

PART D
 PROTISTA 3
 (CHIEFLY RADIOLARIANS AND TINTINNINES)

BY ARTHUR SHACKLETON CAMPBELL AND RAYMOND C. MOORE

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INTRODUCTION

By RAYMOND C. MOORE

The subdivision of protistan organisms which has been effected by allocation of respective groups to Parts B, C, and D of the *Treatise* seems to be unnatural in that several assemblages ranked as phyla are brought together in Protista Section 1 (Part B), whereas only the class Rhizopoda of the subphylum Sarcodina, taking care of a segment of the protozoans, is assigned to Protista Section 2 (Part C), and the remainder of protozoans is covered in this division (Part D). Thus Protista Section 3 deals with the class Actinopoda of the Sarcodina and the subphyla Sporozoa and Ciliophora of the Protozoa. This arrangement is explained by the distribution of various taxonomic groups which are either important or very unimportant to paleontology as one

consideration, and by readiness of materials for publication as another. One of the first-completed contributions to the *Treatise* was the comprehensive description of radiolarians prepared by Dr. ARTHUR S. CAMPBELL, and priority achieved by his industry is a factor in shaping Part D for publication in advance of others. Dr. CAMPBELL has submitted a complete survey of the suborder Tintinnina also, including the only known fossils among the host of ciliate protozoans. Because groups like the Heliozoa, which are unimportant as fossils, are given very brief attention and others are little more than mentioned, this volume is devoted essentially to the radiolarians and tintinnines.

ACTINOPODA

By RAYMOND C. MOORE

GENERAL CHARACTERS

The actinopod protozoans comprise a host of forms which are characterized by very fine radially disposed protoplasmic extensions from the generally spheroidal main body. These extensions consist of somewhat stiffened long axopods (axopodia), unbranched or rarely branching unstiffened slender filopods (filopodia), and, in a few types, anastomosing rhizopods (rhizopodia) that may form a delicate network. Combinations of these types may appear, and even blunt lobose pseudopods (pseudopodia) may be developed temporarily in some species. On the whole, common presence of axopods or filopods distinguishes the group.

A delicate but firmly constructed skeleton composed of silica occurs in a majority of the actinopods (most radiolarians), but one important assemblage (acantharine radiolarians) has a complexly built test of strontium sulfate (Fig. 1). A few forms (some heliozoans) have a netlike exoskeleton of chitinoid nature, more or less impregnated by silica, and several heliozoan genera possess hard parts consisting of siliceous spicules, scalelike plates, and spines which are not firmly joined together. A few encase the body in a covering of diatom tests, mineral grains, and other foreign particles which are loosely embedded in gelatinous or mucilaginous substance surrounding the body. Finally, there are naked actinopods; these are uncommon in the assemblage of radiolarians but relatively numerous among the heliozoans.

The form of the main body is generally subspherical and almost invariably a thick or thin outer zone of ectoplasm can be differentiated from the fine granular, more compact endoplasm of the body interior. A nucleus is located within the endoplasm, most commonly at the center of the spheroidal body, but in some excentrically. Some actinopods are multinucleate. Among radiolarians, the protoplasm may be concealed almost entirely by surrounding skeletal structures of complex nature (Fig. 2).

Actinopods are almost exclusively free-

swimming or floating organisms that predominantly live in oceanic waters, but all heliozoans except a few are confined to fresh-water bodies. Some forms grow in fixed location, attached by a slender stalk. Colonial actinopods are included both among radiolarians and heliozoans, but they are exceptions to the rule. Uncommonly, actinopods are found to occur in moist soil. All kinds depend on other microorganisms for food.

CLASSIFICATION

Divergent interpretation of the taxonomic significance of many morphological features observed in actinopod types of protozoans, as well as incompleteness of knowledge, explains a considerable variation in classifying these protistans both in the past and at present. EHRENBURG (1838) first distinguished typical representatives of the great assemblage now called Radiolaria (MÜLLER, 1858), using for them the name "Polycystina." Although preference for this designation could be expressed on the ground of priority, a universal long-prevailing disuse of EHRENBURG'S term strongly favors continuation of practice that allows it to stay buried. HAECKEL, in 1866, recognized under the name of Heliozoa a group that somewhat resembles the radiolarians in appearance; they lack skeletal structures of comparable sort, however, and are adapted to life in fresh waters rather than a marine environment. HAECKEL also made extensive investigations of the Radiolaria and was first (1862) to distinguish among them a major group which he named Acantharia. These differ from other radiolarians in arrangement of the skeletal structures, which conform to the so-called Müllerian law, and in their composition of strontium sulfate instead of silica (Fig. 1). Subsequently, the main divisions of siliceous-shelled Radiolaria were established by EHRENBURG (1875), who defined the Nassellaria and Spumellaria (Fig. 2), and by HAECKEL (1879), who differentiated the Phaeodaria. These divisions are mainly based on the nature of perforations in the central capsule.

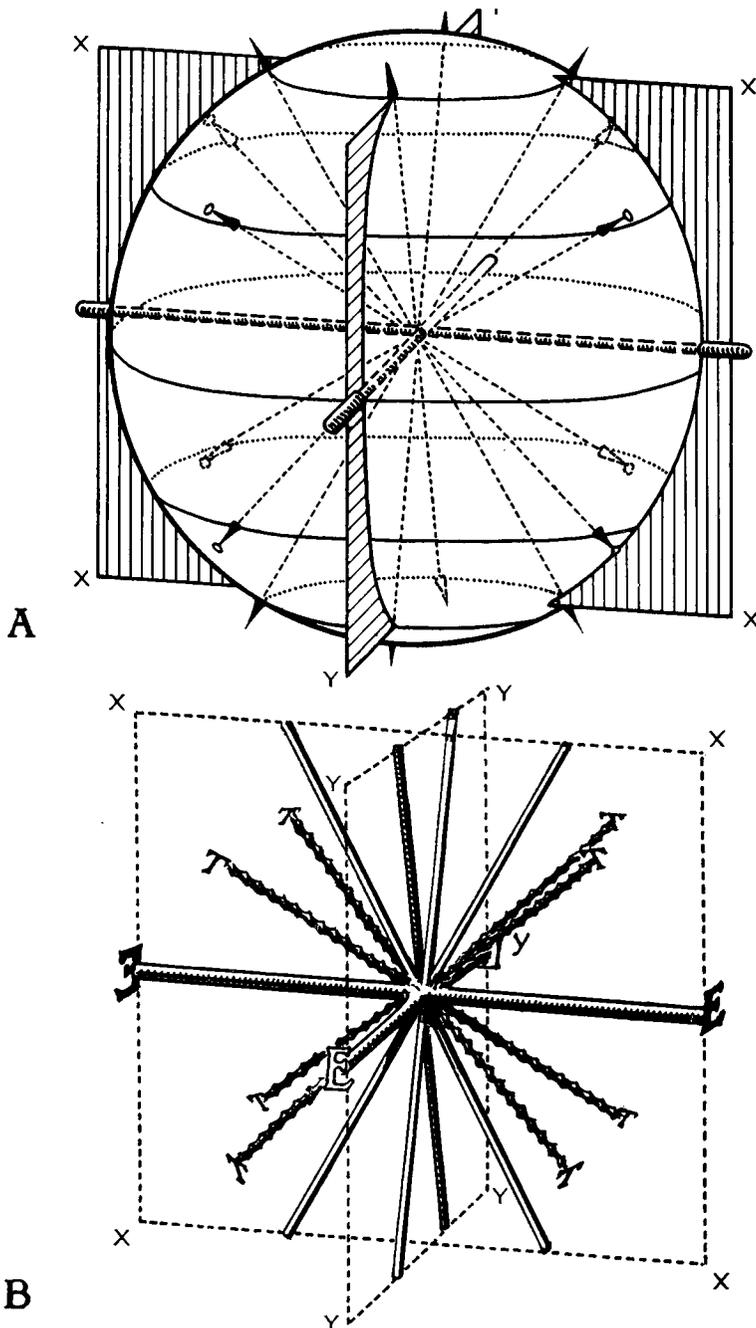


FIG. 1. Arrangement of skeletal spines in acantharine radiolarians, conforming to the so-called Müllerian law. *A*, Spheroidal diagram showing oblique view of equatorial plane and 2 meridional planes (X-X, Y-Y), each intersecting the others at right angles. Junctions of the equatorial plane with meridional ones define the positions of 4 equatorial spines, whereas 8 polar spines are located in the meridional planes at angles diverging 60 degrees from the equatorial plane. Diverging at an angle of 30 degrees from the equatorial plane, 8 tropical spines are located halfway between the polar meridional planes. *B*, Same spine system with spheroid omitted, equatorial spines diagrammatically distinguished by greater thickness and letter "E" at tip, polar spines by smooth slender form, and tropical spines by their crenulate surface and terminal letter "T."

A most common arrangement of protozoan groups given in standard textbooks such as those by HYMAN (*Invertebrates, Protozoa through Ctenophora*, McGraw-Hill, New York, 1940), STORER (*General Zoology*, McGraw-Hill, New York, 1943), BORRADAILE *et al.* (*Invertebrates*, University Press, Cambridge, 1948), and many others defines a class called Sarcodina or Rhizopoda, which is divided into orders named Amoebida (or Lobosa), Foraminifera, Heliozoa, Radiolaria, and Mycetozoa. CALKINS (1909) united the Heliozoa and Radiolaria in a subclass that he named Actinopoda. This arrangement is recognized in standard works on protozoology (MINCHIN, *Study of the Protozoa*, Arnold, London, 1912; KUDO, *Protozoology*, Thomas, Springfield, Ill., 1947; JAHN & JAHN, *How to know the Protozoa*, Brown, Dubuque, 1949; HALL, *Protozoology*, Prentice-Hall, New York, 1953; and others). Recently published comprehensive French works (GRASSÉ *et al.*, *Traité de Zoologie*, Masson, Paris, 1952; DEFLANDRE, in PIVETEAU, *Traité de Paléontologie*, Masson, Paris, 1952) elevate the assemblage of actinopods to the

rank of a subphylum, correlative with Rhizopoda, and among living Actinopoda three classes are defined as Heliozoa, Acantharia, and Radiolaria. The correspondence in characters which supports setting protozoans classed as actinopods apart from others is recognized in the present *Treatise*, and likewise the distinctions which give basis for defining major subdivisions, but classification here adopted is somewhat more conservative in its assignment of lower taxonomic rank to all groups and in retaining HAECKEL'S Acantharia within the span of the radiolarians. This arrangement best reflects a consensus of judgment by specialists.

For the purpose of furnishing in proper sequence appropriate headings and diagnoses which comprise parts of the text devoted to systematic descriptions, the following characterization of the Actinopoda is introduced. References are given at the end of the section on Heliozoa.

Class ACTINOPODA Calkins, 1909

Rhizopod protozoans of typically spherical form characterized by radially pro-

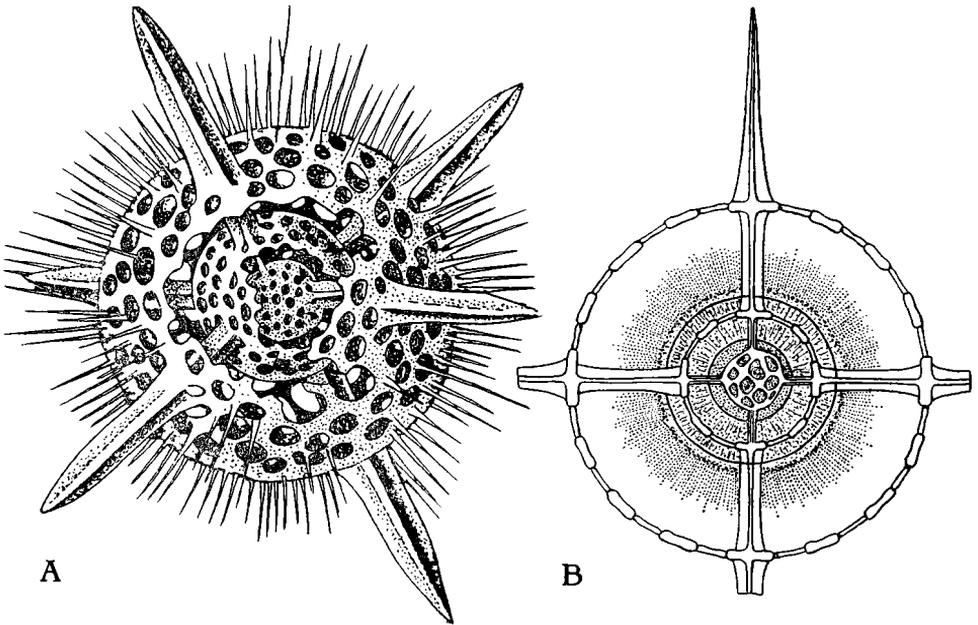


FIG. 2. Siliceous skeleton of a spumelline radiolarian (*Actinomma asteracanthion*) showing large, regularly disposed principal spines that are continuous inward through successive spherical lattice shells so as to form radial beams; very numerous slender by-spines occur also, radiating outward. *A*, View of specimen with parts of the lattice shells broken away in order to reveal interior construction. *B*, Cross section showing relation of skeleton to soft parts (enlarged, after Bütschli).

duced, generally long, fine pseudopodia which in many members of the group are unbranched stiffened axopodia but in others consist of threadlike filopodia or bifurcate and join together so as to make a delicate network; a delicate, complexly built, firm siliceous skeleton distinguishes a majority, in others the test is composed of strontium sulfate or, in a few of a chitinous substance, and in still others there are loose

siliceous hard parts surrounding the body; some types are naked. Protoplasm of the cell is mostly divisible into clearly differentiated ectoplasm and endoplasm, the latter containing a nucleus or nuclei. Predominantly marine but some groups live almost exclusively in fresh waters; typically live as solitary individuals but some are colonial. *Cam.-Rec.*

HELIOZOA

By RAYMOND C. MOORE

The Heliozoa derive their name from resemblance that is shown by a majority of them to the spheroidal body of the sun surrounded on all sides by outward streaming rays. The body comprises the main mass of protoplasm, and the rays are threadlike or fine rodlike pseudopodial extensions. Many heliozoans lack hard parts, but others secrete a reticulate chitinous skeleton partly impregnated by silica or build protection around the body consisting of loose siliceous spicules, scalelike plates, and spines; some utilize foreign material such as sand particles and diatom shells for a covering. Except for a few species found in brackish or marine environments, the Heliozoa are fresh-water protists.

