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THE CILIATED PROTOZOA

Characterization, Classification and Guide to the Literature

SECOND EDITION

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Acknowledgements and Note of Explanation

Acknowledgments and Note of Explanation. The hundreds of figures comprising the plates listed above are either original or (more often) represent redrawings or retouched reproductions from widely scattered sources in the vast protozoological literature of the past 300 years. Specific acknowledgments are generally made in the explanations of figures accompanying the individual plates: there, in place and as appropriate, are named the authors of the papers in which the illustrations originally (with exceedingly rare exception) appeared. Many of the older figures in this book have been used and reused by numerous other writers (both of textbooks and of research papers) in decades past, with the drawings sometimes altered, sometimes not, and with or without proper acknowledgment.

I have made a conscientious effort to ferret out and credit the *earliest* artist (or scientist) involved, though on occasion I have not hesitated to "repair" the original drawing slightly for sake of clarity or accuracy. In the plates of Chapter 20, I have deliberately resurrected some of the oldest ciliate illustrations discoverable, particularly when they have been uncannily accurate (as well as perhaps unusually artistic), in order to preserve such oft-forgotten early efforts so deserving of perpetuation.

When sources are not named, the materials are from my own collections: this is particularly the case with respect to photographs of the "personalia" featured in Chapter 21. However, grateful mention should be made of general contributors to my photographic collection of ciliatologists over the years, *viz.*, colleagues like Jean Dragesco (above all!), Jiří Lom, Enrique Beltrán, Jean and Monique Cachon, J.-B. and J. M. Jadin, and D. N. Zasuchin. Also, I am specifically indebted to Willard D. Hartman, of Yale University, for the photograph of Saville Kent and to Jean-Denis Hufschmid, of the University of Geneva, for the picture of Édouard Claparède.

EXPLANATION OF FRONTISPIECE

The late Professor E. Fauré-Fremiet – fondly known to close associates as "Monsieur Fauré" and to whom this book is dedicated – is shown in the center of a wreath of selected major influences on and interests in his long scientific life, which was dedicated primarily to study of the ciliated protozoa. The photograph was taken (with a very inexpensive camera – befitting a "poverty-striken" postdoctoral fellow!) by the writer at Concarneau in the summer of 1952.

Lefthand column, from top to bottom: (1) The first Mme Fauré-Fremiet, née Jeanne Henneguy, his devoted and artistically talented wife of 54 years (until her passing in 1967). The picture is from a portion of a large painting of "Madame Fauré" executed by her husband at an early time in their marriage. Daughter of L.-F. Henneguy (see below), she was a granddaughter of Pierre-Joseph Proudhon, noted philosopher of the 19th century, and of author and playwright Félix Henneguy. (2) Emmanuel Fremiet, renowned animal sculptor (golden equestrian statue of Jeanne d'Arc in the Place des Pyramides, etc.), maternal grandfather of Monsieur Fauré. Little Emmanuel – an apt pupil – often visited the Fremiet atelier in Paris; and he later took the compound name, Fauré-Fremiet, to honor his son-less grandfather. The picture is of a bust, the original now in a public square, sculptured by M. Fauré himself (who also painted an excellent full length portrait in oils of his namesake). (3) A ship from a remarkable set of drawings of the French navy done by M. Fauré, simply for his own pleasure, at the tender age of *ca.* 13! He was later to draw or paint a number of additional pictures, primarily of members of the family circle, displaying an artistic ability of unusual note. (4) A picture of the 19th-century microscope used in early years by M. Fauré – and by his father-in-law before him – mostly in study of specimens of protozoa. (5) A model of the well-known peniculine ciliate *Urocentrum turbo* made by M. Fauré (later a gift to the writer), who fashioned a number of such forms (from clay) in order to better understand the "whole" organism. Sometimes dividing stages were molded as well, so that morphogenetic movements of certain structures could be more easily visualized.

Righthand column, from top to bottom: (1) The second Mme Fauré-Fremiet, née Marie Hamard (daughter of long-widowed Mme Hamard who was a very dear friend of Jeanne Fauré-Fremiet and her sister Suzanne Henneguy), and many many years faithful secretary and research collaborator of her "Patron," Monsieur Fauré, at the laboratory. They were quietly married in 1971, a scant five months before his untimely passing. (2) Gabriel Fauré, illustrious musician, composer, and organist whose works are played and enjoyed throughout the world perhaps more today than ever before, father of Emmanuel (and of a younger son, Philippe, essayist and drama critic who passed away in 1954). Shown here is a well-known photograph of the celebrated composer, but a bust by his older son now stands in a pretty village park at Foix, southern France, site of the annual Fauré Music Festival. (3) Louis-Felix Henneguy, outstanding microscopist and parasitologist, Membre d'Institut, father-in-law of M. Fauré, and his predecessor in the chair of "comparative embryogeny" at the Collège de France (which split off from the Sorbonne, across Blvd. St. Jacques, in 1543). The picture is of a third bust sculptured by M. Fauré himself. [The ancestral Henneguy "homestead," founded centuries ago, stands sturdily in rustic Précy-sur-Oise, a short distance north of busy metropolitan Paris: M. Fauré spent many an hour of delightful tranquility there.] (4) An unpublished drawing of the (scutico)ciliate *Uronema* sp. prepared by M. Fauré from his study of silver-impregnated specimens. It represents but one of many never published items in the prodigious collection of Faurean materials now housed in a special salon in the Department of Zoology and Protistology, University of Clermont-Ferrand, Aubière. (5) A drawing of another one of M. Fauré's favorite organisms, a species of the pelagic oligotrich genus *Strobilidium*. The picture is taken from his doctoral dissertation of 1924 (he had already published some 189 separate research papers by that date!), a work as noted for its artistic (and accurate) illustrations as for its lasting contribution to our knowledge of the comparative morphology and ecology of the diverse ciliates comprising the fresh-water and marine planktonic communities.

[See also Plate XXXV, views of M. Fauré's small but most compact "living room" enriched by the presence of a number of the objects d'art mentioned above.]

Frontispiece. Emmanuel FAURÉ-FREMIET (1883—1971): ciliatologist sans peer, with indication of major influences and interests in his long and illustrious life. [See page x for fuller explanation.]

Preface to the First Edition

The ciliated protozoa have not been treated monographically, within the confines of a single study, since the encyclopedic works of Bütschli (1887-1889) and Kahl (1930-1935). Even the more recent of these, the invaluable keys and diagnoses by Kahl cited above, omitted consideration of the marine tintinnids, the suctorians, and certain symbiotic groups. Also, since 1935, the number of taxa of ciliates has nearly doubled at every level below the ordinal group: in families, genera, and species. In the meantime, furthermore, important revisions in the scheme of classification of these protozoa, essentially the first major changes since the time of Stein (1867), have been proposed. But these suggested revisions, and the hypotheses on which they are based, have never been presented and discussed extensively in any single paper.

It is time to at least stop and take stock. New genera and families need to be fitted into the framework of the proposed classificational scheme endorsed in the present study. It is becoming increasingly difficult to undertake comparative taxonomic studies today until we have gained a broader background knowledge of the current overall problems facing the ciliate systematist.

The present work represents an attempt to carry out three main objectives: to offer concise characterizations of the major taxa comprising the new scheme of classification; to present an up-to-date list of all the described genera of ciliates considered acceptable; and to include annotated reference to all significant, sizable works, including the most recent, in the principal areas of research in ciliate protozoology. Major concepts are illustrated and "typical" or representative genera are figured. Particular attention is given to nomenclatural problems, since a number of these have gone unattended for many years.

It is earnestly hoped that specialists in all areas, perhaps in systematics above all, will attack with renewed vigor the many important problems remaining to be done. Certainly the present work has revealed more problems than it has solved.

I am indebted to many persons for concrete assistance during the preparation of this work. Specifically, I must at least mention my deep gratitude to Professor E. Fauré-Fremiet, Paris, for his constantly stimulating help, advice, and encouragement first given me during my stay in his laboratories at the Collège de France and at Concarneau, 1951-1952, and continued ever since that most profitable year; to my research assistants and graduate students at the University of Illinois, in particular Miss Margaret Dysart, Miss Louise Weisberg, and Mr. Jacques Berger, for their unstinting aid, especially in checking the bibliographical material involved; to Mr. Lyle Bamber and the library staffs at the University of Illinois for their well-stocked stacks and their patient assistance in locating rare or obscure publications; to Miss Alice Boatright, for her painstaking and most sympathetic execution of all the drawings used here; to Mrs. Ruth Bruckner and Mrs. Suzanne Ford for such cheerful diligence in typing the manuscript; to my understanding wife, Dorothy, for her unselfish moral support in particular; and to Professor P. B. Medawar, University College London, for graciously providing accommodation in his Department of Zoology during completion of the book while I was on sabbatical leave from the University of Illinois, 1960-1961. Finally, I wish to acknowledge the indispensable aid of grants from the National Science Foundation, Washington, D.C.

January 1961 JOHN O. CORLISS

Preface to the Second Edition

This completely revised and necessarily much expanded edition is long overdue. Whether the protistan forms whose taxonomy and evolution are here under consideration are known as the ciliated protozoa, the ciliate Protozoa, the phylum Ciliophora – or even called independent eukaryotic ciliated cells (or supercells) or "pseudometazoa" – the study of so many aspects of the biology of so many of them has increased so greatly during the past 15–16 years that it is again high time to stop and take stock of their systematics in general and their classification in particular. For in these fields, even as in the other areas of their investigation, new data and fresh hypotheses – both owing much to the discovery and application of innovative technical approaches – are rendering former treatments and conclusions obsolete.

In the present situation, however, it is not merely a matter of updating older ideas and outmoded systems of classification. We must also contend with the never-ceasing addition of entirely new taxonomic groups to those already known: not only at the level of species (some 1,500 of which have been described as new since the date of publication of the first edition of this book) but at higher levels as well (e.g., the numbers of orders and classes have both been more than doubled). Furthermore, certain technical advances of recent years, most notably electron microscopy, have so revolutionized the kinds of data obtainable which are potentially of such significance in systematics that we must critically reconsider all past work which, in retrospect, was so often based on inadequate information. For nearly every problem seemingly solved by new approaches, however, fresh difficulties are apt to become evident (such as the distressing unevenness of our knowledge among species of a whole group); so the task which I have undertaken to carry out here has been a much more arduous and time-consuming one than might have been anticipated. Perhaps this has been the reason why, despite a recent flurry of new protozoological textbooks and practical "keys" to selected or restricted ciliate groups, no one else to date has been audacious enough to tackle the job of revising in detail the entire scheme of ciliophoran classification, neglecting no group: free-living or symbiotic, marine or brackish or fresh-water, pelagic or benthic, edaphic or from any other specialized habitat.

The present work, then, represents both a belated (in view of some of the statements made above) and possibly premature (because of the vast quantity of potentially important new data not to be available for many species for perhaps years to come) major overhauling of the systematics of the Ciliophora *sensu lato*, now properly considered a separate phylum in its own right. A rationale has been developed, and criteria defined, to serve as a basis for my own particular reclassification of these intriguing organisms; revised characterizations, admittedly more precise for groups for which we possess more and newer knowledge, are presented; discussions of controversial taxa are offered, with arbitrary but critical resolution of their place in, or rejection from, the new overall system; genera, new and old, are fitted into families, orders, and classes; more than 1,500 figures are included, drawn from classical as well as modern works of quality; and the pertinent literature is reviewed in appropriate places, with a bibliography containing more than one and a half times its former number of references. The latest ideas concerning the evolution of ciliates are also considered; and new "phylogenetic trees" are offered, replacing the aging one of the first edition. Photographs of 185 ciliatologists, spanning 300 years, are included. In short, the whole volume has been completely rewritten, thoroughly updated, and substantially enlarged.

Once again, I am indebted to many persons for help and encouragement over the years. First among them, still and always, is the late Professor E. Fauré-Fremiet (who passed away at the tender age of 88 in 1971), under whom I have had the honor of studying and to whose memory I have thus dedicated this edition with both pleasure and humility (see *Frontispiece*). I must take the liberty of simply listing the names of other valued colleagues, from institutions widespread around the world, whose works and personal contacts I have found most stimulating with regard to various major aspects of ciliate systematics and evolution: Drs. J.-L. Albaret, G. A. Antipa, E. Balech, A. Batisse, J. Berger (and other former University of Illinois graduate students of mine in ciliatology), J. Bohatier, A. C. Borror, M. F. Canella, C. R. Curds, G. Deroux, P. Didier, J. Dragesco, T. Fenchel, H. E. Finley, J. Frankel, J. Grain, C.-A. Grolière, M. F. Greenberg, E. D. Hanson, P. A. Holt, A. W. Jankowski, E. N. Kozloff, M. Laval-Peuto, H. Tappan Loeblich, J. Lom, D. H. Lynn, E. Mayr, D. L. Nanney, D. J. Patterson, J. J. Paulin, P. de Puytorac, I. B. Raikov, H. Sandon, G. G. Simpson, M. A. Sleigh, E. B. Small, T. M. Sonneborn, J. D. Stout, V. Tartar, M. Tuffrau, and K. Vickerman. (Persons kindly supplying photographs for Chapter 21 are acknowledged elsewhere.) Graduate students currently (or recently – time flies!) in residence at the University of Maryland have also provided concrete help and inspiration through seminar courses and frequent "rap" sessions on various topics germane to the text. My wife Ann's moral support has been constant and indispensable; and teenage daughter (only one of our five still at home) Jennifer's perceptive understanding has been touching.

I should also like to express my deepest appreciation to Mrs. Jeanne M. Sievers, a most conscientious fact-finder, index-maker, translator of my scribbled notes, and industrious copyreader without equal; Jeanne has been absolutely indispensable to the entire project. I am grateful to the many ciliatologists who have kindly sent me reprints of their works through the years (or even supplied me with advance copies of papers in press) and to Mr. Michael N. Dadd, of the *Zoological Record*, for prompt aid when needed. Miss Lois Reid, an artistic young lady of great patience and ability, has been of tremendous help in production of the numerous new or redrawn figures throughout the book. Of incalculable value also has been the superior photographic assistance of Dr. D. Wayne Coats and Messrs. Fred Dickson and Allen R. Linder: over the months (= years!), Fred helped first (especially in creating the *Frontispiece*); then Wayne; then, in the final frantic weeks, Allen. Mr. Timothy K. Maugel, TEM and SEM expert, has been most helpful with respect to electron micrographs used. Mrs. Allie May Brown, Mrs. Julia Tossel, Mrs. Linda Kagle Wood, Mrs. Joan M. Bishop, Mrs. Evelyn Zier, and other "gals" in the office have been the skilled and ever-cheerful typists of numerous early and eventually "pentultimate" drafts over the many months of writing, condensing, rewriting, recondensing, etc.! Work on the IBM composer ultimately used to prepare camera-ready copy was faithfully carried out by Mrs. Brown, Mrs. Eileen Peterson, and Mr. Edward Szymanski; particularly deserving of accolades in this difficult work is Allie May who taught herself the technique with most admirable self-discipline and perserverance and put the bulk of the manuscript into its final form.

It is a pleasure, again, to acknowledge the continuous support of research grants for my studies of the ciliates from the Program of Systematic and Evolutionary Biology of the National Science Foundation. Several timely awards from the Graduate School of the University of Maryland made possible some continuity in preparation of the early typescript. Mr. Kenneth Gilmore, astute Business Manager of the Department of Zoology, University of Maryland, and his assistant, Mr. Paul Hopkins, deserve special thanks for help strategically rendered at various critical times. I might also, in all fairness, acknowledge the patience of Pergamon Press, who expected final copy long before I was able to get it to them!

Finally, if I may be permitted to end on a personal note, I should like to make the observation that – despite the anguishes, frustrations, and delays (sometimes considerable!) – the research and writing involved in production of this book have been truly a "labor of love." The fact that much was (had to be) accomplished in the "wee hours" between midnight and 3 a.m. over an e-x-t-e-n-d-e-d period of time may attest to my having been totally captivated by these fascinating, endearing, gentle, minuscule protists who abound all about us in such diversity and such vast but unobtrusive numbers. Enough, when I pass on, if someone remembers me only as (having been) a fervent "philosopher in little things."

JOHN O. CORLISS

December 1977

Chapter 1

Introductory Considerations: Bases, Difficulties, and Result of New Approaches

That there is a pressing need for a fresh review and revision of the overall systematics of the ciliates can scarcely be denied. Not only have hundreds of new taxa (at both species and higher levels) been described since appearance of the first edition of this book, in 1961, but also new kinds of data have now become available (through use of such relatively new techniques as electron microscopy) and new ideas and hypotheses have been promulgated which should be recognized as having a direct effect on systems of classification of the higher-level taxa.

A number of important works on isolated groups of ciliates (generally selected on an ecological rather than taxonomic basis) have appeared in recent years (e.g., Bick, 1972; Borror, 1973a; Curds, 1969; E. E. Jones, 1974a), but these are limited in their approach – set up essentially as field keys – and by their acknowledged incompletenesses. The sections on the Ciliophora in recently published textbooks concerned with protozoology overall (Grell, 1973; Sleigh, 1973; Westphal, 1974, 1976), suffer from the lack of space which can be devoted to such an extensive topic as ciliate systematics. The same point may be made about the elementary ciliate texts published by A. R. Jones (1974) and Matthes & Wenzel (1966). The most comprehensive treatment of the subject has been that of Jankowski (1967a), drastically revised but not particularly modernized in a briefer paper appearing subsequently (Jankowski, 1973c). But, in spite of the admirably innovative nature of the 1967 monograph, it was "dated" with respect to usage of new kinds of data (such as ultrastructural) even at the time of its appearance, a decade ago. Nevertheless, Jankowski's ideas (see especially Chapter 18) have had a definite influence on the scheme of classification supported in the present book.

In 1974, a pair of papers appeared which, in particular, laid much of the groundwork or supplied the framework for subsequent sections of this volume: Corliss (1974a) and de Puytorac et al. (1974). However, some important aspects in the systematics and phylogenetics of the phylum Ciliophora were inadequately treated in those space-restricted works (and even in the "follow-up" presentations of Corliss, 1974b, 1975b), matters thus demanding our attention here in more detail. Especially unfortunate was their lack of provision of a specific rationale containing the analytical criteria on which the revised classification schemes were based. An attempt is made in the present work to meet that explicit need (see particularly Chapter 3), though some approaches have (also) been made, very recently, in papers published while this book has been in final stages of preparation (e.g., see Albaret, 1975; Batisse, 1975; Corliss, 1975c, 1976, 1977a,b; Corliss & Hartwig, 1977; Deroux, 1976a; Gerassimova & Seravin, 1976; Grain et al., 1976; Hutner & Corliss, 1976; Jankowski, 1975; Lynn, 1976a; Orias, 1976; Poljansky & Raikov, 1976; de Puytorac & Grain, 1976; de Puytorac et al., 1976; Small, 1976).

Bases for Change

At a time when the ciliate classification scheme of 1961 seems (at last!) to be receiving very broad acceptance (e.g., in textbooks and the like; and its early heavy support in the widely adopted scheme of Honigberg et al., 1964, may be mentioned in this connection), one may well ask not only why a(nother) change *now* but also what are the bases justifying a second substantial revision seemingly so soon?

Even as light-microscopical observations of the argentophilic infraciliature served in 1961 as a major basis for a better understanding of ciliate systematics over the conventional views of the pre-1950's, today an ultrastructural approach to the infraciliature provides a whole new way of comparing and understanding characteristics of taxonomic value at all levels in the classificational hierarchy. In fact, the combined methods of silver impregnation and electron microscopy produce the most desirable effect of all and provide the relative abundance of morphological characters so sorely needed in comparative taxonomic work.

Still more attention to morphogenetic data represents another basis for revision. Comparative stomatogenesis, for example, is becoming a prerequisite for many systematic studies and is primarily responsible for such major decisions as separation of the order of scuticociliates from the assemblage of hymenostomes *sensu stricto* (Corliss, 1969a, 1974a; Small, 1967). A recently proposed new set of definitions for the modes of stomatogenesis (Corliss, 1973e), although requiring further refinement itself, offers a basis for more precise and more sophisticated descriptions of the phenomenon as it occurs among ciliates belonging to different high-level taxonomic groups. Increased knowledge of the dynamics of all stages in the life cycle is making possible our drawing more reasonable conclusions regarding ciliate group-interrelationships in general (see Chapter 17).

Recognition of the possible taxonomic significance of nuclear differences is another approach often neglected in pre-1960 studies. Ploidy (or genomic) variation and basic functional differences in the life history of the macronucleus, for example, can serve as bases for differentiation of separate orders among the so-called "primitive" gymnostomes (see Corliss, 1974b, 1975b,c, and Corliss & Hartwig, 1977, for the first such taxonomic proposals; and see Raikov, 1969, 1976b, and Raikov & Ammermann, 1974, for reviews of the relevant cytogenetic information).

Even the fact that hundreds of new species (and new higher taxa as well) have been described since 1960 serves as a reason for a revised classification, since such taxonomic activity represents a legitimate indication of a greater diversity among ciliates (i.e., there appear to be a greater number of distinguishably different kinds or groups) than heretofore appreciated. Some 1,200–1,500 bonafide new species, 275 new genera, 75 new families, more than 30 new orders or suborders, and half a dozen new classes or subclasses can hardly be smoothly fitted into a conventional (=outmoded) scheme based on fewer data and involving considerably fewer taxonomic groups.

Added to and intertwined with new approaches, new techniques, new data, and new taxa has been the appearance of fresh ideas and novel hypotheses. Since 1960, positive ideas and constructive criticisms, particularly with respect to possible phylogenetic interrelationships of various major taxa within the Ciliophora, have emanated from a number of quarters. The direct impact of these is noted in appropriate places in subsequent sections of this book, including Chapter 17; and references to a number of them are also cited in such Chapters as 18 and 21. In this realm of synthesis and theory, great progress – or potential progress – has recently been made. The results of such efforts can serve as the basis for development of an improved rationale for resolving some of the most difficult challenges in ciliate systematics.

Difficulties in Application of Any New Approach

There are numerous reasons for the lag in modernization of systematic studies in all protozoan groups, most of which do not seem to be appreciated by taxonomists of many groups of the multicellular plants and animals (see earlier discussions of this situation in Corliss, 1960a, 1962a, 1963a, 1972e, and, especially, 1974c). The very nature of these protists is the main one: their small size, lack of organ systems, frequent absence of demonstrable sexuality, rareness of fossil forms, ecological ubiquity, etc. The paucity of known species compared with the tens of thousands yet to be discovered and described is yet another roadblock to progress in protozoan systematics and phylogenetics. It is extremely difficult to set limits, as it were, on the diversity possible within any given high-level taxon when so much relevant information remains tantalizingly unavailable. Whether new or old approaches are being used, we are also confronted with a general scarcity of morphological characters and a still greater rareness of nonmorphological traits of comparative taxonomic utility. And, although we are now getting some "breakthrough" exceptions, the usual lack of sufficient numbers of characteristics of differential value has precluded the highly desirable use of such sophisticated statistical methods as multivariate morphometrics in treatment of our data.

