington, D. C.

Petrushevskaya, M. G. 1965. Osobennosti i konstruktsii skeleta radiolyarii Botryoidae otr. (Nassellaria) (Peculiarities of the construction of the skeleton of radiolarians Botryoidae [Order Nassellaria]). *Tr. Zool. Inst. Akad. Nauk SSSR*, 35:79-118.

Petrushevskaya, M. G. 1967. Radiolyarii otryadov Spumellaria i Nassellaria Antarkticheskoi oblasti (po materialam Sovetskoi Antarkticheskoi Ekspeditzii). *Issledovaniya Fauny Morei IX(XII), Rezultaty Biologicheskikh Issledovanii Sovetskikh Antarkticheskikh Ekspeditsii 1955-1958*, 3:5-186.

Petrushevskaya, M. G. 1971. Radiolayarii Nassellaria v planktone Mirovogo Okeana. *Issledovaniya Fauny Morei IX(XVII)*, Nauka, Leningrad. pp 5-186

Petrushevskaya, M. G. 1975. Cenozoic radiolarians of the Antarctic, Leg 29, DSDP. *In:* Kennett, J., P., Houtz, R. E., et al., (eds.). *Initial Reports of the Deep Sea Drilling Project, vol. 29*. Washington, D.C.: U. S. Government Printing Office. pp 541-675

Petrushevskaya, M. G. 1981. Radiolyarii otryada Nassellaria Mirovogo Okeana. *Akad. Nauk SSSR, Zool. Inst.*, Nauka, Leningrad. pp 1-405

Petrushevskaya, M. G. 1986. Radiolyarevii analiz. *Akad. Nauk SSSR*, Nauka, Leningrad. pp 1-200

Petrushevskaya, M. G., Cachon, J. & Cachon, M. 1976. Comparative-morphological study of radiolarians: foundations of new taxonomy. *Zool. Zh.*, 55:485-496.

Popofsky, A. 1908. Die Radiolarien der Antarktis (mit Ausnahme der Tripyleen). *In:* Drygalski, E. (ed.), *Deutsche Sudpolar Expedition, 1901-1903*, vol. 10. Berlin, Germany: Georg Reimer. pp 183-306

Popofsky, A. 1912. Die Sphaerellarien des Warmwassergebietes. *In:* Drygalski, E. (ed.), *Deutsche Sudpolar-Expedition, 1901-1903*, vol. 13. Berlin, Germany: Georg Reimer. pp 73-159

Popofsky, A. 1913. Die Nassellarien des Warmwassergebietes. *In:* Drygalski, E. (ed.), *Deutsche Sudpolar-Expedition, 1901-1903*, vol. 14. Berlin, Germany: Georg Reimer. pp 217-416

Renz, G. W. 1976. The distribution and ecology of Radiolaria in the Central Pacific: plankton and surface sediments. *Bull. Scripps Inst. Oceanogrr*, 22:1-267.

Reshetnjak, V. V. 1966. Fauna SSSR. Radiolyarii. Akad. Nauk, SSSR, Nauka, Moskva. pp 1-208

Riedel, W. R. 1957. Radiolaria, a preliminary stratigraphy. *Rep. Swedish Deep Sea Exped. 1947-1948*, 6(3):61-96.

Riedel, W. R. 1958. Radiolaria in Antarctic sediments. *Rep. B.A.N.Z.A.R.E., B*, 6(10):219-255.

Riedel, W. R. 1967a. Some new families of Radiolaria. *Proc. Geol. Soc. Lond.*, 1640:148-149.

Riedel, W. R. 1967b. Subclass Radiolaria. *In:* Harland, W. B., Holland, C. H. & House, M. R. (eds.), *The Fossil Record. A Symposium with Documentation*. London, UK: Geological Society of London. pp 291-298

Riedel, W. R. 1971. Systematic classification of polycystine Radiolaria. *In:* Riedel, W. R. & Funnell, B. M. (eds.), *The Micropalaeontology of Oceans*, Cambridge Univ. Press., Cambridge. pp 649-660

Riedel, W. R. & Sanfilippo, A. 1981. Evolution and diversity of form in radiolaria. *In:* Simpson, T. L. & Volcani, B. E. (eds.), *Silicon and Siliceous Structures in Biological Systems*. Springer-Verlag, New York. pp 323-346

Sanfilippo, A. & Riedell, W. R. 1970. Post-Eocene "closed" theoperid radiolarians. *Micropaleontology*, 16:446-462.

Sanfilippo, A. & Riedel, W. R. 1980. A revised generic and suprageneric classification of the Artiscins (Radiolaria). *J. Paleontol.*, 54(5):1008-1011.

Sanfilippo, A. & Riedel, W. R. 1985. Cretaceous Radiolaria. *In:* Bolli, H. M., Saunders, J. B. & Perch-Nielsen, K. (eds.), *Plankton Stratigraphy*. Cambridge University Press, Cambridge, UK pp 573-630

Sanfilippo, A., Westberg-Smith, M. J. & Riedel, W. R. 1985. Cenozoic Radiolaria. *In:* Bolli, H. M., Saunders, J. B. & Perch-Nielsen, K. (eds.), *Plankton Stratigraphy*. Cambridge Univ. Press, Cambridge, UK. pp 631-712

Steineck, P. L. & Casey, R. E. 1990. Ecology and paleoecology of foraminifera and radiolaria. *In:* Capriulo, G. M. (ed.), *Ecology of Marine Protozoa*. Oxford Univ. Press, New York. pp 46-138

Stohr, E. 1880. Die Radiolarienfauna der Tripoli von Grotte, Provinz Girgenti in Sicilien (The radiolarian fauna of the Tripoli of Grotte, Girenti Province, Sicily). *Palaeontographica*, 26 (ser. 3, vol. 2):71-124.

Swanberg, N. S., Anderson, O. R. & Bennett, P. 1990. Skeletal and cytoplasmic variability of large spongiose spumellarian radiolaria (Actinopodea: Polycystina). *Micropaleontology*, 36:379-387.

Takahashi, K. 1991. Radiolaria: flux, ecology, and taxonomy in the Pacific and Atlantic. *Woods Hole Oceanogr. Inst., Ocean Biocoenosis Series No. 3*. 303 pp

Zhamoida, A. I. & Kozlova, G. E. 1971. Gootnochenie podotryadov i semeistv v otryade Spumellaria; radiolyarii. *Trudy Vsesoyuznogo Neftyanogo Nauchno-Issledovatelskogo Geologorazvedochnogo Instituta*, 291:76-82.