MORPHOLOGICAL FEATURES

The soft body of nearly all heliozoans is divisible clearly into an outer part called **ectoplasm**, which has a hyaline appearance, and an inner part of finely granular or alveolar nature termed **endoplasm**. The ectoplasm generally contains numerous vacuoles, among which one or more relatively large ones (contractile vacuoles) are concerned primarily with nourishment, enveloping captured prey, carrying on functions of digestion, and ultimately discharging waste products; another kind of vacuoles, commonly numerous, pulsates rhythmically, serving probably for control of osmotic pressure in the cell. The endoplasm contains many variously colored granules which are mostly stored food of different sorts, and without exception it includes a relatively large nucleus or several of them. The nuclear bodies are typically spheroidal. In helio-

zoans having only a single nucleus, its location generally is at the center of the cell, but in some species a highly refractive clear body (centroplast) occurs in this position and the nucleus is excentric.

The pseudopods of organisms classed as Heliozoa consist typically of **axopods**, which are relatively long, straight, unbranched protoplasmic extensions that are strengthened by an axial rod of fibrils (Fig. 3). They are by no means stiff and rigid, however. Commonly, the axial rod (axoneme) extends inward through the ectoplasm and endoplasm to the border of the nucleus or to a centroplast. A flow of protoplasmic granules along borders of the axoneme is typical. The outer part of the axopods may be reduced by absorption. Some heliozoans possess threadlike filopods, distinguished by lack of a supporting axial element, and a few exhibit branched or even reticulate pseudopodial extensions. The group of helioflagellids, which are included questionably in the Heliozoa, possess flagella as well as axopods. The pseudopods function in capturing small organisms used as food and there is evidence that they may act in manner serving to numb their prey as by emission of a poison.

Except for some forms (Desmothoraca, Helioflagellida) which are rather doubtfully included among heliozoans, as suggested by the term "pseudoheliozoans" often applied to them, members of this subclass possess no firmly knit skeleton. In this respect, they differ from most Radiolaria. Some heliozoans are naked, but many secrete a protective covering of siliceous spines or thin plates or both; and these discrete hard

parts are embedded in gelatinous or mucilaginous substance of the outer ectoplasm. They may extend outward around basal parts of the axopodia. A few species that secrete no skeletal elements of their own utilize foreign particles of various sorts as a partial or complete armor. Although the siliceous scales and spines of Heliozoa may be preserved as fossils, they are almost invariably so scattered that associations belonging to an individual organism are rarely or never discovered. Therefore, identification of species based on study of preserved skeletal parts is possible only in case of distinctive peculiarities of isolated parts. Even so, it may be possible to recognize the heliozoan nature of the fossils.

Reproduction of the heliozoans is by binary fission or budding, and if buds remain attached to the parent, colonies may be produced.

OCURRENCE

Nearly all Heliozoa are solitary vagile

individuals that live in fresh-water environments, especially in lakes, ponds, and swamps. A few are marine. Some kinds grow attached to algae or an inorganic substratum, fixed by a slender stalk.

Probably the fossilized remains of Heliozoa are widely distributed both stratigraphically and geographically but they are now virtually unknown. Pleistocene heliozoans have been reported from lake and peat deposits in northern Germany and Sweden. An alleged occurrence of heliozoan remains in Oligocene strata of France is based on misidentification of poorly preserved diatoms, according to DEFLANDRE (1952).

SYSTEMATIC DESCRIPTIONS

Subclass HELIOZOA Haeckel, 1866

Mostly spheroidal free-living actinopod protozoans characterized by axopodial pseudopodia, some with filopodia and a few with reticulate rhizopodia. Skeleton, if

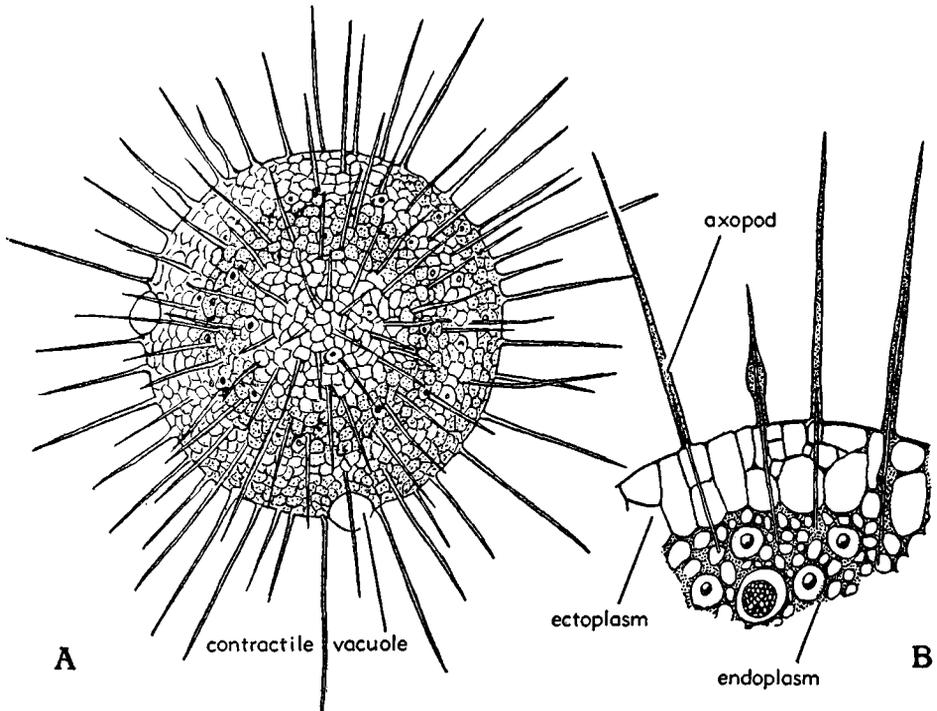


FIG. 3. Typical heliozoan lacking skeletal parts (*Actinosphaerium eichornii* EHR., Rec.). A, Whole organism, showing spheroidal form of body and radially diverging axopods ($\times 700$). B, Section of peripheral region and axopods which penetrate the ectoplasmic layer and terminate in the outer part of the endoplasm ($\times 1,000$) (after Bütschli).

present, consisting typically of discrete siliceous scales and spines but in some uncertainly classified forms comprising a chitinoid network more or less impregnated by silica or rarely composed wholly of silica. Except for a few marine types, exclusively inhabitants of fresh waters. *Pleisto.-Rec.*

Order ACTINOPHRYDEA Hartmann, 1913

Naked heliozoans with one or more nuclei, lacking a centroplast; axopodia commonly reaching to edge of nucleus but may barely penetrate the ectoplasm. *Rec.*

This order includes the very common *Actinosphaerium* STEIN (Fig. 3), with well-differentiated ectoplasm and endoplasm; *Actinophrys* EHR., which lacks such distinction, widely distributed in fresh waters; and *Camptonema* SCHAUDINN, which resembles *Actinosphaerium* but is confined to marine waters.

Order CENTROHELIDIA Kühn, 1926

Heliozoans with excentric location of the nucleus and proved or inferred presence of a centroplast; mostly having a skeleton of siliceous plates or spines and plates but

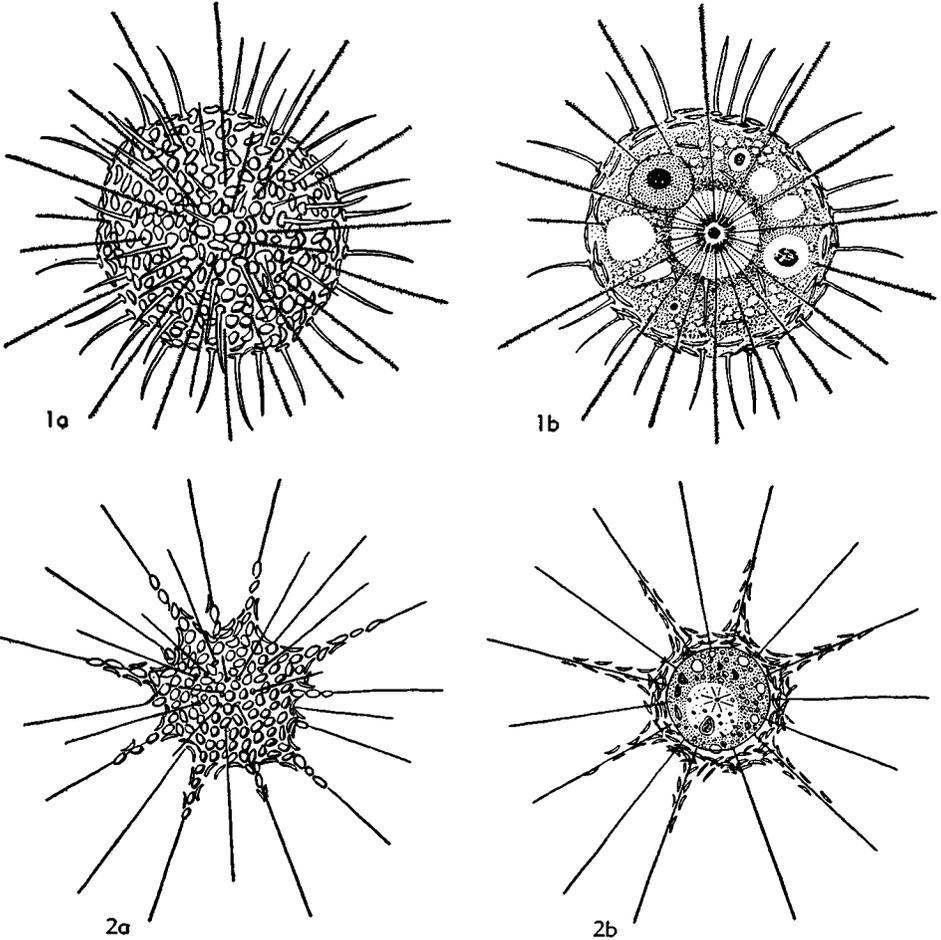


FIG. 4. Heliozoans provided with siliceous hard parts. 1a, b, *Acanthocystis aculeata* HERTWIG & LESSER, Rec., exterior view and cross section, showing skeletal plates and spines; this species has a clearly defined centroplast and an excentric nucleus ($\times 500$) (after Stern). 2a, b, *Radiophrys pallida* SCHULZE, Rec., exterior and cross section, siliceous scales around body and extending outward along basal parts of axopods ($\times 300$) (after Penard).

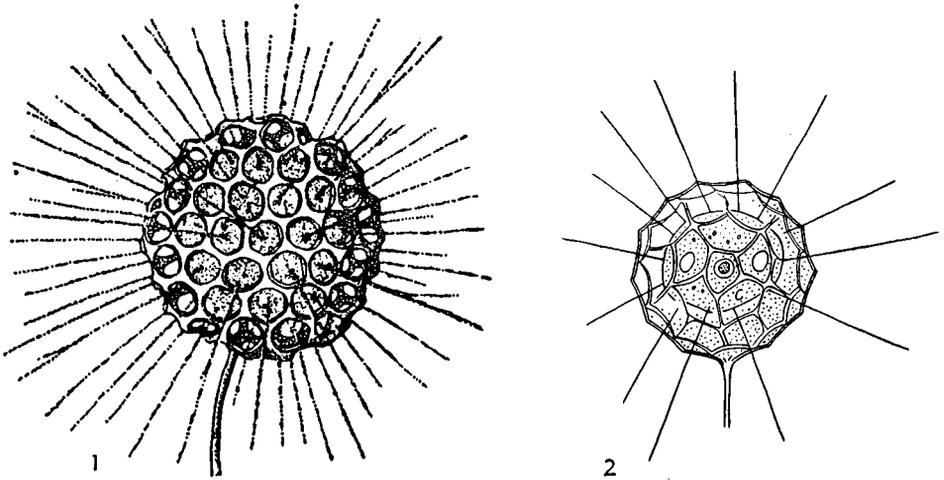


FIG. 5. Desmothoracan heliozoans. 1, *Clathrulina elegans* CIENKOWSKI, Rec., exterior of body and part of stalked attachment ($\times 500$) (after Leidy). 2, *Hedriocystis reticulata* PENARD, Rec. ($\times 600$) (after Penard).

some forms naked; typically spheroidal, free-living but a few sessile. Rec.

This group includes suborders named Aphrothoraca HERTWIG (1871), Chlamydothoraca HERTWIG (1871), and Chalarethoraca HERTWIG & LESSER (1874). Typical skeleton-bearing representatives of the Chalarethoraca are *Acanthocystis* CARTER (1863), *Raphidophrys* ARCHER (1876), and *Raphidocystis* PENARD (1904), which are illustrated to show the nature and arrangement of their hard parts (Fig. 4). Scattered plates and spines of such heliozoans are likely to be found in microfossil collections from fresh-water deposits.

Order DESMOTHORACA Hertwig & Lesser, 1874

Subglobular free or fixed actinopods with continuous reticulate exoskeleton of a chitinoid substance more or less impregnated by silica or rarely consisting entirely of silica; pseudopodia of filopod type, without axoneme, but branching or even anas-

tomosing in some; centroplast lacking. Fresh-water habitat. Pleisto.-Rec.

Clathrulina CIENKOWSKI, 1867 [**C. elegans*]. Family Clathruliniidae CLAUS. Shows typical characters of order; attached by a stalk. Pleisto.(Ger.-Swed.)-Rec.—FIG. 5,1. **C. elegans*, Rec.; adult individual showing test and radiating pseudopodia, $\times 400$ (after Hertwig).

