J. Protozool., 27(1), 1980, pp. 37–58

48

A Newly Revised Classification of the Protozoa*

THE COMMITTEE ON SYSTEMATICS AND EVOLUTION OF THE SOCIETY OF PROTOZOOLOGISTS†
N. D. LEVINE (Chairman), J. O. CORLISS, F. E. G. COX, G. DEROUX, J. GRAIN, B. M. HONIGBERG,‡
G. F. LEEDALE, A. R. LOEBLICH, III, J. LOM, D. LYNN, E. G. MERINFELD,§ F. C. PAGE,
G. POLJANSKY, V. SPRAGUE, J. VAVRA, and F. G. WALLACE

SYNOPSIS. The subkingdom Protozoa now includes over 65,000 named species, of which over half are fossil and ~10,000 are parasitic. Among living species, this includes ~250 parasitic and 11,300 free-living sarcodines (of which ~4,600 are foraminiferids); ~1,800 parasitic and 5,100 free-living flagellates; ~5,600 parasitic "Sporozoa" (including Apicomplexa, Microspora, Myxospora, and Ascetospora); and ~2,500 parasitic and 4,700 free-living ciliates. There are undoubtedly thousands more still unnamed. Seven phyla of PROTOZOA are accepted in this classification—SARCOMASTIGOPHORA, LABYRINTHOMORPHA, APICOMPLEXA, MICROSPORA, ASCETOSPORA, MYXOSPORA, and CILIOPHORA. Diagnoses are given for these and for all higher taxa through suborders, and representative genera of each are named. The present scheme is a considerable revision of the Society's 1964 classification, which was prepared at a time when perhaps 48,000 species had been named. It has been necessitated by the acquisition of a great deal of new taxonomic information, much of it through electron microscopy. It is hoped that the present classification incorporates most of the major changes that will be made for some time, and that it will be used for many years by both protozoologists and nonprotozoologists.

Index Key Words: Protozoa; new classification; revision of 1964 classification.

THE PROTOZOA are essentially single-celled, eukaryotic organisms. They are not a natural group, but have been placed together as a matter of convenience. In the classical, broad classification of living things, which divides them into plants and animals, the Protozoa comprise a phylum of animals. More modern classifications, however, divide living things into 4 to many kingdoms (see Refs. 136, 210). Perhaps the most widely used of these is the 5-kingdom classification (MONERA, PROTISTA, PLANTAE, FUNGI, ANIMALIA). In this, the Protozoa might be considered a subkingdom of the kingdom Protista. If the classical classification is preferred, the Protozoa might be considered a subkingdom of the kingdom Animalia. In either case, the former major groups of Protozoa would become phyla. The Ciliophora have already been formally established as a phylum (Refs. 37, 174), and it seems best to follow suit with the other groups.

The Protozoa range in size from 1 μm to 50 mm or more, most being between 5 and 250 μm. Nearly all are holozoic or saprozoic, but a few are holophytic. The principal line of evolution in the group has been through subcellular specializations or organelles which function in feeding, locomotion, osmoregulation, and reproduction. Most Protozoa have a single, vesicular nucleus, but some are multinucleate and the Ciliophora are heterokaryotic. Sexual and asexual reproduction are present, depending on the group. Some Protozoa are colonial; many live in loricae, and a number are stalked at some time in their life cycle.

The first Protozoa were seen by Antony van Leeuwenhoek in 1674. Linnaeus included 2 species of free-living Protozoa in the 1758 edition of his *Systema Naturae,* but he included no parasitic ones. At present, over 65,000 protozoan species (of which over half are fossil and ~10,000 are parasitic) have been named. Among living species, this includes ~250 parasitic and 11,300 free-living sarcodines (of which ~4,600 are Foraminiferida); ~1,800 parasitic and 5,100 free-living flagellates; ~5,600 parasitic "Sporozoa" (including Apicomplexa, Microspora, Myxospora, and Ascetospora); and ~2,500 parasitic and 4,700 free-living ciliates (43, 145). There are undoubtedly thousands more species still unnamed.

The classical taxonomic scheme of the Protozoa was developed about the turn of the century. In it they were considered a phylum and were divided into 2 subphyla, Plasmodroma (containing the classes Mastigophora, Sarcodina, and Sporozoa) and Ciliophora. This scheme was based primarily on organelles of locomotion. In 1964 the Society of Protozoologists introduced a new but fairly similar classification (110).

It is remarkable how many important and necessary changes have been made in the classification since 1964. Every major group has been affected. The 1964 scheme was a necessary step in the development of the present one, but it is now obsolete. One of the principal sources of many new data of taxonomic significance has been electron microscopy. The present classification will, it is hoped, be used for many years by protozoologists and nonprotozoologists alike, but it is inevitable that it will be modified as new information becomes available.

The present scheme goes only to suborder, but representative genera are included.

Primarily responsible for the various groups were: PHYTOMASTIGOPHOREA—G. F. Leedale; ZOOMASTIGOPHOREA—B. M. Honigberg; SARCODINA—F. C. Page, E. G. Merinfeld; APICOMPLEXA—N. D. Levine, F. E. G. Cox; MICROSPORA—V. Sprague, J. Vávra; MYXOSPORA—J. Lom; ASCETOSPORA—V. Sprague; CILIOPHORA—J. O. Corliss, J. Grain, G. Deroux, J. Lom, D. Lynn.

It should be said that this classification is, to a degree, one of convenience and does not necessarily indicate evolutionary relationships.

As in the Society's 1964 Classification (110), phyla, subphyla, and superclasses end in "-a"; classes in "-ea"; subclasses in "-ia"; orders in "-ida"; and suborders in "-ina"; superorders, not used in the previous scheme, end in "-idea." These uniform endings conform to those recommended by Pearse (165) and employed by Hall (100a) and Jahn & Jahn (110a); they differ from the more precise but longer endings suggested by Levine (142).

In general, the nomenclatural policies of this Committee are

* Reprints of this publication may be purchased for $3.00 US each from the Society of Protozoologists. Requests and orders should be addressed to: Society of Protozoologists, 1041 New Hampshire St., Lawrence, Kansas 66044, USA.

† The members of the Committee were aided in their work by protozoologists too numerous to name, from many countries, some of whom served at various times as members of subcommittees.

‡ The final version of this report was prepared by B. M. HONIGBERG. This became necessary due to the illness of N. D. LEVINE, Chairman of the Committee.

§ E. G. MERINFELD was most helpful by checking the authorities of the various taxa and by providing the correct references. He spared no time and effort in aiding us in these and other aspects of this report; we are grateful for his assistance. NDL, BMH.

also essentially the same as those adopted by the authors of the 1964 scheme (110). Thus, a worker who originally proposed a new name at any level lower than that of suborder is not credited with the name of the new higher taxon, even if essentially the same word is used for it or even if the new taxon (e.g. order or class) contains only a single family. The responsibility for the name of the high-level taxon (suborder or above) is that of the person who established its actual level and its concept. The same situation obtains when a given higher taxon, e.g. an order, has been elevated to another level, e.g. a class, with retention of the original taxon (order)—the name of the higher taxon (class) is credited to the worker who created it. On the other hand, if a group, originally established at the class or subclass level, is now considered to contain several more recently created orders, one of which bears a name similar to that of the class or subclass, the authority and date of the name of either of the latter taxa is automatically employed for this order, with different authorships and dates for the others; the same procedure applies to suborders within an order.

While this Classification is the product of a committee, it should not be assumed that its every member, although responsible for his own group, is in agreement with the entire scheme. Indeed, probably none of them agrees with it completely; however, unanimity can hardly be expected. What we have produced is something with which we can live and which we can modify as suggested by our differing needs and ideas.

Phylum I. **SARCOMASTIGOPHORA** Honigberg & Balamuth, 1963

Single type of nucleus, except in heterokaryotic Foraminiferida; sexuality, when present, essentially syngamy; flagella, pseudopodia or both types of locomotor organelles.

Subphylum I. MASTIGOPHORA Diesing, 1866

One or more flagella typically present in trophozoites; asexual reproduction basically by intrakinetal (symmetrogenic) binary fission; sexual reproduction known in some groups.

Class 1. PHYTOMASTIGOPHOREA Calkins, 1909

Typically with chloroplasts; if chloroplasts lacking, relationship to pigmented forms clearly evident; mostly free-living.

Order 1. **CRYPTOMONADIDA** Senn, 1900

Two subequal flagella arising subapically in ventral groove; chloroplasts brown, red, olive-green, blue or yellow; storage products starch and fat; cells flattened, naked, without wall or pellicle; flagellates, coccoid unicells and palmellae; sexual reproduction unknown.

Cryptomonas

Order 2. **DINOFLAGELLIDA** Bütschli, 1885

Two heterodynamic flagella, inserted apically or laterally, one ribbon-shaped with paraxial rod and single row of fine hairs, other smooth or with 2 rows of stiffer hairs; chloroplasts typically golden-brown or green; storage products starch and fat; cells flattened or of complex symmetry with transverse and ventral grooves and often armor of cellulosic plates; nucleus unique among eukaryotes in having chromosomes that consist primarily only of nonprotein-complexed DNA; mitosis intranuclear; flagellates, coccoid unicells, colonies, and simple filaments; sexual reproduction present.

Ceratium, Gymnodinium, Prorocentrum

Order 3. **EUGLENIDA** Bütschli, 1884

Two (rarely more) flagella, one or both emerging from an anterior invagination of the cell; emergent flagella with single row of fine hairs; flagella with paraxial rods; chloroplasts grass-green, absent in many genera; storage products: paramylon, fat, and cyclic metaphosphates; cell with helical symmetry, naked but with complex pellicle of interlocking proteinaceous strips; nonspindle intranuclear mitosis; flagellates or colonies.

Suborder 1. EUTREPTIINA Leedale, 1967

Two highly mobile emergent flagella, one directed anteriorly and other laterally.

Distigma, Eutreptia

Suborder 2. EUGLENINA Bütschli, 1884

Two flagella, one emergent from cell invagination, highly mobile, other short and non-emergent; one genus colonial, several with envelopes.

Astasia, Euglena, Trachelomonas

Suborder 3. RHABDOMONADINA Leedale, 1967

Two flagella, one emergent from cell invagination, highly mobile during swimming, held straight when cell is stationary; cells colorless, rigid; pellicle composed of strips fused into single continuous structure; canal with intucking scrolls of skeletal material.

Menoidium

Suborder 4. SPHENOMONADINA Leedale, 1967

One or 2 emergent flagella, one always directed anteriorly, straight, not mobile; cells colorless, rigid, usually with pronounced keels or grooves.

Sphenomonas

Suborder 5. HETERONEMATINA Leedale, 1967

One or 2 emergent flagella, one directed anteriorly, straight, with coiling or flickering movement of tip only, causing characteristic gliding locomotion; with special ingestion organelles.

Peranema

Suborder 6. EUGLENAMORPHINA Leedale, 1967

Three or more emergent, homodynamic flagella; endozoic in digestive tracts of tadpoles.

Euglenamorpha

Order 4. **CHRYSOMONADIDA** Engler, 1898

Two unequal flagella, one directed anteriorly and bearing 2 opposite rows of mastigonemes, other trailing and smooth; chloroplasts golden-brown or absent; storage products chrysolaminarin and fat; cells naked, with richly patterned

silicified scales, or with lorica; sexual reproduction present.
Dinobryon, Ochromonas, Synura

Order 5. **HETEROCHLORIDA** Pascher, 1912[1]
Two unequal flagella; chloroplasts yellow-green; storage products oil and possibly chrysolaminarin; supposedly related to xanthophycean algae.
Chloramoeba, Heterochloris

Order 6. **CHLOROMONADIDA** Klebs, 1892
Two heterokont flagella; chloroplasts green; storage product oil; characteristic ring of Golgi bodies at anterior end; sexual reproduction by fusion of 2 flagellates.
Chattonella, Vacuolaria

Order 7. **PRYMNESIIDA** Hibberd, 1976
Two equal or subequal, smooth flagella inserted laterally or anteriorly, with unique 3rd appendage, the haptonema, between them; chloroplasts golden-brown; storage products chrysolaminarin (?) and fat; cells covered with delicate organic scales of diagnostic pattern; scales calcified to form coccoliths in coccolithophorids; sexual reproduction present.
Chrysochromulina, Coccolithus, Prymnesium

Order 8. **VOLVOCIDA** Francé, 1894
Two or 4 equal, smooth, apical flagella; chloroplasts grass-green; storage products starch and fat; sexual reproduction present.
Chlamydomonas, Volvox

Order 9. **PRASINOMONADIDA** Christensen, 1962
One, 2, 4, or 8 flagella, typically covered with rows of finely patterned scales; chloroplasts grass-green; storage product starch; cells typically covered with one or more layers of intricately patterned Golgi-derived scales; sexual reproduction present.
Mesostigma, Prasinomonas

Order 10. **SILICOFLAGELLIDA** Borgert, 1891
One flagellum; chloroplasts golden-brown or green-brown; storage product apparently chrysolaminarin; with star-shaped siliceous skeleton composed of tubular elements; sexual reproduction unknown.
Dictyocha

Class 2. ZOOMASTIGOPHOREA Calkins, 1909

Chloroplasts absent; one to many flagella; ameboid forms, with or without flagella, in some groups; sexuality known in few groups; a polyphyletic group.

Order 1. **CHOANOFLAGELLIDA** Kent, 1880
One flagellum, inserted apically, with proximal part surrounded by ring of tentacles (collar); with membranous sheath or basket-like lorica composed of siliceous costae; stalked or free-swimming; free-living.
Monosiga

[1] These are the unicellular xanthophytes. GFL.

Order 2. **KINETOPLASTIDA** Honigberg, 1963 emend. Vickerman, 1976
One or 2 flagella arising from depression; flagella typically with paraxial rod in addition to axoneme; single mitochondrion (nonfunctional in some forms) extending length of body as single tube, hoop, or network of branching tubes, usually containing conspicuous Feulgen-positive (DNA-containing) kinetoplast (nucleoid) located near flagellar kinetosomes; Golgi apparatus typically in region of flagellar depression, not connected to kinetosomes and flagella; parasitic (majority of known species) and free-living.