Perhaps the most difficult handicap of all is one which is particularly exasperating to the eager young protozoologist anxious to "modernize" the systematics of the group(s) chosen for his or her investigation. I refer to the incredible *unevenness* of our knowledge about the forms which have already been described. On some aspects of the biology of some species comprising a given group, there may be a relative wealth of data. Yet, for other forms (possibly closely related), we may know very little about such aspects, while having some data on different characteristics of these organisms. Filling such gaps in our knowledge is a full-time – if not, in some cases, an impossible – task in itself and may not be very rewarding. But we can hardly draw *comparative* taxonomic conclusions of enduring worth without much of the missing information.

A related problem concerns the many ciliates known only from ancient descriptions, which perhaps were even based on just a few unstained specimens examined briefly under low magnifications of the light microscope. Despite the paucity of data, we can hardly throw out such species, especially if one or two "key" characters have indeed been verified in subsequent studies. The trouble comes principally from the fact that many species – and not necessarily closely related ones – may show various of these same obvious and probably superficial traits. How does one properly sort out the taxonomic "relatedness" of the forms, not to mention the complex nomenclatural tangles so often involved?

We are hardly in a position to require that the thousands of species of ciliates known to date be restudied in exhaustive detail and that the techniques used include such refined (and expensive!) approaches as electron microscopy. Besides, too great a reliance on ultrastructural data raises the problem to which attention has already been briefly called by Cheissin (1965) and the writer (Corliss, 1974a,c, 1976). Too much weight ought not be placed on data from electron microscopy simply because such cytologically exciting information has (suddenly) become available. At least three points may be made here: giving undue emphasis to ultrastructural information may be unfair in view of other (studied or unstudied) potentially just as useful sets of character data; until the presence, absence, or variability of a given fine structural feature in neighboring groups has been determined, its comparative taxonomic worth must be viewed as being at best indeterminate and tentative; and all data from electron microscopy may not be of equal value in phylogenetics, even when considering the species within a single genus.

Major Differences in New Scheme

Historically, as I have recently pointed out in some detail elsewhere (Corliss, 1974a), one may recognize four principal periods in the development of phylogenetically oriented systems of classification of the Ciliophora. The first and second periods (see Table I), which I have named the Age of Discovery and the Age of Exploitation, have essentially the same bases: easily discernible differences in the structural diversification and the topological distribution of the externally borne cilia and compound ciliary organelles. Still today these are valuable taxonomic landmarks, especially as "key" characters. The major significant difference between the dominant schemes of the 1880's and the 1930's is in the greater number of taxa in the latter. This is directly related to the growth in the number of known species, many of the newer ones being forms strikingly different morphologically and often from previously unknown habitats; thus additional taxonomic categories at suprageneric levels were required to accommodate them.

Next came the Age of the Infraciliature, a period extending from about 1950 to 1970. Its dominant scheme of classification stemmed from that proposed by Fauré-Fremiet (1950a), as slightly expanded and modified in the first edition of this book (Corliss, 1961). As comparison of the right-hand column of Table I with that of the left-hand column of Table II will reveal, superficially the differences appear slight between the Kahlian and Faurean schemes. But actually, as discussed in Corliss (1961, 1974a), the changes were profound, related, first, to the use of infraciliary characters rather than the external ciliature and, secondly, to the application of new concepts of phylogenetic interrelationships based, in turn, on the hypothesized evolutionary significance of the infraciliature throughout the various taxonomic groups. Many of the conclusions drawn by Fauré-Fremiet and contemporaries are still in vogue today, and the use of methods of silver impregnation, practically indispensable in ciliate systematics, has, fortunately, become widespread.

The kinds of changes which have been effected or proposed for the post-Faurean or Corlissian scheme of classification adopted in this book are several in number (for discussion of the rationale behind them, see Chapter 3). As may be seen in Table II (and also Table III, in Chapter 4, in which names of all suprafamilial taxa are listed, including authorships and dates), the most obvious one is the great increase in total number of taxa involved. In a word, this is simply an obligatory reflection of our belated recognition of the marvelous diversity of groups within the phylum, a diversity with a greater distinctness among the major units than heretofore acknowledged. The identification of some of these "separatenesses" has been aided by discovery of hundreds of additional new species since 1960, but – more importantly – by ultrastructural evidences of allegedly deep-seated differences undetected or undetectable in earlier years. Thus the fourth, and current, period has been labeled the Age of Ultrastructure.

Significant revisions over the Faurean scheme are, briefly, these:

1. Recognition of three classes of ciliates, rather than only one, divisible further into some seven major subclasses, as compared to the two which are generally currently in vogue; and elevation of the whole assemblage to phylum, rather than subphylum, rank.
2. Removal of the entodiniomorphids from among the spirotrichs and relocating them close to the old trichostomes, on recognition of the nonmembranellar nature of their synciliary tufts and the presence of a vestibulum and a trichostome-like cytopharyngeal apparatus.
3. Full acceptance of the scuticociliates as an independent order, distinct from the hymenostomes *sensu stricto*; reduction of the old "Thigmotrichida" to a scuticociliate suborder, with removal of "rhynchodine" species to the new subclass of hypostomes (see below).
4. Overall reduction in the size of the old spirotrich assemblage, with the loss of the entodiniomorphids (see above) and the amalgamation – at the ordinal level – of the oligotrichs and the tintinnines; but with acceptance of four additional heterotrich suborders.
5. Expansion and radical change in the juxtaposition of the groups (especially the so-called "rhabdophorine" and "cyrtophorine" gymnostomes) formerly comprising the "lower holotrichs," with recognition of four distinct subclasses of a large class (the Kinetofragminophora). The first, the new gymnostomes *sensu stricto*, is divided into five orders; the second, the vestibuliferans, contains the old trichostomes proper (including the blepharocorythines), the entodiniomorphids, and the colpodids; the third, the hypostomes, merits separate consideration (see below). The fourth subclass, the suctorians, is accorded a more independent status than it held in the Faurean scheme but not as much as it had in older (and some modern) classifications; three suctorian suborders are recognized on the basis of morphogenetic data.
6. Establishment of a novel subclass, the hypostomes, resurrecting Schewiakoff's old "tribe" but greatly expanding the taxon in concept, size, and composition. Six groups are given ordinal status within the assemblage, four with their own suborders. Although interrelationships are not entirely clear, the separate orders embrace the old cyrtophorines (a very large group), the nassulids (including the microthoracines), the synhymeniids (presumed to be the most primitive group), the chonotrichs (separated at a still higher level by some workers), the enigmatic rhynchodids, and the long-baffling apostomes.

Less drastic yet still significant alterations in the Faurean scheme – essentially the immediate predecessor of the Corlissian classification endorsed here – are explained in appropriate locations in subsequent chapters.

The "opalinid infusorians," incidentally, continue to be excluded from the ciliate assemblage, a high-level classificational decision first proposed some 25 years ago and one with which few protistologists would quarrel today, despite the many preceding decades (following the pronouncements of the influential worker Metcalf, 1923, 1940) of inclusion of these "superflagellates," as "protociliates," among the truly ciliophoran taxa (for selected references with emphasis on the history of this once controversial problem, see Corliss, 1955, 1960a, 1961, 1977b; Earl, 1971; Grassé, 1952; Honigberg et al., 1964; Kozloff, 1972; and Wessenberg, 1961).

Finally, brief mention may be made here of the numerous nomenclatural problems whose solutions have been proposed, in place, throughout the book, especially in Part II. The matter is complicated by the fact that many such actions are beyond the jurisdiction of the International Code of Zoological Nomenclature, because the names involved are associated with suprafamilial taxa (for further treatment, see Chapter 19).

Brief Guide to Remaining Chapters

The general plan of organization of this book may be realized from a glance at the table of contents, but a brief guide is also in order here.

Part I treats general aspects of the subject, though in some detail, with special attention to basic considerations. It outlines the rationale for the new system of classification, describes or characterizes the major groups of ciliates as the phylum is now reconstituted, and considers evolutionary and phylogenetic interrelationships. Many direct references to the pertinent literature are selectively cited in these chapters, most of them occurring in sections conveniently separated from preceding text pages (concerned with characterizations, comparative diagnoses, etc.) by a set of asterisks (* * * * *). Following the present Chapter 1, the general reader may wish to peruse Chapters 4 and even 17 (overall description of the ciliates and condensed treatment of their presumed evolution, respectively) before referring to Chapter 2 (essentially an illustrated glossary of specialized terms) or turning to Chapters 5–16 (characterizations of the principal taxonomic groups, with a few figures of "representative" forms belonging to the orders and suborders).

Part II, pragmatically the "heart" of the book, is an illustrated classification and brief characterization of all taxa at the level of family and above, with lists of recognized genera, an indication of numbers of included species, and a brief treatment of nomenclatural problems (Chapter 20). Chapter 20 itself is preceded by two short chapters (18 and 19) setting the stage for its better understanding. For the sake of economy of space, overlapping with material already available in Chapters 5–16 has been held to a minimum. [An unexpected "space squeeze" (after completion of the first draft of the book) thwarted my original plan of having at least one figure for each genus; but > 1,000 drawings, representing every major taxon well, were salvaged.]

Part III (Chapters 21, 22) serves as a guide essentially to the research literature (although some textbooks and other references are also listed) and includes direct and full citation to > 2,900 books, papers, review articles, and monographs concerned in the main with ciliates. Photographs of some 185 protozoologists or cell biologists, ciliophoran experts of times past and current, are presented here, too. Some 67% of the references given bear dates more recent than 1959; but the reader is not obliged to consult the first edition (Corliss, 1961) for citation to the "classic" and most important literature of earlier decades and even bygone centuries, for it is also included in the bibliography of the present volume. The main index is limited to the scientific names (> 2,350 are involved!) of taxa. But the glossary of Chapter 2 contains > 700 entries, often identified with specific groups; and I have appended to the Systematic Index a special "Host Index," a brief guide to other organisms with which many ciliates are symbiotically associated.

Because the overall subject of this book is so vast, and space so limited, I have been obliged repeatedly (if unwillingly) to condense material and even introduce "shortcuts" of various kinds to which I hope the reader will take kindly, or, at least, charitably. For example, I have often taken the liberty of using a generic name *as if it were a species*; indeed, specific names are deliberately rarely used anywhere. And I may refer to a given group or taxon by rank, category, or name, or even with reference to the concept behind such a group, *interchangeably*, although I am aware of the differences.

On the immediately following pages are tables of classification which may be usefully compared with the systems appearing at the end of Chapter 4 and throughout Chapter 18.

Table I. Early (pre-1950) major systems of ciliate classification*

Bütschlian Era**
(1880-1930)

Class INFUSORIA

- *Ciliata*
  - Holotricha
    - **Gymnostomata**
    - **Trichostomata**
    - **Astomata**
  - Spirotricha
    - **Heterotricha**
    - **Oligotricha**
    - **Hypotricha**
    - **Peritricha**
- *Suctoria*

Kahlian Era
(1930-1950)

Subphylum CILIOPHORA

- Ciliata
  - *Protociliata*
    - Opalinata
  - *Euciliata*
    - Holotricha
      - **Gymnostomata**
        - Prostomata
        - Pleurostomata
        - Hypostomata
      - **Trichostomata**
      - **Apostomea**
      - **Hymenostomata**
      - **Thigmotricha**
        - Stomodea
        - Rhynchodea
      - **Astomata**
    - Spirotricha
      - **Heterotricha**
      - **Ctenostomata**
      - **Oligotricha**
      - **Tintinnoinea**
      - **Entodiniomorpha**
      - **Hypotricha**
    - Peritricha
      - **Mobilia**
      - **Sessilia**
    - Chonotricha
- Suctoria

*Classes are indicated in either capital letters or in large boldface; subclasses, in italics; orders, in large Roman; suborders, in boldface; and "tribes," further indented, in Roman type.

**It should be carefully noted that Bütschli (1887-1889) himself originally proposed a scheme which differed slightly — but significantly — from that shown (see Corliss, 1962a; Jankowski, 1967a). But later workers in the period re-arranged it so that it came to resemble the form presented in a generalized way here. In all cases, the number of major groups remained essentially the same.

Table II. Faurean classification and system (Corlissian) adopted in this book*

Faurean Era
(1950-1970)

Subphylum
CILIOPHORA

- **Ciliata**
  - *Holotricha*
    - Gymnostomatida
      - Rhabdophorina
      - Cyrtophorina
    - Suctorida
    - Chonotrichida
    - Trichostomatida
    - Hymenostomatida
      - Tetrahymenina
      - Peniculina
      - Pleuronematina
    - Astomatida
    - Apostomatida
    - Thigmotrichida
      - Arhynchodina
      - Rhynchodina
    - Peritrichida
      - Sessilina
      - Mobilina
  - *Spirotricha*
    - Heterotrichida
      - Heterotrichina
      - Licnophorina
    - Oligotrichida
    - Tintinnida
    - Entodiniomorphida
    - Odontostomatida
    - Hypotrichida
      - Stichotrichina
      - Sporadotrichina

Post-Faurean Era
(1970-)

Phylum
CILIOPHORA

- **Kinetofragminophora**
  - *Gymnostomata*
    - Primociliatida
    - Karyorelictida
    - Prostomatida
      - Archistomatina
      - Prostomatina
      - Prorodontina
    - Haptorida
    - Pleurostomatida
  - *Vestibulifera*
    - Trichostomatida
      - Trichostomatina
      - Blepharocorythina
    - Entodiniomorphida
    - Colpodida
  - *Hypostomata*
    - Synhymeniida
    - Nassulida
      - Nassulina
      - Microthoracina
    - Cyrtophorida
      - Chlamydodontina
      - Dysteriina
      - Hypocomatina
    - Chonotrichida
      - Exogemmina
      - Cryptogemmina
    - Rhynchodida
    - Apostomatida
      - Apostomatina
      - Astomatophorina
      - Pilisuctorina
  - *Suctoria*
    - Suctorida
      - Exogenina
      - Endogenina
      - Evaginogenina

- **Oligohymenophora**
  - *Hymenostomata*
    - Hymenostomatida
      - Tetrahymenina
      - Ophryoglenina
      - Peniculina
    - Scuticociliatida
      - Philasterina
      - Pleuronematina
      - Thigmotrichina
    - Astomatida
  - *Peritricha*
    - Peritrichida
      - Sessilina
      - Mobilina

- **Polyhymenophora**
  - *Spirotricha*
    - Heterotrichida
      - Heterotrichina
      - Clevelandellina
      - Armophorina
      - Coliphorina
      - Plagiotomina
      - Licnophorina
    - Odontostomatida
    - Oligotrichida
      - Oligotrichina
      - Tintinnina
    - Hypotrichida
      - Stichotrichina
      - Sporadotrichina

*Classes are indicated in large boldface; subclasses, in italics; orders, in small boldface; and suborders, in Roman type.

Chapter 2

Glossary of Terms and Concepts useful in Ciliate Systematics

With the increasing contribution of data from other fields to the taxonomy of ciliates and the growing interest of biologists of all persuasions in these microorganisms, we ought today to be familiar with a far greater range of terms than was required even 15–20 years ago. The information offered below not only provides, in the aggregate, a "thumbnail sketch" of most aspects in the overall biology of ciliates but also permits use of the terminology in succeeding chapters without the need to reexplain it there. My treatment is not exhaustive – and many commonly known anatomical, cytological, and ecological words are purposely omitted – but the list is >10 times the length of my still rather widely cited "glossary" of 18 years ago (Corliss, 1959), which contained 65 terms; and I am up-dating and correcting those as well as including a myriad of additional ones, many of which were completely unknown at the time of the first edition of this book (Corliss, 1961). A few terms have been established internationally (de Puytorac, 1970b).

An attempt has been made to keep the definitions or explanations succinct; but often I have felt compelled to add a further brief descriptive comment or two, though amplification has simply had to be restricted because of space considerations. Almost always I have included information identifying the taxonomic group or groups of ciliates which possess or show the character or trait being described, for the reader's ease in relating the term to material in subsequent chapters. Cross-referencing is frequently employed, either directly (by "see such-and-such a term") or indirectly (by italicizing selected words in the definition). I have tried to point out controversies, present alternative meanings, give synonyms, etc., although my own preferences will also be apparent, particularly with respect to features in the oral area *sensu lato*.

The bulk of the terms, not surprisingly, are of a morphological or cytological nature; and, within that broad category, they are often based on electron microscopical data, quite appropriate to the "Age of Ultrastructure" (Corliss, 1974a). A number of such features are among those illustrated in the plates of figures at the end of the chapter. Structures chosen for inclusion there are indicated by a pair of stars (★★) and, if labeled, by a "legend" abbreviation [in brackets].

Not wholly neglected are terms from the impinging fields of general ecology, physiology, parasitology, marine biology, genetics, and phylogenetics. Processes and phenomena, as well as structures and functions – and dynamic as well as "static" characteristics – are included; and a number of hypotheses, principles, or concepts are briefly considered, especially relevant tenets or terms from areas of morphogenesis, evolution, vertebrate systematics, and even nomenclature.

The principal dilemma which has arisen with respect to morphological features now being investigated by ultrastructural approaches is that many of the "users" of such characteristics (e.g., field ecologists who may be including protozoan material – which must be properly identified – in their surveys or collections) need to recognize them but do not have recourse to electron microscopical equipment. Thus on the following pages I have tried to describe such features adequately but without undue emphasis on fine structure, at the risk of possibly offending some bench workers in the field of modern cell biology.

Purposely, no citations to the literature are made in this particular chapter (beyond this brief introduction), though it is obvious that I owe much to the scores of workers who have used the terminology, except for that newly introduced, which I am attempting to define or explain here. All such works are included in the bibliography (see Chapter 22); and they are cited appropriately in various chapters, often in association with the particular (genera of) organisms manifesting the structures or characteristics in question.

This glossary serves, in effect, as a kind of "subject index" to the book.

Aboral: away from the *oral area*; in ciliatology almost always used in the most extreme sense, meaning at the opposite (usually antapical) pole from the (other) end (usually apical) of the body bearing the mouth; but – as in the case of peritrichs – the aboral pole is not necessarily the posterior pole of the organism, functionally and/or morphologically and/or evolutionarily.

Abyssal: pertaining to the great depths of the ocean well beyond the continental shelf.

Acellularity Concept: once (and sporadically still) popular hypothesis that protozoa, being individually complete (yet organized without tissues) cannot be cellular and thus must be considered noncellular or acellular organisms; but it is now widely recognized that setting such eukaryotic cells as ciliates – notwithstanding their complex subcellular organization and extracellular specializations – apart from those of the "higher" metazoan groups is a decision basically neither defensible on (ultra)structural grounds nor judicious from a comparative evolutionary point of view; "cell" and "organism" need not be thought of as mutually exclusive terms.

Acetabulum: term rarely used in ciliatology; see **Sucker**.

Aciliferous: see **Nonciliferous**.

Actinophore: structure bearing several or a bundle (or *fascicle*) of *suctorial tentacles*; characteristic of certain suctorians.

Adhesive Disc: thigmotactic cup-shaped organelle at the *aboral pole* of mobiline peritrichs and some other ciliates (e.g., some spirotrichs) used for attachment to the substratum (usually the surface of another organism serving as host). ★★ [AD]

Adhesive Organelle: term often restricted to a secretory structure responsible for or structurally involved in production of a substance (other than cilia or some ciliary derivative) allowing the organism possessing it to adhere or attach to the substratum (e.g., the *podite* of cyrtophorid hypostomes); but also see **Holdfast Organelle**. ★★ [AO]

Adoral Ciliary Fringe: see **Frange**. ★★ [ACF]

Adoral Ciliary Spiral: see **Adoral Zone of Membranelles**. ★★ [ACS]

Adoral Zone of Membranelles: orderly arrangement of three or more *membranelles sensu lato* serially arranged along the left side of the oral area (typically in a *buccal cavity* or *peristome*); the *AZM* is to be found among oligohymenophoran and polyhymenophoran ciliates; in its conspicuous form in peritrich and many spirotrich species, it has also been termed the *adoral ciliary spiral*. ★★ [AZM]

Adult: generalized term; in ciliates it is – depending on the situation – the mature form, the *parental form*, the interfissional form, the sessile or sedentary form, the *tropbont*, etc.

Afferent Canal: cytoplasmic channel (usually several) transporting excreted fluid from the *spongiome* to a *contractile vacuole*; also called a pulsating, nephridial, collecting, or radial canal.

Aire Sécante: see **Système Sécant**.

Akontobolocyst: term used by some workers as a synonym of *spindle tricbocyst*.

Algivorous: feeding on algae; see also **Macrophagous** and **Microphagous**.

Alpha Membranoid: see **Membranoid**.

Alveolus, Pellicular: flattened vesicle or sac, bounded by a *unit membrane*, lying just beneath the surface or *plasma membrane* of the cell (organism) and above the *epiplasm*; typically occurs in pairs in a given *kinetosomal territory*; also known as a *cortical vesicle*. ★★ [PA]

Amacronucleate: without a *macronucleus*; rare, unnatural, unstable condition, realizable only experimentally (e.g., in *Paramecium*).

Ambihymenium: condition of having oral ciliary "membranes" completely surrounding the mouth-area; claimed by some workers to be the situation obtaining in a number of the hypostome kinetofragminophorans.

Amicronucleate: without a *micronucleus*, whether the condition has been brought about naturally or experimentally (e.g., in *Tetrabymena*).

Ampulla, Secretory: *glandular* organelle, generally multiple in number, in some cyrtophorid hypostomes which produces a thigmotactic substance or structure (see **Adhesive Organelle**); but the term is also used for the *collecting canal* (or its enlarged distal end) feeding into the contractile vacuole of a number of ciliates (e.g., certain peniculine hymenostomes): see **Afferent Canal**. ★★ [AS]

Ampullocyst: kind of *mucocyst* found subpellicularly in certain karyorelictid gymnostomes.

Anarchic Field: group of *barren* or *nonciliferous kinetosomes*, in an allegedly (now some doubt) dis- or unorganized array, giving rise to the infraciliary bases of the *buccal organelles* (e.g., in some hymenostomes); it is a transient *primordial field* or ciliary *anlage* in an early stage of (generally parakinetal) *stomatogenesis*. ★★ [AF]

Anisogamonts: see **Gamonts**.

Anisotomic: see **Fission**.

Anlage: *primordium*; a developing, differentiating, or even presumptive structure or organelle; usable with many a preceding modifier: nuclear, cytoplasmic, cortical, oral, somatic, ciliary, etc.; in ciliate morphogenesis, it is often a group of kinetosomes – for example, see **Anarchic Field**, **Germinal Row**, and **Scutica**.