Hedriocystis HERTWIG & LESSER, 1874 [**H. pelliculida*]. Family Clathruliniidae. Resembles *Clathrulina* but polygonal openings of test much larger. Rec.—FIG. 5,2. *H. reticulata* PENARD, Rec.; body and part of stalk, $\times 1,000$ (after Penard).

Various other genera (*Monomastigocystis* DE SAEDELEER, *Orbulinella* ENTZ, *Elaster* GRIMM, etc.) are omitted, for it is sufficient here to indicate general characters of the group.

Order HELIOFLAGELLIDA Doflein, 1907

Mostly subglobular organisms bearing generally both axopodia and flagella, also commonly with a centroplast; hard parts lacking; habitat fresh waters. Rec.

REFERENCES

Doflein, Franz, & Reichenow, Edouard

- (1) 1928, *Heliozoa*: in Lehrbuch der Protozoenkunde, Teil 2, Gustav Fischer, Jena, p. 797-815, fig. 762-782.

Hall, R. P.

- (2) 1953, *Protozoology*: Prentice-Hall, New York, p. 1-682, illus. (Actinopoda, p. 202-226).

Kudo, R. R.

- (3) 1947, *Protozoology*: C. C. Thomas, Springfield,

Ill., p. 1-778, fig. 1-334 (Actinopoda, p. 406-416, fig. 190-193).

Poche, F.

- (4) 1913, *Das System der Protozoen*: Archiv f. Protistenk., v. 30, p. 125-321.

Trégouboff, G.

- (5) 1952, *Classe des heliozoaires*: in Traité de Zoologie, ed. P.-P. GRASSÉ, Masson, Paris, t. 1, fasc. 2, p. 437-489, fig. 333-382.

RADIOLARIA

By ARTHUR SHACKLETON CAMPBELL

INTRODUCTION

Radiolaria are marine protozoans belonging to the lowly organized division (Plasmodroma or Rhizoflagellata) that includes the common *Amoeba*, dinoflagellates, and innumerable foraminifers. These are free-living one-celled animals characterized by the presence of protoplasmic extensions termed pseudopodia or flagella. They are classified by most zoologists as an order (or subclass) of the class Rhizopoda (or subphylum Sarcodina) but by some are grouped with acantharians and heliozoans in a class called Actinopoda. This latter classification is adopted here.

The radiolarians have not been studied in the detail they deserve. Among factors which have tended to retard research on them are: (1) their very small size, which necessitates laborious techniques for isolating them and optimum conditions for examining them; (2) the very great number of different kinds, described in widely scattered publications in several different languages, without comprehensive monographs which unite the fossil and Recent genera into a logical system; and (3) lack of realization, until recently, of the usefulness of these organisms in certain phases of applied paleontology and biological oceanography.

The present contribution had its inception in micropaleontological studies which the late Prof. BRUCE CLARK and I undertook during the period 1936-1945. We realized that taxonomy of the Radiolaria needed revision, and Dr. CLARK suggested that the whole group be re-examined. A start on this task had to be delayed, however, until I was asked to prepare this section of the Protozoa for the *Treatise*.

The taxonomic treatment given is conservative, for only essential changes have been introduced and revision of genera has been limited. Mainly, the changes are those needed to bring designations of Radiolaria into line with provisions of the Inter-

national Rules of Zoological Nomenclature and decisions of the International Zoological Congress meeting at Copenhagen in 1953. If some disagree with features of the classification proposed, they must grant that many problems are exposed. Later examination may lead to better solutions of some of these questions. Practical applications of the study of fossil Radiolaria are assisted not only by records of occurrences, but especially by bringing together into one system both fossil and Recent genera.

Excluded from consideration are generic names to which no species are assigned and those doubtfully placed among Radiolaria by their authors. Among these are plant spores or inorganic bodies.

Illustrations of significant genera accompany the systematic text. Species belonging to some subgenera of especially important genera are also figured. These are mainly those of genera which may have stratigraphic significance.

The systematic text is believed to be complete to July 30, 1952.

The recent treatment of Radiolaria in the new *Traité de Paléontologie* (1953) outlines a different concept of the subclass from that developed herein. The French authors propose an elaborate system including detailed acceptance of SCHEWIAKOFF's studies of the Acantharina. The order of treatment of the families and other divisions of Spumellina and Nassellina differs also from that developed in this section of the *Treatise on Invertebrate Paleontology*. The Phaeodarina are considered essentially as herein developed. Detailed examination of the two contributions will reveal other minor differences.

To all who have assisted in preparation of this work I am obliged, especially for the genial help of Prof. J. W. DURHAM, ICZN Commissioner ROBERT L. USINGER, W. RIEDEL, the Editor and his staff. However, I alone must be held responsible for errors of omission and commission.

MORPHOLOGY

Knowledge of the morphology of the soft parts of Radiolaria is important to understanding the classification and life habits of these organisms.

SOFT PARTS

The living matter of radiolarians, commonly termed **cytoplasm**, may be differentiated into 3 divisions: (1) a cortical layer, termed **extracapsular cytoplasm**; (2) an intracapsular layer containing the **nucleus**; and (3) the **central capsule**, mucoid or chitinous in nature, separating the 2 layers. This capsule distinguishes the Radiolaria from all other Protozoa; even groups such as the Heliozoa, which are intimately related to the Radiolaria, do not possess this unique structure. The extracapsular cytoplasm consists of an assimilative layer (**matrix**), which lies immediately next to the central capsule; a vacuolated layer (**calymma**), which is frothy and appears to vary with the physiological state of the individual; and an enclosing layer (**sarcodictyum**), outside the other 2 layers. Radiating through the whole extracapsular protoplasm are contractile threads that give rise to **axopodial pseudopods**, which seem to arise in the matrix of the extracapsular layer, just outside of the central capsule. The central capsule is single in all but the Phaeodarina, a radiolarian group that is rarely represented among fossils. In this group, the central capsule is multiple. The capsule may be considered a permanent structure, although there is evidence that it may rupture or dissolve during certain phases of reproduction. Generally it is perforated or contains one or more apertures. These apertures constitute one of the bases upon which higher-rank divisions of the group are separated. The central capsule is seldom fossilized.

The intracapsular cytoplasm is denser than the extracapsular portion. Within it are various inclusions, among which are protein reserves, symbiotic cells, and large crystals. At its center is the large spherical nucleus, provided with the usual nuclear components. The whole cell is thus a complicated structure, and each of its elaborations has a peculiar, special physiological function. In a general way, the extracapsular

cytoplasm is concerned with flotation, movement, food-gathering, digestion, respiration, and the reception of external stimuli. The intracapsular cytoplasm, on the other hand, is largely concerned with reproduction and to a limited extent with assimilation and storage. A diagram illustrates relationships of the structures (Fig. 6).

HARD PARTS

The skeleton, or hard parts, of a radiolarian may be termed **scleracoma**, in contrast with the whole soft body of the animal, called **malacoma**. The scleracoma differs greatly in the different suborders of Radiolaria and in appropriate following parts of the text is discussed with special regard to features that distinguish the many genera. Distinction of genera largely depends on skeletal characters, because they provide the only usable basis for differentiating the multitude of forms which occurs among these protistans. It is true undoubtedly that Radiolaria show as great a diversity of form as any of the comparable groups in the animal kingdom, and this diversity invites establishment of many taxonomic divisions. The various kinds of

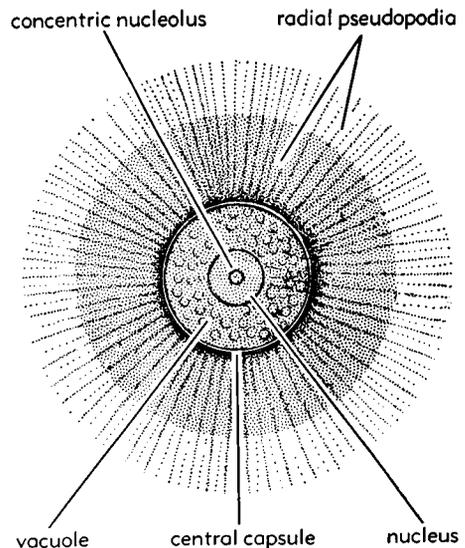


FIG. 6. Diagrammatic cross section of a radiolarian showing relationships of soft parts.

skeletal tests are composed of different materials, and thus shell composition is important at the higher levels of classification. The same essential shapes are repeated in shells of differing composition. Fortunately for the paleontologist, most shells are composed of opaline silica. A few primitive genera in each of the subdivisions lack shells or have only isolated spicules.

Almost nothing is known as to the manner of forming the hard parts of Radiolaria, except that the vacuolated layer is able to secrete silica or other mineral substance. The deposit thus laid down, however, does not conform strictly to the alveolated structure of the sarcodictyum beneath.

Individual variations found in different specimens of the same species of Radiolaria are not well understood. The effect of physical and chemical factors upon shell formation has not been studied specifically. The influence of temperature upon dimensions in some other testate protozoans is well known and, in these forms, size differences commonly are a function of critical temperatures at the moment of deposit. Three chief sorts of structural variation are recognized in Radiolaria: (1) normal genetic variations characteristic of particular species; (2) responses to depth at which the species lives and by which a given species may display differing characters distinctive of deep- or shallow-water environments; and (3) polymorphism related in some way to different stages in a complex life cycle. The last has not been demonstrated satisfactorily by modern methods of investigation. In part at least, the different types of individual variation may be responsible for some of the large number of species which have been described.

The somatic polymorphism occasioned by varying depth environments results in the formation of widely diversified small individuals in warm surface waters and

large individuals in cold deep waters. Generally, the shells of surface-dwelling pelagic Radiolaria are delicate and have numerous slender apophyses, large pores, thin bars between the pores, and diverse spinous armor. Deep-water forms, on the contrary, are massive, solid, less apt to be burrlike, provided with short apophyses, and have small pores with thick trabeculae.

Most of the many shapes found among Radiolaria seem to have been developed as a means of maintaining the animal within certain depth limits. Various structural modifications, such as globular and hat-shaped tests and long pseudopods, serve to retard sinking and thus to keep the more or less passive radiolarian in that upper ocean zone where food is produced by photosynthesis. The various surface extensions of the radiolarian have slight protective function.

MORPHOLOGICAL TERMS APPLIED TO RADIOLARIANS

The general account of morphological features distinguished in the soft and hard parts of radiolarians introduces only a few of the terms which are needed for description of these organisms. Others are given in parts of the text devoted to explanation of main divisions designated as suborders, because the structural characters and nomenclature of parts in each are somewhat different. A compilation of all morphological terms in a single alphabetically arranged list, with accompanying brief definitions, has been judged useful and is given here. The letters A, N, P, and S, which accompany various terms, indicate the suborders Acantharina, Nassellina, Phaeodarina, and Spumellina, respectively, and thus serve to identify the taxonomic divisions within which the terms are mainly or exclusively used. Terms not accompanied by one or more of these index letters have general application.

GLOSSARY OF MORPHOLOGICAL TERMS

abdomen. Third joint of nasselline shell (N).
acanthin. Organic compound of strontium sulfate forming skeletal rods (A).
aglet. Tiny plate pierced by a single pore (A).
alveole. Vacuole or space.
anchor branch. Curved hooklet (P).
aperture. Large main opening of shell.

apical horn. Spine at apex of nasselline or phaeodarine shell (N, P).
apophysis. Lateral transverse process of radial spine (A).
areolate. Weblike or reticulated.
arms. Flat extensions from central region of shell.
articulate. Hollow, septate tube.