Suborder 1. BODONINA Hollande, 1952 emend. Vickerman, 1976
Typically 2 heterodynamic flagella; typical, often large, adbasal kinetoplast (eukinetoplastic condition), or kDNA arranged in several discrete bodies (polykinetoplastic condition) or dispersed throughout mitochondrion (pankinetoplastic condition); free-living or parasitic.
Bodo, Cryptobia, Rhynchomonas

Suborder 2. TRYPANOSOMATINA Kent, 1880
Single flagellum either free or attached to body by undulating membrane; kinetoplast relatively small and compact; parasitic.
Blastocrithidia, Leishmania, Trypanosoma

Order 3. **PROTEROMONADIDA** Grassé, 1952 emend. Vickerman, 1976
One or 2 pairs of heterodynamic flagella without paraxial rods; single mitochondrion, distant from kinetosomes, curving around nucleus, not extending length of body, without Feulgen-positive kinetoplast; Golgi apparatus encircling band-shaped rhizoplast passing from kinetosomes near surface of nucleus to mitochondrion; cysts present; parasitic.
Karotomorpha, Proteromonas

Order 4. **RETORTAMONADIDA** Grassé, 1952[c]
Two to 4 flagella, one turned posteriorly and associated with ventrally located cytostomal area bordered by fibril; mitochondria and Golgi apparatus absent; intranuclear division spindle; "semiopen" mitosis reported from 1 genus; cysts present; parasitic.
Chilomastix, Retortamonas

Order 5. **DIPLOMONADIDA** Wenyon, 1926 emend. Brugerolle, 1975
One or 2 karyomastigonts; genera with 2 karyomastigonts with two-fold rotational symmetry or, in one genus, primarily mirror symmetry; individual mastigonts with 1 to 4 flagella, typically one of them recurrent and associated with cytostome, or, in more advanced genera, with organelles forming cell axis; mitochondria, and Golgi apparatus absent; intranuclear division spindle; "semiopen" mitosis reported in one genus; cysts present; free-living or parasitic.

Superclass 1. **RHIZOPODA** von Siebold, 1845

Locomotion by lobopodia, filopodia, or reticulopodia, or by protoplasmic flow without production of discrete pseudopodia.

Class 1. LOBOSEA Carpenter, 1861

Pseudopodia lobose or more or less filiform but produced from broader hyaline lobe; usually uninucleate; multinucleate forms not flattened or much-branched plasmodia; no sorocarps, sporangia, or similar fruiting bodies.

Subclass 1. **GYMNAMOEBIA** Haeckel, 1862

Without test.

Order 1. **AMOEBIDA** Ehrenberg, 1830

Typically uninucleate; mitochondria typically present; no flagellate stage.

Suborder 1. TUBULINA Bovee & Jahn, 1966

Body branched or unbranched cylinder; no bidirectional flow of cytoplasm; nuclear division mesomitotic.

Amoeba, Entamoeba, Saccamoeba

Suborder 2. THECINA Bovee & Jahn, 1966

Flattened, with more or less regular outline, often oblong, ovate, or flabellate; often with discernible pellicle-like layer, which may be distinctly wrinkled; rolling movement of surface; nuclear division patterns diverse.

Platyamoeba, Thecamoeba, Vannella

Suborder 3. FLABELLINA Page, 1976

Flattened, broad, sometimes discoid, with extensive hyaline zone but no obvious pellicle-like layer; locomotion often accompanied by gentle eruption; nuclear division, where known, mesomitotic.

Flabellula, Rosculus

Suborder 4. CONOPODINA Bovee & Jahn, 1966

Digitiform or mammilliform, usually blunt, normally unbranched hyaline sub-pseudopodia usually produced from a broad hyaline lobe; not discoid; cysts seldom formed; nuclear division typically mesomitotic.

Mayorella, Paramoeba

Suborder 5. ACANTHOPODINA Page, 1976

More or less finely tipped, sometimes filiform, often furcate hyaline sub-pseudopodia produced from a broad hyaline lobe; not regularly discoid; cysts usually formed; nuclear division mesomitotic or metamitotic.

Acanthamoeba, Echinamoeba

Order 2. **SCHIZOPYRENIDA** Singh, 1952

Body with shape of monopodial cylinder, usually moving with more or less eruptive, hyaline, hemispherical bulges; typically uninucleate, nuclear division promitotic; temporary flagellate stages in most species.

Naegleria, Tetramitus, Vahlkampfia

Order 3. **PELOBIONTIDA** Page, 1976

Body with shape of thick cylinder; monopodial, with true bidirectional fountain flow of cytoplasm common; typically multinucleate; lacking mitochondria but with symbiotic bacteria; in microaerobic habitats; no flagellate stage known, but numerous nonmotile cils visible at fine-structural level, with variations of usual microtubular pattern.

Pelomyxa

Subclass 2. **TESTACEALOBOSIA** De Saedeleer, 1934

Body enclosed by test, tectum, or other complex membrane external to plasma membrane and glycocalyx.

Order 1. **ARCELLINIDA** Kent, 1880

Test, tectum, or other external membrane with single aperture and composed of either organic or inorganic material or both.

Arcella, Cochliopodium, Difflugia

Order 2. **TRICHOSIDA** Möbius, 1889

Test composed of fibrous sheath and, in at least one extensive stage of life cycle, with calcareous spicules, and multiple apertures through which short, conical pseudopodia extend; locomotion by broad lobopodium; marine.

Trichosphaerium

Class 2. ACARPOMYXEA Page, 1976[a]

Small plasmodia or much-expanded similar uninucleate forms, usually branching, sometimes forming reticulum of coarse branches; advancing tips lobose; no regular reversal of streaming; no test; no spores or fruiting bodies known.

Order 1. **LEPTOMYXIDA** Pussard, 1973

Typically thin sheets, often polyaxial; sometimes more cylindrical, limax-like forms; cysts produced by soil and freshwater species.

Leptomyxa, Rhizamoeba

Order 2. **STEREOMYXIDA** Grell, 1966

Marine ameboid organisms with more or less branched pseudopodia producing only very slow motion or serving as flotation organelles.

Corallomyxa, Stereomyxa

Class 3. ACRASEA Schröter, 1886

Uninucleate amebae with eruptive, lobose pseudopodia; amebae aggregating to form pseudoplasmodium which gives rise to fruiting bodies without stalk tube; flagellate cells known in only one species; sexuality unknown.

Order 1. **ACRASIDA** Schröter, 1886

With characters of the class.

Acrasis

Class 4. EUMYCETOZOEA Zopf, 1884

Myxamebae with filiform subpseudopodia; flagella, when present nonmastigonemate, in unequal, less often equal, apical pair; producing aerial fruiting bodies; stalk tube typically present in fruiting bodies of first 2 subclasses and in some members of 3rd.

Subclass 1. **PROTOSTELIIA** Olive & Stoianovitch, 1966

Trophic stage varying from single amebae to plasmodia which lack shuttle streaming; flagellate cells present or absent; fruiting bodies consisting of one to several spores on narrow, hollow stalk; sexuality known in one species.

Order 1. **PROTOSTELIIDA** Olive & Stoianovitch, 1966
With characters of the subclass.
Ceratiomyxa, Protostelium

Subclass 2. **DICTYOSTELIIA** Lister, 1909
Amebae aggregate to form multicellular pseudoplasmodium that gives rise to multispored fruiting body; stalk tube present; no flagellate cells; sexuality indicated in some species.

Order 1. **DICTYOSTELIIDA** Lister, 1909
With characters of the subclass.
Dictyostelium

Subclass 3. **MYXOGASTRIA** Fries, 1829
Major trophic stage multinucleate plasmodium typically with shuttle streaming; fruiting bodies multispored; flagellate cells present; syngamy and meiosis in life cycle.

Order 1. **ECHINOSTELIIDA** Martin, 1961
Sporangia stalked, minute; plasmodium small, ameba-like, nonreticulate.
Echinostelium

Order 2. **LICEIDA** Lister, 1909
Spore mass usually light-colored; lime usually absent from sporocarps; true capillitium lacking; pseudo-capillitium often present.
Licea

Order 3. **TRICHIIDA** Masse, 1892
Spore mass usually light-colored; lime usually absent from sporocarps; true capillitium present.
Trichium

Order 4. **STEMONITIDA** Masse, 1892
Spore mass usually dark-colored; lime, when present, restricted to substrate, stipe, and columella.
Stemonitis

Order 5. **PHYSARIDA** Masse, 1892
Spore mass usually dark-colored; peridium and/or capillitium calcareous.
Physarum

Class 5. PLASMODIOPHOREA Cook, 1928
Obligate intracellular parasites with minute plasmodia; zoospores produced in zoosporangia and bearing anterior pair of unequal, nonmastigonemate flagella; resting spores formed in compact sori or loose clusters within host cells; sexuality reported in some species.

Order 1. **PLASMODIOPHORIDA** Cook, 1928
With characters of the class.
Plasmodiophora, Sorosphaera

Class 6. FILOSEA Leidy, 1879
Hyaline, filiform pseudopodia, often branching, sometimes anastomosing; no spores or flagellate stages known.

Order 1. **ACONCHULINIDA** De Saedeleer, 1934
Without external skeletal material; filopodia produced from main mass of cell, not from hyaline lobe.
Nuclearia, Vampyrella

Order 2. **GROMIIDA** Claparède & Lachmann, 1859
Body enclosed by test or rigid external membrane with distinct aperture.
Euglypha, Gromia

Class 7. GRANULORETICULOSEA De Saedeleer, 1934
Delicate, finely granular or hyaline reticulopodia or, rarely, finely pointed, granular but nonanastomosing pseudopodia.

Order 1. **ATHALAMIDA** Haeckel, 1862
Naked.
Arachnula, Biomyxa

Order 2. **MONOTHALAMIDA** Haeckel, 1862
With single-chambered organic or calcareous test, sometimes including foreign matter; no alternation of generations.
Lieberkuehnia

Order 3. **FORAMINIFERIDA** D'Orbigny, 1826
Test with one to many chambers; pseudopodia protruding from aperture, wall perforations or both; reproduction with alternation of sexual and asexual generations, of which one may be secondarily repressed; gametes usually flagellate, rarely ameboid; nuclear dimorphism in developmental stages of some species.

Suborder 1. ALLOGROMIINA Hertog, 1906
Test membranous or tectinous, with ferruginous or, rarely, small quantities of agglutinated material.
Allogromia, Iridia, Myxotheca

Suborder 2. TEXTULARIINA Lankester, 1885
Test agglutinated, with foreign matter held together by various cements.
Saccammina, Textularia

Suborder 3. FUSULININA Wedekind, 1937
Test primitively of micro-granular calcite; 2 or more differentiated layers in test wall of more advanced forms.
Fusulina, Schwagerina

Suborder 4. MILIOLINA Lankester, 1885
Test porcellanous, perforate or imperforate.
Quinqueloculina, Triloculina

Suborder 5. ROTALIINA Lankester, 1885
Test hyaline, calcareous.
Ammonia, Elphidium, Rosalina

Class 8. XENOPHYOPHOREA Schulze, 1904
Multinucleate plasmodium enclosed in branched-tube system composed of transparent organic substance; numerous barite crystals in cytoplasm; fecal pellets retained outside organic tube system as conspicuous dark masses; test of foreign matter surrounding tube system and fecal-pellet masses; marine.

Order 1. **PSAMMINIDA** Poche, 1913
Without linellae (threads forming part of test); body more or less rigid.
Psammetta, Psammina

Order 2. **STANNOMIDA** Tendal, 1972
With linellae (threads forming part of test); body flexible.
Stannophyllum

Superclass 2. **ACTINOPODA** Calkins, 1909

Often spherical, usually planktonic; axopodia with microtubular stereoplasm; skeleton, when present, composed of organic matter and/or silica, or else of strontium sulfate; reproduction asexual and/or sexual; trophic cells rarely flagellated; in many species small flagellated stages whose exact nature (gametes or spores) is still usually uncertain.

Class 1. ACANTHAREA Haeckel, 1881

Strontium sulfate skeleton, usually composed of 20 radial or 10 diametral spines oriented according to Müller's Law, rarely 16 diametrical or 32 radial spines oriented according to Haeckel's Law; sometimes many more spines randomly oriented; spines more or less joined in cell center; extracellular outer (cortex) and inner envelopes usually present; inner envelope (called "capsular membrane") often closely lining central cell mass; marine, usually planktonic.

Order 1. **HOLACANTHIDA** Schewiakoff, 1926
Usually 10, sometimes 16 diametral spines, crossing in center; inner envelope far outside central cell mass, or absent; encystment before sporogenesis, at least in several species.
Acanthochiasma, Acanthocolla, Acanthoplegma

Order 2. **SYMPHYACANTHIDA** Schewiakoff, 1926
Twenty radial spines totally fused in cell center or forming there small sphere by apposition of their basal pyramids; inner envelope far outside central cell mass; encystment before sporogenesis, at least in some species.
Acantholithium, Amphilithium, Pseudolithium

Order 3. **CHAUNACANTHIDA** Schewiakoff, 1926
Twenty radial spines with bases more or less loosely articulated; inner envelope at some distance outside central cell mass, or absent; encystment before sporogenesis in most or perhaps all species.
Conacon, Gigartacon, Stauracon

Order 4. **ARTHRACANTHIDA** Schewiakoff, 1926
Usually 20 radial spines joined at cell center by apposition of bases; inner envelope usually closely lining central cell mass; no cysts.

Suborder 1. SPHAENACANTHINA Schewiakoff, 1926
Bases of spines without lateral wings.
Acanthometra, Dorataspis, Lithoptera

Suborder 2. PHYLLACANTHINA Schewiakoff, 1926
Bases of spines with lateral wings.

Order 5. **ACTINELIIDA** Haeckel, 1885
Variable number of radial spines, not disposed according to Müller's Law; mostly planktonic, one benthic genus.
Actinelius, Astrolophus, Podactinelius

Class 2. POLYCYSTINEA Ehrenberg, 1838[3]

Siliceous skeleton present in most species; made up usually of solid elements, consisting of one or more latticed shells with or without radial spines, or of one or more isolated spicules; capsular membrane composed usually of grossly polygonal plates and containing many more than 3 pores; axonemes often originating from axoplast in endoplasm; marine, planktonic.

Order 1. **SPUMELLARIDA** Ehrenberg, 1875
Capsular membrane with uniformly distributed pores.

Suborder 1. SPHAEROCOLLINA Brandt, 1902
Large, solitary cells, or cell colonies; skeleton absent or consisting of one or more isolated spicules or of usually single, perforated shell.
Collosphaera, Oroscena, Thalassicolla

Suborder 2. SPHAERELLARINA Haeckel, 1881
Small, solitary cells; skeleton always present, of one latticed piece, consisting of one shell, sometimes 2 or more concentric ones, more or less complete, with or without radial spines.
Coccodiscus, Lithelius, Octodendron

Order 2. **NASSELLARIDA** Ehrenberg, 1875
Capsular membrane with pores gathered at a single pole; skeleton of one piece, often basket-shaped.
Eucoronis, Plagiacantha, Plagonium

Class 3. PHAEODAREA Haeckel, 1879[3]

Skeleton (sometimes absent) of mixed silica and organic matter, consisting of usually hollow spines and/or shells; very thick capsular membrane with astropyle (functioning as cytopharynx) at one pole; 2 smaller parapylae, penetrated by axopodia, usually at other pole; ectoplasm with phaeodium (group of dark corpuscles and debris); marine, planktonic.