Annulus: used variously: for example, (1) for the nonliving portion (also called the *sheatb*) of the contractile stalk found in some peritrichs which surrounds the central membrane-bound myofibrillar bundle or *spasmoneme*; (2) for band(s) of fibrous, filamentous, or dense amorphic material encircling the *cytopbaryngeal apparatus* of certain gymnostomes and hypostomes at various levels; and (3) for various ring-like structures or markings in general, including the *pellicular striae* on the zooid of certain peritrichs. ★★ [annular band, ABd]

Antecorpy, Rule of: new somatic kinetosomes always arise anterior to old ones (demonstrated to hold true in at least the case of *Paramecium*).

Apical Funnel: distally drawn-out anterior end of many chonotrichs, sometimes lined with *atrial ciliature* and leading posteriorly to the cytostome; ontogenetically and phylogenetically, the body's ventral surface. ★★ [ApF]

Apokinetal: type of *stomatogenesis* in which the sudden-appearing kinetosomes involved – an *anlage*, in effect – have no apparent pre-association with either somatic kineties or the parental buccal apparatus, as in entodiniomorphids and many spirotrichs; it was formerly known as the *de novo kinetosomal* mode of stomatogenesis. ★★

Apomorph: term used by cladists and some phylogeneticists to designate any *derived* character; for example, one occurring or arising at a branching point and carried through one descending group in a phyletic lineage; a derived character which is (thus) less like (has less resemblance to) the ancestral condition of the attribute in question; admittedly a *relative* term, but to be contrasted with *plesiomorph*.

Arboroid Colony: *zooids* disposed in a dichotomous branching or tree-like manner, interconnected by either stalks or loricae (e.g., as shown by many sessiline peritrichs); *dendroid* and *dendritic* are synonyms of arboroid. ★★

Argentophilic: silver-loving, taking silver stains positively; see Silver-impregnation Techniques.

Argyrome: whole system of pellicular or cortical argentophilic structures or markings revealable by application of techniques of *silver impregnation* (noting that the protargol method may blacken many additional deeper organelles or surfaces, such as the nuclei, kinetodesmata, microtubular ribbons, etc., and even the cilia themselves); often may be indication of points or lines of contact of inner and outer alveolar membranes; the argyrome is *not* identical with the *infraciliature*, although superficially it shows overlapping in some components (e.g., the all-important *kinetosomes* are part of both systems); highly useful in taxonomy, comparative morphology, and morphogenetic studies; principal synonyms are *silverline system*, *Silberliniensystem*, and *neuroformative System*; see Silver-impregnation Techniques. ★★

Astomy: condition of being mouthless, without a cytostome, whether naturally or experimentally derived; one entire order, the Astomatida, exhibits this naturally.

Atrial Ciliature: type of cilia or ciliary organelles found in or associated with the *atrium* (thus limited to occurrence in certain hypostome kinetofragminophorans); relatively simple in organization, with infraciliary bases of kinetofragmental origin; the only cilia in some chonotrichs, where it may line (part of) the *apical funnel*. ★★ [AtC]

Atrium: term generally reserved for the shallow depression found around or in close proximity to the cytostome of certain hypostomes; typically contains cilia of a special type or origin (see Atrial Ciliature). ★★ [At]

Attachment Disc: see Adhesive Disc.

Attachment Knob: enlarged distal end of a *suctorial tentacle* or of the *sucking tube* of rhynchodid hypostomes; adheres to or embeds itself in the body of a prey or host cell; when the knob is particularly prominent, the tentacle is said to be *capitate*.

Attachment Organelle: nonspecific name for all sorts of stalks, filaments, tentacles, knobs, hooks, crochets, spines, mucrons, suckers, discs, or even thigmotactic ciliary fields used in a temporary or permanent manner to attach an individual (or a colony) to some living or inanimate substratum; see Holdfast Organelle. ★★

Aufwuchs Community: see Periphyton Community; but the present term is widely preferred by ciliatologists.

Autogamy: self-fertilization type of *sexual phenomenon*; results in extreme inbreeding, since only single organisms are involved; believed to increase the longevity of a clonal population (best known in the hymenostome *Paramecium*); when autogamy occurs in each member of a paired set of (temporarily fused) organisms, the phenomenon is sometimes termed *cytogamy*; the process is always followed by *fission(s)* of the organism.

Autonomous: now discarded term, along with *semi-autonomous*, for a mode of *stomatogenesis*; see Buccokinetal.

Auxomorphy: morphological-evolutionary relationship between two forms, in a postulated phylogenetic lineage, which is shown in the sameness of certain structures possessed by both but with an apparent increase in the size or number of component parts comprising those structures (by the process of *polymerization*) in one member of the pair (e.g., compare *Dexiotricha* and *Loxocephalus*).

Axenic Culture: laboratory growth of organisms in a "pure" (though not necessarily chemically defined) medium; that is, "without strangers" – no other living organisms of any kind can be present in the clonal culture of the strain or species under study.

Axoneme and Axosome: see Cilium. ★★ [Axn, Axs]

AZM: see Adoral Zone of Membranelles. ★★

Bactivorous: feeding on bacteria; see also Microphagous, essentially a synonymous term.

Barren Kinetosome: basal body not associated (always *or* at a given time) with a cilium; exhibition of a *nonciliferous* (or *aciliferous*) state; a particularly common condition of certain kinetosomes during some stages of *stomatogenesis* in many ciliates.

Basal Body: *kinetosome*, blepharoplast (of flagellates), centriole, etc.; a popular usage of the term is as a synonym of the kinetosome of ciliated protozoa. ★★ [BB]

Basal Disc: see Adhesive Disc.

Basal Fibers: see Basal Microtubules.

Basal Granule: now discarded (as inappropriate) name for *kinetosome* or *basal body*.

Basalkörper: see Basal Granule; Basal Plate: see Cilium. ★★ [BPl]

Basal Microtubules: set, group, ribbon, or bundle (though very few in number) of *microtubules* extending along the left side of somatic kineties at the level of the base (proximal end) of the kinetosomes; found in a number of oligohymenophoran ciliates; sometimes confounded with *subkinetal microtubules*. ★★ [BMt]

Bell: body proper (minus the *stalk*) of many sessiline peritrichs; see Zooid.

Benthic: pertaining to the bottom or near-bottom of an ocean, sea, or (generally large) lake; often implied by the term are the bottom sediments at the greatest depths of the body of water, but bottom-dwelling forms of marine life are also described by the term.

Beta Membranoid: see Membranoid.

Binary Fission: see Fission.

Biogenetic Law: ancestral resemblance during *ontogeny*; recognition, in a broad sense, that some characters or structures seen during the development of an organism may be generally reminiscent of some structure or character known to be possessed by members of an (alleged) ancestral group, in either ontogenetic or adult stages of that predecessor, and often in a more or less modified form (e.g., as proposed in Sewertzoff's principles of *phylembryogenesis*); *to this highly qualified extent and with extreme caution*, Haeckel's old aphorism, "ontogeny recapitulates phylogeny," may be applied to some phylogenetic-systematic problems in ciliatology; a synonym is the *Law of Recapitulation*; see also **Morphogenesis** and **Ontogeny**.

Bipolar Kinety: see **Kinety**; basically, fundamentally, primitively, at least evolutionarily, kineties are assumed to be bipolar – running from pole to pole of the organisim without interruption, without circling the body transversely, without going over the top and down the other side, etc.; in fact, there are many exceptions, but they may generally be considered secondary modifications of the basic original plan of cortical organization in ciliates – and it is noteworthy that the *Rule of Desmodexy* is never upset. ★ ★

Birth Pore: opening or site of emergence of an internally budded *larval form* during the budding process of *reproduction* in some suctorians. ★ ★ [BPor]

Blepharismin: photosensitive cytoplasmic pigment ("pink" in color) found in various species of the heterotrich *Blepharisma*; formerly called *zoopurpurin* (not to be confused with *blepharmone* or *blepharismone*: see below).

Blepharmone: *conjugation*-inducing glycoprotein recently isolated from the heterotrich *Blepharisma*; not to be confused with the pigment *blepharismin* nor with a second *gamone*, *blepharismone*.

Border Membrane: finely striated circumferential band (sometimes called a corona), with fibers, proteinaceous *radial pins*, etc., which is associated with and reinforces the *adhesive disc* of mobiline peritrichs. ★ ★ [BM]

Boring Apparatus: see mention under **Rostrum**.

Bristles: common name for long (or occasionally very short), generally single (or several isolated), resilient cilia of several kinds and functions (sensory, tactile, thigmotactic, locomotor, attachment, etc.) occurring on one or more parts of the body of various ciliates; see **Brosse**, **Caudal Cilium**, **Saltatorial Cilia**, **Sensory Bristle**. ★ ★

Brood Pouch or Chamber: temporaty (in suctorians) or permanent (in chonotrichs) internal chamber or cavity formed by invagination of the pellicle and within which *internal budding* occurs, producing the *larval form* in the life cycle; preferably called a *crypt* in chonotrichs; also known as an *embryo sac* or *marsupium*. ★ ★ [BPch]

Brosse: distinctive "brush" of cilia arising from specialized short kineties, or *kinetal segments*, often oriented obliquely to the body axis on the anterodorsal surface of the nondividing organism; exact infraciliary ultrastructure and function (sensory?) unknown; characteristically found in prorodontine gymnostomes; a primordium may be involved in its reproduction during fission of the organism.

Brow Kinety: see **Ophryokinety**.

Buccal Apparatus: whole complement of *compound ciliary organelles* the bases of which are located in or associated with the *buccal cavity* or *peristome* in oligohymenophoran and polyhymenophoran ciliates; includes *paroral membrane(s)* and *membranelles sensu lato* (plus homologues and possible nonhomologues of these structures) and their infraciliary bases (= *buccal infraciliature*); the whole apparatus functions primarily in food-getting, sometimes in locomotion. ★ ★ [BApp]

Buccal Area: region around the mouth in ciliates which possess a *buccal apparatus* (oligo- and polyhymenophorans); strictly speaking, *not*, therefore, a synonym of the much broader and more generalized term *oral area*.

Buccal Cavity: pouch or depression, typically quite deep though sometimes secondarily flattened out or everted, often at or near the apical end of the body and/or on the ventral surface; contains (the bases of) the *compound ciliary organelles* and inwardly leads ultimately to the organism's cytostome-cytopharyngeal complex, sometimes via a specialized portion of itself known as the *infundibulum*; especially characteristic, under the name "buccal cavity," of many oligohymenophorans, but it is considered to be the structural equivalent of the *peristome* of the polyhymenophorans. ★ ★ [BC]

Buccal Ciliature: see **Buccal Apparatus**.

Buccal Infraciliature: see **Buccal Apparatus**.

Buccal Membranelles: see **Membranelle**.

Buccal Organelles: see **Buccal Apparatus**.

Buccal Overture: outer or distal opening or aperture of the *buccal cavity*, though essentially unrecognizable (i.e., disappears) when the latter is everted or flattened out; typical of and easily visible in hymenostomes such as *Paramecium* and *Tetrahymena*. ★ ★ [BO]

Bucco-anal Striae: see **Director-meridian**.

Buccokinetal: type of *stomatogenesis* in which (at least some of) the fields of kinetosomes involved – as the ultimate *anlage* – have an apparent origin in the (bases of) organelles of the parental buccal apparatus *sensu lato*, as in many hymenostomes (including scuticociliates), peritrichs, and many spirotrichs; formerly known as the *autonomous* and/or *semi-autonomous* mode(s) of stomatogenesis. ★ ★

Bud: filial product of a single or multiple fission characteristically much smaller than the *parental (maternal) form* and typically quite unlike it in both form and function; generally ciliated, playing a migratory role in the organism's life cycle; results from a variety of methods of *budding*; it is a form occurring universally among suctorians and chonotrichs, not uncommonly in rhynchodid hypostomes, some peritrichs, and some apostomes, and occasionally in other groups, including even a species of hypotrich. ★ ★ [Bud]

Budding: binary (though typically *anisotomic*) or multiple method of *reproduction*, producing a single (*monogemmic*) or two or more (*polygemmic*) *filial products*, simultaneously or in succession; the phenomenon (also known as *gemmation*) is classifiable into several types: modified transverse fission, *strobilation*, *endogemmy* (endogenous or internal: a subtype is *cryptogemmy*), *exogemmy* (exogenous or external), *evaginogemmy* (evaginogenous or evaginative), plus additional refinements of some of these (*viz.*, circumvaginative, inva-circumvaginative, invaginative, pseudo-transverse, semi-circumvaginative, and semi-invaginative); budding is typical of suctorians and chonotrichs, but characteristic also of some other species (see **Bud**); here it is not considered to embrace *palintomy* (where perhaps strobilation also belongs) or *catenoid colony-formation*, although distinctions are not always clear-cut. ★ ★

Cannibalistic: see **Carnivorous**.

Capitate Tentacle: *suctorial tentacle* enlarged at its distal end; see **Attachment Knob**.

Capitulum: amorphous material capping the proximal ends of the *nematodesmata* in some dysteriine cyrtophorid hypostomes; these *maxillae* or *teeth*, sometimes quite prominent in appearance, may be enclosing kinetosomes responsible for production of the nematodesmata. ★ ★ [Cap]

Capsules Torquées: see mention under **Tentaculoid**.

Carnivorous: meat-devourer; eater of or feeder on some other or the same (= cannibalistic) ciliate, or some zooflagellate, or some metazoan organism; generally refers to a *holozoic* and predatory, not a *parasitic* or even *histophagous*, mode of life; it is particularly common among various gymnostomes.

Case: see **Lorica**; case is a synonym popular with some ciliatologists.

Catenoid Colony: line or chain of individuals brought about by repeated (and generally *anisotomic*) binary fissions without separation of the resulting *filial products*; a condition commonly found in some astomes, occasionally in certain apostomes, are rarely in species of other groups; sometimes *strobilation* is involved. ★ ★

Cathetodesma: periodically striated, subpellicular fiber, transversely oriented, arising from or near the anterior right region of the posterior somatic kinetosome (of a pair), cutting to the left toward the next row of kinetosomal pairs; found only in certain clevelandelline heterotrichs; a short *kinetodesma*, arising from nearly the same location, is also present in the same ciliates. ★ ★ [Cd]

Caudal Cilium: distinctly longer *somatic* cilium (occasionally more than one) at or near the posterior or antapical pole, sometimes used in temporary attachment to the substratum; it arises from a *PBB-complex*. ★ ★ [CC]

Caudalia: ciliary tufts (of *syncilia*), on short nonretractable stalks, at the posterior or antapical pole of many cycloposthiid entodiniomorphids; may be two or more such structures, depending on the species.

Cavernicolous: cave-dwelling; ciliates speleologically inclined!

Cell Anus: see **Cytoproct**.

Cell Division: see **Fission**.

Cell Envelope: see **Cortex**.

Cell Mouth: see **Cytostome**; but for usage in a very broad and general way, see **Oral Area**.

Chondriome: total *mitochondrial* complex of a cell (or ciliate).

Ciliary Corpuscle: see **Kinetosomal Territory**, now the more popular term for the same structural unit.

Ciliary Girdle: see **Locomotor Fringe**; in a general way, the term is restricted to peritrichs, yet it is also used for any encircling band of somatic ciliature (e.g., as seen in *Didinium*-like gymnostomes). ★ ★ [CG]

Ciliary Meridian: see **Kinety**; but emphasis in the usage of this term has been on the *argentophilic* line (= primary meridian) coursing *above* the kinetosomes, with recognition of secondary (and even tertiary) meridians located interkinetally; visible with *silver techniques* in a great many ciliates, but historically notable in the tetrahymenine hymenostomes. ★ ★ [CM]

Ciliary Organelle: any specific structure, *oral* or *somatic*, compounded of cilia (or cilia-derivatives); see **Ciliature** and **Compound Ciliature**.

Ciliary Rootlet: generally rare in ciliates; sometimes formerly used to include various structures (fibrillar or microtubular in nature) arising from or associated with kinetosomes, particularly the *nematodesmata*; a special case is represented by the striated fibers proceeding from the vicinity of certain kinetosomes and plunging deep into the cytoplasm (direction centripetal), as found in several peritrichs; a little-used synonym is *kinetorhiza*.

Ciliary Row: longitudinal (ordinarily) line of *somatic cilia*; see **Kinety**.

Ciliary Territory: see **Kinetosomal Territory**.

Ciliary Wreath: see **Ciliary Girdle**.

Ciliatology: general term for the study of ciliates; the investigators are therefore *ciliatologists*.

Ciliature: very general term; see definitions under terms denoting specific kinds of ciliature: *atrial*, *buccal*, *circumoral*, *cirral*, *compound*, *coronal*, *oral*, *perioral*, *peristomial*, *perizonal*, *prebuccal*, *scopulary*, *simple*, *somatic*, *synciliary*, *thigmotactic*, and *vestibular*.

Ciliferous: cilium-bearing; used in reference to kinetosomes which regularly produce cilia and also to the cilium-bearing stage of those which have cilia only at some stage(s) in the life cycle of the organism and not at others (at which time they are *nonciliferous*, *naked*, or *barren*).

Ciliospores: now outmoded word for certain tomites arising by *palintomy* (e.g., in the hymenostome *Ichthyophthirius*).

Cilium: cylindrical organelle (diameter *ca.* 0.26 µm; length variable, often 7-10 µm) arising from a kinetosomal base and projecting from the body surface of an organism though covered with the common *plasma membrane*; internally complex, with an axoneme comprised ultrastructurally of microtubular structures in a "9 + 2" arrangement (the nine doublets continuous with the kinetosomal microtubules), etc.; typically disposed over the body in longitudinal rows, though with many exceptions (in "*compound*" forms – see appropriate terms under Ciliature – they occur both on the body, e.g., as *cirri*, and in oral areas, e.g., as *buccal ciliature*); may function in locomotion, especially, with diversity of beating patterns, and in feeding, attachment, sensing, etc.; "*simple*" cilia are present on a wide scale, though scattered, rare, or missing in some of the so-called higher spirotrichs and (along with compound ciliature) entirely absent in one (rarely, all) stage(s) of the life cycle in some kinetofragminophorans; various kinds of specialized cilia are recognized: *caudal*, *clavate*, *marginal*, etc.; two very rarely used synonyms which were proposed to supply a single all-inclusive term for "cilium" and "flagellum" are *pecilokont* and *undulipodium*. ★ ★ [C]

Circumoral Ciliature: line, circle, or band of essentially *simple somatic ciliature* encircling (periorally) all or part of the apical end (including the cytostome) of the body of a number of gymnostomes; basically organized in pairs (but not *dyads*) of kinetosomes (only one of which is typically ciliferous) which also comprise the anterior extremities of the more or less regularly arranged somatic kineties (or, occasionally, of extra, interpolated kinetal segments); variations exist, particularly at the level of the infraciliature, and these are of taxonomic value.

Circumoral Connective: fibril-like line seeming to encircle the buccal overture; a silverline artifact, but of some value, along with other parts of the *argyrome* in general, in the comparative taxonomy of such forms as the tetrahymenine hymenostomes. ★★ [CoC]

Circumoral Kineties: name sometimes used for the two posteriormost of the three oral *kinetofragments* found in cyrtophorid hypostomes anteriad to the complex cyrtos (in the interfissional stage).

Cirral Ciliature: see **Cirrus.**

Cirromembranelle: name used by some workers for parts of the highly organized *vestibular ciliature* of certain colpodid vestibuliferans.

Cirrus: kind of *compound somatic ciliature* typical, especially, of hypotrich polyhymenophorans, though not exclusively found there; a composite tuft of cilia, few to >100, functioning as a unit, though with no special enveloping membrane, and tapering distally or else fimbriate; its infraciliary kinetosomes are also interlinked and joined to other cirral bases by connecting fibers or tracts of microtubules; characteristically, a cirrus is a thick conical locomotor organelle, but some are also occasionally of aid in food-gathering; they occur in lines or in groups in definite patterns on the ventral surface of hypotrichs, with subtypes identifiable by their location; *viz.*, buccal, frontal, frontoventral, midventral, transverse (anal), caudal, and marginal (right and left). ★★ [Cir]

Cisternae: see mention under **Golgi Apparatus.**

Clathrocyst: cytoplasmic *extrusive organelle* in *Didinium* involved in production of the elaborate *mesocystic* layer of the cyst wall. ★★

Clathrum: see **Rhabdos**; total abandonment of the term clathrum (Latin for "lattice") is here proposed, as briefly explained under *rhabdos.*

Clavate Cilia: short immobile cilia lacking the central pair of microtubules in their axoneme; allegedly sensory in function; they occur in a number of ciliates, including several haptorid gymnostomes (e.g., *Didinium*); and they are present in the *scopula* of many peritrichs; also known as *stereocilia*; *Euplotes*' condylocilium = special case?

Clone: population of organisms established in culture from a single isolated individual.

Cnidocyst: special kind of *extrusome* generally found in certain dinoflagellates but now (also) reported from several species of karyorelictid gymnostomes.

Cnidotrichocyst: see **Toxicyst,** of which this term is a seldom used synonym.

Code of Nomenclature: see **International Code of Zoological Nomenclature.**

Collar: term used variously; in chonotrichs it is the neck area (when present) between the often flared apical end and the body proper; ciliate *loricae* also often have collars, and their presence or absence, shape, numbers, etc. are used as diagnostic characteristics in the taxonomy of the tintinnine polyhymenophorans. ★★ [Col]

Collarette: apical, peristomial lip in many sessiline peritrichs which circumscribes the retractable *epistomial disc*; it is equipped with a sphincter "muscle" (see Myoneme). ★★ [Colt]

Collecting Canal: see **Afferent Canal.**

Colonies: definition under major types: see **Arboroid, Catenoid,** and **Spherical.** ★★

Commensalism: very common kind of symbiotic relationship (*symbiosis*) in which the symbiont benefits by the association but the host does not particularly suffer; endo- and ectocommensals exist in many groups; the *ectocommensal* category *sensu lato* could include *epibionts* and *symphorionts*, typical forms in the life cycle of many attached or sessile ciliates; an *inquiline* may be considered a special kind of *endocommensal.*

Compound Ciliary Organelle: see *Compound Ciliature.*

Compound Ciliature: general term for all *ciliature* not comprised of single, separate, or isolated individual cilia or of simple pairs of somatic cilia; various kinds, of both somatic and oral or buccal origin, occur throughout the phylum, though notably above the level of the class Kinetofragminophora; they are particularly well developed in the spirotrichs (presumably arising, evolutionarily, by the process of *polymerization*) – consider, for example, the *cirri* and *membranelles* of that large taxonomic group. ★★

Concrement Vacuole: curious and quite complex subpellicular cytoplasmic inclusion, one to an organism, containing refractile grains (calcium carbonate crystals?), having no opening, and strengthened by surrounding microtubules; characteristic of certain gymnostome and trichostome endocommensals; function unknown, but considered as a kind of *statocyst* with *statoliths* – thus a balancing organelle? – by some workers; possibly homologous with the seemingly simpler *Müller's vesicle.*

Conjugation: reciprocal-fertilization type of *sexual phenomenon*; presumably occurs (successfully) only between members of differing mating types (e.g., as well known in the hymenostomes *Paramecium* and *Tetrahymena*); allegedly significant to both vitality of the clone and survival of the species, although the phenomenon is unknown (unobserved) in many ciliates from various groups; may involve *iso-* or *macro-* and *microconjugants*, with *temporary* (most widespread) or *total* (as in *all* peritrichs and chonotrichs) fusion of members of the pair; pre- and exconjugant stages are recognized; the process is always followed by *fission(s)* of the exconjugants.