- aspiral pore.** Tiny opening in plates which lie immediately at sides of radial spines bordered by primary branches of latter (A).
- astral.** Starlike.
- astropyle.** Nipple-like projection from central capsule of Phaeodarina (P).
- axopodial pseudopod.** Permanent rod-supported protoplasmic extension of radiolarian cell.
- basal feet.** *See* feet.
- basal leaf cross.** Broad wings on radial spines (A).
- basal pores.** Small openings in basal horizontal plate of some Triospyridicae.
- bow.** Curved rod.
- brush.** Bunch of fine terminal branches (P).
- by-spines.** Small accessory spines additional to radial spines (A, S).
- calymma.** Frothy layer of cytoplasm.
- capsule.** *See* central capsule.
- central capsule.** Mucoid or chitinous sac enclosing intracapsular cytoplasm and nucleus (A, N).
- centrogenous skeleton.** Supporting rods which are generated at cell center (A).
- cephalis.** First or apical chamber of Nassellina (N).
- chromatophore.** Colored body within cytoplasm with power of photosynthesis.
- collar pores.** Tiny apertures which occur in horizontal plate at base of cephalis in some Nassellina (N).
- columella.** Vertical rod within shell-cavity; in Stephaniacae, vertical rod between 2 horizontal rings (N).
- comb.** Radial series of knobs or projections (A).
- conrescence.** Union of radial spines.
- condyle.** Swollen knobs on shell surface (A).
- coronal pores.** Tiny openings which lie at periphery of shields, surrounding the aspiral pores but not touching the radial spines (A).
- cortical shell.** Outermost of the concentric shells of Spumellina (S).
- crest.** *See* comb (A).
- cupola.** Large vaulted dome (N, S).
- cytoplasm.** Protoplasm exclusive of the nucleus.
- dendrite.** Branched free style (P).
- dentate.** With small toothlike projections.
- diametral spine.** Opposite radial spines basally fused and passing through diameter of central capsule (A).
- dimple.** Small depression (A).
- diploconical.** Shell formed by fusion of bases of 2 cones opposite in one axis.
- equatorial space.** Four-sided region resulting from formation of basal leaf cross (A).
- equatorial spine.** Radial spine arising on shell equator (A).
- extracapsular cytoplasm.** Protoplasm outside central capsule.
- feet.** Radial appendages extending from ultimate joint of nasselline or phaeodarine shell (N, P).
- fenestrated.** Having open meshwork (N, S).
- frenulum.** Small cylinder connecting nasal mouth and internal part of nasal tube of style near base of galea in Phaeodarina (P).
- galea.** Conical process (P).
- gate.** Large opening or fissure (S).
- geotomical axis.** Minor axis with small spines (A).
- girdle.** Spiral or annular shelf (S).
- girdle zone.** Circular central region with shelves.
- helicoidal.** Asymmetrical coil (S).
- hydrotomical axis.** Major axis with large spines (A).
- icosacanthan law.** *See* Müllerian law (A).
- internal columella.** *See* columella (N).
- intracapsular layer.** Protoplasm within central capsule exclusive of nucleus.
- joint.** Segment of nasselline shell (N).
- keel.** Vertical sail-like plate.
- lattice shell.** Test formed of meshwork (A, N, P).
- leaf cross.** *See* basal leaf cross (A).
- lentelliptical shell.** Lens-shaped shell with elliptical outline.
- malacoma.** Collective name for soft parts.
- mantle.** Various formed covering or coat.
- matrix.** Assimilative portion of cytoplasm.
- medullary shell.** Internal concentric shell (S).
- Müllerian law.** Plan of circles expressed by radial spines dividing the shells of Acantharina into equatorial, temperate, tropical, and polar zones (A).
- nasal tube.** *See* rhinocanna (P).
- nucleolus.** Intranuclear body.
- nucleus.** Kernel or dynamic center of cell responsible for maintenance and heredity.
- operculum.** Flat pore-bearing base of podoconus in Nassellina; in Phaeodarina, central portion of astropyle (N, P).
- oral teeth.** Sharp triangular projections around basal shell opening (P).
- parapylae.** Accessory tubular apertures of central capsule in addition to astropyle (P).
- parmal pores.** Pores piercing the shield and bordered only by united branches of apophyses (A).
- patagium.** Interbrachial spongy veil (S).
- peripolar space.** Three-sided pyramidal space resulting from formation of basal leaf cross (A).
- perispinal pores.** Holes composed of 4 united aspiral pores (A).
- perizonal space.** Four-sided region resulting from formation of basal leaf cross (A).
- perradial plane.** Meridian plane (A).
- phaeodella.** Granule forming part of phaeodium (P).
- phaeodium.** Voluminous aggregate of pigmented cytoplasmic granules (P).
- pharynx.** Internal oral tube (P).
- planispiral.** Plane defined by a flat coil (S).
- podoconus.** Internal cone within central capsule of Nassellina (N).
- polar space.** Four-sided region resulting from formation of basal leaf cross (A).
- polar spine.** Opposite radial spines defining one axis of shell (A).
- polar tubules.** External cylinders opposite in main shell axis (S).
- pore-frame.** Raised edge around area enclosing pore.

- pore-plate.** See operculum.
- post-abdomina.** Joints succeeding third segment of nasselline shell (N).
- principal spines.** Large regularly placed spikes or needles (A, S).
- proboscis.** Distal cylindrical tube extending from astropyle (P).
- pseudopodium.** External cytoplasmic extension from body of cell.
- pylome.** Osculum or large opening usually only in outermost of concentric shells (S).
- radial beam.** Internal rods usually connecting concentric lattice shells (S).
- radial tube.** Centrifugal cylinder (A).
- radial spines.** Tangential rods or needles (A, P).
- rhinocanna.** Curved cylinder or prismatic tube embracing central capsule on one side and the galea on the other side (P).
- rosettes.** Flower-shaped buttons within hexagonal pore frames.
- sagittal ring.** Hoop reinforcing latticed wall in medial vertical plane (N).
- sarcodictyum.** Outermost layer of cytoplasm.
- scleracoma.** Collective name for hard skeletal parts.
- sieve-plate.** Flat, circular porous plate (S).
- sheath.** Receptacle or container.
- shield.** Flat or curved lateral outgrowth at one or more levels of radial spine, forming by fusion the lattice shell of some Acantharina (A).
- spicule.** Discrete skeletal element (P, S).
- spongy.** Foamy or loosely organized tissue (P, S).
- stricture.** Contraction between successive shell joints (N).
- style.** Tubules which arise from the galea (P).
- suture.** Joining of adjacent structures.
- sutural pores.** Pores bordered by sutures along the meeting branches of 2 or more adjacent radial spines (A).
- tabulate.** With smooth plates (P).
- thorax.** Second shell joint in Nassellina (N).
- thorn.** Short, sharply pointed triangular or conical surface extension (S).
- tripod.** Stool-shaped shell formed from divergent rods united at common center (N).
- tropical spine.** Radial spine disposed according to Müllerian law and marking tropical zone (A).
- twin-shell.** Shell with median transverse constriction (S).
- vacuole.** Space inside cytoplasm.
- veil.** Variously formed weblike or netlike film.
- wing.** Solid or fenestrated extension from side wall of nasselline shell (N).
- zooxanthellae.** Yellow intracellular symbionts.

BIOLOGY

REPRODUCTION

The life cycle of Radiolaria is imperfectly understood; much work on it remains to be done. Binary fission certainly occurs, and multiple division or budding has been described in the Thalassicolidae and some Acantharina. The central capsule is said to become irregular and the nucleus to break up into granules which become transformed into minute nuclei. Sexual reproduction and gamete formation is postulated but cannot be said to have been demonstrated. Modern cytological techniques have not been applied to the study of these forms, but chromosomes are certainly formed as among other protozoans. Among Heliozoa, the life cycle is understood in *Actinophrys* and *Actinosphaerium* at least. The marine Radiolaria are less easy to study than these fresh-water forms in which existence of sexual stages is authenticated.

Much of the reproductive activity seems to take place in epidemic form, after local, temporary enrichment of the water with silica. In this way, as among diatoms, vast numbers of individuals are produced sud-

denly. The pulses are seasonal or otherwise periodic.

MODE OF LIFE

Radiolaria usually can live without solid food if light is abundant. This ability is attributed to action of the yellow cells in various parts of the cytoplasm, especially in the calymma. The yellow cells (spherical bodies with distinct cellulose wall, 2 chromatophores, starch grains, and single nucleus) are identified collectively as **zooxanthellae** and belong to the genus *Chrysidella*. Several species are reported to inhabit both foraminifers and radiolarians. They multiply by binary fission in large numbers and, of course, are symbiotic. It is because of these symbionts and dependence of Radiolaria upon them for food that maintenance of the organisms within depth ranges of the sea penetrated by light is so important. Among the Acantharina, the yellow bodies are located only within the intracapsular protoplasm. In the Phaeodarina, which mostly dwell at depths below the light floor of the sea, yellow cells are absent, being replaced by dark bodies. At

least some Radiolaria take in particles of animal food and digest them within temporary vacuoles located in deeper layers of the protoplasm. Some Radiolaria are luminescent.

ECOLOGY

MODERN FORMS

Radiolaria are invariably marine animals which occur in all climates and depths. Under normal conditions, they float freely in the water, at the surface or close to seabottom, and in shallow water or at great depths. Active propulsive movements are lacking, but limited vertical movement is connected with physiological processes affecting the gas content of the alveolated protoplasmic layer. Although radiolarians are greatly favored by water of medium salinity, they are not absent in seas of high or low salinity. Scarcely any radiolarians are peculiarly coastal or neritic in distribution. A few may drift accidentally into larger bays.

No radiolarians inhabit fresh waters, although one supposed family (Traquiriidae), of the suborder Acantharina is claimed to have inhabited coal swamps. These so-called radiolarians have proved to be misidentified plant spores. Other reported fresh-water forms have been shown to belong to the Heliozoa.

With respect to local distribution, Radiolaria generally show the same relations as other pelagic organisms. Since they are incapable of active horizontal locomotion, the dispersion of different species depends on oceanic currents, winds and waves, and all accidental agencies that affect transport of other planktonic forms. Such passive movements bring about wider distribution of individual species than commonly is attained by active wandering. As a result of migrations, the number of cosmopolitan species is relatively large. Similar species occur in the 3 great ocean basins, but local species also are found, and local faunas may be distinguished by species peculiar to them. The Radiolaria are distributed throughout all the seas. Like most other organisms, they reach maximum richness in tropical waters, whereas frigid zones are characterized by great numbers of individuals of relatively few kinds. The surface

of the sea everywhere at a little distance from land appears replete with radiolarians. In the Pacific Ocean, however, they flourish most richly. Those of the Atlantic are less numerous in kinds. The Arctic, Antarctic, and temperate seas are filled with radically different types from those of the warmer oceans. Surface faunal zones differ sharply from those of deeper waters.

Vertical distribution in the ocean is imperfectly divided into several life zones: (1) the region penetrated by abundant light, which reaches from the surface to 25 fathoms (45.5 m.); (2) intermediate depths, which contain floating members of the group beneath the light floor; and (3) the bottom of the deep sea, which is characterized by a browsing fauna. The middle zone is divided into 3 subzones: an upper, ranging from 25 to 150 fathoms (45.5 to 274 m.); a middle, from 150 to 2,000 fathoms (274 to 3,650 m.); and a lower, from 2,000 to 3,000 fathoms (3,650 to 5,475 m.). Among the 4 recognized suborders of radiolarians, the Phaeodarina and some Nassellina generally are found in abyssal waters. Nearly all Spumellina, Nassellina, and Acantharina occur near the surface. HAECKER (13) makes an ecological distinction between microradiolarians and macroradiolarians, which may have some importance in connection with the vertical distribution of these organisms. Since deep-water and near-surface types may often be distinguished by their morphology, not only in characters mentioned previously but in the abundance of foamy kinds among surface dwellers, it becomes possible to determine something of the conditions under which radiolarian-bearing sediment was laid down.

Rich accumulations of Radiolaria occur in deep-sea oozes. Although pelagic material skimmed from the surface of the sea and collected in nets which draw plankton from intermediate depths are more or less filled with these organisms, a still greater number of species is obtained from bottom deposits. The skeletons found in ocean mud may belong to species which live at or near the surface, at intermediate levels, or at the bottom, and they may even include fossils. Almost all observed remains belong to the Spumellina or Nassellina; the Phaeodarina occur only sparingly and Acantharina gener-

ally are wanting, for their soft skeletons readily dissolve. Abundance of Radiolaria varies greatly according to composition and origin of the deposits. In general, marine deposits may be divided into (1) terrigenous muds and (2) abyssal deposits. The terrigenous muds include all sediment derived from the coasts of adjacent land masses, extending outward from these coasts for distances of 200 miles or more. They contain varying amounts of Radiolaria. The abyssal oozes mostly commence at 100 to 200 miles offshore. Commonly they are very uniform, corresponding to the constancy of the sea above them, and they may be distinguished as (1) radiolarian ooze, (2) foraminiferal (*Globigerina*) ooze, and (3) red clay.

Radiolarian ooze includes oceanic deposits, the greater part of which (75 per cent or more) is composed of the siliceous shells of these creatures. Such relatively pure oozes are limited to certain areas of the Pacific and Indian oceans. Deposits in which Radiolaria comprise less than 5 per cent of the organic contents are called mixed radiolarian ooze. This kind is more common than the relatively pure ooze and has wider distribution on many parts of the ocean floor. When carefully treated with acids, radiolarian ooze appears as a fine, white powder; in the raw state, it is yellowish or may be red.

Foraminiferal ooze rich in the siliceous skeletons of radiolarians covers extensive areas at depths below 1,800 fathoms (3,280 m.); it is replaced by red clay at depths of 2,200 fathoms (4,000 m.) or more. When dried, such ooze is a fine white or gray powder, containing 50 to 80 per cent CaCO_3 . Removal of the calcium carbonate leaves a residue consisting mainly of the tests of siliceous organisms.

Red clay is quantitatively the most important deep-sea deposit, covering a large part of the deep-sea floor. Calcareous matter is largely lacking in the red clay, but volcanic ash, pumice, particles of lava, and radiolarian tests are common. Some investigators believe that the red clay is formed largely by decomposition of radiolarian ooze.

Some long deep-sea cores taken by modern methods display mixed faunas of Recent and Tertiary species. The significance of

such core samples has only lately come to be realized in oceanographic investigations (21).

FOSSIL FORMS

About 60 per cent or more of the Recent deep-sea sediments containing radiolarians occur between 1,800 and 2,200 fathoms (3,300 and 4,000 m.), and in minor part extending downward to about 3,750 fathoms (6,800 m.). Accordingly, the argument has been advanced that beds containing fossil Radiolaria must have been formed at similar depths. Radiolarians may be deposited in much shallower water, however, and it is even probable that some deposits consist of strand-line accumulations carried inland under special circumstances, as is inferred in explanation of some early Tertiary deposits of Trinidad. No information on the rate of accumulation of radiolarian-bearing sediments seems to be available, but a modern deposit of diatoms, 10 to 15 cm. in thickness and 20 miles in length, is known to have been formed on the Oregon coast during a 3-day storm with high winds and rains. Tests of *Globigerina* are reported to have been carried by local winds several miles inland from the coast of Ireland and mixed with fresh-water and wind-blown sediments. Obviously, these are not abyssal sediments, and the contained organisms give no hint of the origin of the deposit. It is also evident that they are rare accidental accumulations. The extensive Eocene siliceous shales of California, with alternating beds of Radiolaria and Foraminifera, may have accumulated in a shallow sea at some distance from land as a result of alternating periods of accelerated reproduction during frequently recurrent times of favorable conditions for each of the 2 types of organisms. Occurrence of fossil Radiolaria in abundance is not *ipso facto* proof of deep-water sedimentation but only of pelagic origin of the fossils. Deep-water deposits generally lack large, land-derived fragments such as logs or sizable clastic detritus. They do not contain rooted plants. Shells of typical shallow-water animals, such as rudistids, tide-flat snails, and sand-dollars, are absent. The clastic deposit is commonly in the form of fine or flocculent material. Man-

ganese oxide and phillipsite are important minerals. Deep-sea deposits mostly occur as sheets which cover wide areas. Structures produced by wind and waves are lacking. Coarse sandstones are absent. All features must be examined before judgment is pronounced as to the mode of making any given radiolarian-bearing deposit. Few deposits on present-day lands offer indisputable evidence of deep-sea origin.