Order 1. **PHAEOCYSTIDA** Haeckel, 1879
Skeleton absent, or consisting of spicules either free or radiating from common junction point.
Astracantha, Aulacantha, Phaeodina

Order 2. **PHAEOSPHAERIDA** Haeckel, 1879
Skeleton consisting mainly of very large latticed shell with wide polygonal meshes.
Aulosphaera, Cannosphaera, Sagosphaera

Order 3. **PHAEOCALPIDA** Haeckel, 1887
Skeleton consisting mainly of small shell, usually with numerous pores, often with one large opening; shell texture usually porcellanous, sometimes alveolar, never diatomaceous; radial spines often present.
Castanella, Circoporus, Tuscarora

Order 4. **PHAEOGROMIDA** Haeckel, 1879
Skeleton consisting mainly of small diatomaceous or alveolar shell with one large opening;

---

[3] The classes POLYCYSTINEA and PHAEODAREA are equivalent to the Radiolaria. FCP, EGM.

shell, sometimes greatly reduced, may bear spines.
Atlanticella, Challengeron, Medusetta

Order 5. **PHAEOCONCHIDA** Haeckel, 1879
Skeleton consisting of 2 thick, usually hemispherical valves pressed against each other.
Concharium, Conchopsis, Neosphaeroconchidium

Order 6. **PHAEODENDRIDA** Haecker, 1908
Skeleton consisting of 2 noncontiguous valves, from which originate long, branching spines with ramifications that may produce enormous external latticed spongious shells.
Coelodendrum, Coelographis, Coelothamnus

Class 4. HELIOZOEA Haeckel, 1866

Without central capsule; skeletal structures, if present, siliceous or organic; axopodia radiating on all sides; most species freshwater, some marine.

Order 1. **DESMOTHORACIDA** Hertwig & Lesser, 1874
Cell enclosed in usually spherical, latticed organic capsule stalked in most species; no centroplast; microtubular stiffening elements, not discernible as axonemes, present in axopodia of some species; uni- or diflagellate zoospores.
Clathrulina

Order 2. **ACTINOPHRYIDA** Hartmann, 1913
No skeleton; no centroplast or axoplast; microtubular stiffening elements of axopodia usually discernible as axonemes by light microscopy; some with flagella or flagellated stage; sexuality known in some genera.
Actinophrys, Actinosphaerium, Ciliophrys

Order 3. **TAXOPODIDA** Fol, 1883
Bilaterally symmetrical, planktonic cells with siliceous spines; swimming by rowing action of axopodia arranged in parallel longitudinal rows; axopodia insert on complex, thick nucleotheca; small biflagellated species; marine.
Sticholonche

Order 4. **CENTROHELIDA** Kühn, 1926
Frequently with a skeleton of siliceous plates and/or spines or of organic spicules; with centroplast or axoplast on which axonemes insert or, if centroplast absent, with large, eccentric nucleus; microtubular elements of axopodia frequently discernible by light microscopy as axonemes; some species with flagella or flagellated stages.
Acanthocystis, Gymnosphaera, Raphidiophrys

Phylum II. **LABYRINTHOMORPHA** phyl. n.[4]

Trophic stage, ectoplasmic network with spindle-shaped or spherical, nonameboid cells; in some genera ameboid cells move within network by gliding; with sagenogenetosome, unique cell-surface organelle, associated with ectoplasmic network; heterokont zoospores produced by most species; saprobic and parasitic on algae, mostly in marine and estuarine waters.

Class 1. LABYRINTHULEA Levine & Corliss, 1963

With characters of the phylum.

Order 1. **LABYRINTHULIDA** Lankester, 1877
With characters of the class.
Labyrinthula, Thraustochytrium

Phylum III. **APICOMPLEXA** Levine, 1970[5]

Apical complex (visible with electron microscope), generally consisting of polar ring(s), rhoptries, micronemes, conoid and subpellicular microtubules present at some stage; micropore(s) generally present at some stage; cilia absent; sexuality by syngamy; all species parasitic.

Class 1. PERKINSEA Levine, 1978[6]

Conoid forming incomplete cone; "zoospores" (sporozoites?) flagellated, with anterior vacuole; no sexual reproduction; homoxenous.

Order 1. **PERKINSIDA** Levine, 1978
With characters of the class.
Perkinsus

Class 2. SPOROZOEA Leuckart, 1879[7]

Conoid, if present, forming complete cone; reproduction generally both sexual and asexual; oocysts generally containing infective sporozoites which result from sporogony; locomotion of mature organisms by body flexion, gliding, or undulation of longitudinal ridges; flagella present only in microgametes of some groups; pseudopods ordinarily absent, if present used for feeding, not locomotion; homoxenous or heteroxenous.

Subclass 1. **GREGARINIA** Dufour, 1828
Mature gamonts large, extracellular; mucron or epimerite in mature organism; mucron formed from conoid; generally syzygy of gamonts; gametes usually similar (isogamous) or nearly so, with similar numbers of male and female gametes produced by gamonts; zygotes forming oocysts within gametocytes; life cycle characteristically consisting of gametogony and sporogony; in digestive tract or body cavity of invertebrates or lower chordates; generally homoxenous.

Order 1. **ARCHIGREGARINIDA** Grassé, 1953
Life cycle apparently primitive, characteristically with merogony, gametogony, sporogony; gamonts (trophozoites) aseptate; in annelids, sipunculids, hemichordates, or ascidians.
Exoschizon, Selenidioides

---

[4] LABYRINTHOMORPHA phyl. n. was created by **F. C. Page**, with the diagnosis given in the body of this classification. NDL, BMH.

[5] Members of the old "Sporozoa" have now been assigned to 4 phyla—APICOMPLEXA, MICROSPORA, MYXOZOA, AND ASCETOSPORA. The last 3 have spores, but many members of the Apicomplexa do not. NDL.

[6] This class contains at present only a single species, *Perkinsus marinus*. NDL.

[7] As originally conceived by Leuckart (141), this group contained only the gregarines and coccidia. Other authors added other groups (see Ref. 143). The present concept essentially returns to the original one as modified by newer knowledge gained during the last hundred years. NDL.

Order 2. **EUGREGARINIDA** Léger, 1900
Merogony absent; gametogony and sporogony present; locomotion progressive, by gliding or undulation of longitudinal ridges, or nonprogressive; typically parasites of annelids and arthropods, but some species in other invertebrates.

Suborder 1. BLASTOGREGARININA Chatton & Villeneuve, 1936
Gametogony by gamonts while still attached to intestine, with anisogamous gametes budding off of gamonts; no syzygy; gametocysts absent; oocysts with 10–16 naked sporozoites; gamont composed of single compartment with mucron, without definite protomerite and deutomerite; in marine polychaetes.
Siedleckia

Suborder 2. ASEPTATINA Chakravarty, 1960
Gametocysts present; gamont composed of single compartment, without definite protomerite and deutomerite, but with mucron (epimerite?) in some species; syzygy present.
Lecudina, Monocystis, Selenidium, Urospora

Suborder 3. SEPTATINA Lankester, 1885
Gametocysts present; gamont divided into protomerite and deutomerite by septum; with epimerite; in alimentary canal of invertebrates, especially arthropods.
Actinocephalus, Cephaloidophora, Gregarina, Stenophora

Order 3. **NEOGREGARINIDA** Grassé, 1953
Merogony, presumably acquired secondarily; in Malpighian tubules, intestine, hemocoel, or fat tissues of insects.
Caulleryella, Gigaductus, Mattesia

Subclass 2. **COCCIDIA** Leuckart, 1879
Gamonts ordinarily present; mature gamonts small, typically intracellular, without mucron or epimerite; syzygy generally absent, if present involves markedly anisogamous gametes; life cycle characteristically consisting of merogony, gametogony, and sporogony; most species in vertebrates.

Order 1. **AGAMOCOCCIDIIDA** Levine, 1979
Merogony and gametogony absent.
Rhytidocystis

Order 2. **PROTOCOCCIDIIDA** Kheisin, 1956
Merogony absent; in invertebrates.
Eleutheroschizon, Grellia

Order 3. **EUCOCCIDIIDA** Léger & Duboscq, 1910
Merogony present; in vertebrates and/or invertebrates.

Suborder 1. ADELEINA Léger, 1911
Macrogamete and microgamont usually associated in syzygy during development; microgamont producing 1–4 microgametes; sporozoites enclosed in envelope; no endodyogeny; homoxenous or heteroxenous.
Adelea, Haemogregarina, Klossiella

Suborder 2. EIMERIINA Léger, 1911
Macrogamete and microgamont developing independently; no syzygy; microgamont typically producing many microgametes; zygote not motile; sporozoites typically enclosed in sporocyst within oocyst; homoxenous or heteroxenous.
Aggregata, Eimeria, Isospora, Sarcocystis, Toxoplasma

Suborder 3. HAEMOSPORINA Danilewsky, 1885
Macrogamete and microgamont developing independently; no syzygy; conoid ordinarily absent; microgamont producing 8 flagellated microgametes; zygote motile (oökinete); sporozoites naked, with 3-membraned wall; heteroxenous, with merogony in vertebrates and sporogony in invertebrates; transmitted by blood-sucking insects.
Haemoproteus, Leucocytozoon, Plasmodium

Subclass 3. **PIROPLASMIA** Levine, 1961[8]
Piriform, round, rod-shaped or ameboid; conoid absent; no oocysts, spores and pseudocysts; flagella absent; usually without subpellicular microtubules, with polar ring and rhoptries; locomotion by body flexion, gliding, or, in sexual stages (in Babesiidae and Theileriidae, at least), by large axopodium-like *Strahlen*; asexual and probably sexual reproduction; parasitic in erythrocytes and sometimes also in other circulating and fixed cells; heteroxenous, with merogony in vertebrates and sporogony in invertebrates; sporozoites with single-membraned wall; so far as known, vectors are ticks, but vectors of dactylosomatids unknown.

Order 1. **PIROPLASMIDA** Wenyon, 1926
With characters of the subclass.
Babesia, Dactylosoma, Theileria

Phylum IV. **MICROSPORA** Sprague, 1977

Unicellular spores, each with imperforate wall, containing one uninucleate or dinucleate sporoplasm and simple or complex extrusion apparatus always with polar tube and polar cap; without mitochondria; often, if not usually, dimorphic in sporulation sequence; obligatory intracellular parasites in nearly all major animal groups.

Class 1. RUDIMICROSPOREA Sprague, 1977

Spore with simple (rudimentary) extrusion apparatus consisting of polar cap and thick (manubroid) polar tube extending backward from cap, bending laterally and terminating in funnel (infundibulum); polaroplast and posterior vacuole absent; spore spherical or subspherical; sporulation sequence with dimorphism, oc-

[8] This subclass probably arose from the HAEMOSPORINA. Our respondents' opinions were strongly divided as to whether this group should form a separate class or a suborder under the Eucoccidiida. The present position is a compromise. NDL.

curring either in parasitophorous vacuole or in thick-walled cyst; hyperparasites of gregarines in annelids.

Order 1. **METCHNIKOVELLIDA** Vivier, 1975
With characters of the class.
Amphiacantha, Metchnikovella

Class 2. MICROSPOREA Delphy, 1963

Spore with complex extrusion apparatus of Golgi origin, often including polaroplast and posterior vacuole in addition to polar tube and polar cap; polar tube typically filamentous, extending backward from polar cap and coiling around inside of spore wall; spore shape various, depending largely on structure of extrusion apparatus; spore wall with 3 layers: proteinaceous exospore, chitinous endospore, and membranous inner layer; outer 2 layers varying considerably in structure; sporocyst present or absent; often dimorphic in sporulation sequence.

Order 1. **MINISPORIDA** Sprague, 1972
General tendency toward minimum development of accessory spore organelles (components of extrusion apparatus and spore wall) and accompanying tendency toward maximum development of sporocysts; spore without well developed polaroplast; usually with relatively short polar filament, with little or no endospore; shape spherical or slightly ovoid; merogony present or absent(?); sporulation stages usually separated from host cell cytoplasm by intracellular sporocyst; some genera dimorphic in the sporulation sequence.
Burkea, Chytridiopsis, Hessea

Order 2. **MICROSPORIDA** Balbiani, 1882
General tendency toward maximum development and varied specialization of accessory spore organelles (components of extrusion apparatus and spore wall), with accompanying reduction of sporocysts; sporocysts inside host cell present or absent; cysts of other kinds sometimes formed from host cell membrane or other host material; merogony present; spore shape variable; often dimorphic in sporulation sequence.

Suborder 1. PANSPOROBLASTINA Tuzet, Maurand, Fize, Michel & Fenwick, 1971
Sporulation sequence occurring within more or less persistent intracellular (in host cell) sporocyst (pansporoblastic membrane); often dimorphic, with another sporulation sequence not involving such membrane; sporoblasts and spores usually uninucleate when membrane present, dinucleate when membrane absent.
Amblyospora, Pleistophora, Thelohania

Suborder 2. APANSPOROBLASTINA Tuzet, Maurand, Fize, Michel & Fenwick, 1971
Pansporoblastic membrane usually absent, vestigial when present, never persisting as sporophorous vesicle; sporoblast most often dinucleate.
Encephalitozoon, Glugea, Nosema

Phylum V. **ASCETOSPORA** Sprague, 1978[9]

Spore multicellular (or unicellular?); with one or more sporoplasms; without polar capsules or polar filaments; all parasitic.

Class 1. STELLATOSPOREA Sprague, 1978

Haplosporosomes present; spore with 1 or more sporoplasms.

Order 1. **OCCLUSOSPORIDA** Perkins, in Sprague, 1978[10]
Spore with more than 1 sporoplasm; sporulation involving series of endogenous buddings that produce sporoplasm(s) within sporoplasm(s); spore wall entire.
Marteilia

Order 2. **BALANOSPORIDA** Sprague, 1978[11]
Spore with one sporoplasm; spore wall interrupted anteriorly by orifice; orifice covered externally by operculum or internally by diaphragm.
Haplosporidium, Minchinia, Urosporidium

Class 2. PARAMYXEA Levine, in Sprague, 1979

Spore bicellular, consisting of parietal cell and one sporoplasm; spore without orifice.

Order 1. **PARAMYXIDA** Chatton, 1911
With characters of the class.
Paramyxa

Phylum VI. **MYXOZOA** Grassé, 1970 emend.[12]

Spores of multicellular origin, with one or more polar capsules and sporoplasms; with 1, 2, or 3 (rarely more) valves; all species parasitic.

Class 1. MYXOSPOREA Bütschli, 1881

Spore with 1 or 2 sporoplasms and 1–6 (typically 2) polar capsules, each capsule with coiled polar filament; filament function probably anchoring; spore membrane generally with 2, occasionally up to 6, valves; trophozoite stage well developed, main site of

---

[9] The Greek word *asketos* means curiously wrought. It refers to the strange and complex spore structure recently shown with the aid of electron microscopy. VS.