Conocyst: very recently described novel *extrusome* in the cortex of the pleurostomatid gymnostome *Loxophyllum.*

Constellation of Characters Principle: use of characters multiple in number and from diverse approaches or fields in assessment of differences or similarities between or among groups of organisms under comparative taxonomic study; its application helps overcome biases and prevents the extreme splitting likely when only very few characters – or data from but a single field – are taken into account in drawing conclusions concerning phylogenetic and taxonomic relationships.

Contractile Vacuole: liquid-filled organelle (sometimes multiple), serving as an osmoregulator in the cytoplasm of nearly all ciliates; generally pulsates with a regular frequency (under natural conditions): grows (*diastole*) to a certain size and then "contracts" (*systole*), typically emptying its contents (dissolved "waste materials") to the exterior via one or more *pores*; the CV is more widespread in ciliates than the CYP (*cytoproct*); some workers prefer the synonymous term (*water*) *expulsion vesicle*, but I believe that this is an improper use of the term *vesicle*; I also consider *nephridial apparatus* an inappropriate synonym. ★ ★ [CV]

Contractile Vacuole Pore: minute permanent opening(s), with *argentophilic* rim(s) and reinforced by microtubular fibers, in the pellicle through which contents of the *contractile vacuole* are expelled to the outside milieu; CVP's are *corticotypic* structures characteristically stable in number and location and thus of diagnostic value in comparative taxonomy; also known as *expulsion vesicle pores* (but *vesicle* inappropriate here). ★ ★ [CVP]

Convergent Evolution: development of similar characters (generally morphological ones are implied) separately in two or more groups which do not share a close common ancestry, such characters coming about (and preserved by natural selection) through adaptation to similar ecological pressures or habitat features.

Corona: apical, cytostome-bearing extremity of the body of certain haptorid gymnostomes; often set off by longer cilia from an extensible posteriorly adjacent neck; but the term is also sometimes used for the *border membrane* of mobiline peritrichs.

Coronal Ciliature: term used in different ways, but most commonly refers to the circlet of relatively long cilia surrounding the apical cytostomal area (the *corona*) of various haptorid gymnostomes and located anterior to the extensible neck region of the body, at the ends of somatic kineties or isolated from them.

Cortex: in the broadest sense, the outer portion or "layer" of the ciliate body, sometimes termed the *cell envelope*; contains the *pellicle* and the *infraciliature sensu lato* and bears the cilia; its various openings, ridges, alveoli, ciliary kinetosomes, their fibrous and microtubular associates, etc. comprise the *corticotype* so useful in studies of both morphogenesis and systematics; mitochondria are in the cortex of many ciliates.

Cortical Vesicle: see **Alveolus, Pellicular**.

Corticotype: specific pattern, especially as made visible following application of a *silver-impregnation technique*, of cortical structures or organelles found to be characteristic of a given organism or population of organisms within a species.

Cristae: see mention under **Mitochondria**.

Crypt: see **Brood Pouch**; but this is the preferred term for use with chonotrichs; also occasionally employed in a more general sense for any cleft or depression, in the body or elsewhere. ★ ★ [Crp]

Cryptogemmy: see **Budding** and **Endogenous Budding**. ★ ★

Crystallocyst: minute, enigmatic (extrusible or not?) body, quite numerous in the cortex of the thigmotrichine *Conchophthirus*.

Cursorial: adapted to or specialized for running; true of some hypotrich *cirri*.

Cuticular Pores: see *Pellicular Pores*.

Cyrtocyst: type of short, curved *extrusome* found subpellicularly in the haptorid gymnostome *Didinium*.

Cyrtos: tubular *cytopharyngeal apparatus*, often *curved* (even reminiscent of a cornucopia), the walls of which are strengthened by longitudinally arranged *nematodesmata* derived from apically located kinetosomes and lined with extensions of *postciliary microtubules*; the nematodesmata may be interconnected and/or wrapped circumferentially by annular sheaths of diffuse fibrous material, an amorphous electron-dense substance which may form *capitula* proximally; contains no toxicysts; septa and specialized *phagoplasm* may be present; typical of members of the kinetofragminophoran subclass Hypostomata (including especially the "cyrtophorine gymnostomes" of older classifications); principal synonyms include *nasse* and *(cyto)pharyngeal basket*; of Greek derivation, the word literally means "curved" but also may be extended to imply "basket" or "cage," all three descriptively appropriate to its usage here; the cyrtos is to be compared with the *rhabdos* (recently inadvisedly called the *clathrum*, so here renamed), the other major type of cytopharyngeal apparatus recognized for kinetofragminophoran ciliates, allegedly less complex, noncurved, often containing toxicysts, and lined with *transverse* microtubules. ★ ★

Cyst: nonmotile inactive stage in the life cycle of many ciliates, generally thought to serve a role of either protection or dispersal; organism typically rounded up, mouthless, and surrounded by one or more layers of secreted cystic membranes (ectocyst, mesocyst, endocyst, etc.) or envelopes or walls; when considered a protective stage, its walls may sometimes be quite thick, sculptured on the outside, and with or without an emergence pore, which may have an *operculum*; several (generally self-explanatory) types have been described; *viz.*, digestive; division, multiplicative, propagative, or reproductive; infective; invasion (cuticular); phoretic; protective; reorganization or reconstructive; resting; and temporary; the widespread phenomena of *en-* and *excystment* are in need of renewed study, generally with experimental and more sophisticated approaches – the causes of their occurrence are still poorly understood in almost all cases. ★ ★

Cystic Membrane: see Cyst.

Cytobrain: see Neuromotorium.

Cytogamy: see Autogamy.

Cytokinesis: often used in a general sense, as a synonym of *cell division* (see Fission); but cell biologists today usually restrict this term to mean the terminal stage in the division of solely the cytoplasm.

Cytopharyngeal Apparatus: term generally reserved for reference to either the *cyrtos* or the *rhabdos*; see also Cytopharynx.

Cytopharyngeal Armature: refers to the nematodesmal elements of a *cytopharynx*, especially of the *cyrtos* found in hypostome kinetofragminophorans. ★ ★

Cytopharyngeal Basket: see Cyrtos.

Cytopharyngeal Pouch: reservoir-like enlargement or *receiving vacuole* of the cytopharynx of a few ciliates (e.g., *Tetrahymena vorax*), present in a carnivorous macrostome stage of their life cycle; when food-filled, it pinches off as a regular membrane-bound food vacuole.

Cytopharyngeal Rod: see **Nematodesma**, especially as it relates to the *cytopharynx* of gymnostome kinetofragminophorans (therefore, see also **Rhabdos**).

Cytopharynx: nonciliated tubular passeway, of different lengths in different ciliates, leading from the *cytostome* proper into the inner cytoplasm of the organism; typically, food vacuoles are formed at its inner or distal end, when it retains its own integrity during the feeding process; when its walls are particularly strengthened, the *cytopharyngeal apparatus* may be known by such specialized names as *cyrtos* or *rhabdos*. ★ ★ [Cph]

Cytoproct: cell anus; generally permanent (when present at all), slit-like opening (though actually usually closed) through the pellicle, near the posterior end of the body, through which *egesta* may be discharged; its edges, resembling a kind of pellicular ridge and reinforced with microtubules, are *argentophilic*; in some species, the Cyp is a cortical landmark of taxonomic significance, located in or just to the left of the posterior portion of *kinety number 1*; of phylogenetic interest is its general absence in gymnostomes ("lower" ciliates). ★ ★ [Cyp]

Cytopyge: see Cytoproct, the preferred term.

Cytoskeleton: generalized term referring to any secreted inorganic or proteinaceous material within or below or on the surface of a ciliate, covering or involving all or some specific part of the body and lending considerable rigidity to the shape of the organism; see **Skeletogenous Structure**, a term with which it is broadly synonymous, although the emphasis in meaning may vary in usage by different workers.

Cytostome: cell mouth; the "true" mouth or oral opening; simply a two-dimensional aperture, most commonly permanently open (when present at all), through which food materials pass into the endoplasm of the organism (via a more or less distinct *cytopharynx*); may open directly to the exterior or be sunken into a depression or cavity of some kind, such as an *atrium*, *vestibulum*, or *buccal* or *peristomial cavity*; definable as the level at which pellicular alveolar sacs are no longer present (end of ribbed wall), it may occur as an angled or tipped elliptical opening with a long axis of considerable length. ★ ★ [Cs]

Cytostome-cytopharyngeal Complex: convenient generalized term to refer to the inseparable complement of the cytostomal opening and the adjacent (really continuous) cytopharyngeal tube or funnel. ★ ★

Cytotaxis: broad concept which holds that the ordering of cortical structure(s) is determined by the preexisting organization of the cytoplasm underlying the particular site concerned; the ordering and arranging of new cell structure under the influence of preexisting cell structure; see also **Structural Guidance Principle**.

Dactylozoite: infective stage in the most unusual life cycle of the suctorian *Tachyblaston*; the forms arise by several rapid fissions of the (at that stage) loricate parental organism; they then, though nonciliated and with but one tentacle, reach the body of another suctorian, *Ephelota*, "burrow" in, and grow into forms producing a ciliated *swarmer* stage individuals of which settle down (often on the stalk of the same *Ephelota*), produce their own stalk and lorica, and repeat the cycle; a synonym is *Dactylophrya*-stage.

Daughter Organisms: see **Filial Products**.

Deme: natural population within a species; the concept is particularly used by parasitologists to indicate populations of different types: for example, *monodemes*, *nosodemes*, *serodemes*, *topodemes*, and *xenodemes*; the last-mentioned – meaning differing in hosts – is useful in consideration of the echinoid *inquilines* (mostly scuticociliates); the organisms comprising different demes may possess distinctive morphological and/or physiological characters and, in some cases, may be incipient subspecies (or even species).

Dendritic or Dendroid Colonies: essentially synonyms of *arboroid colony*.

De Novo Cytoplasmic: now discarded term (and concept) for a mode of *stomatogenesis*; see **Telokinetal** for its modified replacement.

De Novo Kinetosomal: now discarded term for a mode of *stomatogenesis*; see **Apokinetal**.

Denticle: one of many similar structures or interlocked component parts of a supporting ring underlying the *adhesive disc* of mobiline peritrichs; a proteinaceous subpellicular *skeletal* element; each denticle is a hollow cone, fitted into the one next in front; associated with this conical centrum is usually an inwardly directed spine or ray and an outer blade. ★ ★ [Dent]

Denticulate Ring: *skeletal* organelle, made up of *denticles*, found in mobiline peritrichs; see **Denticle**. ★ ★

Desmodexy, Rule of: true *kinetodesmata*, when present, lie to or extend (anteriad) to the (organism's) right of the *kinety* (line of kinetosomes) with which they are associated; thus polarity is recognizable, etc. (see **Bipolar Kinety**). ★ ★

Dictyosome: see **Golgi Apparatus**.

Diploid: 2N number of chromosomes: characteristic of ciliate micronuclei and of the nondividing macronuclei in the karyorelictids (though some karyorelictid macronuclei may show *oligoploidy*, a low *polyploid* number).

Diplokinety: used variously by different workers; often it is a kinety (with its kinetosomes) doubled in some specific fashion; but also see **Diplostichomonad**.

Diplostichomonad: type of double *paroral membrane* the infraciliature of which is composed of two parallel rows or files of identically oriented kinetosomes; this is the characteristic condition found in the clevelandelline heterotrichs and in many hypotrichs; the kinetosomes are never in dyads nor do they form a zigzag pattern, and all are *ciliferous*; some workers consider this a type of *diplokinety*.

Director-meridian: *argentophilic* nonkinetosomal (though occasionally with nonciliferous basal bodies near its anterior end) line on the mid-ventral surface of many scuticociliates, coursing from the posterior margin of the buccal cavity to the cytoproct near the posterior end of the body; its locale is part of the site of formation of new buccal organelles during *stomatogenesis*; a little-used synonym is *bucco-anal strie*. ★ ★ [DM]

Dorsal Brush: see **Brosse**.

Dorsal Zone of Membranelles: an older term referring, somewhat inaccurately, to tufts of *syncilia* (which are not *membranelles*) located anteriorly and dorsally on the bodies of many entodiniomorphids.

Dyad: used in ciliatology to refer to the paired set or couplet of kinetosomes in which the kinetosomal axes are at right angles (perpendicular) to the axis of the line or file of the kinetal structure of which they are a part; in the case of many *paroral membranes*, only the outermost kinetosome of the dyad is *ciliferous*; the term is *not* used for the differently arranged pairs of kinetosomes comprising the *circumoral ciliature*. ★ ★

Ectoplasmic Flange: see **Flange.**

Ectosymbiont (*of* **Ciliates**)**:** microorganism, occasionally another ciliate, attached to the outside of the host; it is becoming known today that many species of protozoa have a thick covering or carpet of bacteria (especially) living on the pellicle, sometimes flat in grooves, sometimes perpendicular to the surface; common examples of ciliates as hosts include many psammophilic species from various taxa, commensalistic scuticociliates, and sessiline peritrichs (in which both bell and stalk may be involved).

Edaphic: in a broad sense, pertaining to all kinds of soil, forest litter, and other types of *terrestrial biotopes*, including bryophilic or lichenophilic kinds of habitats and even trunks and leaves of trees.

Embryo: see **Larval Form.**

Embryo Sac: see **Brood Pouch.**

Enantiotropic: name once given to a kind of *fission* typical of oligotrichs, said to involve a condition of inverse *homothety* and shifting body axes via pronounced morphogenetic movements during stomatogenesis.

Encystment: see mention under **Cyst.**

Endogemmy: see **Budding** and **Endogenous Budding.**

Endogenous Budding: type of single or multiple fission taking place within a *brood pouch*, with the embryo or *larval form(s)* completely free of the *parental body* before emergence through the *birth pore*; this is the characteristic mode of reproduction of certain chonotrichs (where the process is, however, better called *cryptogemmy*) and, especially, of certain suctorians; the phenomenon is also known as *endogemmy*.★★

Endoplasmic Reticulum: system of paired internal membranes in the form of vesicles and/or flattened cisternae, the interiors of which are not in direct continuity with the surrounding cytoplasm; surfaces of the membranes are sites of the ribosomal activity involved in protein synthesis. ★★ [ER]

Endoral Membrane: see **Paroral Membrane.**

Endoskeletal System: see **Cytoskeleton**; endoskeleton is the term preferred by many students of the astome oligohymenophorans.

Endosome: somewhat transient brightly Feulgen-positive body in the *paramere* moiety of the *heteromerous macronucleus* of cyrtophorid hypostomes and chonotrichs; in ciliatology the term is sometimes misused for the Feulgen-negative, RNA-containing *nucleolus* so commonly found, generally as numerous small bodies, in the nucleoplasm of the *homomerous macronucleus* and the *orthomere* of the heteromerous macronucleus. ★★ [End]

Endosprit: old term for the very short *suctorial tentacle* known for the curious evaginogenine suctorian *Cyathodinium*.

Endosymbiont (*of* **Ciliates**)**:** organism, generally bacterial or algal in nature, living within the cytoplasm or nucleoplasm of a ciliate cell; they range from *kappa particles* and other "Greek-letter parasites" of *Paramecium*, gram-negative bacteria often intimately involved (genetically and metabolically) with their host, to the common "*zoochlorellae*" found widespread among ciliate groups, especially in fresh-water gymnostomes, peritrichs, heterotrichs, and hypotrichs; recently reported, as *xenosomes*, from marine scuticociliates.

Envelope: used variously; for example, see **Cell Envelope, Lorica, Nuclear Envelope,** etc.

Epiplasm: fibrillar or filamentous layer in the outer cytoplasm directly underlying (and sometimes considered a part of) the *pellicle*; may be confounded by some workers with the *lamina corticalis*. ★★ [Ep]

Epistomial Disc: retractable, nonciliated, vaulted center of the concentric *peristomial field* characteristic of many sessiline peritrichs; in some of the Operculariidae, it is in the form of a prominent stalked *operculum*. ★★ [ED]

Ergastoplasm: now a generally discarded term, formerly variously used: for the so-called lifeless cell inclusions (stored fats, starches, etc.); for cytoplasmic components with affinity for basic dyes; and for a form of the *endoplasmic reticulum*.

Erratic Kinetosomes: generalized term referring, literally, to a single or a few kinetosomes (*ciliferous* or *nonciliferous*) which appear to have "wandered off" from some larger, more stable, well-known infraciliary structure or organelle; they may appear, or be revealable, only at certain stages in the life cycle of the organism, becoming involved (in effect as an *anlage* or as a *vestige*-turned-*anlage*) in some explicit morphogenetic process such as *stomatogenesis* (in a number of ciliates) or *budding* of ciliated larvae (e.g., in suctorians). ★★ [EK]

Esophagus: outmoded term in ciliatology, not needed and misleading in description of any structure or cavity in the oral area.

Eupelagic: see **Pelagic.**

Eutrophic: pertaining to an aquatic habitat with high primary productivity; high rate of anabolism; rich in minerals and dissolved organic nutrients but with low oxygen content; similar to *polysaprobic* in some ways, but generally *not* used with regard to *pollution*; term seldom employed by ciliatologists with reference to their organisms.

Evaginative Budding: type of fission involving formation of a temporary *brood pouch* but (in contrast to *endogenous budding*) in which the larval form is *not* freed within the *parental body*; in emergence, the entire wall of the pouch evaginates and cytokinesis takes place on the outside of the parental body; this is the characteristic mode of reproduction of members of an entire suborder of suctorians; it might also be called *evaginogemmy*. ★★

Evaginogemmy: see **Budding** and **Evaginative Budding.** ★★

Evolutionary Series: arrangement of groups of organisms in a supposed phylogenetic sequence using some major character or, better, *constellation of characters*, as a basis for indicating a graded series from, for example, primitive to (more) complex forms; a hypothesis difficult to apply, however, especially because of factors of *convergent evolution*; and see **Orthogenetic Lines** for an example of the danger of possibly arbitrary and nonphylogenetic sequencing.

Excystment: see mention under **Cyst.**

Exogemmy: see **Budding** and **Exogenous Budding.** ★★

Exogenous Budding: type of single or multiple fission taking place essentially on the surface of the *parental body*; larvae are pinched off singly or multiply, in the latter case, synchronously or consecutively; the characteristic mode of reproduction in certain chonotrichs and in one large group of suctorians; also known as *exogemmy*. ★★

Explosive Radiation: rapid diversity of forms (e.g., into many different taxa at a given level) brought about evolutionarily by invasion of a vast new and quite different biotope by some "stem" group, with subsequent adaptation to the variety of specialized habitats and niches thus made available to the (presumably unopposed) invader; the chonotrichs, largely *symphorionts* on certain crustaceans, may well serve as an example of an expanding group which has taken advantage of such a situation.

Explosive Trichocyst: see **Trichocyst**. ★★

Expulsion Vesicle: see **Contractile Vacuole**; but the present term is preferred by some workers today, despite the inappropriateness of *vesicle* in this context.

Extensor Membrane: largely disused term today referring to the ciliature of the anterior part of the *paroral membrane* of certain ciliates when it is in an immobile state; its cilia, forming a coalesced stiff membrane, aid in guiding food particles into the buccal cavity; it is called *Lachmann's bristle* in peritrichs, and is at least partially synonymous with another seldom used term, *semi-membrane*.

External Budding: see **Exogenous Budding**.

Extrusive Organelle: see **Extrusome**.

Extrusome: membrane-bound extrusible body subpellicularly located; a generalized term useful in referring to various types of often, admittedly, probably nonhomologous structures (*mucocysts*, *trichocysts*, *toxicysts*, *haptocysts*, *fibrocysts*, *clathrocysts*, *cyrtocysts*, *rhabdocysts*, *pexicysts*, *cnidocysts*, *conocysts*, and possibly *crystallocysts*) *in toto*; extrusion occurs under conditions of appropriate chemical or mechanical stimulation. ★★

Fascicle: generalized term; but used specifically in ciliatology with reference to a group or bundle of *suctorial tentacles* on the body of a suctorian, sometimes (but not necessarily) borne on an *actinophore*.

Fibers, Postciliary: see **Postciliary Microtubules**.

Fibers, Transverse: see **Transverse Microtubules**.

Fibrils: see **Microfibrils**.

Fibrocyst: unique *trichocyst* characteristic of the microthoracine hypostomes; fusiform, explosive, and revealing a conspicuous parachute- or umbrella-like tip after discharge; recently termed a *compound* trichocyst. ★★

Fibrous Trichocyst: see **Fibrocyst** and **Trichocyst**.

Filamentous Annulus: "elastic," expansible binding of fine fibrils surrounding (and considered a part of) the cytopharyngeal *rhabdos* near its proximal (outer) end; it allows for the great expansion required by certain carnivorous gymnostomes when feeding; it is said to be continuous with the *tela corticalis* in the vicinity of the *corona* of various haptorid gymnostomes.

Filamentous Reticulum: three-dimensional lattice of kinetosome-associated microfibrils present in the wall of the *buccal cavity* or *infundibulum* of certain ciliates; often they are united at condensation nodes, giving a striking hexagonal pattern at the ultrastructural level (e.g., in some peritrichs). ★★ [FR]

Filaments: see **Microfilaments**.

Filial Products: generalized term for (daughter) organisms resulting from any mode of ciliate *fission*; it includes *tomites*, *buds*, etc., as well as the usual *proter* and *opisthe*.

Fission: *cell division*; the sole mode of *reproduction* (nuclear mitosis but never meiosis involved) in ciliates; many kinds or types: iso- or anisotomic (filial products of equal or unequal size) and mono- or palintomic (two or multiple filial products); strobilation (products temporarily held together, chain-like); and budding (exogenous, endogenous, evaginative; mono- or polygemmic; synchronous or consecutive); a cystic stage is sometimes regularly involved; in the usual binary fission, the anterior filial product is called the *proter*, the posterior the *opisthe*; see more detailed definitions under specialized terms: those above and also *homothetogenic*, *interkinetal*, *perkinetal*, and *symmetrogenic*. ★★

Fixation Organelle: see **Holdfast Organelle**.