Most radiolarian-bearing cherts are thought to be of shallow-water origin. Extensive chert beds of this sort are found in supposedly Jurassic rocks (Franciscan) of California, Ordovician strata of New York, and Cretaceous and Eocene deposits of Ecuador.

The Franciscan formation comprises a heterogeneous but rather distinctive assemblage of shallow-water marine clastics, chemical deposits, and some organic sediments. These beds of great thickness were deposited in a sinking geosynclinal trough that extended the whole length of the Coast Ranges in California and Oregon. Extensive volcanism, particularly during accumulation of the upper Franciscan, resulted in outpourings of pillow basalts and andesites. Sills, dikes, and laccoliths of diabase and basalt were formed commonly. Association of the Franciscan cherts, well described by DAVIS (9), with pillow basalts and serpentine indicates introduction of the silica from volcanic sources. The cherts are chemical sediments and the Radiolaria are accidental inclusions. The great amount of silica supplied by the volcanoes created conditions favorable for the multiplication of these animals. Nearly conclusive evidence indicates that the Franciscan is of shallow-water origin. In southwestern Ecuador, analogous Cretaceous and Eocene cherts with Radiolaria are similarly associated with volcanics.

RUEDEMANN & WILSON (22) maintain that the Ordovician cherts of New York are of deep-water origin. It is possible, in-

deed, that some cherts were accumulated in deep water, whereas others were laid down in shallow seas. The same is true of soft siliceous radiolarian shales, novaculites, and other sediments of different ages which contain these fossils. CLARK & CAMPBELL (8) judge that upper Eocene radiolarian shale of the Mt. Diablo area (California) is of shallow-water origin, although some other geologists think that depths may have been as much as 1,000 fathoms (1,800 m.). Estimating the depth of deposition of fossil Radiolaria on the basis of depth range for the same genera in modern seas, RUEDEMANN believes that a mixed fauna of shallow- and deep-water forms must have been deposited at depths no less than the greatest inhabited by the deep-water forms. ABERDEEN (1), however, points out that almost every genus has both shallow- and deep-water species and that modern species vary greatly in depth distribution; accordingly, interpretation of the environment of fossil species by analogy is not necessarily reliable. ABERDEEN believes that best evidence of depth lies in structures of the shell. Nearly all deposits of fossil Radiolaria are those of upper-zone pelagic types. The great array of spherical, elliptical, and especially spongy kinds, which occur in vast numbers in deposits of Barbados, Trinidad, California, and elsewhere, are all free-floaters, differing almost only in detail from Recent planktonic faunas, especially those of the tropics. Representatives of the Nassellina in the same deposits are kinds that freely developed radial apophyses. It must be remembered also that empty shells of these floating organisms may drift a long way from their point of origin before they settle down and become enclosed in sediment. For this reason, some deposits of these fossils are not autogenous. Bottom- and middle-zone forms may become associated in this way with surface-dwelling kinds and a death assembly (thanatocoenose) results.

DISTRIBUTION

STRATIGRAPHIC VALUE

The value of fossil Radiolaria for stratigraphy is diminished by the long ranges of many genera. Some seem to extend through-

out the whole post-Precambrian geological column and others through a number of systems. Only a few genera are limited sharply to part of a single system. Furthermore, the number of species is tremendous,

so that, despite general limitation to very short geological ranges (21), identifications and establishment of the ranges of individual species are very difficult indeed. Many species remain to be described. The selection of index forms and correlation of faunas in widely separated geographic provinces cannot be undertaken satisfactorily under conditions of present knowledge.

On the other hand, the usefulness of Radiolaria in local correlations is well recognized and is especially important where a number of different radiolarian-bearing rocks occur in a stratigraphic sequence and where these display differences in faunal composition or ecological conditions. Some formations can be followed and identified positively for long distances by their radiolarian contents. Extensive use has been made of these fossils in this manner in Ecuador (30). Thus, Radiolaria seem to be as useful as Foraminifera and other fossils in localities where they occur, especially if they are abundant. Also, often they can be used in the solution of stratigraphic problems (14, pp. 166-167) where other fossils have little value or are absent. The principal difficulty lies in our lack of knowledge of these organisms and in the relatively elaborate processing required to prepare them for study. Few micropaleontologists understand the necessary research techniques, and most are bewildered by the multitude of finely differentiated species encountered. However, the Radiolaria can be mastered as easily as other groups which have been used for stratigraphic purposes, and they offer the possibility of solutions not readily arrived at by study of various other fossils.

GEOLOGICAL OCCURRENCE

Radiolaria are found in important groups of marine sedimentary rocks in all continents and on some of the larger islands. By the aid of modern methods it has been demonstrated that many hard rocks contain numerous well-preserved specimens of these primitive organisms. Some rocks are composed essentially of closely compacted masses or radiolarian shells. Soft marls and clays may be filled with such shells, and even quartzites may contain them. Radiolarites extend throughout nearly the whole column of fossiliferous geological forma-

tions. They are most common in strongly folded pre-orogenic sediments of the flysch type in geosynclines. Volcanic products are commonly adjacent.

SUPPOSED PRECAMBRIAN

The presence of Radiolaria in Precambrian rocks of Brittany, along the Vendée coast, has been reported (6), largely upon insecure evidence. All described specimens (19 genera, 45 species, and many indeterminate forms) came from a single sample. Most of these Radiolaria are poorly preserved and illustrations of them are highly reconstructed. The shells are much smaller than modern forms to which they seem to be related. The fossil-bearing matrix is interbedded with gneiss, and its exact age is open to question. Somewhat arbitrarily, it is herein classed as Cambrian.

Radiolaria found near Adelaide, Australia, which commonly have been assigned to the Precambrian, now are credited to the Cambrian (14). Until the stratigraphy of these deposits is more clearly understood, the presence of Radiolaria in Precambrian formations cannot be affirmed reliably.

PALEOZOIC

The number of Radiolaria known from Paleozoic strata is much smaller than that from Mesozoic or Cenozoic deposits. Rüst (25) counted 109 genera and 261 species which had been reported up to 1892 in rocks of this era. In the Ordovician of New York, 19 genera and 33 species belonging to planktonic types were recorded but only 27 species from the Silurian. Devonian rocks, according to Rüst, contain 64 species, but numerous others have been added since his time. Cherts, limestones, and tuffs rich in these organisms occur in New South Wales, and the Caballos chert of the Marathon basin of Texas contains a fauna of 18 genera and 24 species. The greater part of these pre-Carboniferous rocks contain forms which belong to the Sphaerellari. Only a few records of Carboniferous Radiolaria are trustworthy, for most of the 199 so-called Carboniferous species reported by Rüst come from radiolarian-bearing rocks in Sicily now classified as Jurassic. Only 8 genera and 12 species are known from the Permian, the Word and Leonard formations of the Texas Marathon basin being the

best-known North American occurrences of Radiolaria of this age. With few exceptions, all Paleozoic Radiolaria are of simple form, consisting mostly of latticed spherical, elliptical, or lens-shaped shells. Many Nassellina belong to the Plectellari, although some large Cyrtellari are known.

MESOZOIC

Well-preserved Radiolaria have been recovered from the principal divisions of the marine Mesozoic. Rüst counts 421 species, of which only 21 are from the Triassic. For the most part, the great development occurs in the Jurassic (232 species), especially from the Alps, where marine subdivisions are more or less prolific in these fossils. Silicified coprolites, flints, jaspers, novaculites, hornstones, and cherts are fertile sources of these fossils everywhere in the Jurassic. The age of some radiolarian-bearing rocks assigned to the Jurassic in Asia, particularly Japan (14), and also in California is now considered uncertain. Rocks of the Danau plateau of Kalimantan (Dutch Borneo), with an area of about 40,000 square miles, which seem to comprise a nearly flat elevated sea-bottom, are assigned to the Jurassic by most students. The Danau formation contains a radiolarian fauna of 32 genera and 100 species. The Franciscan radiolarian chert of California, similarly assigned to the Jurassic and often correlated with the Danau formation, carries a uniform but very small fauna of only 10 genera and 13 species in an area of 25,000 square miles or more. These 2 formations have the greatest areal extent of any known radiolarian-bearing rocks.

Rüst reports only 168 Cretaceous Radiolaria, but about 3 times as many have been added since his records were made. Extensive studies of various Italian localities provide most of these new records. Rocks elsewhere are known to contain rich undescribed faunas, among which those from the Funks formation (northern California) and Water Canyon formation of the San Joaquin Valley (central California) are especially abundant in kinds and numbers. Extensive deposits of Radiolaria occur in Ecuador and large faunas are known to occur in Java, Rotti, and other parts of the East Indies.

Mesozoic radiolarian faunas contain

great numbers of different kinds of very large Triacartilae and abound in basally fenestrated Nassellina. The number of ringed Spumellina (*Saturnalis* and similar genera) is great. The genus *Cenellipsis* is common but Triospyridicae generally are scarce. These Mesozoic faunas are easily distinguished from those of other eras. Some students of fossil Radiolaria believe that Mesozoic faunas are widely distributed (21).

CENOZOIC

The great majority of described fossil Radiolaria belong to Cenozoic formations, and these are mainly from upper Eocene formations. One report describes these fossils in Paleocene strata (Missouri).

Lower and middle Eocene faunas are recorded in Alabama, Trinidad, and New Zealand but are poorly known. Upper Eocene marls and clays, especially in Barbados, are very rich in radiolarians and afford some of the classic examples of these fossils; nearly every geological and biological collection possesses some specimens from Barbados. About 500 species from this island have been described. Sicily also abounds in fruitful tripoli deposits, long known for their utility as polishing powders.

The Oligocene of New Zealand (Omaru), famous for its beautiful and varied diatom flora, is rich in Radiolaria. Oligocene beds of Cuba and Trinidad contain large but undescribed faunas.

Among the best-known Miocene radiolarian deposits are those of the Mohnian and Delmontian stages of California. Faunas from Italy, particularly that of Reggio Emilia, near Naples, are important. Smaller Miocene faunas occur elsewhere in Europe and North and South America.

The Pico formation of the Los Angeles area (California) yields an interesting Pliocene fauna, but the largest and most varied fauna (328 species) of this age is found on Rotti (East Indies). Hardly any other Pliocene faunas are known. Undifferentiated Cenozoic Radiolaria have been described from several parts of South America.

Cenozoic Spumellina and Nassellina are intimately related in general character to forms which now occur in Recent deep-sea oozes, especially those of the Pacific area (21). At least 1,500 species have been described from Cenozoic deposits.

METHODS OF STUDY

SEPARATION

Methods of separating the shells of Radiolaria from matrix containing them differ greatly from techniques generally employed by students of Foraminifera.

RECENT FORMS

Radiolaria, especially those from deep-sea cores with much calcareous matrix, can be prepared by boiling a small sample in a glass beaker or test tube in concentrated HCl under a chemical hood or with arrangement to direct the fumes away from the operator. Much gas usually is evolved, and care must be taken that particles do not cling to sides of the container or overflow. The acid should be added to the container little by little before flame is applied. After the material has broken down, the sample should be allowed to cool and the residue to settle. The supernatant liquid may then be decanted carefully. The residue should next be boiled in H_2O_2 , and, after cooling, it should be washed in distilled water and stored in weak alcohol in tightly corked bottles. Refractory samples must be treated according to directions given for preparation of fossils.

FOSSIL FORMS

Samples of sedimentary deposits, especially shales containing fossil shells of Radiolaria, are broken into fragments, put into a beaker, and boiled under a chemical hood for 15 to 20 minutes in concentrated HCl. Without washing, an equal volume of concentrated HNO_3 is added and boiled in the same beaker for a similar length of time, or until brown fumes disappear. After thorough washing with water and careful decanting, the sample is boiled in concentrated H_2SO_4 until organic matter is removed. The process may take an hour, or exceptionally more than 12 hours, and judgment must be used to determine when it has been completed. The sulphuric acid treatment may be repeated if necessary. The sample is next washed in a liberal amount of water with repeated decantations. After all trace of acid disappears, NaOH pellets or small portions of sticks should be added and boiling repeated. If

the sample has not disintegrated previously, it will do so now. Care must be taken to avoid an excess of NaOH which may destroy the specimens. Wash the sample once more and boil with a few drops of HCl in order to neutralize the alkali. The sample, generally consisting of very clean beautiful specimens, may now be stored in weak alcohol in small vials.

Another method sometimes employed is as follows: (1) Place a 10-gram sample of dry fragmented sediment in a 400-ml. beaker with distilled water to which 4 or 5 grams of tetrasodium pyrophosphate has been added, and set the sample aside for 24 hours. If undispersed clay remains, add more of the reagent and allow the sample to soak for another day. The next steps are directed to segregation and concentration of the Radiolaria. (2) Rotate the sample rapidly in a beaker and allow it to stand 10 minutes, after which the water should be poured off gently. Repeat until a clean residue is obtained. If clay remains, more reagent may be added and the sample boiled for a half hour. Further decanting at 10-minute intervals should be continued until a clay-free residue remains. (3) Decant now at 5-minute intervals, saving the decanted part, and gradually reduce the decanting period to 1- or 2-minute intervals. (4) Next, boil the decanted residues for about 30 minutes in distilled water with 10-per cent concentrated H_2SO_4 until the organic matter is removed. (5) Wash the residue in distilled water and store as usual. This process sometimes proves successful when other methods fail, especially in samples containing much clay matrix.

EXAMINATION

SLIDE PREPARATION

To make slides of specimens prepared by one of the methods described, small amounts of sample residue should be withdrawn by pipette from a bottle and dropped on a clean glass slide. Allow the water to evaporate on a warm electric plate until the preparation is completely dry. Place a drop of mounting medium over the specimen-containing area while the slide is warm, lay a cover slip in position, and

reheat the slide gently until the medium spreads evenly to all edges of the slip. Then the slide may be withdrawn from the plate and allowed to cool. Hyrax, because of its high refractive index, is preferable to Canada balsam but may not be available. Specimens mounted in this way are not arranged in order.