[10] This is MARTEILIIDA Desportes & Ginsburger-Vogel, 1977. These authors rejected the view of Perkins that *Marteilia* "is shown to be a member of the protozoan class HAPLOSPOREA" and placed it in the "Cnidosporidies." Later, Ginsburger-Vogel & Desportes (78) assigned MARTEILIIDAE, along with PARAMYXIDA, to the phylum MYXOZOA Grassé, 1970. One member of the Committee (Lom) rejected this position and pointed out a 3rd possible disposition of these 2 orders—they could constitute an independent phylum, the ASCETOSPORA. Although each of the 3 alternatives has merit, there seems to be no compelling argument for any of them. Therefore, this classification follows the scheme of Sprague (196), who accepts the view of Perkins, leaving it provisionally unchanged. VS.

[11] This order includes that part of the original order "Aplosporidies" which has been retained in the present classification scheme. Some other genera have been left in limbo. The present name, derived from the Greek word *Balanos*, refers to a stage in sporogenesis that resembles an acorn in its cupule. VS.

[12] Grassé (89) wrote simply "Embranchement des myxozoaires." Subsequently Grassé & Lavette (90) Latinized this term using "Myxozoa."

proliferation; coelozoic or histozoic in cold-blooded vertebrates.

Order 1. **BIVALVULIDA** Shulman, 1959
Spore wall with 2 valves.

Suborder 1. BIPOLARINA Tripathi, 1948
Spores with polar capsules at opposite ends of spore, or with widely divergent polar capsules located in sutural plane or sutural zone.
Myxidium, Sinuolinea, Sphaeromyxa

Suborder 2. EURYSPORINA Kudo, 1920 emend. Shulman, 1962
Spores with 2–4 polar capsules at one pole in plane perpendicular to sutural plane.
Ceratomyxa, Chloromyxum, Sphaerospora

Suborder 3. PLATYSPORINA Kudo, 1920 emend. Shulman, 1962
Spores with 2 polar capsules at one pole in sutural plane; spores bilaterally symmetrical, unless with single polar capsule.
Henneguya, Myxobolus, Thelohanellus

Order 2. **MULTIVALVULIDA** Shulman, 1959
Spore wall with 3 or more valves.
Hexacapsula, Kudoa, Trilospora

Class 2. ACTINOSPOREA cl. n.[13]

Spores with 3 polar capsules, each enclosing coiled polar filament; membrane with 3 valves; several to many sporoplasms; trophozoite stage reduced, proliferation mainly during sporogenesis; in invertebrates, especially annelids.

Subclass 1. **ACTINOMYXIA** Štolc, 1899
Spores with 3 polar capsules, each enclosing polar filament; membrane with 3 valves; several to many sporoplasms; in invertebrates, especially annelids.

Order 1. **ACTINOMYXIDA** ord. n.[14]
With characters of the subclass.
Triactinomyxon

Phylum VII. **CILIOPHORA** Doflein, 1901[15,16]

Simple cilia or compound ciliary organelles typical in at least one stage of life cycle; with subpellicular infraciliature present even when cilia absent; 2 types of nuclei, with rare exception; binary fission transverse, basically homothetogenic and generally parakinetal, but budding and multiple fission also occur; sexuality involving conjugation, autogamy, and cytogamy; nutrition heterotrophic; contractile vacuole typically present; most species free-living, but many commensal, some truly parasitic, and large number found as symphorionts on variety of "hosts."

Class 1. KINETOFRAGMINOPHOREA de Puytorac, Batisse, Bohatier, Corliss, Deroux, Didier, Dragesco, Fryd-Versavel, Grain, Grolière, Hovasse, Iftode, Laval, Roque, Savoie & Tuffrau, 1974[17]

Oral infraciliature only slightly distinct from somatic infraciliature and differentiated from anterior parts, or other segments, of all or some of somatic kineties; stomatogenesis generally telokinetal; cytostome often apical (or subapical) or mid-ventral, on surface of body or at bottom of atrium or vestibulum; cytopharyngeal apparatus commonly prominent; compound ciliature, oral or somatic, typically absent.

Subclass 1. **GYMNOSTOMATIA** Bütschli, 1889
Cytostomal area superficial, apical or subapical; circumoral infraciliature without kinetosomal differentiation other than closer packing of kinetosomes, insertion of supplementary segments of kineties, or pairing (not as dyads) of kinetosomes; cytopharyngeal apparatus of rhabdos type; toxicysts common; somatic ciliation usually uniform.

Order 1. **PROSTOMATIDA** Schewiakoff, 1896
Cytostome apical or subapical; circumoral infraciliature involving anterior parts of all somatic kineties; typical polyploid independent macronucleus; body often large; commonly carnivorous.

Suborder 1. ARCHISTOMATINA de Puytorac et al., 1974[17]
Cytostome apical; simplest type of circumoral infraciliature (closely packed kinetosomes); somatic ciliature mostly in tufts or bands; concrement vacuoles; no toxicysts; all known species commensals, principally in equids.
Alloiozona, Blepharoprosthium, Bundleia, Didesmis

Suborder 2. PROSTOMATINA Schewiakoff, 1896
Cytostome apical, round; circumoral ciliature unspecialized; kineties bipolar, with axial-radial symmetry; no toxicysts.
Holophrya, Metacystis, Pelatractus

---

[13] ACTINOSPOREA cl. n. was created by **E. R. Noble**, with the diagnosis given in the body of this classification. NDL, BMH.

[14] ACTINOMYXIDA ord. n. was created by **J. Lom**, with the diagnosis given in the body of this classification. NDL, BMH.

[15] The present classification of CILIOPHORA is a compromise between that of Corliss (42) and that of de Puytorac et al. (172). NDL.

[16] Publications, some 4 to 6 years ago (37, 38, 40, 83, 113, 115, 116, 172) suggested revolutionary changes in the concepts and bases for classification of the ciliates over the essentially Faurean scheme (32, 34, 65, 110). Although, for the most part, the French and American proposals differed rather little, some additional refinements and/or criticisms have been made since the time of the original schemes, and still newer data have been accumulating (e.g., see, among scores of papers which might appropriately be cited, Refs. 1, 4, 5, 19, 39, 41-43, 45, 51-55, 58, 59, 71, 76, 77, 81, 101, 106, 117, 151, 152, 166, 167, 169, 171, 173, 176, 178, 191, 192, 212, 213). Thus, the Committee's ciliatologists have been faced with the formidable task of finding a single agreeable "compromise" classification for the present paper. To meet such a need and yet recognize the legitimacy of significant differences of opinion, footnotes have been used throughout this section—they generally contain comments of greatest value to specialists on the systematics of the groups concerned. In general, spellings of taxonomic names and data on authorships and dates conform to those used in Corliss (42, 43), except for the slight modification, here, of the suffixes on class and subclass names. JOC.

[17] Because of the large number of authors responsible for the names of this and some of the other ciliophoran taxa included in the present classification, all the authors' names are given only once, in connection with the first name of their authorship cited in this scheme. Subsequently, this "authority" is referred to as "de Puytorac et al., 1974." BMH.

Suborder 3. PRORODONTINA Corliss, 1974[a]
Cytostome apical or subapical, round or oval, sometimes in shallow atrium; distinctive "brosse" typically present near oral area; toxicysts somatic; mostly carnivores or scavengers.
Coleps, Prorodon, Urotricha

Suborder 4. HAPTORINA Corlis, 1974[a][18]
Cytostome apical or subapical, oval or slit-like; cytopharyngeal rhabdos complex; field of clavate "sensory" cilia prominent near anterior end of body; toxicysts in oral or circumoral area or in proboscis or tentacles; rapacious carnivores.
Didinium, Dileptus, Lacrymaria, Spathidium

Order 2. **PLEUROSTOMATIDA** Schewiakoff, 1896
Cytostome slit-like, lateral; circumoral infraciliature including anterior parts of only few somatic kineties and showing differentiation into left and right components; body often large, laterally compressed; macronucleus possibly of low ploidy number; voracious carnivores.
Amphileptus, Litonotus, Loxophyllum

Incertae sedis[19] in subclass **GYMNOSTOMATIA**

Order **PRIMOCILIATIDA** Corliss, 1974[a]
Nuclei homokaryotic, with prominent RNA-rich nucleolus or endosome; cytostome apical, slit-like; somatic ciliature sparse, ventral; small, marine benthic forms, thigmotactic, often algivorous.
Stephanopogon

Order **KARYORELICTIDA** Corliss, 1974[a]
Macronucleus diploid (with possible exceptions) and nondividing; fragile, highly thigmotactic; oral area apical or ventral slit; somatic toxicysts; postciliodesmata characteristically present; contractile vacuoles absent; mainly interstitial sand-dwelling forms, often carnivorous.
Geleia, Kentrophoros, Loxodes, Trachelocerca

Subclass 2. **VESTIBULIFERIA** de Puytorac et al., 1974[17]
Apical or near-apical (occasionally at posterior pole) vestibulum commonly present, equipped with cilia derived from anterior parts of somatic kineties (normal or reorganized) and leading to cytostome; stomatogenesis sometimes involving 2 anlagen; cytopharyngeal apparatus resembling rhabdos; free-living or parasitic, especially in digestive tract of vertebrates and invertebrates.

Order 1. **TRICHOSTOMATIDA** Bütschli, 1889
No reorganization of somatic kineties at level of vestibulum other than more packed alignment of kinetosomes or addition of supernumerary segments of kineties; many species endocommensals in vertebrate hosts.

Suborder 1. TRICHOSTOMATINA Bütschli, 1889
Somatic ciliature not reduced.
Balantidium, Isotricha, Sonderia

Suborder 2. BLEPHAROCORYTHINA Wolska, 1971
Somatic ciliature markedly reduced; all species in herbivorous mammals, especially equids.
Blepharocorys, Ochoterenaia, Raabena

Order 2. **ENTODINIOMORPHIDA** Reichenow, in Doflein & Reichenow, 1929
Oral and somatic ciliature functioning as syncilia; somatic ciliature in form of unique ciliary tufts or bands, otherwise body naked; oral area sometimes retractable; pellicle generally firm, sometimes drawn out into processes; skeletal plates in many species; stomatogenesis apokinetal; commensals in mammalian herbivores, including anthropoid apes.
Cycloposthium, Entodinium, Ophryoscolex, Troglodytella

Order 3. **COLPODIDA** de Puytorac et al., 1974[17]
Vestibular ciliature and infraciliature highly organized by reorganization of parts of somatic kineties in vestibulum, but stomatogenesis basically telokinetal (sometimes involving 2 anlagen); body often contorted, rendering morphogenetics of division complex; somatic kinetids typically with kinetosomes in pairs; cysts common; mostly free-living, often in edaphic habitats.
Colpoda, Platyophrya,[20] *Tillina, Woodruffia*

Subclass 3. **HYPOSTOMATIA** Schewiakoff, 1896[21]
Cytostome nonpolar, on ventral surface; body cylindrical or flattened dorsoventrally, often with re-

[18] This taxon was considered an order by Corliss (37, 43). It is reduced here as a compromise with the French position (e.g. Refs. 59, 172) in which both this group and the prorodontines are not even recognized as separate suborders. JOC.

[19] The *Incertae sedis* category is used here advisedly, although with some reluctance. The problem of a homokaryotic ciliate has been complicated by preliminary findings in an ultrastructural (as yet unpublished) study of *Stephanopogon*—a number of its characteristics appear to be significantly *flagellate*-like! In the case of the karyorelictids, which French workers generally place in the order PLEUROSTOMATIDA, the location of *Geleia* has become particularly controversial: Nouzarède (158) has recently created a new order for it, the PROTOHETEROTRICHIDA (not included in the present scheme), in the class POLYHYMENOPHORA. JOC.

[20] Grain (in Ref. 58) has recently proposed a new order, PLATYOPHRYIDA (in a superorder PLATYOPHRYIDEA), for this problematic genus and several alleged relatives (e.g., *Cyrtolophosis* and *Woodruffia*), placing it as the most primitive group in the subclass HYPOSTOMATA. Such a taxonomic arrangement, although endorsed by McCoy (155) and others, is not followed here, awaiting further data with regard to the ultrastructure of the cytopharyngeal apparatus, especially. JOC.

[21] French workers (e.g., Refs. 171, 172) have insisted on insertion of superordinal taxa among the several orders comprising this large subclass of kinetofragminophorans; these are adopted here, except for PLATYOPHRYIDEA (see preceding footnote) and SUCTORIDEA (see below), although Corliss (e.g., Refs. 42, 43) maintains that they are of limited taxonomic value at the present state of our knowledge. The most striking and most extensive changes in the present ciliate scheme over that of the Society's earlier classification (110) are to be seen among the groups here assembled under the HYPOSTOMATIA—

duction of somatic ciliature; cytopharyngeal apparatus typically of cyrtos type; oral area may be sunk into atrium, with atrial ciliature present; morphogenesis often complex, with stomatogenesis of advanced telokinetal type or even para- or buccokinetal-like; some species astomatous; free-living or ecto- or endocommensals, principally of invertebrates.

Superorder 1. NASSULIDEA Jankowski, 1967

Hypostomial frange of many parts, running obliquely across anterior end of ventral surface, or extremely reduced to few adoral "pseudomembranelles" (sometimes in oral atrium); body often cylindrical, with complete somatic ciliature; cyrtos of numerous nematodesmata; free-living, most often in freshwater habitats.

Order 1. **SYNHYMENIIDA** de Puytorac et al., 1974[17,22]

Parts of generally extensive hypostomial frange more or less fused (=synhymenium); kineties bipolar; body often cylindrical, with complete ciliation; stomatogenesis parakinetal-like.

Nassulopsis, Orthodonella, Scaphidiodon

Order 2. **NASSULIDA** Jankowski, 1967

Parts of hypostomial frange individualized, limited to left side of ventral surface, sometimes reduced to few "pseudomembranelles"; distinct preoral suture; stomatogenesis para- or buccokinetal-like.

Suborder 1. NASSULINA Jankowski, 1967

Frange of variable composition, always distinct from suture line; body often large, cylindrical, fully ciliated; best-known forms from freshwater habitats, feeding on filamentous algae.

Furgasonia,[23] *Nassula, Paranassula*

Suborder 2. MICROTHORACINA Jankowski, 1967

Circumoral ciliature (frange) commonly reduced to 3 "pseudomembranelles"; somatic ciliation typically reduced; body often small and laterally flattened; unique kind of trichocyst characteristically present; cysts common; species freshwater or, often, edaphic.

Leptopharynx, Microthorax, Pseudomicrothorax

Superorder 2. PHYLLOPHARYNGIDEA de Puytorac et al., 1974[17]

Cyrtos complex, embedded in foliated or laminated phagoplasm; commonly relatively few but distinctive nematodesmata, often partly recurved, with "teeth-like" capitula; circumoral ciliature restricted to 3 short rows of kinetosomes near oral opening; somatic ciliature only on ventral surface, in 2 dissymmetric fields; preoral suture skewed to left; macronucleus commonly heteromerous.