Flange: generalized term (literally, "a projecting rim") used variously in ciliatology (e.g., an *ectoplasmic flange* underlies part of the paroral membrane in the hymenostome *Glaucoma*).

Food Vacuoles: intracellular vacuoles formed (usually) at the distal end of the cytopharynx, containing food materials in either a particulate or dissolved state; the food vacuolar membrane, supplied in the region of the cytopharynx, may originate in discs or packets delivered with the aid of certain microtubules in the vicinity; within the vacuoles digestion takes place, with appropriate enzymes supplied by nearby *lysosomes*; solid egesta are often discharged through a *cytoproct*; these are the *phagocytic* ("cell-engulfing") *vacuoles* or *gastrioles*; in the broadest sense, a second type of food "vacuole" may be recognized: the *pinocytotic* ("cell-drinking") *vesicles* (with "liquid" contents); these latter vesicles may be found anywhere along the plasma membrane: see also **Parasomal Sac**.

Forma: see mention under **Variety**.

Fragmon: see **Kinetofragment**.

Frange: band of *perioral ciliature* characteristic of certain hypostomes; it varies in composition from an extensive line of specialized ciliature winding helically around much of the anterior end of the organism to a short linear group of as few as three *pseudomembranelles* (or *pavés*) adjacent to the cytostome proper; it is sometimes called an *adoral ciliary fringe*, but more often the *hypostomial frange*. ★★ [ACF, HF]

Fringe: see **Locomotor Fringe**; but, on occasion, the word "fringe" is also used alone or in other combinations, with different (but generally self-explanatoty) meanings; it is sometimes used when *frange* is meant.

Fusiform Trichocyst: see **Trichocyst**.

Gamma Membranoid: see **Membranoid**.

Gamones: soluable "mating type" substances active in inducing conjugation (e.g., see **Blepharmone**).

Gamonts: members of a conjugating pair (iso- or anisogamonts, equal or unequal in size, with the latter kind including micro- and macrogamonts); but usage of this terminology is not widespread in ciliatology; see **Conjugation**.

Gastrioles: see Food Vacuoles.

Gemmation: see Budding.

Generative Nucleus: see Micronucleus.

Germinal Row: line of *nonciliferous kinetosomes* associated with the terminal portion of the infraciliary base of the *paroral membrane* (or *haplokinety*) of peritrichs; it plays a productive role (as an *anlage*) in *stomatogenesis* in such ciliates, and may be homologous with the *scutico-vestige* of scuticociliates. ★ ★ [GR]

Glandule, Secretory: see Ampulla, Secretory.

Golgi Apparatus or **Body**: intracytoplasmic membranous structure consisting of flattened saccules (*cisternae*), often stacked in parallel arrays, and *vesicles*; involved in elaboration or storage of products of cell synthesis; the Golgi apparatus (syn. *dictyosomes*) is not prominent in ciliates, in contrast to the condition in many other protozoa.

Grain Convention: see Numbering Conventions. ★ ★

Gullet: unnecessary term sometimes used for the *buccal cavity* of such ciliates as *Paramecium*.

Haploid: N set of chromosomes; in ciliate life cycles, haploidy is characteristic of "gametic" or pronuclear (sexual) stages only.

Haplokinety: once-popular term for the infraciliary base of a generalized *paroral membrane*, especially in ciliates belonging to the present subclasses Hymenostomata and Peritricha; typically a double row of kinetosomes (paired tangentially, as *stichodyads*) joined in a zigzag pattern, generally with only the outermost basal bodies ciliferous; some workers have also used the term to mean the entire paroral membrane, the ciliated portion *plus* its infraciliary base; in scuticociliates, the haplokinety has been described as comprised of one, two, or three kinetosomal segments (see remarks under Membranoid), depending on the species under consideration. ★ ★ [Hk]

Haptocyst: minute *extrusive organelle* in the *suctorial tentacles* of suctorians; presumed to contain lytic enzymes useful in the capture of prey organisms; sometimes still referred to as a *microtrichocyst*, a *missile-like body*, or a *phialocyst*. ★ ★ [Hpc]

Head: generalized term, variously used in ciliatology but usually in a nonspecific way.

Heterokaryotic: possessing more than one kind of nucleus (i.e., exhibiting *nuclear dualism*); characteristic of the great majority of ciliates, with their *micro-* and *macronuclei*. ★ ★

Heteromembranelle: specialized term for each of the several (often many) adoral *buccal membranelles* of the clevelandelline (all symbiotic) heterotrichs, the infraciliary bases of which are slightly different (in the leftmost row of kinetosomes) from those of the *paramembranelle* of the free-living heterotrichs and other spirotrichs. ★ ★ [Hmem]

Heteromerous Macronucleus: nucleus partitioned into two moities or *karyomeres* (*orthomere* and *paramere*) with strikingly different DNA and RNA contents and, therefore, with differential staining capacities; found especially in cyrtophorid and chonotrich hypostomes; to be contrasted with the *homomerous macronucleus*. ★ ★

Histophagous: tissue-eating; the feeding habit of ciliates living on or in the usually unhealthy (i.e., wounded, moribund, or decaying) bodies of aquatic or edaphic metazoa, including vertebrates (generally larval forms) as well as many kinds of invertebrates of all sizes; blood is one of the preferred tissues for certain ciliates; examples of histophagous forms include species of the hymenostomes *Ophryoglena* and *Tetrahymena* and such scuticociliates as *Porpostoma*; the term was formerly often misspelled as "*histiophagous*."

Holdfast Organelle: when broadly used (see Attachment Organelle), refers to any structure(s) by which a given ciliate can affix or attach, temporarily or permanently, to a living or inanimate substratum (e.g., by use of cilia, hooks, uncini, crochets, tails, loricae, mucous filaments, spines, stalks, suckers, tentacles, and the like); in the usual, more restricted sense, it refers to specific, specialized organelles such as *stalks* of various kinds, the *adhesive disc* of mobiline peritrichs, the *sucker* of some astomes or clevelandelline heterotrichs, or the localized *thigmotactic ciliature* of many thigmotrichine scuticociliates. ★ ★ [HO]

Holozoic: mode of nutrition or feeding; see mention under the contrasting mode, Saprozoic.

Homokaryotic: fundamentally possessing but one kind of nucleus, neither a micronucleus nor a macronucleus; among the ciliates, this characteristic is limited (in our present state of knowledge) to species of the primociliatid gymnostome *Stephanopogon*; it is not to be confused with the *amicronucleate* condition. ★ ★

Homologous Characters: traits or structures or organelles which are similar (resemble one another) due solely to inheritance from a common ancestry; if such ancestry is unknown or unknowable it may be *inferred* (with great caution), keeping in mind the possibility of convergent evolution and other such confounding factors; various tests for homology have been formulated for use with material (such as ciliates) not having a usable fossil record.

Homomerous Macronucleus: nucleus with no differentiation into zones containing differing DNA and RNA contents; essentially uniform staining capacity exhibited; this is the type of macronucleus found in the great majority of ciliates; to be contrasted with the *heteromerous macronucleus*. ★ ★

Homonym: one of two or more names identical in orthography (spelling) applied to different organisms or taxa; the earlier published name (of two) is the *senior* homonym (and must prevail); the other is the *junior* homonym (which must be replaced, unless it is a junior synonym).

Homopolar Doublet: individual ciliate with two sets of mouthparts, generally 180° apart around the anterior end of the body; a teratological, unstable condition.

Homothetogenic Fission: type of division (generally transverse or *perkinetal*) of a *parental organism* in such a manner that there is a point-to-point correspondence (exhibition of the condition of homothety) between structures or "landmarks" in both *filial products*, the *proter* and the *opisthe*; typical of ciliates, to be contrasted with the *symmetrogenic* or mirror-image *fission* of flagellates and of opalinids (*interkinetal* division). ★ ★

Host: independent or so-called dominant member of a symbiotic pair, unless the relationship is mutualistic; the dependent partner, the *symbiont*, lives in or on the host.

Hyperparasitism: see Parasitism.

Hypostomial Frange: see Frange. ★ ★ [HF]

Indicator Organisms: as used with respect to "pollution ecology" studies, see **Saprobity System**; ciliates employed in most laboratory assay work of a biochemical nature are not so called.

Infraciliary Lattice: branching filamentous tract or mat at the boundary of ectoplasm and endoplasm, running parallel to and not far from the surface of the organism's body but at a deeper level than that of either the *epiplasm* or the layer of *striated bands* (as known in *Paramecium*). ★ ★ [IL]

Infraciliature: assembly of all kinetosomes and associated subpellicularly located microfibrillar (or microfilamentous) and microtubular structures, both somatic and oral in location; the *argentophilic* nature of most such organelles and structures (not to mention their easy revealability, now, via electron microscopy) and their universality and stability make the infraciliature an ideal system for study to gain significant information in areas of morphogenesis, evolution, and phylogeny as well as in comparative systematics at all taxonomic levels. ★ ★

Infundibulum: lower or inner or posterior part or section of the *buccal cavity* in certain ciliates, particularly peritrichs; often funnel-shaped or in the form of a long tube or canal; the cavity may contain some of the buccal ciliature and its infraciliature (such as the special *peniculi* of peritrichs). ★ ★ [Inf]

Ingestatory Apparatus: see **Oral Apparatus**.

Inquiline: term often used for the *endocommensal* organism living in a body cavity of some *host* and not obtaining nourishment directly from or at the expense of it; the term is employed in this book primarily for those echinophilic ciliates essentially endemic in the digestive tract of their (mainly echinoid) hosts (e.g., certain scuticociliates).

Interkinetal: between the kineties; as a kind of division in protozoa, see **Symmetrogenic Fission**.

Intermeridional Connectives: apically located concentric *silverlines* encircling the anterior part of the body of certain ciliates (e.g., *Tetrahymena*); probably *argentophilic* artifacts of some sort, but their constancy and nonvarying nature – true also of other, similar lines (e.g., **Circumoral Connective**) – make them of value taxonomically. ★ ★ [IC]

Internal Budding: see **Endogenous Budding**.

International Code of Zoological Nomenclature: authoritative dicta regarding all matters nomenclatural (for animals: to date, this is assumed to include the protozoa), essentially to the level of familial taxa; provisions of the *Code* affect systematics and classification to the obvious yet significant extent that nearly all taxonomic decisions ultimately require use of scientific names – and that only by proper usage everywhere can the laudable and welcome goals of stability, universality, and uniqueness of names be achieved on an international and lasting basis.

Interstitial: living between or among, or in the interstices of, sand grains (or similar sediments); many gymnostomes, especially, are among such *psammophilic* forms, obligately or facultatively, in both fresh-water and (especially) marine biotopes – but other groups of ciliates are well represented, too.

Intracytoplasmic Pouch: temporary depression or cavity or "vacuole," present in the *opisthe* during fission (especially in entodiniomorphids, oligotrichs, and some hypotrichs), in which the anlagen of oral ciliature appear – or come to be located – during the overall process of stomatogenesis. ★ ★ [IcP]

Isoconjugants: conjugants of the same size; see **Conjugation**.

Isogamonts: see **Gamonts**.

Isotomic: see **Fission**.

Kappa Particles: see **Endosymbiont**.

Karyological Relict: organism which is presumed to be a remnant or direct and little-changed descendant of an early or phylogenetically ancient group of ciliates, at least with respect to its nuclear condition or properties; this is particularly assumed to be the case for primociliatid (homokaryotic) and karyorelictid (diploid, nondividing macronuclei) species of gymnostomes; the idea is important in phylogenetic and evolutionary – and thus taxonomic-classificational – considerations; see also **Macronuclear Evolution Hypothesis**.

Karyomeres: see **Heteromerous Macronucleus**.

Karyonide: laboratory clonal population of organisms, started from a single individual, in which no (subsequent) nuclear reorganization has been allowed to occur.

Karyophore: strands or sheets of specialized and generally conspicuous fibers emanating from subpellicular locations and surrounding and suspending the macronucleus; a characteristic structure in certain ciliates belonging to the suborder of clevelandelline heterotrichs. ★ ★ [Kph]

Kinetal Segment: see **Kinetofragment**; in a broader sense, some workers have used the term for a section of any row or line of kinetosomes, oral or somatic and anywhere on the ciliate's body. ★ ★

Kinetal Suture System: see **Système Sécant**. ★ ★

Kinetid: elementary repeating organizational unit of the typical ciliate cortex, consisting of a *kinetosome* (or pair, occasionally more, of kinetosomes) and certain intimately associated structures or organelles; commonly the latter include *cilia*, *unit membranes*, *alveoli*, *kinetodesmata*, and various ribbons, bands, or bundles of *microtubules* (including some *nematodesmata*), and sometimes also *microfibrils*, *myonemes*, *parasomal sacs*, *mucocysts* or *trichocysts*, etc.; a currently popular synonym is *kinetosomal territory*, formerly also known as a *ciliary corpuscle*. ★ ★

Kinetodesma: periodically striated, longitudinally oriented, subpellicular fiber (of component fibrils) arising close to the base of a somatic kinetosome (posterior one, if paired), near its microtubular triplets 5-8 (*Grain convention*), and extending anteriad toward or parallel to the organism's pellicular surface and on the right side of the kinety involved (*Rule of Desmodexy*); rare, seemingly similar structures showing exception to such orientation (or to any of the other characteristics given above) are considered by the writer not to be true kinetodesmata; when kinetodesmata are of a length greater than the interkinetosomal distance along the kinety, they overlap, shingle-fashion, producing a bundle of fibers; they are well developed in apostomes, hymenostomes, scuticociliates, and peritrichs, and present as large and heavy bundles (part of *endoskeletal system*) in certain astomes. ★ ★ [Kd]

Kinetodesmal Fiber: see **Kinetodesma**.

Kinetofragments: novel term (based in large measure on an expansion of Jankowski's *kinetofragmon* concept) referring to the patches or short files of basically *somatic kinetids* in the general vicinity of the more or less apical (or subapical and ventral) cytostomal or *oral area*; the (evolutionary) origin of these particular kinetosomes *sensu lato* is presumed to have been the nearby anterior terminations of the (present or one-time present) somatic kineties converging onto the general oral region; these kinetal segments, sometimes only partially ciliferous, may play active roles in stomatogenesis, in production of *atrial* and *vestibular ciliature*, and in the evolutionary origin of the *buccal apparatus* of "higher" ciliates; the *hypostomial frange* may be considered to be composed of kinetofragments, so complex in some species that the term *pseudomembranelle* (or *pavé*) has been used to describe some of its ciliary groups; kinetofragments are characteristically found in many members of its namesake class, the Kinetofragminophora. ★★ [Kf]

Kinetofragmon: compound word to describe the assembly of fragments of somatic kineties around the mouth area in, for example, hypostome and trichostome ciliates; see Kinetofragments. ★★

Kinetome: assembly of all (generally longitudinal rows of) *kinetids* (i.e., the *kineties*) covering the body of a given ciliate; the total mosaic of an organism's repeating *kinetosomal territories*. ★★

Kinetorhiza: little-used synonym of *ciliary rootlet*.

Kinetosomal Territory: see Kinetid, of which it is essentially a (very popular) synonym. ★★

Kinetosome: subpellicularly located tubular cylinder of nine longitudinally oriented (at right angles to cell's surface), equally spaced, skewed, peripheral structures each composed of three *microtubules*; typical size of a kinetosome, in ciliates, is *ca.* 1.2 X 0.3 μm; when ciliferous, this embedded *basal body* (or, by accepted homology, *centriole*) produces a *cilium* at its distal end; when viewed from deeper in the cytoplasm of the organism looking outward, the nine triplets of microtubules (numbered by the *Grain convention*) are skewed inwardly, clockwise. ★★ [Ks]

Kinetosome Triplet Numeration: see Numbering Conventions. ★★

Kinety: single structurally and functionally integrated (somatic) row, typically oriented longitudinally, of single or paired (or, in special cases, possibly greater number of) kinetosomes (not all necessarily ciliferous) plus cilia and other associated cortical organelles and structures, *viz.*, a line of *kinetids*; these *ciliary* and infraciliary *meridians* are basically *bipolar* (though some may be interrupted, fragmented, intercalated, partial, shortened, etc.), with an asymmetry allowing recognition of anterior and posterior poles of the organism itself; better *not* used in reference to buccal infraciliary structures. ★★ [K]

Kinety Number 1: meridian or *ciliary row* which, in a number of ciliates (e.g., tetrahymenine hymenostomes), has three unique features or properties: it is the *stomatogenic kinety* (or *stomatogenous meridian*), functioning in new mouth-formation during fission; it bears, or is topologically associated with, the *cytoproct* at its extreme posterior end; and it is terminated anteriorly by the posterior margin of the buccal overture as the rightmost *postoral meridian*. ★★ [K1]

Kinety Numeration: see Numbering Conventions. ★★

Kinoplasm: see mention under Spasmoneme.

Km Fiber: structure composed of a stack of *microtubular ribbons* derived from an origin near triplet 9 (*Grain convention*) of the (posterior, if pairs of) kinetosomes in a given kinety; first described, as unique, in certain heterotrich polyhymenophorans; but it is a *postciliodesma*, an organelle now also known in many of the kinetofragminophorans; running posteriorly, the large bundle courses along the right side of its associated row of kinetosomes, perpendicular to the organism's surface; its function may involve extension of the body following contraction; it is not to be confused either with true *kinetodesmata* (generally absent in both groups of these ciliates) or with the *M fibers* (deeper bundles of fibrils involved in contraction); on the other hand, it is to be considered as (only) a special formation of *postciliary microtubules*. ★★ [KmF]

Lachmann's Bristle: see Extensor Membrane. ★★ [L'sB]

Lamina Corticalis: dense fibrillar or filamentous layer beneath the pellicle of various ciliates, marking the ecto-endoplasmic boundary; in certain groups, it seems to be indistinguishable from the *epiplasm*, as that term is used by some workers; and it is probably reasonably considered a synonym of *tela corticalis*, as the latter term is often used; it appears to be continuous with the *filamentous annulus* of the *rhabdos* in certain haptorid gymnostomes.

Larval Form: widely used to denote a motile migratory or dispersive form in the life cycle of, particularly, free-living sessile or sedentary ciliates (fresh-water and marine); includes the *bud* of suctorians and chonotrichs (etc.) but also the *telotroch* of peritrichs and the migratory stage of many loricate organisms not confined to membership in the Peritricha – for example, folliculinid (coliphorine) heterotrichs; such forms (sometimes called *swarmers*) are usually morphologically dissimilar to their parental forms (or even the other filial product of the fission), possessing special adaptations for making rapid progress through their aqueous medium, for finding food, and/or for settling down in a favorable spot for new lorica- or stalk-production; a number of *tomites* or *phoronts* of various taxonomic groups (especially comprising parasitic species), which may well serve the same purpose, are traditionally *not*, however, referred to as larval forms. ★★

Lieberkühn's Organelle: lenticular refractile structure invariably and exclusively found beneath the pellicle close to the left side of, or in the left wall of, the buccal cavity of ophryoglenine hymenostomes; the function (sensory?) of this "*watchglass organelle*" remains enigmatic.

Lips: generalized term, variously used; experts on different groups of ciliates (e.g., the tintinnines and some loricate peritrichs) may employ it for specific yet nonhomologous structures.

Lithosome: vesicular, membrane-bound cytoplasmic inclusion or small body, found in a number of ciliates, comprised of some inorganic material laid down in concentric layers.

Littoral: pertaining to the zone (of the beach) between high- and low-water marks; this intertidal zone is the biotope of many marine *psammophilic* ciliates from all three classes comprising the phylum.

Lkm Fiber: compound microtubular structure, perhaps unique to the vestibuliferan *Woodruffia*, similar to the *postciliodesma* (in composition, direction, etc.) of allegedly distantly related forms except that it runs on the *left* side of the associated kinety and has its origin near kinetosomal microtubular triplets 4 and 5 (*Grain convention*) instead of 9; totally different from a *kinetodesma*, with which some workers have confused it.

Locomotor Fringe: ring of specialized "compound" ciliature (sometimes called *pectinelles*) around the posterior part of the body of the telotrochs of sessiline peritrichs and around the *basal disc* of mature mobilines; used in swimming by the migratory *larval forms*, generally resorbed in the adult forms; also popularly known as a *trochal band*; locomotor fringe *sensu stricto* is unique to peritrichs. ★★ [LF]

Locus of Stripe Contrast: "ramifying zone" in forms like the heterotrich *Stentor*; a ventral region of the body showing the greatest contrast with respect to width of contiguous granular (pigmented) stripes; in *Stentor*, it represents the primordial site of new mouth formation and also the region of stripe proliferation; see also **Système Sécant**.

Longitudinal Microtubules: present in some (oligohymenophoran) ciliates as a sheet or band in the *pellicle* close to the *plasma membrane*; run longitudinally down the body near the rows of kinetosomes (kineties). ★★ [LMt]

Lorica: test, envelope, case, or shell (or, occasionally, theca) secreted and/or assembled (using various materials) by a number of ciliates from several different taxa (most commonly peritrichs, folliculinids, and tintinnines), with the important properties of fitting (the body) loosely, opening at one (anterior) end (or occasionally both ends), and being either attached to the substratum (common) or carried about by the freely swimming organism (true of the tintinnines); may occur in a multiple (arboroid-tree) state; such a "house" or "tube" may be occupied only temporarily (e.g., as is true in the case of some hypotrichs); may be calcareous, composed of some proteinaceous or mucopolysaccaride secretion, including chitin, pseudochitin, or tectin, or made up of foreign matter (sand grains, diatom frustules, coccoliths, debris) ingeniously cemented together in a species-specific pattern. ★★ [Lor]

Loricastome: specialized opening or aperture, surrounded by thickened but movable lips, in the rigid *loricae* of lagenophryid peritrichs; the buccal ciliature may be extended through the aperture when it is open, the migratory larval form exits through it, and microconjugants can enter through it.

Lysosomes: cytoplasmic organelle bounded by a single *unit membrane* and containing hydrolytic (digestive) enzymes; not yet widely studied in ciliates.

Macroconjugant: larger member of a conjugating pair, and the only surviving conjugant in cases (such as in peritrichs) of so-called *total conjugation*; a little-used synonym is *macrogamont*.

Macronuclear Evolution Hypothesis: origin of the complex, nearly autonomous, polyploid macronucleus (stage 3) typical of the great majority of contemporary ciliates from a preceding diploid and nondividing form (stage 2) which, in turn, supposedly arose – concomitant with the first micronucleus – from a single "plain" nucleus (i.e., *homokaryotic* stage 1, before the differentiation which led to *nuclear dualism*); application of this idea to ciliate systematics is enhanced by recognition of the actual existence today (preservation of *karyological relicts*?) of species assignable (on nuclear characteristics, at least) to the first two postulated stages as well as the last, stage 3 (contemporarily the predominant one).