Sometimes, for special reasons, ordered rows of specimens are prepared before the cover slip is added. In order to make such arrangement of shells, one should add a small amount of gum arabic to the center of the slide and put the specimens near by. When the gum is dried, small brushes or fine needles may be used under a compound binocular dissecting microscope to arrange the specimens in suitable order. Individuals are picked up singly and placed in regular rows in the gum. When so placed, the specimens may be fixed in position by breathing upon the slide gently. Further treatment with mounting medium is according to schedule. For diagnostic purposes and usual laboratory routine, the unsorted mount is satisfactory, but ordered rows of specimens are desirable in a reference collection or for exhibition.

THIN SECTIONS

Specimens enclosed in a very hard matrix, such as chert, novaculite, and other refractory material, generally are examined in thin sections. It is best to grind a small polished surface first in order to find a plane containing a large number of suitably oriented specimens. Sections should not be ground as thin as those usually made for mineral determinations.

Thin sections of radiolarian shells require special interpretation, for specimens sectioned obliquely may appear as ovals, and cross sections as circles. Conical forms in these views may appear to belong to radically different genera. KOBAYASHI (14) gives an excellent discussion of some of these difficulties.

CLASSIFICATION

PRINCIPLES

The classification of Radiolaria depends mostly upon hard parts which form the shell. The outstanding feature of the dif-

MICROSCOPIC METHODS

A compound biological microscope with powers ranging from $\times 50$ to $\times 700$ is required for the study of these minute organisms. A binocular instrument is most satisfactory. Good lighting is required and should come from an artificial source. Green light obtained by interposing a suitable filter is desirable, especially for continued observations. A camera lucida helps the worker. With aid of this instrument, drawings made to scale can be accumulated rapidly. Simple photographic methods have been described (6).

AGE DETERMINATION

For determining the age of a previously unstudied radiolarian fauna, the traditional method has been to ascertain the percentage of species of Cyrtellari in the whole fauna and to compare it with similar percentages in classic European faunas. In Europe, the Cyrtellari comprise 22 per cent of known Paleozoic faunas, 55 per cent of the Jurassic, 35 per cent of the Cretaceous, and 50 per cent of the Cenozoic. Percentages are sometimes calculated on number of individuals counted in thin sections or by taking genera as the unit. All this comes about because the Cyrtellari are best known in the European Jurassic and less so in formations of other ages. Recent studies (14) do not bear out age determinations based on this method. Many questions as to specific identifications, influence of ecological factors, geographic distribution, accidental assemblies, conditions of differential fossilization, deformation of individuals due to fossilization, and effect of other factors cast doubt on the reliability of this method and any conclusions drawn from it. By this method the Franciscan and Danau formations were correlated with each other. The study of radiolarian assemblages by comparison with faunas of known ages probably is more sound. Statistical methods may be useful.

ferent families, genera, and species of Radiolaria is the geometrical form of the test. Nearly every figure found in symmetrical 3-dimensional geometrical structures is

reproduced in some member of this group. Irregular shapes are rare and they are derived from regular forms. The geometrical system thus seems to be a logical, simple plan capable of expressing the genetic history and relations of the multitudinous forms belonging to Radiolaria.

HISTORY

The classification of Radiolaria by early authors (to 1884) has been stated by HAECKEL (12), who gives reasons for rejection of systems proposed by EHRENBURG, MÜLLER, HERTWIG, BÜTSCHLI, and others. Later monographers, especially RÜST, HAECKER, and POPOFSKY, largely have followed the system proposed by HAECKEL. None of these or other authors, most of whom have been concerned principally with description of particular faunas, has reviewed the Radiolaria as a whole. Neither HAECKER nor POPOFSKY considered fossil radiolarians especially, and RÜST (23-26) did not treat Recent forms. HAECKER (13) removed the Orosphaeridae from the Phaeodarina to the Spumellina, and rejected HAECKEL'S Prunoidea, which he included with the Sphaeroidea, at least in part. POPOFSKY (19) united the Stephaniidae and Cannobotrydidae as Orboidea, in the Nassellina, but otherwise followed HAECKEL and HAECKER in most other divisions.

The system herein adopted is mainly that of HAECKEL but accepts HAECKER'S placement of the Orosphaeridae and rejects the union of HAECKEL'S Prunoidea and Sphaeroidea, and also POPOFSKY'S Orboidea. HAECKER'S Lamprocycladidae and Plectopyramididae in the Nassellina are also rejected. Other unaccepted categories are evident in organization of the systematic text. These exclusions are based on a re-examination of the various groups as a whole, rather than on the partial basis of their arrangement.

The complex classification of the Phaeodarina presents a special problem. HAECKEL'S arrangement of these forms, which is adopted in the *Treatise*, differs chiefly from that of HAECKER, followed by POPOFSKY (20), in separation of the Coelodendridae and Coelographididae. The general system here presented is the first since HAECKEL'S Challenger report, which treats

Radiolaria as a whole, including both fossil and Recent genera.

PHYLOGENY

For the purpose of constructing a genealogical tree of the Radiolaria, available sources of information are: (1) paleontology, (2) comparative development, and (3) comparative structure. The third of these is the most satisfactory, and by its aid we are able to recognize the general features of probable radiolarian phylogeny.

The agreement of all Radiolaria in essential structure of the central body (capsule) distinguishes them from other Protozoa and justifies the conclusion that the whole group developed from a common undifferentiated stem form. The simplest Spumellina, without a skeleton but with a spherical body, seems to be the radical form, and the genus *Procyttarium* closely approximates the common ancestor of the whole group. The Radiolaria are judged to be closely related to the Heliozoa, which probably gave rise to them.

The Spumellina may be regarded as the common stem of Radiolaria, for they possess in simplest, least differentiated form all characters that distinguish Radiolaria essentially from other protozoans. Furthermore, the Spumellina lack the positive characters which set apart the remaining suborders. The Acantharina, Nassellina, and Phaeodarina are interpreted as divergent branches of the genealogical tree which have separated in different directions and are only connected through their respective simplest members, viz., *Actinelius*, *Cystidium*, and *Phaeodina* (FIG. 7).

The Acantharina are distinguished by (1) the centrally generated skeleton, (2) the peculiar chemical nature of the skeleton, and (3) the disposition of pores of the central capsule. All forms of the Acantharina may be derived from *Actinelius*, which seems to have arisen from *Procyttarium* by division of some primitive pseudopods into soft, flexible extensions, while others became firm and rigid, with skeletal supporting rods. The Acantharina are widely divergent from other suborders and are treated first in the systematic text in order to stress this difference.

The Nassellina are peculiarly distinguished from other suborders by the pore-

bearing plate which closes off the oral pole of the conical structure (podocone) within the central capsule. The Nassellina are connected through *Cystidium* to *Procyttarium*. *Cystidium* may be considered a *Procyttarium* with a very different central capsule. It may have arisen from *Procyttarium* by obliteration of numerous, evenly distributed pores of the central capsule at one pole of the capsule, accompanied by better development of them at the opposite pole. The concentration of these pores at one pole led to further development of the podoconus (Fig. 8).

The Phaeodarina are sharply marked off from other Radiolaria by (1) the double membrane of the central capsule, (2) the tubular opening (astropyle) at one pole, and (3) the presence of an aggregate of dark granules (phaeodium). The stem form is *Phaeodina* and others may derive from it. *Phaeodina*, in turn, may have arisen from *Procyttarium*, presuming that the 3 essential characters listed above appeared mostly by successive steps through intermediate stages. Thus, the gradual reduction of numerous fine pores of the central capsule may have resulted in a tubular main aperture approximately in the fashion postulated for the Nassellina, and the phaeodium may have appeared progressively from some sort of modified symbiontism. The double capsule membrane could have formed in a single step. In any case, these are easy evolutionary developments. The Phaeodarina are among the most complex Radiolaria. With respect to their multiform skeletons, most of the series seem to be due to genetic factors and few to adaptive modifications. Of the last, those related to flotation are the most important.

Suprageneric Divisions of Radiolaria

(First figures in parentheses indicate number of genera and second the number of subgenera.)

- Porulosida (order) (474;504) *Cam.-Rec.*
 Acantharina (suborder) (72;86) *Eoc.-Rec.*
 Astrolophi (division) (32;39) *Eoc.-Rec.*
 Astrolophicae (superfamily) (5;8) *Eoc.-Rec.*
 Astrolophidae (family) (2;3) *Rec.*
 Litholophidae (1;2) *Rec.*
 Acanthochiasmatae (2;3) *Eoc.-Rec.*
 Acanthochiasmatae (subfamily) (1;3) *Rec.*
 Chiasoliniae (1) *Eoc.-Rec.*
 Actinastriacae (superfamily) (3) *Rec.*
 Actinastriidae (family) (1) *Rec.*
 Rosettidae (1) *Rec.*
 Trizonidae (1) *Rec.*
 Astrolonchicae (superfamily) (24;31) *Mio.-Rec.*
 Astrolonchidae (family) (14;19) *Mio.-Rec.*
 Astrolonchiniae (subfamily) (5;2) *Rec.*
 Stauracanthinae (4;4) *Rec.*
 Zygacanthinae (5;13) *Mio.-Rec.*
 Acanthostauridae (family) (7;7) *Rec.*
 Acanthostaurinae (subfamily) (4;2) *Rec.*
 Lithopterinae (3;5) *Rec.*
 Acantholonchidae (family) (3;5) *Rec.*
 Acanthophracti (division) (40;47) *Rec.*
 Dorataspidicae (superfamily) (28;30) *Rec.*
 Dorataspididae (family) (18;25) *Rec.*
 Dorataspidinae (subfamily) (10;17) *Rec.*
 Dorataspidides (tribe) (8;13) *Rec.*
 Phractaspidides (2;4) *Rec.*
 Tessarapelmatinae (subfamily) (8;8) *Rec.*
 Tessarapelmatides (tribe) (4;6) *Rec.*
 Stauraspidides (4;2) *Rec.*
 Astrocapsidae (family) (5) *Rec.*
 Astrocapsinae (subfamily) (2) *Rec.*
 Cenocapsinae (subfamily) (1) *Rec.*
 Porocapsinae (subfamily) (2) *Rec.*
 Aspidommatidae (family) (5;5) *Rec.*
 Belonaspidicae (superfamily) (12;17) *Rec.*
 Belonaspididae (family) (6;5) *Rec.*
 Belonaspidinae (subfamily) (5;2) *Rec.*
 Phatnaspidinae (1;3) *Rec.*
 Hexalaspididae (family) (4;8) *Rec.*
 Diploconidae (2;4) *Rec.*
 Spumellina (suborder) (402;418) *Cam.-Rec.*
 Collodari (division) (26;28) *Ord.-Rec.*
 Thalassicolicae (superfamily) (7;11) *Dev.-Rec.*
 Thalassicolidae (family) (5;6) *Dev.-Rec.*
 Cristallosphaeridae (1) *Rec.*
 Collozoidae (1;5) *Rec.*
 Thalassosphaericae (superfamily) (15;11) *Ord.-Rec.*
 Thalassosphaeridae (family) (5;5) *Rec.*
 Sphaerozoidae (3;6) *Ord.-Rec.*
 Meynellidae (2) *Jur.*
 Thalassothamnidae (3) *Rec.*
 Lithacanthidae (2) *Rec.*
 Orosphaericae (superfamily) (4;6) *Rec.*
 Orosphaeridae (family) (4;6) *Rec.*
 Orosphaerinae (subfamily) (2;2) *Rec.*
 Orospheninae (2;4) *Rec.*
 Sphaerellari (division) (376;390) *Cam.-Rec.*
 Liosphaericae (superfamily) (149;133) *Cam.-Rec.*
 Liosphaeridae (family) (16;24) *Cam.-Rec.*
 Liosphaerinae (subfamily) (2;6) *Ord.-Rec.*
 Ethmosphaerinae (4;6) *Cam.-Rec.*
 Thecosphaerinae (3;6) *Jur.-Rec.*
 Cromyosphaerinae (1) *Cret.-Rec.*
 Caryosphaerinae (1) *Dev.-Rec.*
 Plegmosphaerinae (5;6) *Cam.-Rec.*
 Protosphaeridae (family) (1) *Cret.*
 Collosphaeridae (17;13) *Ord.-Rec.*
 Collosphaerinae (subfamily) (15;11) *Ord.-Rec.*
 Clathrosphaerinae (2;2) *Rec.*
 Dorysphaeridae (family) (5;2) *Ord.-Mio.*
 Stylosphaeridae (18;22) *Cam.-Rec.*
 Stylosphaerinae (subfamily) (3;8) *Dev.-Rec.*
 Xiphostylinae (4;10) *Cam.-Rec.*
 Amphistylinae (3;4) *Jur.-Rec.*
 Cromyostylinae (2) *Rec.*

Caryostyliinae (1) *Rec.*
 Spongostyliinae (5) *Cret.-Rec.*
 Triposphaeridae (family) (5) *Ord.-Cret.*
 Staurosphaeridae (14;12) *Cam.-Rec.*
 Staurosphaerinae (subfamily) (3;4) *Ord.-Rec.*
 Staurolonchinae (5;4) *Cam.-Rec.*
 Stauracontiinae (1;4) *Jur.-Rec.*
 Staurocromyinae (2) *Cret.-Rec.*
 Staurocaryinae (1) *Rec.*
 Staurodoradinae (2) *Ord.-Rec.*
 Pentasphaeridae (family) (1) *Cret.*
 Cubosphaeridae (21;14) *Dev.-Rec.*