Order 1. **CYRTOPHORIDA** Fauré-Fremiet, in Corliss, 1956

Three rows of oral ciliature arising from kineties of left field, composed of pairs of kinetosomes with inverted polarity; body dorsoventrally flattened or laterally compressed; ventral ciliature often thigmotactic; many species with "glandular" adhesive organelle near posterior end.

Suborder 1. CHLAMYDODONTINA Deroux, 1976

Ventral ciliature thigmotactic, without specialized glandular organelle; body broad and dorsoventrally flattened, with ventral surface in contact with substrate; macronucleus heteromerous; free-living or commensal, with some species parasitic, harmful to gills of freshwater fishes.

Chilodonella, Chlamydodon, Lynchella

Suborder 2. DYSTERIINA Deroux, 1976

Generally reduced ciliature and relatively narrow body, nematodesmata of cyrtos may be few in number and more conspicuous, sometimes with very prominent capitula ("teeth"); adhesive organelle well developed, often with protruding mobile appendix (podite); macronucleus heteromerous; species numerous, mainly marine, free-living or commensal.

Dysteria, Hartmannula, Plesiotrichopus

Suborder 3. HYPOCOMATINA Deroux, 1976

Ventral surface quite densely ciliated; dorsal surface humped; cytopharyngeal tube, not surrounded by nematodesmata, may protrude from body; adhesive organelle inconspicuous in right-ventral pit or fosette; macronucleus not heteromerous; ecto- or endocommensals of marine hosts.

Crateristoma, Hypocoma, Parahypocoma

Order 2. **CHONOTRICHIDA** Wallengren, 1895

Variously vase-shaped, sessile and sedentary forms; naked, except for ciliature of ventral surface (displaced to apical end of body); cytopharynx without nematodesmata; adhesive organelle active in stalk production; macronucleus heteromerous; reproduction by budding; marine and freshwater species, ectocommensal principally on crustaceans.

Suborder 1. EXOGEMMINA Jankowski, 1972

External budding, often with single bud at a time; body relatively large, long, cylindrical, with well developed collar, but spines often absent; stalks almost universal; freshwater,

---

dozens of significant papers have been published on them within the past 10-12 years, one of the most heuristic being Fauré-Fremiet's (67) succinct but perceptive contribution. JOC, GD, JG.

[22] Two suborders, the SYNHYMENIINA and the NASSULOPSINA, have been recognized by some workers as comprising this order, following the original proposal of de Puytorac et al. (172); but Corliss (43) and others believe that more data are needed firmly to establish such a suprafamilial separation. JOC.

[23] *Furgasonia* (better known by its preoccupied name, *Cyclogramma*) has been considered by a number of workers (81, 82) to belong in a new order, PARAHYMENOSTOMATIDA, of the subclass HYMENOSTOMATA and class OLIGOHYMENOPHORA. Principally because of its seemingly inexplicable possession of a cyrtos, Corliss (42, 43) (the present scheme) has retained it among the nassulids. Like other similar problems treated in these footnotes, the matter is perhaps best left unresolved until further comparative ultrastructural information becomes available. JOC, GD, JG.

brackish, and marine hosts, including alga.
Heliochona, Phyllochona, Spirochona

Suborder 2. CRYPTOGEMMINA Jankowski, 1975
Internal budding, with up to 8 tomites in brood pouch; body small, flattened, angular, with spines but reduced collar; stalk may be absent; marine crustacean/hosts (including "whale-lice").
Chonosaurus, Isochona, Stylochona

Superorder 3. RHYNCHODEA Chatton & Lwoff, 1939
Aberrant, small rostrate forms, with sucking tube and toxicysts; body of mature stage often nearly naked or with somatic ciliature limited to thigmotactic field; buds or "larvae" typically ciliated (in 2 fields); commensal or pathogenic, most commonly on gills of marine bivalves.

Order 1. **RHYNCHODIDA** Chatton & Lwoff, 1939
With characters of the superorder.
Ancistrocoma, Gargarius, Sphenophrya

Superorder 4. APOSTOMATIDEA Chatton & Lwoff, 1928
Cytostome inconspicuous or, in certain stages of polymorphic life cycle, absent; glandular complex (rosette) typically near oral area; in mature forms somatic ciliature spiraled, often widely spaced; commonly anterior thigmotactic ciliary field; stomatogenesis specialized, derived from telokinetal type; life cycle complex, sometimes involving alternation of hosts (unique in phylum); palintomy and cysts common; most species associated with marine crustaceans.

Order 1. **APOSTOMATIDA** Chatton & Lwoff, 1939
With characters of the superorder.

Suborder 1. APOSTOMATINA Chatton & Lwoff, 1928
Cytostome present in both trophont and tomite stages, typically with rosette; palintomy usually within cysts; hosts mostly marine crustaceans, but a few species associated with polychaetes or freshwater crustaceans.
Foettingeria, Gymnodinioides, Hyalophysa

Suborder 2. ASTOMATOPHORINA Jankowski, 1966
Cytostome absent; remnants of oral ciliature present; body often elongate, vermiform; marked thigmotactism; strobilation type of budding, producing catenoid colonies; life cycles incompletely known; some species in coelomic fluid of amphipods and isopods, others in organs of squid and octopus.
Chromidina, Collinia, Opalinopsis

Suborder 3. PILISUCTORINA Jankowski, 1966
Trophonts nonciliated, immobile, in cysts; some species impaled on setae of crustacean hosts; migrating tomites, produced by strobilation or budding, flattened and ciliated, but apparently mouthless; on marine crustaceans of various kinds and, perhaps, terrestrial mites.
Ascophrys, Askoella, Conidophrys

Subclass 4. **SUCTORIA** Claparède & Lachmann, 1858[24]
Suctorial tentacles, generally multiple (polystomy), containing haptocysts; adult body sessile and sedentary, seldom with cilia; reproduction by budding; stalk commonly present, noncontractile, produced by scopuloid; conjugation often involving micro- and macroconjugants; migratory larva ciliated (with right field and possibly vestigial left field), without tentacles or stalk; widespread on marine and freshwater organisms, occasionally endocommensal.

Order 1. **SUCTORIDA** Claparède & Lachmann, 1858
With characters of the subclass.

Suborder 1. EXOGENINA Collin, 1912
Budding exogenous, without invagination of parental cortex; reproduction generally monogemmic, but polygemmy also occurring; some species with both prehensile and suctorial tentacles; larvae of some species long and vermiform, practically devoid of cilia and nonmotile; mostly large, solitary, and marine, free-living or ectocommensal; some species loricate and colonial.
Ephelota, Paracineta, Podophrya, Thecacineta

Suborder 2. ENDOGENINA Collin, 1912
Budding endogenous, with larvae free in pouch before emergence; reproduction monogemmic and polygemmic; some species stalkless; several with atypically huge ramified body; bundles of tentacles may be branched; migratory larvae often small; diverse habitats, with some species endocommensal in various hosts.
Acineta, Dendrosoma, Endosphaera, Tokophrya

Suborder 3. EVAGINOGENINA Jankowski, 1975
Budding involves evagination of entire pouch with bud still attached; large, single larva, flattened, with distinct patterns of ventral ciliature; some adults with branched tentacular bundles; common freshwater or marine symphorionts, with few endoparasitic species.
Cyathodinium, Dendrocometes, Discophrya, Heliophrya

[24] The SUCTORIA present at least 2 problems: (a) whether or not they should be considered taxonomically closer to the hypostomes [by incorporation there as a separate superorder, as originally suggested by de Puytorac et al. (172)] and (b) whether or not the order SUCTORIDA should be composed of 2 [after Corliss (42)], 3 [after Corliss (43)], or 7 [after Batisse (4)] distinct suborders. The generally more conservative positions have been taken here; i.e., the subclass has been considered deserving a separate status at the subclass level (many workers have made the separation at even higher ranks; see reviews in Refs. 35, 43) and the number of suborders has been placed at the intermediate figure of 3 (formerly, none has been recognized). JOC.

Class 2. OLIGOHYMENOPHOREA de Puytorac et al., 1974[17]

Oral apparatus, at least partially in buccal cavity, generally well defined, although absent in one group; oral ciliature, clearly distinct from somatic ciliature, consisting of paroral membrane (stichodyad) on right side and small number of compound organelles (membranelles, peniculi, or polykineties) on left side; stomatogenesis parakinetal or buccokinetal; cytostome usually ventral and/or near anterior end, present at bottom of buccal or infundibular cavity; cysts not uncommon; various species loricate; colony-formation common in some groups.

Subclass 1. **HYMENOSTOMATIA** Delage & Hérouard, 1896[25]

Body ciliation often uniform and heavy; buccal cavity, when present, ventral; kinetodesmata regularly present, usually conspicuous; sessile forms and stalk, colony, and cyst formation relatively rare; freshwater forms predominant.

Order 1. **HYMENOSTOMATIDA** Delage & Hérouard, 1896

Buccal cavity well defined, containing membranelles or peniculi with infraciliary bases typically 3–4 rows of kinetosomes wide; oral area on ventral surface, usually in anterior half of body; no scutica appearing during stomatogenesis.

Suborder 1. TETRAHYMENINA Fauré-Fremiet, in Corliss, 1956

Uniformly ciliated; 3 oral membranelles on left and undulating or paroral membrane (stichodyad) on right; preoral but no postoral suture; seldom any thigmotactic ciliature, with even caudal cilia uncommon; no nematodesmata or trichocysts, but mucocysts common, stomatogenesis parakinetal; mostly free-living, freshwater, microphagous forms, although few species facultative or even obligate endoparasites.

Colpidium, Glaucoma, Tetrahymena, Turaniella

Suborder 2. OPHRYOGLENINA Canella, 1964

Large, primarily freshwater, histophagous forms; life cycle polymorphic, with palintomic cyst stage; oral apparatus including 3 ciliary organelles on left and associated structure, enigmatic "watchglass organelle"; stomatogenesis parakinetal but complicated by life cycle; no nematodesmata or trichocysts; several species causing white spot disease in marine and freshwater fishes.

Ichthyophthirius, Ophryoglena

Suborder 3. PENICULINA Fauré-Fremiet, in Corliss, 1956

Large, free-living, monomorphic, predominantly freshwater microphagous forms; mucocysts uncommon; explosive fusiform trichocysts occurring widely throughout group; 3 peniculi, often located deep in buccal cavity; stomatogenesis buccokinetal; nematodesmata and pre- and postoral sutures often present, as is depression or oral groove leading to buccal cavity; many species with endosymbiotic algae or gram-negative bacteria; cysts known for only few groups.

Frontonia, Neobursaridium, Paramecium, Stokesia

Order 2. **SCUTICOCILIATIDA** Small, 1967

Body uniformly to sparsely ciliated; thigmotactic area common in many species; buccal ciliature often dominated by tripartite (anterior, middle, and posterior segments) paroral membrane on right side; mucocysts, director-meridian, and caudal cilia common; stomatogenesis buccokinetal, with appearance of prominent unique scutica during morphogenesis; mitochondria long, interkinetal, sometimes fused to form gigantic "chondriome"; no nematodesmata and probably no trichocysts; cysts common.

Suborder 1. PHILASTERINA Small, 1967

Infraciliature of paroral membrane with reduced "a" and "c" segments; scutica very transient; mucocysts prominent, rod-shaped; director-meridian distinct; numerous species, especially in brackish or marine habitats, including sand; some inquilines of sea urchins, others endocommensals of molluscs, polychaetes, and other hosts.

Entodiscus, Loxocephalus, Philaster, Uronema

Suborder 2. PLEURONEMATINA Fauré-Fremiet, in Corliss, 1956

Body commonly small or very small; paroral membrane often prominent (sometimes as stiff velum); cytostome equatorial to subequatorial; infraciliary base of paroral membrane clearly trisegmented, with segment "c" serving as permanent scutica; caudal cilia often conspicuous; mucocysts prominent; cytoproct typically present; widely distributed, mostly free-living, but some commensals.

Conchophthirus, Cyclidium, Pleuronema, Thigmocoma

Suborder 3. THIGMOTRICHINA Chatton & Lwoff, 1922

Prominent thigmotactic region, typically near anterior end, commonly present; cytostome often at or near posterior end; body usually heavily ciliated and laterally compressed; prominent sucker at anterior end in some groups; segment "c" of paroral membrane may be indistinct "scutico-vestige"; director-meridian absent; cytoproct generally ab-

---

[25] One problem has been mentioned in footnote 24 (above). Some workers (e.g., see Ref. 152) would elevate the hymenostomatid suborder PENICULINA to ordinal status, very likely a good idea (but arriving too late for detailed consideration by the Committee). French specialists (e.g., see Refs. 171, 172) suggest amalgamation of the 2nd and 3rd scuticociliatid suborders, with others (see Ref. 43) arguing for their separation; all 3 orders are tentatively retained here. JOC. JG, DL.

sent; all species parasitic, especially in lamellibranchs and oligochaetes.

Ancistrum, Boveria, Cheissinia, Ptychostomum

Order 3. **ASTOMATIDA** Schewiakoff, 1896

Body usually large or long, uniformly ciliated; mouth absent; complex infraciliary endoskeleton and often elaborate holdfast organelles (hooks, spines, or sucker) may be present at anterior end; silverline system resembling that of hymenostomatids; fission may be by budding, with chain-formation; cytoproct absent; contractile vacuoles present; all endoparasitic, mostly in oligochaetes (soil, freshwater, marine); few species in other annelids, molluscs, and turbellarians; one major group in caudate amphibians.

Anoplophrya, Cepedietta, Intoshellina, Radiophrya

Subclass 2. **PERITRICHIA** Stein, 1859

Oral ciliary field prominent, covering apical end of body and dipping into infundibulum; paroral membrane, generally called "haplokinety," and adoral membranelles, "polykineties," becoming "peniculi" in infundibulum present; somatic ciliature reduced to temporary posterior circlet of locomotor cilia; stomatogenesis buccokinetal; widely distributed species, many stalked and sedentary, others mobile, all with aboral scopula; dispersal by migratory telotroch (larval form); mucocysts and pellicular pores universal; myonemes associated with strong contractility of stalk or parts of body; conjugation total, involving fusion of micro- and macroconjugants.

Order 1. **PERITRICHIDA** Stein, 1859

With characters of the subclass.

Suborder 1. SESSILINA Kahl, 1933

Sedentary and sessile, with rare exceptions; body characteristically bell- or goblet-shaped, with stalk at tapered end; mouthless telotroch with locomotory posterior ciliary girdle; many species colonial, some loricate; scopulary kinetosomes typically producing aboral stalk or thigmotactic (adhesive) disc; adults generally filter-feeding bactivores, attached to various substrates in wide range of habitats.