Macronucleus: so-called vegetative or trophic nucleus of ciliates; controls the organism's phenotype; may be multiple, but even then is typically much larger than the micronucleus; most often compact, spherical or ellipsoidal, but sometimes of diverse other shapes (reniform, moniliform, filiform, dendritic, halteriform, C- or E-shaped); polyploid (diploid in the karyorelictids) with respect to its genomic content; commonly contains numerous small nucleoli (sometimes single very large one – e.g., in some karyorelictids); may be *homomerous* or *heteromerous* (see those terms); divides "amitotically" (though totally incapable of division in the karyorelictids); has regenerative powers, but normally is resorbed during sexual phenomena and replaced by products of a *synkaryon* itself derived from fusion of haploid pronuclei of micronuclear origin. ★★ [Mac]

Macrophagous: feeding on relatively large particles of food; see especially **Carnivorous**, but *algivorous* may also be included unless only the very smallest algae are involved; to be contrasted with *microphagous*.

Macrozooid: see **Zooid**.

Marginal Cilia: circumferential band of long, stout cilia located above the aboral *locomotor fringe* of many mobiline peritrichs; sometimes called *cirri* because of their stoutness.

Marsupium: see **Brood Pouch**.

Maternal Form: see **Parental Form**.

Maxillary Armature: see **Capitulum**.

M-band: see **Myoneme**.

Meganucleus: see **Macronucleus**, the preferred word.

Membrana Quadripartita: see **Quadrulus**.

Membrane: generalized term with a variety of particular meanings depending on its specific modifier: for example, see **Cystic Membrane**, **Nuclear Membrane**, **Paroral Membrane**, **Plasma Membrane**, **Undulating Membrane**, etc.; in ciliate systematics, however, it is often understood, when used alone (and unless otherwise indicated), to mean a ciliary membrane, specifically, the *paroral membrane*, usually in the context of contrasting it with the *membranelles* of the *AZM*. ★★

Membranelle: used in this book in a broad, nearly all-inclusive sense to refer to one of the several serially arranged *compound ciliary organelles* (together known as the *AZM*) found on the (basically) left side of the *buccal cavity* or *peristomial field* in oligo- and polyhymenophoran species; its cilia, sometimes seemingly fused or partially coalesced (if only hydrodynamically), may be used in food-getting or locomotion; the generally rectangular infraciliary base is commonly composed of three rows of densely set kinetosomes which may (or may not!) be associated with parasomal sacs and/or microtubular or microfibrillar structures in specific patterns not necessarily identical for each row of the base or for the similar-appearing "membranelle" in a different taxonomic group; membranelle *sensu stricto* may be used to refer to the (left-hand) buccal ciliary organelles of the tetrahymenine Hymenostomatida, undoubtedly being homologous structures throughout the species of at least that suborder; but membranelle *sensu lato* includes organelles very likely *not* homologous (a supposition supported in part by the different origins of some of them during stomatogenesis): for some specific types of the latter kind, see **Heteromembranelle, Membranoid, Paramembranelle, Peniculus, Polykinety,** and **Quadrulus.** ★★ [Mem, M1-3]

Membranoid: used by some workers to indicate either the definitive membranellar fields (including, for some ciliatologists, even the paroral membrane) or some stage in their ontogenetic development in species belonging to the oligohymenophoran order Scuticociliatida; at one time, "*alpha*," "*beta*," "*gamma*," and "*zeta*" types were differentially defined, the first three referring to the *polykineties* on the left side of the buccal area, from anterior to posterior, and the fourth to the (haplokinetal base of the) *paroral membrane* on the right; the *zeta membranoid* in some scuticociliate species was (is) said to consist of three more or less separable segments ("a," "b," and "c"), with terminal fragmentation (probably of "b," in this case) into a dozen additional pieces in one genus (*Schizocalyptra*) and with "a" most anteriad and "c" (= *scutico-vestige*?) at end and farthest to the left.

Meridian: see **Ciliary Meridian.**

Mesosaprobic: see mention under **Polysaprobic.**

M Fibers: see **M-band.**

Microbiocenosis: restricted community of interacting microorganisms (including ciliates) in nature, with a stability of limited duration (but temporary equilibrium may be repeatedly regained).

Microconjugant: smaller member of a conjugating pair; completely absorbed by the macroconjugant — sometimes many times its volume — in cases of *total conjugation* (e.g., in chonotrichs and peritrichs); a little-used synonym is *microgamont.*

Microfibrils: generalized term, perhaps better considered without the prefix; many structures and organelles are (micro)fibrillar in composition, sometimes quite densely so; the term is most frequently used in its adjectival form; fibrillar or microfibrillar constituents of ciliates may include such prominent and organized structures as the *kinetodesmata* and the *myonemes* (including *M fibers*, *spasmoneme*, etc.) and perhaps the *karyophore*, the *filamentous annulus*, etc.; however, some workers use "filamentous" to describe the very same organelles; see also **Microfilaments.**

Microfilaments: generalized term, perhaps better considered without the prefix; the finer or finest composition (*ca.* 5 nm in diameter) of a number of important organelles appears to be (micro)filamentous in nature, often dense and with or without nodes — for example, the *epiplasm*, the *infraciliary lattice*, and the *filamentous reticulum*; if this is the ultimate or lowest macromolecular level of organization, then there should be a distinction, even in very generalized usage, between this term and *(micro)fibrils* — but this has *not* always been the case in the literature, the terms, in fact, being used interchangeably by some workers; if many fibers are made up of fibrils, then perhaps the fibrils should be considered as composed of filaments: a possible solution to much of the dilemma; see also **Microfibrils.**

Micronucleus: so-called generative nucleus of ciliates; may be multiple, but is typically much smaller than the macronucleus; generally spherical or ovoid in shape and diploid in its genomic content; without nucleoli; its envelope is with pores in some species, without them in others; divides mitotically or meiotically, playing a major role in sexual phenomena such as autogamy and conjugation; absent in *amicronucleate* strains or races. ★★ [Mic]

Microphagous: feeding on small or very small particles of food; a generalized term embracing especially *bactivorous* (feeding on bacteria) and sometimes *algivorous* (when very small algae are involved); to be contrasted with *carnivorous*, *histophagous*, *saprozoic*, and especially *macrophagous*.

Microstome-Macrostome Transformation: see **Stomatogenesis.**

Microtoxicyst: used as a synonym of *haptocyst*, but might also refer to some other minute *toxicyst*.

Microtubule: hollow, cylindrical structure of indeterminate length, *ca.* 2.5 nm in diameter, composed of subunits of *tubulin*; rigid, often cross-linked with others to form a ribbon, band, or bundle; microtubules in the cytoplasm are typically (but not exclusively) associated with, if not derived from, kinetosomes; they comprise the "9 + 2" structure of cilia, and they also occur in many subpellicular locations with possibly different functions; some occur in the nucleoplasm (with no kinetosomal association); the most striking microtubular configurations in ciliates include the ribbons of *transverse* and *postciliary microtubules*, the bundles of *nematodesmata*, and the microtubular arrays in the *suctorial tentacle*. ★★ [Mt]

Microzooid: see **Zooid.**

Migratory Form: see **Larval Form.**

Missile-like Body: see **Haptocyst.**

Mitochondria: generally conspicuous organelles in the cytoplasm, composed of a complex membrane system (inner membrane forming *cristae* of several types, usually tubular in ciliates) and indispensably functioning as the "powerhouse" of the cell (energy transformations); in some ciliates they are arranged in specific (often linear) patterns or formations; in scuticociliates there seems to be a single interconnected "compound" mitochondrion, a giant *chondriome* located immediately under the pellicular alveoli; in many parasitic ciliates they are often deeper in the cytoplasm. ★★ [Mit]

Monogemmic: production of a single *bud* (at a time); a mode of *fission*.

Monophyletic: condition of a taxon (at any level) being comprised of members all derived from a single common ancestor or from an ancestral group of the same or lower rank via one or more lineages; careful application of this as a principle can have a significant effect on ciliate systematics, especially at the higher taxonomic levels; contrast with the term *polyphyletic*.

Monostomy: condition of having but one *mouth*; typical of most ciliates.

Monotomic: division of a single individual into but two *filial products*; the mode of *fission* typical of most ciliates.

Monoxenic Culture: laboratory growth of two kinds or species of living organisms with no others present; for example, a ciliate plus one "stranger" — a bacterium, an alga, a yeast, or another ciliate species; the second organism is typically present in the medium to serve as food for the ciliate, which is usually being studied biochemically or (competitive-)ecologically; *zweigliedrige Kultur* is an older term with essentially the same meaning.

Morphogenesis: coming-into-being of characteristic and specific form; the transformation involved in growth and differentiation, resulting – in ciliates – in reproduction of (the preexisting) form, with the same patterned array of cytoarchitectural substructures, etc.; morphogenetic movements, etc. are particularly involved in the processes of ***reproduction***, but also in cystation, conjugation, regeneration, etc., and in ***stomatogenesis***; the consistent patterns describable in observation of such dynamic ***ontogenetic*** phenomena may be recognized as of considerable value in both phylogenetic and comparative taxonomic work; see also **Biogenetic Law**.

Mosaic Evolution: process resulting in an organism's showing unequal development or advancement in different structures or organelles possessed by it, since the evolutionary rate of change need not have been identical (different selection pressures, etc.) for each part of the organism; thus, depending on the character chosen for comparative study, a given taxonomic group of ciliates might, relative to other groups, appear in a position on one worker's proposed phylogenetic tree different from that on another's tree.

Motorium: see **Neuromotorium.**

Mouth: of value only as a very general term, used in reference to the ***oral area*** of any mouth-bearing ciliate; the "true" mouth of a ciliate should be called the *cytostome*.

Mucigenic Body: see **Mucocyst.**

Mucocyst: subpellicularly located, membrane-bound, saccular or rod-shaped organelle of a paracrystalline structure, dischargeable through an opening in the pellicle as an amorphous, mucus-like mass; probably involved in cyst formation (in some species), among other possible functions; occurs in regular, longitudinal, interkinetal rows in many ciliates; formerly known as a ***protrichocyst*** (especially), a ***mucous trichocyst***, or a ***mucigenic body***; an ***ampullocyst*** has been considered a special type of mucocyst. ★★ [Muc]

Mucous Trichocyst: not a *trichocyst*; see **Mucocyst.**

Müller's Vesicle: small vacuole containing mineral concretions; actual function unknown; described from various karyorelictid gymnostomes; possibly homologous with the ***concrement vacuole*** of certain commensalistic prostomatid and trichostomatid groups.

Mutualism: kind of symbiotic relationship in which both partners benefit from the association, the host as well as the ecto- or endosymbiont; verifiable cases rare involving ciliates as the symbiont, but there are several with the ciliate as the host – for example, the situation obtains for a number of species with endosymbiotic *zoochlorellae*.

Myoneme: fibrillar (ultimately filamentous) organelle with a known or presumed contractile function; in the broadest sense, it may include the ***spasmoneme*** found in the stalk of many peritrichs, the *M-band* or *M fibers* coursing beneath the ciliary rows in the bodies of certain contractile heterotrichs, retractors and sphincters in various other groups, and still additional (micro)filamentous strands, bands, sheets, or bundles active in contraction or retraction of all or part of a ciliate's body in a number of forms; the fibrils, sometimes running deep in the cytoplasm, may be (inter)connected to one another, the pellicle, and/or certain kinetosomes; ≠ *Km fiber*. ★★ [My]

Nasse: see **Cyrtos.**

Nebenkörper: used variously in protozoology; in the case of ciliates, it has been applied – formerly but now inappropriately – to the ***parasomal sacs*** which are so often found in the near vicinity of kinetosomes.

Neck: term used variously; most appropriately for the often highly extensible region of the body in some haptorid gymnostomes which is immediately posterior to the apical cytostome (and ***corona***); the neck in chonotrichs (non-extensible but sometimes quite elongate) is better called a ***collar***.

Nematodesma: birefringent bundle of parallel ***microtubules***, often showing a hexagonal, paracrystalline arrangement in cross-section; typically, it is kinetosome-associated; it plunges into the cytoplasm at right angles to the pellicle, forming (with others) the major reinforcement of the walls of the *cytopharyngeal apparatus* (*rhabdos* and *cyrtos*) of gymnostomes and hypostomes, respectively, though to be found in other groups as well (e.g., in frontoniids); nematodesmata comprise the armature of the oral area of kinetofragminophorans formerly identified with light microscopy as *trichites*, *cytopharyngeal rods*, or the *cytopharyngeal basket*. ★★ [Nd]

Neoteny: retention of major larval characters in the mature form or adult stage of an organism; the ***trophont*** of mobiline peritrichs is sometimes considered a matured or permanently arrested *telotroch* (the larval form in sessiline peritrichs).

Nephridial Apparatus: see **Contractile Vacuole.**

Nephridial Canal: see **Afferent Canal.**

Nephridioplasm: see **Spongioplasm.**

Neritic: pertaining to the region of shallow water along a seacoast; the biotope near the shoreline (edge) of an ocean; to be contrasted with ***pelagic***.

Nesselkapseltrichocyste: see **Toxicyst.**

Neuroformative System: see **Silverline System.**

Neuromotor Apparatus: see **Neuromotorium.**

Neuromotor Concept: see **Neuromotorium.**

Neuromotorium: presumed center or ***cytobrain*** or ***motorium*** of a ciliate's entire ***neuromotor apparatus*** (associated with the now discarded but once very popular *Neuromotor Concept*); a chromophilic fibrillar bundle or node, often cytologically "discoverable" in or near the oral area of the selected ciliates studied, which was formerly thought to have played a conductive or active coordinating role in locomotion, feeding, avoidance, etc.; identified as the rest of the apparatus were various parts of the ***silverline system*** and/or structures today known to be microtubular or microfibrillar organelles of diverse sorts.

Nomen Conservandum: name to be conserved; a name preserved (with appropriate permission) as an exception to some provision of the *International Code of Zoological Nomenclature*.

Nomen Dubium: dubious or doubtful name; a name of uncertain application through lack of sufficient information about it or the organism or taxon with which it might be associated.

Nomen Novum: new name; a name expressly proposed and published as replacement of another name (usually a junior homonym requiring such action); often abbreviated to "n. n.," as in this book.

Nomen Nudum: "naked" name; a name published without description of its associated taxon, a diagnosis necessary to validate both the name and taxon involved; abbreviation can be "n. n.," but not so used here: see above.

Nomen Oblitum: forgotten name; a name unused as a senior synonym for more than 50 years; a long unused invalid name often literally "forgotten" by taxonomists of the group and generally best left in that condition.

Nonciliferous: see **Barren Kinetosome**.

Nonhomologous: see **Homologous (characters)**, of which this term is the exact opposite; however, either kind (of structures, for example) may have an ***analogous*** function with some other structure.

Nuclear Dualism: presence or existence of two different kinds of nuclei; for example, the micro- and macronuclei so characteristic of the great majority of ciliates; exhibition of the ***heterokaryotic*** condition. ★ ★

Nuclear Envelope: system of membranes or coverings of a nucleus; often replete with minute pores.

Nuclear Membrane: older term — better called ***nuclear envelope***.

Nucleolus: see mention under **Endosome**; but the nucleolus is quite a different organelle, and one much more commonly found in ciliate nucleoplasm. ★ ★ [Nuc]

Nucleus: in general, see **Macronucleus** and **Micronucleus**; however, in the homokaryotic gymnostome *Stephanopogon* the nucleus is of but one sort, which is neither a micro- nor a macronucleus. ★ ★

Numbering Conventions: (1) *Kineties* are numbered — following the method of Chatton-Lwoff — around the body clockwise when viewed from the apical pole, with ***number 1*** being the rightmost ***postoral meridian***, which (in certain hymenostomes) also bears the *cytoproct* posteriorly and is normally the ***stomatogenic kinety***; the operational equivalent of the first kinety in other ciliate groups may generally be determined with relative ease; no matter the total number, the last one, immediately to the viewer's right of number 1, is conventionally labeled as "n." (2) *Microtubular triplets of a kinetosome* are numbered — following the *Grain convention* — clockwise around the proximal end of the basal body, viewed (as in cross-section) from the inside of the organism looking out, with ***number 1*** being the triplet lying in the axis of the kinety; but it is often more convenient (and perhaps safer!) to make use of the location of the *postciliary microtubular ribbon* which is (or is assumed to be) always associated with number 9, the last triplet — thus number 1 would be the next one on the viewer's left. There are alternative systems of numeration for both of the matters treated above. For counting kineties, the method of von Gelei — proposed in the same year, 1931, but subsequently generally ignored — gives results exactly the opposite from those of the French system; that is, number 1 is the same, but the suggested direction of counting is counterclockwise, and thus the nth meridian is on the right rather than the left side of the first kinety. For the microtubular triplets, the ***Pitelka convention*** — proposed in 1969, also the year of Grain's suggestion — considers numbers 1-3 to be on the right anterior margin of the kinetosome (again, looking at a cross-section from the base outward), associated with the ***kinetodesma*** (of *Paramecium*); the counting similarly proceeds clockwise around the base. In this convention, the triplet associated with the postciliary microtubular ribbon is always number 5 (which equals number 9 of the Grain convention, the system adopted in this book). ★ ★

Occam's Razor: equivalent to the principle of parsimony, *viz.*, when faced with two assumptions or alternatives equally unproven or nonverifiable, choose the simpler of the two as the tentative solution of the problem at hand; perhaps it should be more frequently applied in taxonomic dilemmas!

Ogival Field: transitory group of kinetosomes, bearing *thigmotactic cilia*, which appears anterior to the *rosette* during tomitogenesis in many apostomes; the pointed arch-shaped patch of specialized cilia facilitates attachment of the tomite to a new substratum (generally crab integument).

Oligomerization: postulated evolutionary process of reduction or diminution (but not necessarily simplification) in the usual numbers of some organelle: for example, in numbers of ***kineties*** over a ciliate's body; to be contrasted with ***polymerization***, as these terms are conventionally used by ciliate phylogeneticists.

Oligoploidy: see mention under **Diploid** and **Polyploid**.

Oligosaprobic: see mention under **Polysaprobic**.

Omnivorous: eats everything(!); such ciliates are not at all "fussy" in their feeding habits.

Ontogeny: history of an individual, from egg to adult; by analogy, in the case of a ciliate, it is the growth and development from a fission product, the ***tomite***, to the mature ***trophont*** or ***tomont*** (ready for another fission) in the full life cycle of the organism; comparative study of the ***patterns*** revealed in the *morphogenesis* associated with such ontogenetic development may throw light on the ***phylogeny*** of the group concerned (phylembryogenesis); see also **Biogenetic Law**.

Operculum: literally, lid or covering flap; used variously (e.g., as the cover of the emergence pore of some cysts), but mostly for two quite different structures both in sessiline peritrichs: (1) the stalked *epistomial disc* present in many of the opercularids; and (2) the organelle attached to the anterior end of the body, as a stalked "cap" at an oblique angle to the epistomial disc, which may wholly or partially cover the opening of the lorica (on retraction of the organism into its case) in some of the loricate vaginicolids (e.g., *Pyxicola*). ★ ★ [Operc]

Ophryokinety: one of 3-5 short, parallel rows of cilia (with pairs of kinetosomes and single associated parasomal sac forming the triangular group so neatly revealed in silver-impregnated material) on the ventral surface near the anterior end of the body and located immediately to the right of the buccal cavity proper, as found in such peniculine ciliates as *Frontonia*; these "brow" kineties have generally been called ***vestibular kineties***, now an inappropriate term for them; differing from true ***somatic kineties***, they may represent a legitimate part of the buccal ciliature ***sensu lato*** in the organisms bearing them, though their topological position is unique and their role in stomatogenesis not fully understood. ★ ★ [Ok]

Opisthe: posterior ***filial product*** of a regular binary ***fission*** of the parental organism; the anterior ciliate resulting from such a division is the ***proter***. ★ ★ [Op]

Oral Apparatus: general term to denote the entire complex of structures and organelles involved in or quite directly related to the mouth *sensu lato* and its ingestatory function; it is multiple in suctorians and absent as such in astomatous ciliates.

Oral Area: general term for that part of the ciliate's body bearing the *oral apparatus*; convenient to use in a nonspecific way, and it is to be contrasted with the *somatic area* (the rest or bulk of the body); *buccal area*, a more restrictive term, is *not* to be considered a synonym.

Oral Atrium: see **Atrium**.

Oral Ciliature: general term for cilia, simple or compound, which are directly associated with the *oral apparatus*; associated with it would be the bases of all such structures, the *oral infraciliature* (as opposed to kinds of *somatic infraciliature*).

Oral Disc: specialized name for the apically located *oral area* of a ciliate when it is conspicuously separated from the rest of the body, such as in the hourglass-shaped heterotrich *Licnophora*.

Oral Groove: generalized term for a depression leading to a buccal cavity or a cytostome; widely used in the past for *Paramecium* to indicate what was more recently termed *vestibulum* and which I am now considering to be a kind of *prebuccal area* in that organism, reserving vestibulum for a different usage.

Oral Infraciliature: see **Oral Ciliature**.

Oral Replacement: see **Stomatogenesis**.

Oral Ribs: argentophilic pellicular crests of a non-naked *ribbed wall*; they appear, under light microscopy, to represent lines coursing inwardly in a one-to-one ratio from the kinetosomal bases of the right-hand *paroral membrane*, as seen in many oligohymenophoran species (in silver-impregnated preparations). ★★ [OR]

Organelle of Fixation: see **Attachment Organelle**.

Organic Pollution: for our purposes, see **Polysaprobic** and **Saprobity System**.

Orthogenetic Lines: supposed *evolutionary series* which have allegedly followed a *predetermined* pathway and have not invoked nor been subject to the laws of natural selection; such proposed phylogenetic lines are rejected by modern evolutionary theory.

Orthomere: DNA-rich *karyomere* of a *heteromerous macronucleus*; to be contrasted with the *paramere*, the other kind of karyomere in that type of nucleus. ★★ [Om]

Osmotrophic: see **Saprozoic**.

Palintomy: rapid sequence of binary fissions, typically within a cyst and essentially without intervening growth; results in production of numerous, small-sized *filial products* or *tomites*; characteristic of various parasitic ciliates, including some apostomes, the hymenostome *Ichthyophthirius*, and a few others; the net result is similar to that of *polytomic fission*.

Palp: variously used, often for a protuberance of the body with an alleged *sensory* function.

Papilla: variously used; but often refers to the pellicular or extrapellicular wart-like bumps or small protuberances on the surface of an organism (e.g., on the *bell* of some sessiline peritrichs and on the body of certain chonotrichs); in a broad sense, *tubercle* may be considered a synonym.