Cubosphaerinae (subfamily) (2) *Rec.*
 Hexastyliinae (5;4) *Jur.-Rec.*
 Hexalonchinae (4;6) *Dev.-Rec.*
 Hexacromyinae (3;4) *Eoc.-Rec.*
 Hexacromyinae (1) *Mio.-Rec.*
 Centralonchinae (3) *Rec.*
 Hexadoradinae (3) *Cret.-Rec.*
 Astrosphaeridae (family) (50;46) *Cam.-Rec.*
 Astrosphaerinae (subfamily) (9;16) *Cam.-Rec.*
 Heliosphaerinae (6;14) *Ord.-Rec.*
 Actinommatinae (4;6) *Dev.-Rec.*
 Cromyommatinae (3;2) *Cam.-Rec.*

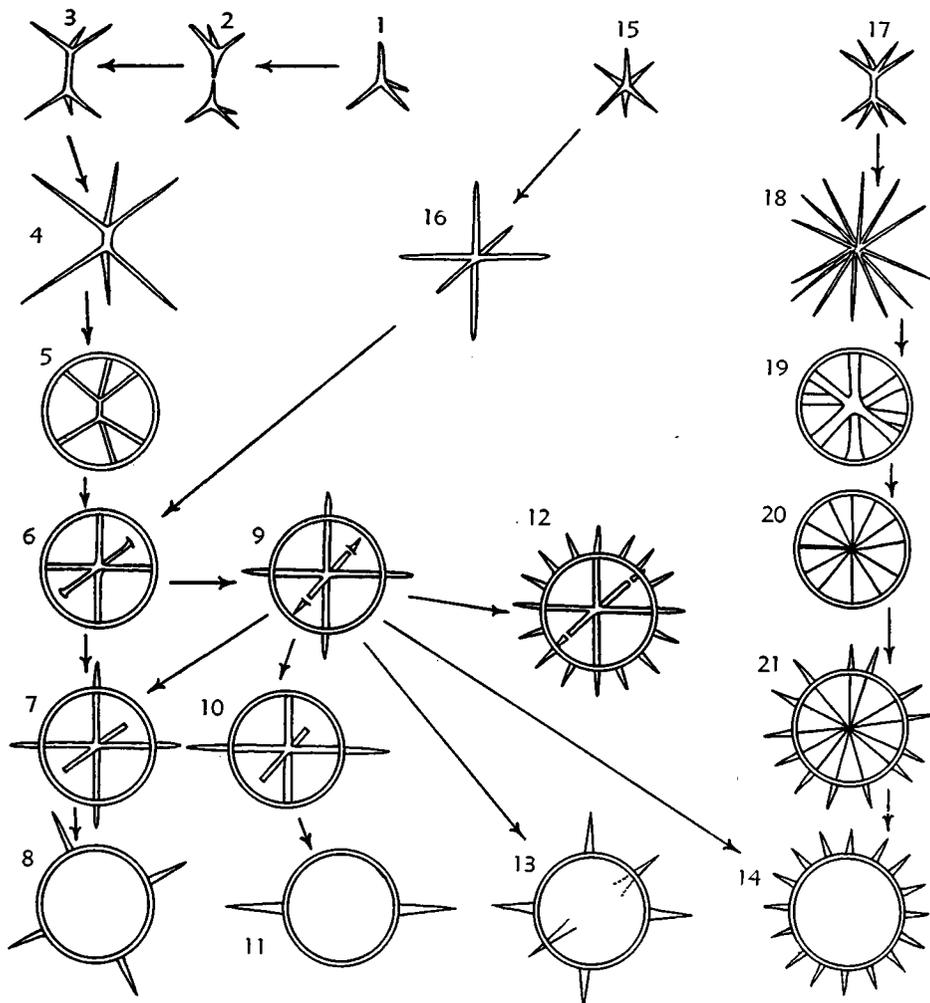


FIG. 7. Phylogenetic relationships of the Spumellina, showing inferred evolution of skeletal ray patterns in Radiolaria. Primitively these consist of radially arranged spines alone (1-4, 15-16, 17-18) or, in more complex forms, of spines and a spheroidal lattice shell. Monocentric 4-ray types (1, 2) by pairing may produce dicentric forms (3-5) which give rise to secondarily monocentric 6-ray and other patterns. Similar evolution of multiray skeletons is suggested. Evolutionary trends are indicated by arrows and architectural types by letters: (1) 4-ray, (2-4) double 4-ray, (5,6) *Stigmosphaera*, (7) hypothetical intermediate form, (8) staurosphaerid, (9) *Centrolonche*, (10) *Stigmosphaerostylus*, (11) stylosphaerid, (12) *Acanthosphaera*, (13) cubosphaerid, (14) astrosphaerid, (15) thalassosphaerid, (16) *Lithacanthus*, (17) double 4-ray, (18) *Cytocladus*, (19,20) *Stigmosphaera*, (21) *Heterosoma* (48).

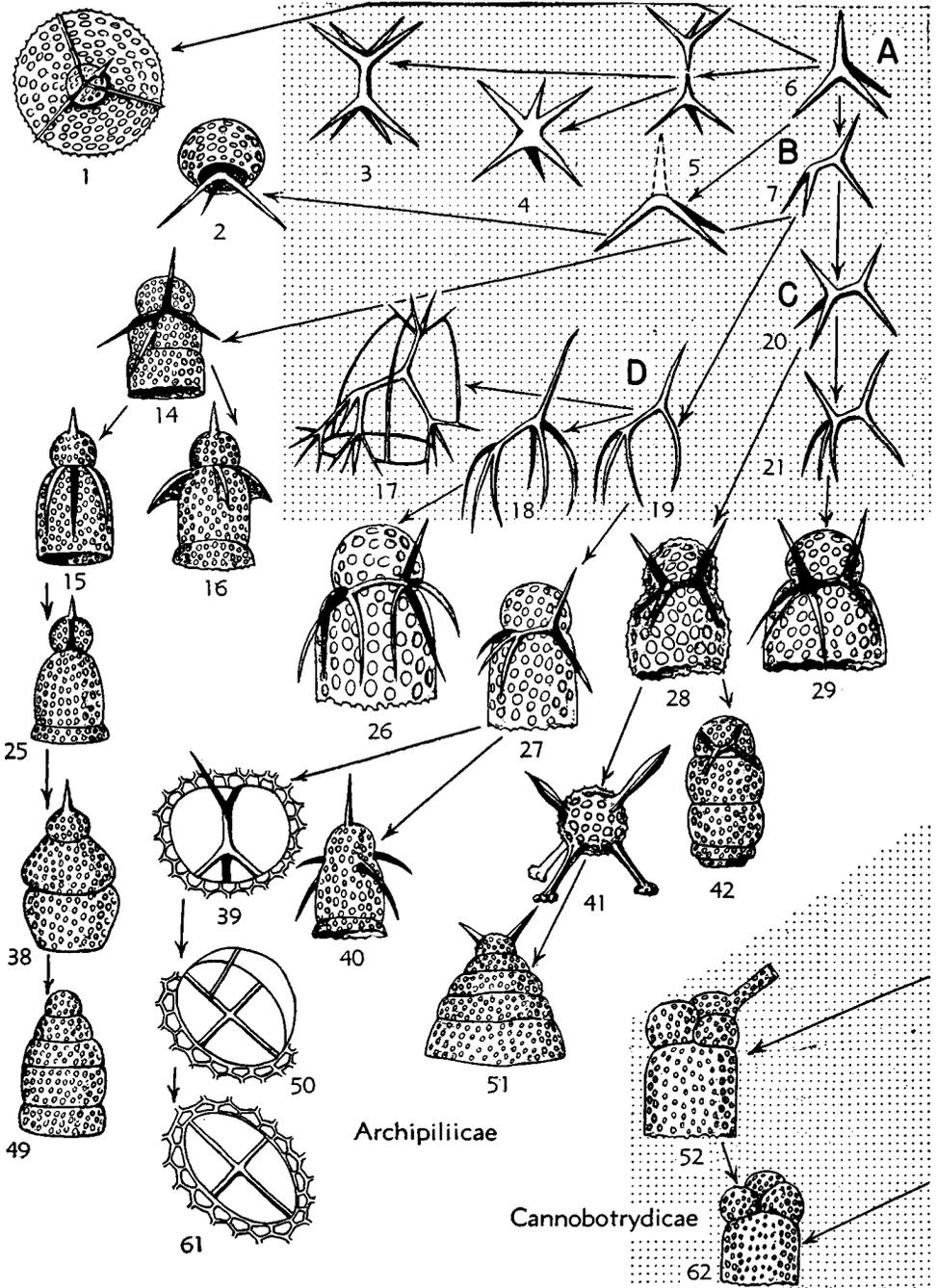
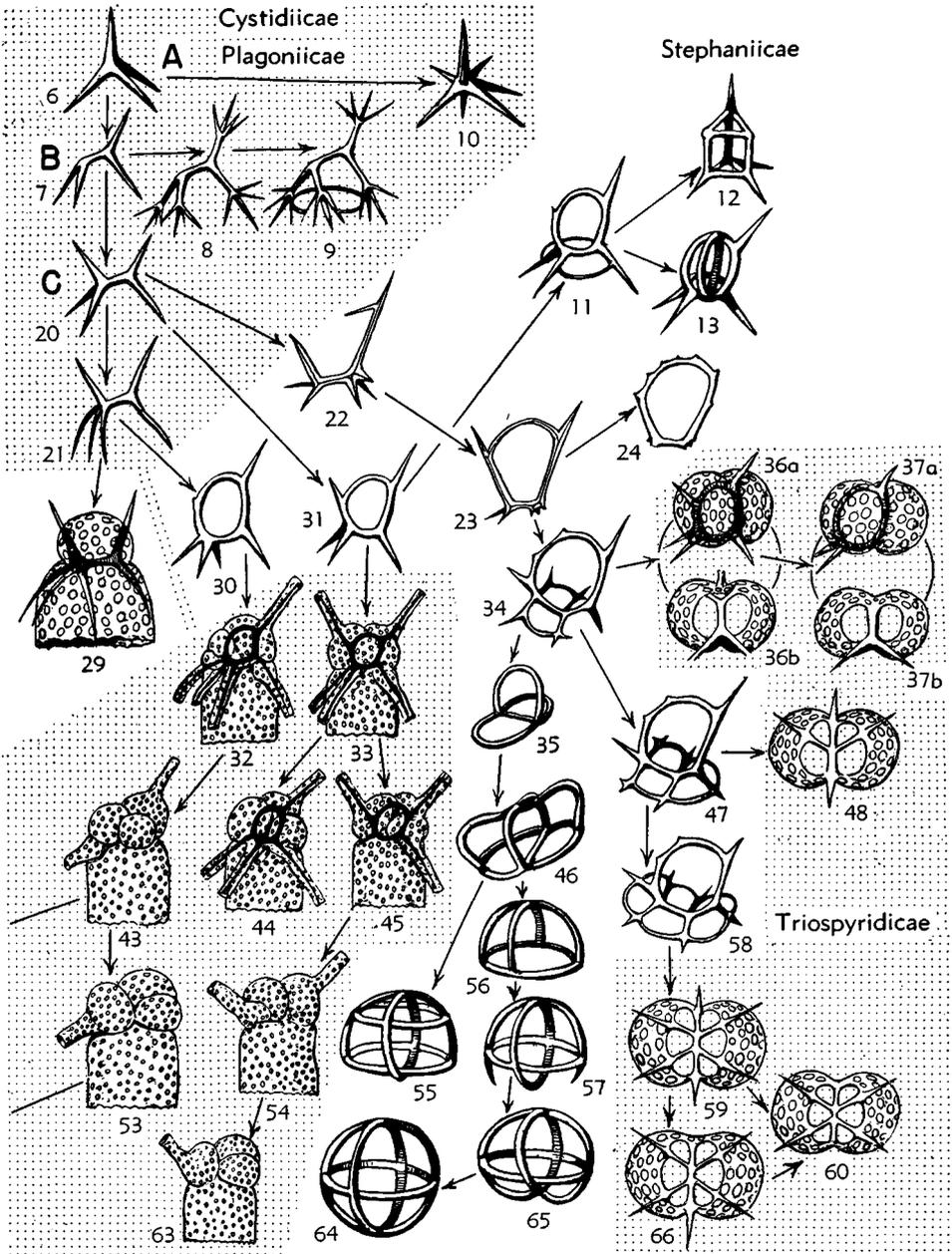


FIG. 8. Phylogeny of the Nassellina. All of these radiolarians are thought to be derivatives of relatively simple types illustrated by (A) *Plagoniscus*, (B) *Periplecta*, (C) *Plagiocarpa*, and (D) *Campylacantha*. The superfamilies Cystidiace and Plagioniace are represented by 3-10, 17-21, and the Stephaniace by 11-13, 30, and other numbers in the unshaded area at right; these belong to the division Plectellari. The



superfamily Archipiliaceae is represented by 26-29 and other numbers in the unshaded area at left; the Cannobotrydaceae by 52 and other numbers in the central shaded area below; and the Triospyridaceae by figures in the shaded area at lower right; they belong to the division Cyrtellari (48).