Carchesium, Epistylis, Opercularia, Vaginicola, Vorticella, Zoothamnium

Suborder 2. MOBILINA Kahl, 1933

Mobile forms, usually conical or cylindrical (or discoidal and orally-aborally flattened), with permanently ciliated trochal band (ciliary girdle); complex thigmotactic apparatus at aboral end, often with highly distinctive denticulate ring; all species ecto- or endoparasites of freshwater or marine vertebrates and invertebrates; forms on gills of fishes pathogenic.

Polycycla, Trichodina, Urceolaria

Class 3. POLYMENOPHOREA Jankowski, 1967[26]

Dominated by well-developed, conspicuous adoral zone (AZM) of numerous buccal or peristomial organelles (para- or heteromembranelles), often extending out onto body surface; on right side, one or several lines of "paroral" ciliature (mono- or diplo- or polystichomonads or pairs of kinetosomes); stomatogenesis parakinetal or apokinetal; somatic ciliature complete or reduced, or appearing as cirri; cytostome at bottom of buccal cavity or infundibulum; somatic infraciliature rarely including kinetodesmata; postciliodesmata common and prominent; cytoproct often absent; cysts, and especially loricae, very common in some groups; often large and commonly free-living, free-swimming forms in great variety of habitats.

Subclass 1. **SPIROTRICHIA** Bütschli, 1889

With characters of the class.

Order 1. **HETEROTRICHIDA** Stein, 1859

Generally large to very large forms, often highly contractile, sometimes pigmented; body dominated by AZM, but also commonly bearing heavy holotrichous ciliation; macronucleus oval or, often, beaded; parasitic and free-living species.

Suborder 1. HETEROTRICHINA Stein, 1859

Somatic ciliature well developed; body very contractile, often with simple axis of symmetry; single, conspicuous contractile vacuole at posterior end; peristomial ciliature comprised of numerous paramembranelles and paroral membranes of diplostichomonad type or with pairs of basal bodies; no loricae; cysts common; stomatogenesis either parakinetal or apokinetal; free-living forms large, widely distributed.

Blepharisma, Metopus, Spirostomum, Stentor

Suborder 2. CLEVELANDELLINA de Puytorac & Grain, 1976

Somatic ciliature well developed, sometimes separated into distinct areas by well defined suture lines ("systèmes sécants"); buccal ciliature composed of heteromembranelles and diplostichomonad paroral line(s); several specialized unique fibers associated with kinetosomes; macronuclear karyophore and/or

[26] Several taxonomic problems remain unresolved at this time. Is *Bursaria* no longer to be recognized as a heterotrich [see the startling announcement by Fernández-Galiano (70)]? Should the order OLIGOTRICHIDA be raised to (a 2nd) subclass in the class? Is *Strobilidium* more properly assigned to the tintinnines than the oligotrichines? Should the hypotrichs be subdivided into more than 2 suborders? But some very important changes over earlier "spirotrich" classifications *are* agreed on: for example, (a) removal of the entodiniomorphids to the VESTIBULIFERIA, of class KINETOFRAMINOPHOREA [following findings of Grain (79), Noirot-Timothée (157), and Wolska (211)]; (b) recognizing 6 separate suborders of heterotrichs [based especially on works of Albaret (1) and Jankowski (111, 113)]; and (c) clarifying problems within the oligotrich and hypotrich taxa [see Borror (7), Deroux (50), Fauré-Fremiet (68), Fauré-Fremiet & Ganier (69), Grain (80), Laval (134), Radoičič (175), Remane (177), Tappan & Loeblich (199), and Tuffrau (201)]. JOC, GD, JG.

conspicuous dorsoanterior sucker characteristic of many species; endoparasitic in digestive tract of insects (and related arthropods) or lower vertebrates, occasionally in oligochaetes or molluscs.

Clevelandella, Nyctotherus, Sicuophora

Suborder 3. ARMOPHORINA Jankowski, 1964
AZM commonly encircling body, spiraling posteriad; cytostome near antapical end; somatic ciliature absent except for caudal tuft, several anterior cirri, and "ciliary stripe" accompanying AZM; pellicle rigid, armor-like, with 1 or 2 posterior spines; few species, small, all polysaprobic.

Caenomorpha, Cirranter, Ludio

Suborder 4. COLIPHORINA Jankowski, 1967
AZM borne on pair of prominent "peristomial wings" extending out from lorica-encased body; somatic ciliation uniform and holotrichous; stomatogenesis parakinetal; in division, proter becoming vermiform migratory stage in life cycle; adult attached (by lorica) to various substrates; all but very few species marine.

Ascobius, Folliculina, Lagotia

Suborder 5. PLAGIOTOMINA Albaret, 1974
Body laterally flattened, with extensive AZM and 2 diplostichomonad paroral lines on right side; cytostome subequatorial; stomatogenesis parakinetal; no macronuclear karyophore; body uniformly ciliated, with groups of cilia highly reminiscent of cirri of primitive hypotrichs; few species, all endocommensals in oligochaetes.

Plagiotoma

Suborder 6. LICNOPHORINA Corliss, 1957
Hourglass-like shape; prominent oral disc bearing massive wreath of membranelles; conspicuous basal disc at antapical pole, latter disc with particularly complex substructure, serving as attachment organelle; body proper without cilia, possibly with infraciliature; several ectocommensal species associated with variety of marine invertebrates, with one species on alga.

Licnophora

Order 2. **ODONTOSTOMATIDA** Sawaya, 1940
Laterally compressed, wedge-shaped, with armor-like cuirass and often posterior spines; somatic ciliature reduced; AZM with only 8 or 9 membranelles and no paroral membrane; cytoproct absent; several small species, chiefly in putrefying organic matter in freshwater habitats, few marine.

Epalxella, Mylestoma, Saprodinium

Order 3. **OLIGOTRICHIDA** Bütschli, 1887
Body ovoid to elongate, sometimes with tail; pellicle thickened, with perilemma external to cell membrane in many species; somatic ciliature reduced; AZM (of paramembranelles) extensive, often separable into one part inside buccal cavity and another on nearby body surface; paroral membrane and its infraciliary base single (monostichomonad); stomatogenesis apokinetal; macronuclear reorganization bands present; cytoproct absent; free-swimming, macrophagous, mainly pelagic.

Suborder 1. OLIGOTRICHINA Bütschli, 1887
Somatic ciliature commonly, but not universally, reduced to few short rows of cirrus-like bristles; prominent bipartite AZM (forming open or closed ring), with perioral region used in locomotion; body seldom loricate; endoskeletal "trichites" and polysaccharide platelets may be present; mostly marine, but several widely distributed freshwater species and at least one strongly edaphic.

Halteria, Strobilidium, Strombidium

Suborder 2. TINTINNINA Kofoid & Campbell, 1929
Ciliature dominated by AZM, always forming closed ring; somatic ciliation reduced; body cylindrical or cone-shaped, highly contractile; loricae universally present; tentaculoids sometimes located between adjacent paramembranelles; great majority of species pelagic, some neritic, with a few abundant in freshwater habitats; fossil forms known.

Codonella, Dictyocysta, Epiplocylis, Tintinnopsis

Order 4. **HYPOTRICHIDA** Stein, 1859
Dorsoventrally flattened, highly mobile (yet often thigmotactic), with unique cursorial type of locomotion; body dominated by compound ciliary structures, consisting of prominent AZM (of numerous paramembranelles) near anterior end, multiple paroral lines (diplo- or polystichomonads) on right side of peristomial field, and cirri on ventral surface; rows of widely spaced "sensory-bristle" cilia common on dorsal surface; complex fibrillar system; some species loricate, few colony-forming; stomatogenesis typically apokinetal; macronuclear reorganization bands common; species numerous and very widespread.

Suborder 1. STICHOTRICHINA Fauré-Fremiet, 1961
Body generally elongate; cirri often small and quite inconspicuous, typically in 3 to 12 longitudinal, sometimes spiraled, rows on ventral surface; stomatogenesis presumably parakinetal in more primitive forms; predominantly free-living, but one species ectocommensal on hydras.

Holosticha, Hypotrichidium, Kerona, Urostyla

Suborder 2. SPORADOTRICHINA Fauré-Fremiet, 1961
Body often oval to elliptical; cirri, nonaligned, typically heavy and conspicuous, in isolated groups in specific regions of ventral surface; stomatogenesis apokinetal; most species free-living in widely diverse habitats (freshwater, edaphic, interstitial, marine, etc.), but few inquilines of echinoids or ec-

51. ——— 1976. Le plan cortical des Cyrtophorida unité d'expression et marges de variabilité. I. Le cas des Plesiotrichopidae, fam. nov., dans la nouvelle systématique. *Protistologica* **12**, 469-81.

52. ——— 1976a. Le plan cortical Cyrtophorida unité d'expression et marges de variabilité. II. Cyrtophorida à thigmotactisme ventral généralisé. *Protistologica* **12**, 483-500.

53. ——— 1977. Le plan cortical des Cyrtophorida. III. Structures differenciatrices chez les Dysteriina. *Protistologica* **12**, 505-38.

54. ——— 1978. The hypostome ciliate order Synhymeniida: from *Chilodontopsis* of Blochmann to *Nassulopsis* of Fauré-Fremiet. *Trans. Am. Microsc. Soc.* **97**, 458-69.

55. ———, Iftode F, Fryd G. 1974. Le genre *Nassulopsis* et les Ciliés fondamentalement hypostomiens. *C. R. Acad. Sci., Paris* **278**, 2153-6.

56. Doflein F. 1901. *Die Protozoen als Parasiten und Krankheitserreger, nach biologischen Gesichtspunkten dargestellt.* G. Fischer, Jena. xiii + 274 pp.

57. ———, Reichenow E. 1929. *Lehrbuch der Protozoenkunde.* 5 Aufl. *2 Teil. Spezielle Naturgeschichte der Protozoen. 2 Hälfte: Sporozoa, Ciliata und Suctoria.* G. Fischer, Jena, pp. 865-1262.

58. Dragesco J, Fryd-Versavel G, Iftode F, Didier P. 1977. Le Cilié *Platyophrya spumacola* Kahl, 1926: morphologie, stomatogenèse et ultrastructure. *Protistologica* **13**, 419-34.

59. ———, Iftode F, Fryd-Versavel G. 1974. Contribution à la connaissance de quelques Ciliés Holotriches Rhabdophores. I. Prostomiens. *Protistologica* **10**, 59-76.

60. Dufour L. 1828. Note sur la Grégarine, nouveau genre de ver qui vit en troupeau dans les intestines de divers Insectes. *Ann. Sci. Nat.* **13**, 366-8.

61. Ehrenberg CG. 1830. *Organisation, Systematik und geographisches Verhaltniss der Infusionsthierchen.* K. Acad. Wiss., Berlin, 108 pp. + 8 pl.

62. ——— 1838. *Die Infusionsthierchen als vollkommene Organismen.* Leopold Voss, Leipzig. xviii + 547 pp.

63. ——— 1875. Fortsetzung der mikrogeologischen Studien als Gesammt-Uebersicht der mikroskopischen Paläontologie gleichartig analysierter Gebirgsarten der Erde, mit specieller Rücksicht auf den Polycystinen-Mergel von Barbados. *Phys. Math. Abh. K. Akad. Wiss. Berlin,* Jahrgang 1875, 1-226 + pl. 1-30.

64. Engler A. 1898. *Syllabus der Pflanzenfamilien,* 2nd Ed. Bornträger, Berlin, xii + 214 pp.

65. Fauré-Fremiet E. 1950. Morphologie comparée et systématique des Ciliés. *Bull. Soc. Zool. Fr.* **75**, 109-22.

66. ——— 1961. Remarques sur la morphologie comparée et la systématique des Ciliata Hypotrichida. *C. R. Acad. Sci., Paris* **252**, 3515-9.

67. ——— 1967. La frange ciliaire des Nassulidae (Ciliata Cyrtophorina) et ses possibilités évolutives. *C. R. Acad. Sci., Paris* **264**, 68-72.

68. ——— 1970. Remarques sur la systématique des Ciliés Oligotrichida. *Protistologica* **5**, 345-52.

69. ———, Ganier MC. 1970. Structure fine du *Strombidium sulcatum* Cl. et L. (Ciliata Oligotrichida). *Protistologica* **6**, 207-23.

70. Fernández-Galiano D. 1978. La position systématique de *Bursaria truncatella.* Un nouveau ordre des Ciliés. *J. Protozool.* **25,** 54A.

71. Foissner W. 1978. Das Silberliniensystem und die Infraciliatur der Gattungen *Platyophrya* Kahl, 1926, *Cyrtolophosis* Stokes, 1885 und *Colpoda* O. F. M., 1786: ein Beitrag zur Systematik der Colpodida (Ciliata, Vestibulifera). *Acta Protozool.* **17**, 215-31.

72. Fol H. 1883. Sur le *Sticholonche zanclea* et un nouvel ordre des Rhizopodes. *Mem. Inst. Genevois* **15**, 3-35.

73. Francé R. 1894. Die Polytomeen, eine morphologisch-entwicklungsgeschichtliche Studie. *Jahrb. Wiss. Bot.* **26**, 295-378.

74. Fries E. 1829. *Systema Mycologicum.* Vol. **3**, *Myxogastres.* E. Mauritius, Gryphiswaldae, pp. 67-129.

75. Fursenko AV. 1959. Subclasis Foraminifera, obschaya chast'. [Subclass Foraminifera, general part. In Russian.] *in, Osnovy Paleontologii,* Akad. Nauk SSSR, Moscow, **1**, 115-168.

76. Gates MA. 1978. An essay on the principles of ciliate systematics. *Trans. Am. Microsc. Soc.* **97**, 221–35.

77. Gerassimova ZP, Seravin LN. 1976. Ectoplasmic fibrillar system of Infusoria and its role for the understanding of their phylogeny [in Russian, English summary]. *Zool. Zh.* **55**, 645-56.

78. Ginsburger-Vogel T, Desportes I. 1979. Etude ultrastructurale de la sporulation de *Paramarteilia orchestiae* gen. n., sp. n., parasite de l'Amphipode *Orchestia gammarellus* (Pallas). *J. Protozool.* **26**, 390-403.

79. Grain J. 1969. Le cinétosome et ses dérivés chez les Ciliés. *Ann. Biol.* **8**, 53-97.

80. ——— 1972. Etude ultrastructurale d'*Halteria grandinella* O.F.M. (Cilié Oligotriche) et considérations phylogénétiques. *Protistologica* **8**, 179-97.

81. ———, Didier P, Peck RK, Rodrigues de Santa Rosa M. 1978. Etude ultrastructurale et position systématique des Ciliés du genre *Cyclogramma* Perty, 1852. *Protistologica* **14**, 225-40.

82. ———, Peck RK, Didier P, Rodrigues de Santa Rosa M. 1976. Importance de la microscopie électronique dans les études de systématique chez les unicellulaires; un exemple: les Ciliés du genre *Cyclogramma. C. R. Acad. Sci., Paris* **282**, 735-8.