Parakinetal: type of *stomatogenesis* in which the (supposedly *anarchic*) field of kinetosomes involved in the developing opisthe is derived directly from (or appears alongside) one or more of the parental organism's *postoral somatic kineties* at a level destined to be slightly posterior to the eventual fission furrow; the primordial field (*anlage*) for the opisthe's oral apparatus thus appears subequatorially on the ventral surface at a location (far) removed from the parental mouthparts; partial or full replacement or restructuring (see **Oral Replacement**) of the parental (now proter) buccal organelles, involving oral kinetosomes and kinetosomes from the anterior termination of the (same) *stomatogenic kinety*, may occur simultaneously; the parakinetal mode is characteristic of some hymenostomes and some spirotrichs; it was formerly known as *somatic-meridional* stomatogenesis. ★★

Paralabial Organ: enigmatic structure in a crypt near one of the adoral *syncilia* in certain entodiniomorphids; composed of pellicular folds and several cilia; considered a kind of *sensory organelle*, but really of unknown function.

Paramembranelle: specialized term for each of the several (often many) adoral *buccal membranelles* characteristic of free-living heterotrich (and other polyhymenophoran) ciliates; it is unique in having its *transverse microtubules* limited to the kinetosomes of the left (outermost, distal) row of its infraciliary base. ★★ [Pmem]

Paramere: DNA-poor *karyomere* of a *heteromerous macronucleus*; to be contrasted with the *orthomere*, the other kind of karyomere in that type of nucleus. ★★ [Pm]

Parasitic: see **Parasitism**.

Parasitism: kind of symbiotic relationship in which one member (the parasite) lives at the expense (to various degrees) of the other (the host); the association (from the point of view of the parasite) may be facultative or obligate; the phenomenon is not common among ciliates: many species loosely called "parasitic" are more likely just exhibiting *commensalism*; but, in a general way, many workers (including the writer) often use "parasitism," "parasite," and "parasitic" *sensu lato* as handy (but admittedly imprecise) synonyms of *symbiosis*, *symbiont*, and *symbiotic*; *hyperparasitism*, relatively even rarer among ciliates, is the parasitic association of a form with a host (protozoan or metazoan) which is itself a parasite on or in still another host (e.g., the several apostome species which have stages on or in other apostomes which themselves are parasitic on crustaceans; or chonotrichs on "whale-lice").

Parasomal Sac: small, membrane-lined, pit-like invagination or diverticulum in the pellicle, characteristically alongside (usually to the right of) a *ciliferous kinetosome*; a site of pinocytosis ("cell-drinking") – that is, *pinocytotic vesicles* may be pinched off from its distal portion; perhaps the *pellicular pore* of peritrichs is a kind of parasomal sac. ★★ [PS]

Parateny: condition or presence of recognizable repeating *kinetidal patterns* at right angles to the longitudinal axis of the ciliate's body, thus parallel to the (eventual) fission furrow; paratenes superficially give the impression that the organism's ciliary rows run circumferentially rather than longitudinally in the part of the body affected; the anterior end of *Loxocephalus* serves as an outstanding example, with other scuticociliates and various hymenostomatids also manifesting the condition quite clearly. ★ ★ [Par]

Parental Form: generalized term to denote the mature or about-to-divide (e.g., *trophont-tomont*) stage in the life cycle; the form capable of producing offspring – one or more, depending on the mode of *fission* invoked; generally, this form is itself lost in the process, typically by becoming one of the individuals of the reproduced generation (though this kind of immortality may involve a considerable degree of de- and redifferentiation, etc.); but in some ciliates, and/or under certain conditions, the parental or maternal form persists (e.g., living to produce subsequent generations of filial products, as is true of many suctorians with their budding method of reproduction) and/or even dies a natural death itself in due time.

Paroral Kinety: see **Paroral Membrane**; but I reserve the word "kinety" for *somatic* structures, though some other workers do use it in connection with various *oral* organelles.

Paroral Membrane: preferred term, used in a broad sense, for the ciliary organelle (sometimes multiple) lying along the right side or border of the *buccal cavity* in oligo- and polyhymenophoran ciliates; its cilia may be undulatory as a single unit (but this is *not* universally true) because of their fully or partially coalescent nature (see **Undulating Membrane**); different types – some very likely nonhomologous – are recognized by their variation in the pattern and organization of the kinetosomes comprising their infraciliary bases; the haplokinetal arrangement in many oligohymenophorans – zigzag configuration with inner kinetosomes barren and outer ciliferous (a pair, one inner one outer, being a *stichodyad*) – is well known; the *stichomonad* and *diplostichomonad* arrangements in polyhymenophorans have only very recently been exposed; other kinds of parorals may show additional, if minor, ultrastructural differences; but in all cases the topological position and the probable function are at least analogous; major synonyms include *endoral membrane* (e.g., in *Paramecium*) and *undulating membrane* (e.g., in tetrahymenines); with emphasis on the infraciliary base, *haplokinety* has long been used with reference to the paroral membrane of many oligohymenophorans, including peritrichs, sometimes even meaning the whole organelle (ciliary part as well as kinetosomal); the paroral of many scuticociliates is a bi- or tripartite structure, with segments (not always truly separable) which are labeled as "a," "b," and "c" from anterior to posterior, with "b" sometimes forming a great curve around the cytostomal area proper (see **Zeta Membranoid**). ★ ★ [PM]

Pavés: "blocks" of ciliary organelles or kinetofragments (called *pseudomembranelles* by some workers) characteristic of the *frange* of certain hypostome species; their infraciliary bases are particularly clearly revealed by methods of silver impregnation. ★ ★ [Pav]

PBB-complex: polar basal body-complex at the posterior end of the body of a number of forms, especially scuticociliates; found ultrastructurally in some species to be an infraciliary kinetosome, bearing a long and often stiff *caudal cilium*, plus a pair of *parasomal sacs*. ★ ★ [PBB]

PCA: see **Preoral Ciliary Apparatus**.

Pecilokont: seldom used word once proposed to include both "cilium" and "flagellum" together under a single convenient(?!) term; see also **Undulipodium**.

Pectinelle: one of a circumferential band of short rows of closely apposed cilia oriented at an oblique angle to the long axis of the body; used by some workers to describe the composition of both the *locomotor fringe* of peritrichs and the *ciliary girdle* of didiniid gymnostomes. ★ ★ [Pec]

Pedicel: term used variously in ciliatology, but generally with reference to a very short attachment *stalk*, such as in certain chonotrichs. ★ ★ [Ped]

Peduncle: term generally used as a synonym of *stalk* when referring to ciliates; often reserved for long, highly visible stalks, such as those, not necessarily homologous organelles, found in many peritrichs and suctorians; the adjectival form, "peduncular," is also often used with reference to stalk structures. ★ ★ [Pdc]

Pelagic: pertaining to the open ocean (beyond the continental slope) or the "high seas" as an ecological habitat, in contrast to the near-shore or *neritic* biotope; many tintinnines are especially representative of pelagic ciliates; *eupelagic*, for our purposes, is essentially a synonym.

Pellicle: outer "living" covering of a ciliate, composed of the typical cell or *plasma membrane* plus the membrane-lined *alveoli* and, often, the closely apposed underlying fibrous layer known as the *epiplasm*; sometimes loosely used as synonymous with *cortex*, but the majority of the infraciliary cortical structures and organelles are mostly *sub*pellicular in location. ★ ★ [Pel]

Pellicular Alveolus: see **Alveolus, Pellicular**. ★ ★ [PA]

Pellicular Crest: in a general way, any ridge or crest formed on the surface of the body by the underlying pellicle; often it is the *argentophilic* line of contact or juncture of the (membranes of the) adjacent, contiguous *pellicular alveoli*; when, in the buccal cavity of various oligohymenophorans, the crests are underpinned by postciliary microtubules, they are identified as *oral ribs* of a so-called non-naked *ribbed wall*.

Pellicular Pores: self-explanatory term, but particularly used in reference to the numerous minute openings in the pellicle on the *bell* (and perhaps in the area of the *scopula*) of sessiline peritrichs through which are secreted substances involved in mucus-coatings, *lorica*-formation, and (in part) *stalk*-production; in many cases, these pores *may* be, in effect, some kind of *parasomal sac*, even kinetosomeless in the case of the bell of peritrichs and the *scopuloid* of suctorians; they have also been called *cuticular pores*.

Pellicular Striae: ridges or markings in or on the pellicle; the term is particularly applied to the circumferential *annuli* on the *zooid* of many sessiline peritrichs, rings which may be comprised of argentophilic *pellicular pores* and/or *pellicular crests* or – perhaps most likely – just "silverlines" of unknown significance. ★ ★ [PelStr]

Peniculus: kind of *membranelle* or compound buccal ciliary organelle in the form of a long band of often short, seemingly fused cilia; its infraciliary base, typically coursing along the left wall of a buccal cavity, may be as many as 11 kinetosomes in width but is usually only 3-7, with a tapering to still lower numbers at either end; its metachronal movement and details in its ultrastructure lend further distinctiveness; it is known classically in such peniculine hymenostomes as *Paramecium*, where there is one dorsal and one ventral peniculus; but the term has also been used for the membranellar organelles found in the *infundibulum* of peritrichs (although see Polykinety) and various other oligohymenophorans. ★ ★ [P1-3, in figures of *Frontonia* and *Campanella*]

Perforatorium: see mention under **Rostrum**.

Perilemma: additional outermost membrane covering the pellicle in various oligotrichid ciliates (and possibly present in species of a few other groups).

Perioral Ciliature: see **Circumoral Ciliature**, although perioral is sometimes used in a looser way to include *any* ciliature, even buccal, which is, in effect, around (in the vicinity of) the ciliate's *cytostome*.

Periphyton Community: in the broadest sense, a loose association of organisms living on (generally attached to) various submerged substrata, often plant material or inanimate objects (in fact, the investigator's submerged glass slide — for collecting the material — often provides the ideal substratum); the predominantly sessile forms, including many ciliates, which comprise the community may be found in marine, fresh-water, or brackish habitats; generally considered today to be a synonym is *aufwuchs community*, the term actually preferred by many protozoologists.

Peristome: in a broad sense, a synonym of *buccal cavity*; but the term is well entrenched in the literature to mean the entire expansive oral area (*peristomial field*) of the so-called higher ciliates (peritrichs and various of the spirotrichs) in which the buccal ciliature has often emerged from a true cavity to encircle (though usually only partially) much of the anterior (or ventro-anterior or oral) end or pole of the organism's body. ★ ★ [Pst]

Peristomial Area or Field: see **Peristome**. ★ ★

Peristomial Ciliature: see **Buccal Ciliature**.

Perizonal Ciliature: *somatic ciliature* in the vicinity (usually to the right) of the *oral area* the rows of which appear to run transversely (see **Parateny**); the often closely packed cilia are said to function in intensification of the (food-carrying) water currents which are being directed toward the ciliate's ingestatory apparatus.

Perkinetal: across or through the kineties, the common mode of *homothetogenic fission* in ciliates; the division furrow cuts across the body at essentially right angles to the rows of *somatic ciliature*. ★ ★

Pexicyst: type of small toxicyst-like *extrusome* in certain haptorid gymnostomes (perhaps uniquely in *Didinium*) which, on discharge, adheres to the pellicle of the prey without subsequent penetration.

Phagocytic Vacuoles: see **Food Vacuoles**.

Phagoplasm: specialized cytoplasm, vacuolated and allegedly rich in digestive enzymes, found in or around the *cytopharyngeal apparatus* in, for example, predaceous carnivorous gymnostomes.

Pharyngeal Basket: see **Cytopharyngeal Basket**.

Pharynx: see **Cytopharynx**.

Phialocyst: see **Haptocyst**.

Phoront: stage in a polymorphic life cycle during which the organism is carried about by (generally on or in the integument of) another (generally metazoan) organism; the term is used, however, in a much more restrictive sense (than is the word *symphoriont*) to indicate the condition exhibited primarily by certain polymorphic apostomes, where it is a stage which is typically preceded by a *tomite* and followed by a *trophont*. ★ ★ [Phor]

Phylembryogenesis: see mention under **Biogenetic Law** and **Ontogeny**.

Phylogeny: history of the race; lines of evolution involving groups of organisms through time and space; a continuum of ontogenies; without the advantage of a helpful fossil record, ciliates must be studied phylogenetically via indirect means: identification of trends in comparative morphology, recognition and tracing of homologous structures and organelles, appropriate application of well-known evolutionary tenets, etc., using material exclusively from contemporary groups.

Phytoplankton: see **Plankton**.

Pigment Granules: not uncommon — as endogenous pigmentation — in ciliates, either in the cortex near the pellicle (e.g., see **Stentorin**) or deeper in the cytoplasm; of various colors; but many "colored" ciliates derive their hues exogenously — from endosymbiotic *zoochlorellae* or, temporarily, from pigmented ingested food materials.

Pinocytotic Vesicles: see **Food Vacuoles**, also **Parasomal Sac** and **Saprozoic**.

Pitelka Convention: see mention under **Numbering Conventions**. ★ ★

Plankton: community (*sensu lato*) of predominantly passively floating or weakly motile organisms (including various stages in their life cycles) on or near the surface of a body of water — fresh, brackish, or marine; ciliates may be found in abundance, whether the plankton is largely plant (e.g., algae) or animal (e.g., eggs, larval stages of microcrustaceans, and the like) in composition (*phyto-* or *zooplankton*, respectively); classification into *meso-*, *micro-*, or *nannoplankton* is based on body size of the plankters (diameter ⟩ 1000 µm, 50-1000 µm, ⟨ 50 µm).

Plasmalemma: sometimes used in the sense of *plasma membrane*, other times as a synonym of *pellicle*; not to be confused with *perilemma*.

Plasma Membrane: see **Unit Membrane**. ★ ★ [PlM]

Plesiomorph: term used by cladists and some phylogeneticists to designate an *original* character in a branching phyletic lineage; a character found only in an ancestral form; primitive, as in the ancestral condition; admittedly a *relative* term, but to be contrasted with *apomorph*.

Podite: term reserved, in ciliatology, for the often conical-shaped projection from the ventral surface, near the posterior pole, of certain cyrtophorid hypostomes; this foot-like appendage, rigid though usually slightly rotatable, is the structure through which or from which a glutinous, mucus-like filament may be extruded which, in turn, serves to attach or anchor (usually only temporarily) the ciliate to or over a desirable substratum; the organelle is also known as a *stylet* (or *stylus* or *style*); to a degree, it may be homologous to (part of?) the *stalk* of the related chonotrichs. ★ ★ [Pod]

Polar Basal Body-complex: see **PBB-complex**.

Polyenergid: state of having either multiple nuclei and/or multiple ploidy in a nucleus within a single cell or protistan body; all *heterokaryotic* ciliates exhibit this condition, generally to a high degree.

Polygemmic: production of multiple *buds*, synchronously or consecutively; a mode of *fission* exhibited by some suctorians and chonotrichs.

Polygenomic: may be considered to be a term reasonably similar to *polyploid*, with respect to ciliate macronuclei; but some protistan evolutionists use it to mean the presence of many nonhomologous genomes, a definition appropriate to the endosymbiotic theory of the origin of the eukaryotic cell.

Polyhymenium: little-used term for denoting the multiple-*membranelle* situation manifest especially in the *peristomial area* of the so-called higher ciliates (e.g., many spirotrichs).

Polykinety: persistingly popular term for the infraciliary bases (or sometimes the whole structure, *with* its cilia) of the buccal membranelles *sensu lato* of certain groups of ciliates (particularly the scuticociliates); in very recent times it has been restricted by some workers to description of the oral membranelles of the peritrichs (but, in which case, should not one also include the pleuronematine and thigmotrichine scuticociliates?); there are specialized ultrastructural infraciliary differences – among the various types of membranelles – detectable in the relatively few species subjected to comparative study to date; but exact homologies rest unclear, and the picture is complicated by the seemingly *peniculus*-like nature of the peritrich polykinety in its lower portion in the *infundibular* part of the buccal cavity *sensu lato*. ★★ [Pk]

Polymerization: postulated evolutionary process of multiplication or increase in usual numbers of some organelle: for example, in numbers of *membranelles* comprising an *AZM*; it may lead to hypertelic development of certain organelles or structures and it may be involved in *somatization* as well as in *auxomorphy*; this principle is to be contrasted with *oligomerization*, as these terms are conventionally used by ciliate phylogeneticists.

Polyphyletic: condition of a taxon (at any level) being comprised of members some of which are descended from (or presumed to have been derived from) ancestors which are quite different from the predecessors of other members in the group; this is an undesirable situation from a taxonomic-classificational point of view, and it is to be contrasted with the favored *monophyletic* condition.

Polyploid: multiple sets of the N chromosome number within a single nucleus; characteristic of the great bulk of ciliate *macronuclei*; a low polyploid condition may be called *oligoploidy*.

Polysaprobic: pertains to an aquatic habitat poor in dissolved oxygen and rich in decomposition products (thus exhibiting a high degree of *organic pollution*, generally including high production of ammonia and hydrogen sulfide); physicochemically similar to *eutrophic*, though the terms are not used in the same way at all; it is to be contrasted with *mesosaprobic* and *oligosaprobic* habitats which show, respectively, either a medium degree or a low degree of organic pollution; broadly usable more or less as synonyms of polysaprobic, for our purposes, are terms such as *sapropelic* and *sapropelebiotic*; see also **Saprobity System**.

Polystichomonad: type of multiple *paroral membrane* the infraciliature of which is composed of more than two parallel rows or files of identically oriented kinetosomes; found in a few hypotrichs; see also **Diplostichomonad**.

Polystomy: condition of being equipped with many or multiple *mouths*; best illustrated by the suctorians, with their typically numerous *suctorial tentacles*.

Polytomic: division of a single individual into numerous *filial products*, presumably at one time or in quick succession; generally rare in ciliates, but this type of *fission* may occur in certain kinds of *budding*; the net result is similar to that realized in *palintomy*.

Pores: generalized term for variety of holes or generally small openings – into or through membranes, envelopes, pellicle, loricae, cysts, brood pouch, etc.; the *contractile vacuole pore* may serve as an example of a pore of considerable taxonomic value.

Positional Control Principle: use of gradient-fields (or the like) in defining the local properties responsible for placement of major cortical (and other) organelles which develop anew during fission of an organism (e.g., new groups of cirri on the ventral surface of hypotrichs); that is, invoking their geometrical relationships to certain "boundary zones" to explain the ultimate positioning of such structures arising during the morphogenetics of division, reorganization, or regeneration; a developmental hypothesis applicable to ciliate *morphogenesis* which is experimentally testable.

Postciliary Fibers: see **Postciliary Microtubules**, the more widely used term today for the structures involved.

Postciliary Microtubules: ribbon or band of *microtubules* occurring widely throughout the ciliate taxa and strongly developed (in stacks or sheet of ribbons known collectively as the *postciliodesma*) in many kinetofragminophoran and polyhymenophoran groups; it is always found in association with a kinetosome, arising at that organelle's right-posterior side very close to triplet number 9 (*Grain convention*); the ribbon, which may be composed of 2-8 cross-linked (in some ciliates) microtubules, first extends diagonally (to the right) upward into a *pellicular crest* and then – if well developed – continues posteriorly, parallel to and midway between the kinety containing its kinetosome and the next kinety to the right, with the sheet perpendicular to the pellicle; in the buccal cavity of many oligohymenophorans, postciliary microtubules are implicated in formation of the *ribbed wall*; in the oral area of hypostomes, they are involved in the composition of the *cytopharyngeal apparatus* (see **Cyrtos**); see also the specialized **Km Fiber** and **Postciliodesma**. ★★ [PcMt]

Postciliodesma: recently coined term for the conspicuous, posteriorly running (on the right side of the associated kinety) fiber, composed of stacks of *postciliary microtubular ribbons*, which is found in various groups of species (e.g., in such currently widely separated taxa as the karyorelictids and the heterotrichs); the ciliates in which it is strongly developed allegedly have short or no *kinetodesmata*, a fact with interesting phylogenetic implications; an earlier name for the postciliodesma in certain heterotrichs is the *Km fiber*. ★★ [Pcd]

Posterior Microtubules: see **Postciliary Microtubules**, the more acceptable term today for the structures involved.

Postoral Meridian: ventral kinety terminating anteriorly at the posterior border of the *buccal overture* or of the general *oral area*; in a number of ciliates, POM #1 (rightmost if more than one) is the *stomatogenic kinety* (in *parakinetal* stomatogenesis) and bears the *cytoproct* in its left posterior extremity as well; particularly characteristic of tetrahymenine hymenostomes. ★★ [PoM]

Postoral Somatic Kinety: see **Postoral Meridian.**

Postoral Suture: typically, a midventral *système sécant* or line coursing from the *oral area* toward the posterior pole of the organism; and onto it some kineties (i.e., their posterior extremities) from both sides converge (or run roughly parallel to it); it exists in a number of groups of ciliates, though sometimes it is less distinctive than the *preoral suture*. ★ ★ [PoS]

Prebuccal Area: new term, here proposed, for the depression or *oral groove* leading to the *buccal cavity* (in forms like the hymenostome *Paramecium*) and lined with somatic or slightly modified *somatic ciliature*; the area was formerly included under *vestibulum*, a term now restricted to ciliates without "true" buccal cavities. ★ ★ [PbA]

Prebuccal Ciliature: new term, here proposed, for some of the ciliature formerly called *vestibular*; it is composed of the more or less modified somatic cilia lining the *oral groove*, that is, the *prebuccal area*, which leads to the *buccal cavity* in such peniculine hymenostome ciliates as *Paramecium*.

Prehensile Tentacle: noningestatory organelle (with pointed rather than knobbed end) possessed by a few suctorians which – with others of the same kind – is allegedly used to capture or hold a prey organism in such a manner as to bring it into contact with the more common *suctorial tentacle*.

Preoral Ciliary Apparatus: rather all-inclusive term used by some workers to indicate all categories of *oral ciliature* (from *atrial* to *buccal*), differentiating them from *somatic* (including *thigmotactic*) ciliature; called the *PCA*.

Preoral Kinety: name sometimes used for the anteriormost of the three oral *kinetofragments* found in certain cyrtophorid hypostomes.

Preoral Suture: typically, a short, midventral (or often skewed to left) line or *système sécant* coursing from the oral area to the apical pole of the organism; onto it the anterior ends of a number of somatic kineties from either side may converge; common in ciliates from various taxonomic groups. ★ ★ [PrS]

Primary Meridian: see **Ciliary Meridian.**

Primary Ribbed Wall: see **Ribbed Wall.**

Primordium: see **Anlage.**

Proboscis: elephant trunk-like extension of the anterior end of certain ciliates (e.g., *Dileptus*); it differs from a neck in that the *oral area* is situated at its base rather than at its distal extremity; it is heavily armed with *toxicysts*, and – though ciliated and active – it is not capable of effecting extreme changes in its length; the nonhomologous "proboscis" of *Didinium* is that organism's everted *cytopharyngeal apparatus*.