- Arachnosphaerinae (3;2) *Rec.*
 Sphaeropylinae (3) *Dev.-Rec.*
 Stomatospaerinae (1) *Rec.*
 Spongiommatinae (21;6) *Cam.-Rec.*
 Dactylosphaeridae (family) (1) *Cret.*
 Ellipsidiidae (superfamily) (65;76) *Cam.-Rec.*
 Ellipsidiidae (family) (11;6) *Cam.-Rec.*
 Druppulidae (19;27) *Ord.-Rec.*
 Sponguridae (10;11) *Ord.-Rec.*
 Spongurinae (subfamily) (6;7) *Ord.-Rec.*
 Spongodruppinae (4;4) *Carb.-Rec.*
 Artiscidae (family) (3;4) *Cret.-Rec.*
 Cyphantidae (9;12) *Dev.-Rec.*
 Panartidae (6;12) *Rec.*
 Zygartidae (7;4) *Rec.*
 Zygartinae (subfamily) (2) *Rec.*
 Ommatocampinae (2;4) *Mio.-Rec.*
 Desmocampinae (2) *Rec.*
 Monaxoniinae (1) *Rec.*
 Cenodiscicae (superfamily) (109;129) *Cam.-Rec.*
 Cenodiscilae (subsuperfamily) (48;46) *Cam.-Rec.*
 Cenodiscidae (family) (7;8) *Cam.-Rec.*
 Cenodiscinae (subfamily) (2) *Sil.-Rec.*
 Trochodiscinae (5;8) *Cam.-Rec.*
 Phacodiscidae (family) (22;28) *Cam.-Rec.*
 Phacodiscinae (subfamily) (5;4) *Eoc.-Rec.*
 Dorydiscinae (2) *Mio.*
 Heliosestrinae (12;14) *Dev.-Rec.*
 Heliodiscinae (3;10) *Cam.-Rec.*
 Coccodiscidae (family) (19;10) *Dev.-Rec.*
 Coccodiscinae (subfamily) (2) *Dev.-Rec.*
 Stylocyclinae (6) *Jur.-Rec.*
 Atracturinae (11;10) *Trias.-Rec.*
 Euchitoniidae (subsuperfamily) (61;83) *Cam.-Rec.*
 Euchitoniidae (family) (38;63) *Cam.-Rec.*
 Euchitoniinae (subfamily) (25;42) *Dev.-Rec.*
 Archidiscinae (2;5) *Jur.-Rec.*
 Flustrellinae (2;5) *Cam.-Rec.*
 Ommatodiscinae (2;2) *Paleoc.-Rec.*
 Stylodictyinae (7;9) *Perm.-Rec.*
 Pylodiscidae (family) (8) *Eoc.-Rec.*
 Pylodiscinae (subfamily) (3) *Rec.*
 Triopylinae (3) *Rec.*
 Discopylinae (2) *Eoc.-Rec.*
 Spongodiscidae (family) (15;20) *Ord.-Rec.*
 Spongodiscinae (subfamily) (2;4) *Dev.-Rec.*
 Spongopylinae (1;2) *Eoc.-Rec.*
 Spongotrochinae (6;6) *Ord.-Rec.*
 Spongobrachiinae (6;8) *Jur.-Rec.*
 Laracariidae (superfamily) (53;52) *Cam.-Rec.*
 Laracariidae (family) (7) *Eoc.-Rec.*
 Laracariinae (subfamily) (2) *Rec.*
 Coccolarcinae (2) *Eoc.-Rec.*
 Spongolarcinae (2) *Rec.*
 Larcopylinae (1) *Rec.*
 Larnacillidae (family) (8) *Paleoc.-Rec.*
 Larnacillinae (subfamily) (2) *Rec.*
 Larnacalpidinae (5) *Paleoc.-Rec.*
 Cenolarcopylinae (1) *Plio.*
 Pyloniidae (family) (10;14) *Jur.-Rec.*
 Pyloniinae (subfamily) (4;8) *Rec.*
 Monozoniinae (3;6) *Jur.-Rec.*
 Tetrapyloinae (3) *Jur.-Rec.*
 Tholoniidae (family) (12;18) *Rec.*
 Tholoniinae (subfamily) (4;6) *Rec.*
 Amphitholinae (4;4) *Rec.*
 Staurotholinae (4;8) *Rec.*
 Zonariidae (family) (3) *Rec.*
 Litheliidae (6;12) *Dev.-Rec.*
 Litheliinae (subfamily) (2;4) *Dev.-Rec.*
 Larcospirinae (4;8) *Dev.-Rec.*
 Strebloniidae (family) (3) *Rec.*
 Strebloniinae (subfamily) (2) *Rec.*
 Streblopylinae (1) *Rec.*
 Phorticae (family) (2;4) *Cam.-Rec.*
 Soreumatidae (2;4) *Rec.*
 Osculosida (order) (427;258) *Cam.-Rec.*
 Nassellina (suborder) (324;224) *Cam.-Rec.*
 Plectellari (division) (70;26) *Ord.-Rec.*
 Cystidiidae (superfamily) (2) *Rec.*
 Cystidiidae (family) (2) *Rec.*
 Plagoniidae (superfamily) (25) *Ord.-Rec.*
 Plagoniidae (family) (9) *Ord.-Rec.*
 Plagoniinae (subfamily) (2) *Ord.-Rec.*
 Triplagiinae (2) *Dev.-Rec.*
 Tetraplagiinae (4) *Ord.-Rec.*
 Enneaplagiinae (1) *Rec.*
 Plectaniidae (family) (16) *Rec.*
 Plectaniinae (subfamily) (3) *Rec.*
 Triplectinae (5) *Rec.*
 Triplectinae (7) *Rec.*
 Enneaplegmatinae (1) *Rec.*
 Stephanicae (superfamily) (43;26) *Trias.-Rec.*
 Stephanidae (family) (7;2) *Trias.-Rec.*
 Stephaniinae (subfamily) (2) *Eoc.-Rec.*
 Lithocircinae (5;2) *Trias.-Rec.*
 Cyrtostephanidae (family) (1) *Rec.*
 Semantididae (9) *Jur.-Rec.*
 Semantidinae subfamily (6) *Jur.-Rec.*
 Cortiniscinae (3) *Eoc.-Rec.*
 Acanthodesmiidae (family) (11;15) *Jur.-Rec.*
 Acanthodesmiinae (subfamily) (2) *Rec.*
 Zygostephaninae (2;2) *Jur.-Rec.*
 Eucoronidinae (3;7) *Eoc.-Rec.*
 Trissocyclinae (4;6) *Rec.*
 Paratympanidae (family) (15;9) *Jur.-Rec.*
 Protympaniinae (subfamily) (6;9) *Cret.-Rec.*
 Paratympaninae (2) *Rec.*
 Dystympaniinae (1) *Jur.-Rec.*
 Eutympaniinae (6) *Jur.-Rec.*
 Cyrtellari (division) (254;198) *Cam.-Rec.*
 Triospyrididae (superfamily) (46;33) *Jur.-Rec.*
 Triospyrididae (family) (28;27) *Jur.-Rec.*
 Triospyridinae (subfamily) (4;9) *Eoc.-Rec.*
 Dipodospyridinae (6) *Eoc.-Rec.*
 Pentarrhabdinae (2;2) *Eoc.-Rec.*
 Tetraspyridinae (3) *Eoc.-Rec.*
 Hexaspyridinae (3;2) *Eoc.-Rec.*
 Therospyridinae (4;2) *Cret.-Rec.*
 Petalospyridinae (4;8) *Jur.-Rec.*
 Circospyridinae (2;4) *Jur.-Rec.*
 Tholospyrididae (family) (5;2) *Mio.-Rec.*
 Tholospyridinae (subfamily) (2;2) *Mio.-Rec.*
 Tiarospyridinae (2) *Rec.*
 Spyridobotrydinae (1) *Rec.*
 Phormospyrididae (family) (6) *Eoc.-Rec.*
 Phormospyridinae (subfamily) (2) *Eoc.-Rec.*
 Rhodospyridinae (4) *Eoc.-Rec.*
 Androspyrididae (family) (7;4) *Eoc.-Rec.*
 Androspyridinae (subfamily) (2) *Rec.*
 Perispyridinae (3;2) *Rec.*
 Paradictyinae (2;2) *Eoc.-Rec.*

- Archipiliaceae (*superfamily*) (194;165) *Cam.-Rec.*
- Archipiliidae (*subsuperfamily*) (45;25) *Cam.-Rec.*
- Archipiliidae (*family*) (19;8) *Cam.-Rec.*
- Archipiliinae (*subfamily*) (12;4) *Cam.-Rec.*
- Archiperinae (7;4) *Rec.*
- Archiphormididae (*family*) (16;10) *Ord.-Rec.*
- Archiphormidinae (*subfamily*) (12;6) *Ord.-Rec.*
- Archiphatninae (4;4) *Jur.-Rec.*
- Archicorythidae (*family*) (10;7) *Cam.-Rec.*
- Archicorythinae (*subfamily*) (6;5) *Cam.-Rec.*
- Archicapsinae (4;2) *Perm.-Rec.*
- Sethopiliidae (*subsuperfamily*) (60;48) *Cam.-Rec.*
- Sethopiliidae (*family*) (27;12) *Jur.-Rec.*
- Sethopiliinae (*subfamily*) (17;12) *Jur.-Rec.*
- Sethoperinae (10) *Jur.-Rec.*
- Sethophormididae (*family*) (18;29) *Cam.-Rec.*
- Sethophormidinae (*subfamily*) (16;29) *Cam.-Rec.*
- Sethophatninae (2) *Rec.*
- Lophophaenidae (*family*) (15;7) *Cam.-Rec.*
- Lophophaeninae (*subfamily*) (9;7) *Cam.-Rec.*
- Adelocytidinae (6) *Cam.-Rec.*
- Theopiliidae (*subsuperfamily*) (51;50) *Cam.-Rec.*
- Theopiliidae (*family*) (21;15) *Jur.-Rec.*
- Theopiliinae (*subfamily*) (15;13) *Jur.-Rec.*
- Theoperinae (6;2) *Jur.-Rec.*
- Theophormididae (*family*) (11;19) *Jur.-Rec.*
- Theophormidinae (*subfamily*) (8;19) *Jur.-Rec.*
- Theophatninae (3) *Rec.*
- Theocorythidae (*family*) (19;16) *Cam.-Rec.*
- Theocorythinae (*subfamily*) (12;10) *Cam.-Rec.*
- Theocapsinae (7;6) *Dev.-Rec.*
- Triacartidae (*subsuperfamily*) (38;42) *Ord.-Rec.*
- Triacartidae (*family*) (10;8) *Perm.-Rec.*
- Triacartinae (*subfamily*) (7;4) *Perm.-Rec.*
- Stichoperinae (3;4) *Perm.-Rec.*
- Artophormididae (*family*) (8;9) *Jur.-Rec.*
- Artophormidinae (*subfamily*) (4;7) *Jur.-Rec.*
- Stichophatninae (4;2) *Cret.-Rec.*
- Stichocorythidae (*family*) (20;25) *Ord.-Rec.*
- Stichocorythinae (*subfamily*) (16;23) *Ord.-Rec.*
- Stichocapsinae (4;2) *Dev.-Rec.*
- Cannobotrydicae (*superfamily*) (14) *Jur.-Rec.*
- Cannobotrydidae (*family*) (3) *Jur.-Rec.*
- Glycobotrydidae (7) *Eoc.-Rec.*
- Pylobotrydidae (4) *Eoc.-Rec.*
- Pylobotrydinae (*subfamily*) (2) *Rec.*
- Botryocampinae (2) *Eoc.-Rec.*
- Phaeodarina (*suborder*) (103;34) *Cret.-Rec.*
- Phaeodinicae (*superfamily*) (14;10) *Rec.*
- Phaeodinidae (*family*) (2) *Rec.*
- Caementellidae (1) *Rec.*
- Cannorrhaphididae (3) *Rec.*
- Cannorrhaphidinae (*subfamily*) (2) *Rec.*
- Catinulinae (1) *Rec.*

- Aulacanthidae (*family*) (7;10) *Rec.*
- Aulacanthinae (*subfamily*) (6;10) *Rec.*
- Aulaciniinae (1) *Rec.*
- Astracanthidae (*family*) (1) *Rec.*
- Aulosphaericae (*superfamily*) (20;6) *Cret.-Rec.*
- Sagosphaeridae (*family*) (8) *Rec.*
- Sagosphaerinae (*subfamily*) (5) *Rec.*
- Sagmariinae (3) *Rec.*
- Aulosphaeridae (*family*) (9;6) *Rec.*
- Aulosphaerinae (*subfamily*) (6;6) *Rec.*
- Auloniinae (3) *Rec.*
- Cannosphaeridae (*family*) (3) *Cret.-Rec.*
- Challengeriicae (*superfamily*) (41;16) *Rec.*
- Challengeriidae (*family*) (7;9) *Rec.*
- Challengeriinae (*subfamily*) (4;9) *Rec.*
- Pharyngellinae (3) *Rec.*
- Cadiidae (*family*) (1) *Rec.*
- Medusettidae (8;4) *Rec.*
- Medusettinae (*subfamily*) (3) *Rec.*
- Gazellettinae (5;4) *Rec.*
- Porospathididae (*family*) (1) *Rec.*
- Atlanticellidae (6) *Rec.*
- Castanellidae (8) *Rec.*
- Castanellinae (*subfamily*) (7) *Rec.*
- Circocastaneinae (1) *Rec.*
- Circoporidae (*family*) (7) *Rec.*
- Circoporinae (*subfamily*) (6) *Rec.*
- Haeckelianinae (1) *Rec.*
- Tuscadoridae (*family*) (3;3) *Rec.*
- Conchariicae (*superfamily*) (9) *Rec.*
- Conchariidae (*family*) (9) *Rec.*
- Conchariinae (*subfamily*) (2) *Rec.*
- Neosphaeroconchidiinae (5) *Rec.*
- Conchopsidinae (2) *Rec.*
- Coelodendricae (*superfamily*) (19;2) *Rec.*
- Coelodendridae (*family*) (4;2) *Rec.*
- Coelodendrinae (*subfamily*) (2;2) *Rec.*
- Coelodryminae (2) *Rec.*
- Coelographididae (*family*) (15) *Rec.*
- Coelographidinae (*subfamily*) (7) *Rec.*
- Coelothyrinae (2) *Rec.*
- Coelotetraceradinae (3) *Rec.*
- Coelotholinae (3) *Rec.*

The following synoptic table shows the distribution of the systematic categories of Radiolaria herein recognized.

Statistical Summary

Orders	Sub-orders	Super-families	Families	Sub-families	Genera	Sub-genera
Porulosida	Acantharina	5	15	14	72	86
	Spumellina	7	42	81	402	418
	Total	12	57	95	474	504
Osculosida	Nassellina	6	27	62	324	224
	Phaeodarina	5	19	25	103	34
	Total	11	46	87	427	258
Grand Total		23	103	182	901	762