83. ———, de Puytorac P, Bohatier J. 1973. Essai de systématique des Ciliés gymnostomes fondée sur les caractéristiques de l'infraciliature circumorale. *C. R. Acad. Sci., Paris* **277**, 69-72.

84. Grassé P-P. 1952. Ordre des Protéromonadines (Proteromonadina Nov. Ord.), *in* Grassé P-P, ed., *Traité de Zoologie,* Masson et Cie., Paris, **1**, fasc. 1, 694-703.

85. ——— 1952a. Ordre des Pyrsonymphines (Pyrsonymphina n. ord.), *in* Grassé P-P, ed., *Traité de Zoologie,* Masson et Cie., Paris, **1**, fasc. 1, 789-800.

86. ——— 1952b. Ordre des Oxymonadines nov. (Oxymonadina ord. nov.), *in* Grassé P-P, ed., *Traité de Zoologie,* Masson et Cie., Paris, **1**, fasc. 1, 801-23; bibliography, 957-62.

87. ——— 1952c. Ordre des Retortamonadines nov. (Retortamonadina n. nov.), *in* Grassé P-P, ed., *Traité de Zoologie,* Masson et Cie., Paris, **1**, fasc. 1, 824-35.

88. ——— 1953. Sous-embranchement des Sporozoaires (Sporozoa Leuckart, 1879); Rabdogeniae Delage et Hérouard, 1896; Telosporidia Schaudinn, 1900), *in* Grassé P-P, ed., *Traité de Zoologie,* Masson et Cie., Paris, **1**, fasc. 2, 545-797; bibliography, 890-9.

89. ——— 1970. Embranchement des Myxozoaires, *in* Grassé P-P, Poisson RA, Tuzet O, eds., *Précis de Zoologie* **1**, *Invertébrés,* 2nd Ed., Masson et Cie., Paris, pp. 107-12.

90. ———, Lavette A. 1978. La Myxosporidie *Sphaeromyxa sabrazesi* et le nouvel embranchement de Myxozoaires (Myxozoa). Recherches sur l'état pluricellulaire primitif et considérations phylogénetiques. *Ann. Sci. Nat. Zool.,* Paris, **20**, 193-285.

91. Grassi GB, Foà A. 1911. Intorno ai protozoi dei termitidi. *Atti R. Accad. Lincei, Roma. Rendic. Cl. Sci. Fis., Mat. Nat.* 5. s., **20**, 725-41.

92. Grell KG. 1966. Amöben der Familie Stereomyxidae. *Arch. Protistenk.* **109**, 147-54.

93. Haeckel E. 1862. *Die Radiolarien (Rhizopoda Radiolaria). Eine Monographie.* I. G. Reimer, Berlin. xiv + 572 pp. + 35 pl.

94. ——— 1866. *Generelle Morphologie der Organismen.* I. G. Reimer, Berlin, **1**, xxxii + 574 pp.; **2**, clx + 462 pp.

95. ——— 1879. Ueber die Phaeodarien, eine neue Gruppe kieselschaliger mariner Rhizopoden. *Sitzungsber. Med.-Naturwiss. Ges., Jena,* **1879**, 151-7.

96. ——— 1881. Entwurf eines Radiolarien-Systems auf Grund von Studien der Challenger-Radiolarien. *Jena Z. Naturwiss.* **15**, n.F. 8, 418-72.

97. ——— 1883. Über die Ordnungen der Radiolarien. *Sitzungsber. Med.-Naturwiss. Ges., Jena,* **1883**, 18-36.

98. ——— 1885. Ueber das System der Acantharien. *Jena Z. Naturwiss.* **19**, n.F. 12 (Suppl.), *Sitzungsber. Med.-Naturwiss. Ges., Jena,* **1885**, 168-72.

99. ——— 1887. Report on the Radiolaria collected by H. M. S. Challenger during the years 1873-1876. *Report on the Scientific Results of the Voyage of H. M. S. Challenger During the Years 1873-76. Zoology* **18**, viii + clxxxviii + 1893 pp. + 140 pl.

100. Haecker V. 1908. Tiefsee-Radiolarien. *Wiss. Ergeb. Deut. Tiefsee-Expedition* **14**, x + 706 pp.

100a. Hall RP. 1953. *Protozoology.* Prentice-Hall, New York. 682 pp.

101. Hanson ED. 1977. *The Origin and Early Evolution of Animals.* Wesleyan Univ. Press, Middletown, Connecticut. 670 pp.

102. Hartmann M. 1913. Rhizopoda, *in* Hartmann M, *Handwörterbuch der Naturwissenschaften*. G. Fischer, Jena, **8**, 422-46.
103. Hartog MA. 1906. Protozoa, *in* Harmer SF, Shipley AE, eds., *The Cambridge Natural History,* MacMillan, London, **1**, 1-162.
104. Hertwig K, Lesser E. 1874. Ueber Rhizopoden und denselben nahestehende Organismen. Morphologische Studien. *Arch. Mikrosk. Anat.* **10**(Suppl.), 35-243.
104a. Hibberd DJ. 1976. The ultrastructure and taxonomy of the Chrysophyceae and Prymnesiophyceae (Haptophyceae): a survey with some new observations on the ultrastructure of the Chrysophyceae. *Bot. J. Linn. Soc.* **72**, 55-80.
105. Hollande A. 1952. Ordre des Bodonides (Bodonidea Ord. Nov.), *in* Grassé P-P, ed., *Traité de Zoologie,* Masson et Cie., Paris, **1**, fasc. 1, 669-93.
106. Holt PA, Lynn DH, Corliss JO. 1974. An ultrastructural study of the tentacle-bearing ciliate *Actinobolina smalli* n. sp. and its systematic and phylogenetic implications. *Protistologica* **9**, 521-41.
107. Honigberg BM. 1963. A contribution to systematics of the non-pigmented flagellates, *in* Ludvík J, Lom J, Vávra J, eds., *Progress in Protozoology,* Proc. 1st Int. Conf. Protozool., Prague, 1961, Czechoslovak Acad. Sci., pp. 68-9.
108. ——— 1973. Remarks upon trichomonad affinities of certain parasitic protozoa, *in* de Puytorac P, Grain J, eds., *Progress in Protozoology,* Abstracts of Papers Read at 4th Int. Congr. Protozool., Sept. 1973, Université de Clermont, Clermont-Ferrand, p. 187.
109. ———, Balamuth W. 1963. Subphylum SARCOMASTIGOPHORA nom. nov. to embrace the flagellate and amoeboid assemblages of protozoans. *J. Protozool.* **10**(Suppl.), 27.
110. ———, ———, Bovee EC, Corliss JO, Gojdics M, Hall RP, Kudo RR, Levine ND, Loeblich AR Jr, Weiser J, Wenrich DH. 1964. A revised classification of the phylum Protozoa. *J. Protozool.* **11**, 7-20.
110a. Jahn TL, Jahn FF. 1949. *How to Know the Protozoa.* Brown, Dubuque, Iowa. 234 pp.
111. Jankowski AW. 1964. Morphology and evolution of Ciliophora. I. The new system of sapropelebiotic Heterotrichida [in Russian, English summary]. *Zool. Zh.* **43**, 503-17.
112. ——— 1966. Morphology and evolution of Ciliophora. VI. Morphology and development cycle of *Conidophrys enkystotrophos* sp. nov. in connection with phylogenetic and systematic problems of the family Conidophryidae Guilcher 1951 [in Russian]. *Mat. IV Konf. Mold. Zool.* pp. 123-9.
113. ——— 1967. A new system of ciliate Protozoa (Ciliophora) [in Russian]. *Akad. Nauk SSSR, Trudy Zool. Inst.* **43**, 3-54.
114. ——— 1972. Recapitulation of phylogenesis in ciliate ontogeny [in Russian, English summary], *in* Vorontsov NN, ed., *Problems of Evolution,* **2**, 95-123. *Akad. Nauk SSSR, Nauka, Novosibirsk.*
115. ——— 1973. Podklass Chonotricha. Infuzorii. [Subclass Chonotricha. Infusoria. In Russian], *in* Bykhorskii BE, ed., *Fauna SSSR, Zool. Institut, Akad. Nauk SSSR, Nauka, Leningrad,* Nov. Ser. No. 103, **2**(1), 1-356.
116. ——— 1973a. Taxonomic revision of subphylum Ciliophora Doflein, 1901 [in Russian]. *Zool. Zh.* **52**, 165-75.
117. ——— 1975. A conspectus of the new system of subphylum Ciliophora Doflein, 1901 [in Russian], *in* Balashov US, ed., *Account of Scientific Sessions on Results of Scientific Work, Year 1974: Abstracts of Reports. Akad. Nauk. SSSR, Zool. Inst. Leningrad,* pp. 26-7.
118. Kahl A. 1932. Ctenostomata (Lauterborn) n. subordo. Vierten Unterordnung der Heterotricha. *Arch. Protistenk.* **77**, 231-304.
119. ——— 1933. Ciliata libera et ectocommensalia, *in* Grimpe G, Wagler E, eds., *Die Tierwelt der Nord- und Ostsee, Akademische Verlag, Leipzig,* Lieferung 23 (Teil II, c_3), 29-146.
120. ——— 1930-5. Urtiere oder Protozoa. I: Wimpertiere oder Ciliata (Infusoria), eine Bearbeitung der freilebenden und entocommensalen Infusorien der Erde, unter Ausschluss der marinen Tintinnidae, *in* Dahl F, ed., *Die Tierwelt Deutschlands.* G. Fischer, Jena, pts. 18, 21, 25, 30, 886 pp.
121. ——— 1934. Ciliata entocommensalia et parasitica, *in* Grimpe G, Wagler E, eds., *Die Tierwelt der Nord- und Ostsee, Akademische Verlag, Leipzig,* Lieferung 26 (Teil II, c_4), 147-83.
122. ——— 1934a. Suctoria, *in* Grimpe G, Wagler E, eds., *Die Tierwelt der Nord- und Ostsee, Akademische Verlag, Leipzig,* Lieferung 26 (Teil II, c_5), 184-226.
123. Kent WS. 1880. *A Manual of the Infusoria: Including a Description of All Known Flagellate, Ciliate, and Tentaculiferous Protozoa, British and Foreign, and an Account of the Organization and Affinities of the Sponges.* David Bogue, London, 432 pp.
124. Kheisin EM. 1956. Sistema sporovikov. [Taxonomy of the Sporozoa, in Russian]. *Zool. Zh.* **35**, 1281-98.
125. Kirby H. 1947. Flagellate and host relationships of trichomonad flagellates. *J. Parasitol.* **33**, 214-28.
126. ——— 1949. Systematic differentiation and evolution of flagellates in termites. *Rev. Soc. Mex. Hist. Nat.* **10**, 57-79.
127. Klebs G. 1892. Flagellatenstudien. *Z. Wiss. Zool.* **55**, 265-351, 353-445.
128. Kofoid CA, Campbell AS. 1929. A conspectus of the marine and fresh-water Ciliata belonging to the suborder Tintinnoinea, with descriptions of new species principally from the Agassiz expedition to the eastern tropical Pacific, 1904-1905. *Univ. Calif., Berkeley, Publ. Zool.* **34**, 1-403.
129. Kudo RR. 1920. Studies on Myxosporidia. A synopsis of genera and species of Myxosporidia. *Ill. Biol. Monogr.* **5**(3, 4), 265 pp. + 25 pl.
130. Kühn A. 1926. Rhizopoda, 2 Teil, *in* 2. Heft: *Protozoen, Morphologie der Tiere in Bildern,* Bornträger, Berlin, pp. i-iv + 107-272.
131. Kulda J, Nohýnková E. 1978. Flagellates of the human intestine and of intestines of other species, *in* Kreier JP, ed., *Parasitic Protozoa,* Academic Press, New York, **2**, 1-138.
132. Lankester ER. 1877. Notes on the embryology and classification of the animal kingdom: comprising a revision of speculations relative to the origin and significance of the germ-layers. *Q. J. Microsc. Sci.* n. s. **17**, 399-454 + 25 pl.
133. ——— 1885. Protozoa. *Encycl. Brit., 9th Ed.* **19**, 830-66.
134. Laval M. 1973. Ultrastructure de *Petalotricha ampulla* (Fol): Comparaison avec d'autres Tintinnides et avec les autres ordres de Ciliés. *Protistologica* **8**, 369-86.
135. Leedale GF. 1967. *Euglenoid Flagellates.* Prentice-Hall, Inc., Englewood Cliffs, NJ, xiii + 242 pp.
136. ——— 1974. How many are the kingdoms of organisms? *Taxon* **23**, 261-70.
137. Léger, L. 1900. Le genre *Eimeria* et la classification des Coccidies. *C. R. Soc. Biol., Paris,* **52**, 576-7.
138. ——— 1911. *Caryospora simplex,* Coccidie monosporée, et la classification des Coccidies. *Arch. Protistenk.* **22**, 71-88.
139. ———, Duboscq O. 1910. *Selenococcidium intermedium* Lég. et Dub. et la systématique des Sporozoaires. *Arch. Zool. Exp. Gen.* **45** (ser. 5, **5**), 187-238.
140. Leidy J. 1879. Fresh-water rhizopods of North America. *Rep. U.S. Geol. Surv. Territories* **12**, 1-324.
141. Leuckart K. 1879. *Allgemeine Naturgeschichte der Parasiten.* G. F. Winter, Leipzig and Heidelberg, x + 216 pp.
142. Levine ND. 1959. Uniform endings for the names of higher taxa. *System. Zool.* **7**, 134-5.
143. ——— 1961. Problems in the systematics of the "Sporozoa." *J. Protozool.* **8**, 442-51.
144. ——— 1970. Taxonomy of the sporozoa. *J. Parasitol.* **56**, No. 4, Sect. II, Pt. 1, 208-9.
145. ——— 1978. Recent advances in classification of Protozoa. *Beltsville Symp. in Agric. Res. II. Biosystematics in Agriculture,* pp. 71-87.
146. ——— 1978a. *Perkinsus* gen. n. and other new taxa in the protozoan phylum Apicomplexa. *J. Parasitol.* **64**, 549.
147. ——— 1979. Agamococcidiorida ord. n. and Rhytidocystidae fam. n. for the coccidian genus *Rhytidocystis* Henneguy, 1907. *J. Protozool.* **26**, 167-8.
148. ———, Corliss JO. 1963. Two new subclasses of sarcodines, LABYRINTHULIA subcl. nov. and PROTEOMYXIDIA subcl. nov. *J. Protozool.* **10**(Suppl.), 27.
149. Light SF. 1927. *Kofoidea,* a new flagellate, from a California termite. *Univ. Calif., Berkeley, Publ. Zool.* **29**, 467-92.
150. Lister JJ. 1909. The Mycetozoa, Sect. C of The Protozoa, *in* Lankester ER, ed., *A Treatise on Zoology,* A & C Black, London, Pt. 1, Fasc. 1, 37-67.
151. Lynn DH. 1976. Comparative ultrastructure and systematics of the Colpodida: structural conservatism hypothesis and a description of *Colpoda steinii* Maupas, 1883. *J. Protozool.* **23**, 302-14.

152. ———, Didier P. 1978. Caractéristiques ultrastructurales du cortex somatique et buccal du Cilié *Colpidium campylum* (Oligohymenophora, Tetrahymenina) quant à la position systématique de *Turaniella*. *Can. J. Zool.* **56**, 2336-43.

153. Martin GW. 1961. The systematic position of the Myxomycetes. *Mycologia* **52**, 119-29.

154. Masse G. 1892. *A Monograph of the Myxogastres*. Methuen, London, iii + 367 pp. + 12 pl.

155. McCoy JW. 1978. *Cyrtolophosis*: a "lower" ciliate with a mantle cavity. *Protistologica* **13**, 497-502.

156. Möbius KA. 1889. Bruchstücke einer Rhizopodenfauna der Kieler Bucht. *Phys. Abh. K. Akad. Wiss. Berlin*, 1888 (1889) Abh. ii, 31 pp. + 5 pl.

157. Noirot-Timothée C. 1969. Les affinités des Entodiniomorphida (Ciliata), *in* Strelkov AA, Sukhanova KM, Raikov IB, eds., *Progress in Protozoology*, Proc. 3rd. Int. Congr. Protozool., Leningrad, 1969, Nauka, Leningrad, p. 371.

158. Nouzarède M. 1977. Cytologie fonctionnelle et morphologie expérimentale de quelques Protozoaires Ciliés mésopsammiques géants de la famille des Geleiidae (Kahl). *Bull. Stat. Biol. Arcachon* (N.S.) **28**(Suppl.), 1-315.

159. Olive LS. 1975. *The Mycetozoans*. Academic Press, New York and London, 293 pp.

160. ———, Stoianovitch C. 1966. *Schizoplasmodium*, a mycetozoan genus intermediate between *Cavostelium* and *Protostelium*; a new order of Mycetozoa. *J. Protozool.* **13**, 164-71.

161. D'Orbigny A. 1826. Tableau méthodique de la classe des Céphalopodes. *Ann. Sci. Nat.* **7**, 96-169, 245-314.

162. Page FC. 1976. A revised classification of the Gymnamoebia (Protozoa: Sarcodina). *Zool. J. Linn. Soc.* **58**, 61-77.

163. ——— 1976a. *An Illustrated Key to Freshwater and Soil Amoebae*. Freshwater Biol. Assoc. Sci. Publ. No. 34, Cumbria, England. 155 pp.

164. Pascher A. 1912. Zur Gliederung der Heterokonten. (Kleine Beiträge zur Kenntnis unserer Mikroflora 3.) *Hedwigia* **53**, 6-22.

165. Pearse AS, ed. 1936. *Zoological Names. A List of Phyla, Classes, and Orders*. Duke Univ. Press, Durham, N.C., 24 pp.

166. Peck RK. 1975. Morphology and morphogenesis of *Pseudomicrothorax*, *Glaucoma*, and *Dexiotricha*, with emphasis on the types of stomatogenesis in holotrichous ciliates. *Protistologica* **10**, 333-69.

167. ——— 1978. Ultrastructure of the somatic and buccal cortex of the tetrahymenine hymenostome *Glaucoma chattoni*. *J. Protozool.* **25**, 186-98.

168. Poche F. 1913. Das System der Protozoen. *Arch. Protistenk.* **30**, 125-321.

169. Poljansky, GI, Raikov IB. 1976. Polymerization and oligomerization phenomena in protozoan evolution. *Trans. Am. Microsc. Soc.* **95**, 314-26.

170. Pussard M. 1973. Position systématique des genres *Leptomyxa* Goodey et *Gephyramoeba* Goodey (Proteomyxida), *in* de Puytorac P, Grain J, eds., *Progress in Protozoology*, Abstracts of Papers Read at 4th Int. Congr. Protozool., Sept. 1973, Université de Clermont, Clermont-Ferrand, p. 334.

171. de Puytorac P, Grain J. 1976. Ultrastructure du cortex buccal et évolution chez les Ciliés. *Protistologica* **12**, 49-67.

172. ———, Batisse A, Bohatier J, Corliss JO, Deroux G, Didier P, Dragesco J, Fryd-Versavel G, Grain J, Grolière C-A, Hovasse R, Iftode F, Laval M, Roque M, Savoie A, Tuffrau M. 1974. Proposition d'une classification du phylum Ciliophora Doflein, 1901 (Réunion de Systematique, Clermont-Ferrand). *C. R. Acad. Sci., Paris* **278** D, 2799-802.

173. ———, Grain J, Rodrigues de Santa Rosa M. 1976. A propos de l'ultrastructure corticale du Cilié Hypotriche *Stylonychia mytilus* Ehrbg., 1838: les caractéristiques du cortex buccal adoral et paroral des Polyhymenophora Jankowski, 1967. *Trans. Am. Microsc. Soc.* **95**, 327-45.

174. Raabe Z. 1964. Remarks on the principles and outline of the system of Protozoa. *Acta Protozool.* **2**, 1-18.

175. Radoičič R. 1969. La branche aberrante des tintinnines fossiles (sous-ordre Tintinnina). [In Serbo-Croatian and French.] *Palaeont. Jugosl.* **9**, 1-71.

176. Raikov IB. 1976. Evolution of macronuclear organization. *Annu. Rev. Genet.* **10**, 413-40.

177. Remane J. 1969. Nouvelles données sur la position taxonomique des Calpionellidea Bonet (1956) et sur leurs rapports avec les Tintinnina actuels et les autres groupes de "tintinnoïdiens" fossiles, *in* Brönnimann P, Renz HH, eds., *Proc. 1st Int. Conf. Planktonic Microfossils, Brill, Geneva and London,* **2**, 574-87.

178. Rodrigues de Santa Rosa M, de Puytorac P. 1976. A propos de l'ultrastructure du Cilié *Parauronema virginianum* Thompson, 1967: les caractéristiques ultrastructurales des Ciliés Scuticociliatida Small, 1967. *Protistologica* **12**, 321-34.

179. Saedeleer H de. 1934. Beitrag zur Kenntnis der Rhizopoden: Morphologische und systematische Untersuchungen und ein Klassifikationversuch. *Mem. Mus. Roy. Hist. Nat. Belg.* **60**, 1-112.

180. Sawaya MP. 1940. Sôbre um ciliado nôvo de S. Paulo: *Blepharisma sinuosum* sp. n. (Ciliata, Heterotricha) e sôbre a sub-ordem Odontostomata, nom. nov. *Bol. Fac. Filos. Ciênc. S. Paulo* **19** (Zool. No. 4), 303-8.

181. Schewiakoff VT. 1896. Organizatsiya i sistematika Infusoria *Aspirotricha* (Holotricha auctorum). [Organization and systematics of the Infusoria *Aspirotricha* (Holotricha auctorum). In Russian.] *Mem. Acad. Imp. Sci. St. Petersb., Cl. Phys.-Math.*, 8. s., **4**(1), ix + 395 pp.

182. ——— 1926. Die Acantharia des Golfes von Neapel. [Fauna e Flora del Golfo di Napoli.] *Monographia 37, Staz. Zool. Napol.*, Bardi, Rome (and Friedlander, Berlin). 2 vols. xxiv + 755 pp. + 46 pl.

183. Schmarda LK. 1871. *Zoologie*. Braumüller, Vienna. x + 372 pp.

184. Schröter J. 1886. Pilze, *in* Cohn F, eds., *Kryptogamen-Flora von Schlesien,* Kern, Breslau **3** (Lieferung 2), 91-135.

185. Schulze FE. 1904. Über der Bau und die Entwickelung gewisser Tiefsee-Organismen. *Sitzber. Ak. Berlin* **1904**, 1387.

186. Senn G. 1900. Cryptomonadineae, *in* Engler A, Prantl K, eds., *Die natürlichen Pflanzenfamilien,* 1st Ed., Teil I, Abt. la, pp. 167-9.

187. Shulman SS. 1959. Osnovnye napravleniya evolyutsii v otryade Myxosporidia. [Basic trends of evolution in the order Myxosporidia. In Russian, English summary.] *Zool. Zh.* **38**, 1481-97.

188. ——— 1962. Prosteishie presnovodnykh ryb SSSR. [Protozoa of freshwater fishes in the USSR. In Russian], *in* Bykhovskii BE, ed., *Opredelitel' Parazitov Presnovodnykh Ryb SSSR.* [*Key to Parasites of Freshwater Fishes in the USSR.*] *Opred. Faune SSSR,* Zool. Inst., Akad. Nauk SSSR, Leningrad (80), pp. 7-151.

189. Siebold CTE von. 1845. Bericht über die Leistungen in der Naturgeschichte der Würmer, Zoophyten und Protozoen während des Jahres 1843 und 1844. *Arch. Naturgesch.* **11**, 256-96.

190. Singh BN. 1952. Nuclear division in nine species of small free-living amoebae and its bearing on the classification of the order Amoebida. *Phil. Trans. R. Soc. Lond.* **236**B, 405-61.

191. Small EB. 1967. The Scuticociliatida, a new order of the class Ciliatea (phylum Protozoa, subphylum Ciliophora). *Trans. Am. Microsc. Soc.* **86**, 345-70.

192. ——— 1976. A proposed subphyletic division of the phylum Ciliophora Doflein, 1901. *Trans. Am. Microsc. Soc.* **95**, 739-751.

193. Sprague V. 1969. Need for drastic revision of the classification of subphylum Amoebogena, *in* Strelkov AA, Sukhanova KM, Raikov IB, eds. *Progress in Protozoology,* Abstracts of Papers Read at 3rd Int. Congr. Protozool., Leningrad, July, 1961, Nauka, Leningrad, p. 372.

194. ——— 1972. Classification of the Microsporidia. *Handout, 469th Mtg. Helm. Soc. Wash.,* College Park, Md., USA, 20 Oct., 1972, Chesapeake Biol. Lab. Ref. No. 72-106. [Mimeo.]

195. ——— 1977. Classification and phylogeny of the Microsporidia, *in* Bulla LA, Jr, Cheng TC, eds., *Comparative Pathobiology. Vol.* **2**. *Systematics of the Microsporidia*. Plenum Press, New York, pp. 1-30.

196. ——— 1979. Classification of the Haplosporidia. *Marine Fish. Rev.* **41**, 40-4.

197. Stein F von. 1859. Der Organismus der Infusionsthiere nach eigenen Forschungen in systematischer Reihenfolge bearbeitet. Abt. I: Allgemeiner Theil und Naturgeschichte der hypotrichen Infusionsthiere. Engelmann, Leipzig, 206 pp.

198. Štolc A. 1899. Actinomyxidia, nová skupina Mesozoů, příbuzná Myxosporidií. [Actinomyxidia, a new group of Mesozoa, related to Myxosporidia. In Czech.] *Rozpr. České Akad. Císaře Františka Josefa Trida II, Mat.-Prirod.* **8**(22), 12 pp.

199. Tappan H, Loeblich AR Jr. 1968. Lorica composition of mod-

ern and fossil Tintinnida (ciliate Protozoa), systematics, geologic distribution, and some new Tertiary taxa. *J. Paleontol.* **42**, 1378-94.

200. Tendal OS. 1972. Xenophyophorerne [in Danish]. *Naturens Verd.* **1972**, 302-10.

201. Tripathi YR. 1948. Some new Myxosporidia from Plymouth with a proposed new classification of the order. *Parasitology* **39**, 110-8.

201a. Tuffrau M. 1972. Caractères primitifs et structures évoluées chez des Ciliés Hypotriches: le genre *Hypotrichidium*. *Protistologica* **8**, 257-66.

202. Tuzet O, Maurand J, Fize A, Michel R, Fenwick B. 1971. Proposition d'un nouveau cadre systematique pour les genres de microsporidies. *C. R. Acad. Sci., Paris* **272**, 1268-71.

203. Vickerman K. 1976. The diversity of the kinetoplastid flagellates, *in* Lumsden WHR, Evans, DA, eds. *Biology of the Kinetoplastida.* Academic Press, New York and London, **1**, 1-34.

204. Vivier E. 1975. The Microsporidia of the Protozoa. *Protistologica* **11**, 345-61.

205. Wallengren H. 1895. Studier öfver Ciliata infusorier. II. Slägtet *Heliochona* Plate, slägtet *Chilodochona* n. g., slägtet *Hemispeira* Fabre-Domergue. [In Swedish, English summary.] *Acta Univ. Lund,* 77 pp.

206. Wedekind R. 1937. *Einführung in die Grundlagen der historischen Geologie.* **2**. Band: *Mikrobiostratigraphie. Die Kerallen- und Foraminiferzeit,* Enke, Stuttgart, 136 pp. + 16 pl.

[27] 207. Weiser J. 1974. Morphological basis of the taxonomy of Microspora. *Proc. 3rd Int. Congr. Parasitol.,* Munich, 1974. Facta Publication, H. Egermann, Vienna, **1,** 12-3.

[27] 208. ——— 1977. Contribution to the classification of Microsporidia. *Véstnik Česk. Spol. Zool.* **41**, 308-20.

209. Wenyon CM. 1926. *Protozoology. A Manual for Medical Men, Veterinarians and Zoologists.* 2 vol. Wood, New York. xxv + 1563 pp.

210. Whittaker RH. 1977. Broad classification: the kingdoms and the protozoans, *in* Kreier JP, ed., *Parasitic Protozoa.* Academic Press, New York and London, **1**, 1-34.

211. Wolska M. 1971. Studies on the family Blepharocorythidae Hsiung. VI. Phylogenesis of the family and the description of a new genus *Circodinium* gen. n. with the species *C. minimum* (Gassovsky, 1918). *Acta Protozool.* **9**, 141-94.

212. ——— 1978. *Tripalmaria dogieli* Gass., 1928 (Ciliata, Entodiniomorphida). Structure and ultrastructure. Part I. Light-microscope investigations. *Acta Protozool.* **17**, 13-20.

213. ——— 1978a. *Tripalmaria dogieli* Gass., 1928 (Ciliata, Entodiniomorphida). Structure and ultrastructure. Part II. Electron-microscope investigations. *Acta Protozool.* **17**, 21-30.

214. Zopf W. 1884. Die Pilzthiere oder Schleimpilze, nach dem neuesten Standpunkte bearbeitet, *in* Jäger G, et al., eds., *Encyklopaedie der Naturwissenschaften,* Abt. I, Theil 1: von Schenk JA, ed., *Handbuch der Botanik,* Breslau **3**, 1-174.

[27] Although Weiser's classification of MICROSPORA is not used in the present scheme, the references to his important works are included in the list. NDL, BMH.