Proter: anterior *filial product* of a regular binary *fission* of the parental organism; it often retains the mouthparts of the parent; the posterior daughter is the *opisthe*. ★ ★ [Pr]

Protomite: relatively rare stage in the polymorphic life cycle of a few ciliates (e.g., some apostomes) which is recognizable as a separate form between the *tomont* and the *tomite*; see Tomite.

Protomont: relatively rare stage in the polymorphic life cycle of a few ciliates (e.g., some apostomes) which is recognizable as a separate form between the feeding *trophont* and the often encysted true *tomont* (dividing) stage; see Tomont.

Protrichocyst: older, once popular term for *mucocyst*, an *extrusome* found in many ciliates (and some other protozoa).

Psammophilic: sand-loving; descriptive term for *interstitial forms* found in, on, or at least temporarily associated with the sands of intertidal zones (marine *littoral* biotope) or of fresh-water beaches and the like.

Pseudomembranelle: rather imprecise term used variously in the literature to describe oral or somatic ciliary complexes which seem to defy other classifications and do appear to resemble some kind of membranelle *sensu lato*; some complex *kinetofragments* have been so called: see Frange and Pavés.

Pseudonasse: see **Rhabdos.**

Pseudoperistome: term formerly used by some workers for the *vestibulum* of trichostomatid and colpodid ciliates.

Pulsating Canal: see **Afferent Canal.**

Pulsating Vacuole: see **Contractile Vacuole.**

Quadrulus: buccal *ciliary organelle* with long cilia and an infraciliary base four kinetosomes in width and many in length; the lengthy rows are more loosely associated than is the case in *peniculi* and *membranelles sensu stricto*; it is well known in *Paramecium*, and its homologue may exist in certain other peniculine hymenostomes; synonyms include *membrana quadripartita*, *Vierermembran*, and *vierteilige Membran*.

Radial Canal: see **Afferent Canal.**

Radial Fibers: see **Postciliary Microtubules**, the more acceptable term today for the structures involved.

Radial Pins: see mention under **Border Membrane.**

Recapitulation, Law of: see **Biogenetic Law.**

Receiving Vacuole: see **Cytopharyngeal Pouch.**

Reorganization Band: lightly staining (though with a narrow Fuelgen-positive leading edge) cross-band of a *macronucleus* which migrates or sweeps along (through) one-half the length of the nucleus, typically (e.g., in hypotrichs) with a similar band traversing the other half (from either midpoint out to the ends or ends into the center); the area is involved in DNA replication and histone synthesis, the amount of these substances doubling just behind the moving bands; the phenomenon occurs periodically in a number of hypotrich and oligotrich ciliates, forms with *homomerous macronuclei*, preceding macronuclear fission and cytokinesis of the organism itself; it also takes place in the *heteromerous macronucleus* of certain cyrtophorid hypostomes and chonotrichs where there is only one band, moving across the *orthomere* to its free end; two *zones* may be recognized; the *reticular* ("forward zone" or "solution plane," as formerly known) and the *diffuse* ("rear zone" or "reconstruction plane": locus of the DNA synthesis); a more modern and perhaps more meaningful name is *replication band*, but "reorganization band" is firmly entrenched in the literature. ★ ★ [RB]

Replication Band: see **Reorganization Band.**

Reproduction: see **Fission**; note that, though there are a number of types of fission, the only kind of reproduction in ciliated protozoa is asexual, textbook statements notwithstanding (i.e., conjugation, for example, is a sexual phenomenon but *not* sexual reproduction).

Reticulated Fiber: see **Filamentous Reticulum**, the newer and more accurate name.

Retractor Fibers: generalized term for bundles of *myonemes*, in various ciliates, used to draw back some extended part of the body or a protuding oral area. ★★ [RF]

Retrodesmal Fiber: rarely occurring (known, to date, from only certain clevelandelline heterotrichs) nonstriated fiber arising close to the base of a somatic kinetosome near its microtubular triplets 5-7 (*Grain convention*) and – unlike the *kinetodesma* – extending *posteriad* parallel to the pellicle; it could be called a "retrodesma" (pl. retrodesmata). ★★ [Rd]

Rhabdocyst: short, rod-like *extrusome* or *trichocyst* (in the broadest sense) found subpellicularly in certain karyorelictid gymnostomes. ★★

Rhabdos: new term, here proposed, for the tubular *cytopharyngeal apparatus* the walls of which are strengthened on the outside by bundles of *nematodesmata* and often lined longitudinally by *transverse microtubules* derived from circumoral (perioral) kinetosomes; contains specialized *phagoplasm*, sometimes with included *toxicysts*; may be bound, near its proximal (outer) end, by an expansible *filamentous annulus*; it is considered evolutionarily more primitive than the *cyrtos* and was formerly associated with only the "lower" (formerly "rhabdophorine") gymnostomes, but it shows a range of complexity in its own composition – for example, it is loosely organized in archi- and prostomatines and vestibuliferans (and generally lacks toxicysts in the last group), whereas it is more elaborate (and sometimes eversible) in prorodontines and haptorids; principal synonyms of rhabdos include *pseudonasse* and the recently used *clathrum*; but the latter term is here considered totally inappropriate in view of its clear implication of a lattice work (or grate or screen), whereas actually the rhabdos is both overall, and in its principal separate parts, highly reminiscent of a *rod* or *rods* (thus its name), arranged in a *straight*, noncurved, encircling palisade formation, with perhaps a suggestion of fluting; the rhabdos is to be compared with the *cyrtos* (a name also, appropriately, of Greek derivation), the other major type of cytopharyngeal apparatus recognized for kinetofragminophoran ciliates, more complex, often curved like a "horn of plenty," lacking toxicysts, and lined with *postciliary* microtubules. ★★

Ribbed Wall: nonciliated lining or surface of the right side of the *buccal cavity* of many oligohymenophoran ciliates which, ultrastructurally, appears ribbed due to the presence there of *postciliary microtubules* (arising in association with the kinetosomes of the nearby *paroral membrane*) which approach the outer pellicular surface perpendicularly at orderly spaced intervals; it is considered to be naked (posterior to the cytostome, thus in the cytopharynx) when no *pellicular alveoli* are involved, and non-naked (the much more common condition) when *oral ribs* – argentophilic pellicular crests of the alveoli underpinned by the postciliary microtubules – are present; the ribbed wall is sometimes called the *primary ribbed wall*: a much rarer *secondary ribbed wall* is said to occur on the *left* side of the buccal cavity in some ciliates. ★★ [RW]

Rod, Cytopharyngeal: see **Nematodesma** and also **Rhabdos**.

Rosette: unique septate structure near the cytostome of many apostomes, complex ultrastructurally and its function still unclear; but the term is also used to describe the result of several rapid preconjugation divisions of certain peritrich zooids (e.g., *Carchesium*) in production of free-swimming microconjugants; there are still other meanings used for certain nonciliate protozoan structures.

Rostellum: small *rostrum* (see following term).

Rostrum: usually employed in a generalized way, with reference to the apical end of an organism's body when it has the appearance of a beak or shows a distinctive protuberance of some kind; it may bear the *cytostome*, as in the haptorid gymnostome *Chaenea*, or a *sucking tube*, as in the entire order Rhynchodida; a small rostrum is sometimes called a *rostellum*; the apically located *perforatorium* or *boring apparatus* of the ciliate literature might better be referred to by this less specific term, rostrum, until we know more from both ultrastructural and more sophisticated functional studies; many a genuine *attachment organelle*, on the other hand, *is* recognizably distinct and should *not* be called a rostrum.

Rule of Desmodexy: see **Desmodexy, Rule of.**

Rules of Nomenclature: see **International Code of Zoological Nomenclature**.

Saltatorial Cilia: long cilia (often stiff or heavy when not in motion) distributed sparsely around the body of certain ciliates (e.g., the oligotrich *Halteria*) and used in a quick, jerky sort of locomotion readily recognizable by its uniqueness; the *Springborsten* of the older literature.

Sanguicolous: living in the circulatoty system (blood) of the host.

Saprobity System: method of potential *saprobiological* classification of aqueous habitats and their contained communities of microorganisms by recognizing that distinct zones exist with respect to degrees of *pollution* present (with attendant "unique" combinations of chemical and physical features: see **Polysaprobic**) and that these provide certain protists (*indicator organisms*) with optimal conditions for their own growth; species of ciliates are considered valuable in such "pollution ecology" studies because of their measurable organic pollution tolerance.

Sapropelebiotic: see **Polysaprobic**.

Sapropelic: see **Polysaprobic**.

Saprozoic: type of nutrition in which the organism feeds on, takes in, or absorbs food substances in the dissolved state in (from) the surrounding medium (often via the process of pinocytosis, with production of *pinocytotic vesicles*); this *osmotrophic* mode is to be contrasted with the *holozoic*, *phagocytic*, *macrophagous*, *carnivorous*, *histophagous*, or other feeding or nutritional habits which essentially involve the ingestion of sizable particulate materials, often including whole prey organisms.

Scopula: compound organelle or structure (or area, in effect), often cup-shaped with a thickened peripheral border or lip, at the *aboral pole* of (especially sessiline) peritrichs which is comprised of a plaque or field of numerous *kinetosomes* typically equipped with very short and immobile cilia; *pellicular(?) pores* (= *parasomal sacs?*) are also present; the scopula may function directly as a *holdfast organelle* or, more commonly, may be involved (presumably mostly via its kinetosomes and/or its pores) in secretion or elaboration of a *peduncle* or *stalk* of considerable complexity (contractile or noncontractile, etc.). ★★ [Sa]

Scopulary Ciliature: see Scopulary Organelles.

Scopulary Kinetosomes: see Scopulary Organelles.

Scopulary Organelles: basically the *kinetosomes* of the *scopula*, although their *clavate cilia* (also known as *stereocilia*), when present, may be included in the definition as well as the associated *pellicular(?) pores* (here possibly = *parasomal sacs?*); various additional fibrillar and microtubular structures are associated with these scopulary kinetosomes, and presumably they are also involved in production of the inner fibers (etc.) of the stalk when one is present (as it frequently is).

Scopuloid: organelle found at the posterior pole of the body of most suctorians; analogous to but not homologous with the *scopula* of peritrichs; comprised mainly of some kind of pellicular(?) pores (here = kinetosomeless *parasomal sacs?*), secretory in nature, which are presumably responsible for production of the sometimes lengthy, complex, nonliving, never contractile *stalk* characteristic of suctorians. ★★ [Sd]

Scutica: transient "compound" *kinetosomal* structure or organelle identifiable by its shape, location, and presence during the developmental process of *stomatogenesis*, thus appearing in a late ontogenetic stage in the binary fission of the group of ciliates possessing it; quite conspicuous but generally nonciliated at the time of its (fleeting) existence, the scutica represents the remainder of an often much larger stomatogenic field of kinetosomes (buccal *anlage*, in effect) located near (and slightly to the right of) the posterior termination of the presumptive infraciliary base of the *paroral membrane* in both the proter and opisthe; typically, it manifests a *hook-like* or *whiplash configuration* (giving it its name), recurving back to the right; presumably its basal bodies have arisen from parts of the *buccal infraciliature* of the parental organism; its typical ultimate fate, if it does not disappear altogether or become entirely incorporated into the haplokinetal base of the paroral membrane, is to persist as a ciliferous or nonciliferous *vestige* of varying size and shape, in close juxtaposition to the base of the trophont's *paroral membrane* and/or at the anterior end of the *director-meridian*, the scutica is thought to be limited to members of its namesake, the Scuticociliatida, but its homologue may be present in species of other orders; the term has been erroneously spelled "*scuticus*" in the recent literature – but it is a perfectly good Latin word of feminine gender requiring the terminal "a" in the nominative singular. ★★ [Sc]

Scutico-field: see Scutica; often used with reference to the slightly earlier multi-kinetosomal "anlage" stage.

Scutico-hook: term emphasizing what is the most typical appearance of the *scutica*, its hook-like configuration – thus the words are practically synonymous; see Scutica.

Scutico-kinetosomes: basal bodies comprising the *scutica*.

Scutico-vestige: structure (residual field of recognizable *scutico-kinetosomes*) visibly remaining in the (new) trophont(s) after the identifiable stage of the dynamic *scutica* has passed; see Scutica. ★★ [ScV]

Scuticus: misspelling of *scutica* which should be dropped from any further usage.

Seizing Organ: long ago described in *Didinium* as a special, structured, discrete organelle associated with the "*proboscis*" of this haptorid gymnostome; but it is (only) a bundle of discharged *toxicysts* and *pexicysts*; however, they (it) play(s) an essential role in the feeding process of *Didinium* and deserve(s) continued recognition.

Secondary Meridian: see Ciliary Meridian. ★★ [2°CM]

Secretory Organelle: see **Ampulla, Secretory**; but the term also may be used in a broader, more generalized way to refer to any vesicles, glands, pores, adhesive structures, and the like if they are involved in some form of secretion.

SEM: scanning electron microscopy, a technique of growing usefulness in ciliate systematics.

Seme: unit of phylogenetic information; a unit character (ancestral or derived) of high information content; usable in reference to any structural part or function of an organism, from the molecular level up to large and complex organelles or organellar systems.

Semi-autonomous: now discarded term, along with *autonomous*, for a mode of *stomatogenesis*; see **Buccokinetal**.

Semi-membrane: see **Extensor Membrane**; but also formerly used by some workers as a synonym of the *undulating membrane* (= *paroral membrane*) in certain ciliate groups.

Sensory Bristles: rather widely applied term to many "*bristles*" or "*setae*" in ciliates, even when the exact function is unknown; particularly used to describe both (1) the several short rows of *clavate cilia* in such haptorid gymnostomes as *Didinium*, and (2) the nonhomologous very short nonmotile cilia occurring in several longitudinal rows of pits on the dorsal surface of many hypotrichs; sensory bristles are the *Tastcilien* of older literature. ★★ [SB]

Sensory Organelle: generalized term probably often improperly or imprecisely applied to a variety of structures found in ciliates which may or may not actually possess a "sensing" function; frequently implicated organelles (defined elsewhere under their names as listed here) include diverse *bristles* and *setae*, the *brosse*, other specialized cilia (e.g., *caudal, clavate, tactile, thigmotactic*), the *concrement vacuole* (and *Müller's vesicle*), *Lieberkühn's organelle*, *palps*, the *paralabial organ*, *tentaculoids*, and the like.

Setae: see **Bristles** (essentially synonymous terms in ciliatology).

Sexual Phenomena: see **Autogamy, Conjugation, Cytogamy**; meiosis, haploid "gametic" nuclei, a diploid *synkaryon*, etc. are involved, but any *reproduction* which takes place (at the end of the process) is purely by *asexual* fission (the only kind of reproduction exhibited by ciliates).

Sheath: see **Annulus**; also used in other, generalized ways. ★★ [Sh, as outer portion of peritrich stalk]

Shell: see **Lorica**, of which it is a synonym; but it is seldom used in reference to ciliates.

Silberliniensystem: see **Silverline System**.

Silver-impregnation Techniques: cytological staining methods which permit deposition of silver ions onto argentophilic sites where they are reduced, under UV light or appropriate chemicals, blackening the coated structures or areas affected and thus rendering them beautifully visible under subsequent light microscopic examination; the *argyrome* or *silverline system* so revealed in ciliates has proven of immeasurable value in comparative taxonomy and morphogenesis (thus in evolutionary and phylogenetic studies as well); the Klein "dry" method and the "wet" methods of von Gelei and especially of Chatton and Lwoff (classically *the* silver-impregnation technique) show up the argyrome *sensu stricto*, the more or less superficial "cortical" structures such as the silverlined *meridians*, the *contractile vacuole pores*, the *cytoproct*, and – most importantly – the (general sites of the) *kinetosomes*, both somatic (comprising the *kineties* proper) and oral (e.g., the infraciliary bases of the *buccal organelles*); other methods, especially Bodian's protargol (activated silver albumose) technique and the Rio-Hortega method, *additionally* blacken many truly cortical organelles of the *infraciliature sensu lato*, subpellicularly deeper in the organism, such as the *kinetodesmata*, the *nematodesmata*, *extrusive organelles*, ribbons of *microtubules*, *myonemes*, etc., and – further – even the *nuclei*, *mitochondria*, *contractile vacuoles*, etc., and the *cilia* themselves (thus allowing distinction between ciliferous and barren or nonciliferous kinetosomes, a very important consideration in morphogenetic studies); one or more of these techniques, ideally in combination with electron microscopy (TEM and SEM), are nearly indispensable tools today for any precise cytological-systematic work in ciliatology.

Silverline System: see **Argyrome**; once popular synonyms are *Silberliniensystem* and *neuroformative System*. ★★

Simple Ciliature: general term restricted to meaning individual cilia (e.g., those comprising a somatic ciliary row) or single isolated cilia, such as most bristles, or ordinary pairs of cilia; but excluded are formations or arrangements of cilia which are closely apposed in special groups or packets or blocks with some sort of interconnection (often at the infraciliary level), morphologically and/or functionally (real or apparent), such as found in the case of *syncilia*, some *atrial* and *vestibular ciliature*, *all* buccal "compound" ciliature (*paroral membranes*, *membranelles sensu lato*), and "compound" somatic ciliature (best exemplified by *cirri*).

Skeletal Plaques: term recently applied to the numerous polysaccharide granules assembled in the unique *sucker* of certain clevelandelline heterotrichs.

Skeletal Plates: term usually reserved for the long recognized and generally highly conspicuous subpellicular structures composed of polysaccharide reserves (amylopectin) within a fibrillar lattice which are found in the entodiniomorphid vestibuliferans (ophryoscolecids and relatives); but also used in reference to the uniquely calcified cuirass of the prorodontine gymnostome *Coleps*. ★★ [SP]

Skeletal Ring: see **Denticulate Ring**.

Skeletogenous Structure: nonspecific term usable for any organelle or system (e.g., various microtubular sheets or ribbons, kinetodesmata, nematodesmata, various proteinaceous rods, polysaccharide formations, etc.) which may lend a certain firmness or rigidity to the cortex or to all or part of the body of an organism; see **Cytoskeleton**, a term with which it is broadly synonymous, though usage may vary among different workers and for different groups of ciliates.

Solitary Forms: individual ciliates; but used principally in reference to *noncolonial* forms in a contrasting sense; for example, there are colonial and solitary peritrich species, sometimes within a single family.

Somatic Area: general term for all of a ciliate's body except the *oral area*; but some workers also recognize a (separate) *thigmotactic area*.

Somatic Ciliature: all-inclusive term for any cilia or compound ciliary organelles found anywhere on the body outside the *oral area*; associated with it would be the bases of all such structures, the somatic infraciliature (as opposed to kinds of *oral infraciliature*: atrial, vestibular, buccal, peristomial, etc.).

Somatic Infraciliature: see **Somatic Ciliature**.

Somatic-meridional: now discarded term for a mode of *stomatogenesis*; see **Parakinetal**.

Somatization: evolutionary process of increasing the separation of "generative" from "somatic" functions in protozoa, demonstrated in ciliates in the development of *nuclear dualism*, in the complications of *sexual phenomena*, in the manifestation of epigenetic morphogenesis, and in the general diversification and differentiation (often involving *polymerization*) of more complex structures and functions which approach almost a metazoan level of organization.

Spasmoneme: see **Myoneme**; the present term is limited to usage for describing the membrane-bound bundle of contractile fibrillar (myofibrillar) material found in the *stalks* of various (e.g., vorticellid sessiline) peritrichs which arises from and maintains continuity with the *bell* or *zooid* proper; it is capable of contraction at an amazing speed; its former structural subdivision into *thecoplasm* and *kinoplasm* has not been confirmed by electron microscopy. ★★ [Sn]

Spherical Colony: zooids dispersed throughout a rounded, usually gelatinous (but firm), colonial mass, with body axes perpendicular to the surface; because of attachment to a flat substratum, the overall shape may more often be *hemispherical*; the framework of such a globular colony may be basically *arboroid*, however, as shown by some species of the peritrich *Ophrydium* the individuals of which are interconnected by long and slender "penduncular fibers" produced by their scopulae. ★★

Spindle Trichocyst: see **Trichocyst**.

Spines: variously used, though especially for certain apically located *holdfast organelles* (e.g., in some astomes); but the term is also applied to quite elaborately developed structures, with exact function unknown, on the outside of the body of a number of chonotrichs. ★★ [Sp]

Spongiome: see **Spongioplasm**.

Spongioplasm: specialized secretory (in the sense of *collecting* fluid) cytoplasm, of spongy appearance, found in the vicinity of the *contractile vacuole*; sometimes known as the *spongiome*.

Springborsten: see **Saltatorial Cilia**.

Stalk: term broadly used for any kind of cylindrical (generally tubular) supporting structure (either totally nonliving or with a nonliving *sheath* or *annulus*) running from the posterior end of a ciliate's body to a point of fixation on on the underlying substratum (living or inanimate); typically found in attached, sedentary, or sessile forms or stages (with or without involvement of a lorica) of a life cycle, serving as an *attachment* or *holdfast organelle*; may be of varying length, composition, and origin (from *secretory ampullae*, kinetosomes, or possibly *pellicular*(?) *pores*); may be contractile (with a *spasmoneme*) or noncontractile; may have an expanded attachment disc at its distal end; ramified in some groups, associated with colonial organization of the supported *zooids*; most commonly known in chonotrichs, suctorians, and peritrichs, but undoubtedly is a nonhomologous structure in these diverse taxonomic groups; some workers reserve the term stalk solely for the scopula-produced organelle of the sessiline peritrichs, where it is a structure variously composed depending on the taxonomic subgroup: generally, the entire matrix of the stalk is either filled with striated (or, in some species, nonstriated) fibrillar tubules (or with such nonliving material plus a central essentially vacuous cavity) or composed of an outer (nonliving) *sheath* or *annulus*, of varying complexity, and an inner membrane-bound contractile myoneme (the *spasmoneme*). ★ ★ [St]

Statocyst: see **Concrement Vacuole** and **Müller's Vesicle**.

Statolith: see **Concrement Vacuole** and **Müller's Vesicle**.

Stentorin: "blue" cytoplasmic *pigment* distributed in subpellicular granules or vesicles appearing in longitudinal rows in certain species of the heterotrich *Stentor*.

Stereocilia: see **Clavate Cilia**; the term is erroneously used by some metazoological cytologists for what are simply long, slender microvilli.

Stichodyad: type of *paroral membrane* the infraciliature of which is composed of pairs of kinetosomes so oriented that each is perpendicular to the anteroposterior axis of the membrane; furthermore, the kinetosomes are arranged in a zigzag pattern with only the outer member of the dyad being ciliferous (see **Haplokinety**); common condition in oligohymenophorans; compare with *stichomonad*.

Stichomonad: type of *paroral membrane* the infraciliature of which is composed of a single file or line of identically oriented kinetosomes; the characteristic condition found in most polyhymenophorans; the kinetosomes are never in dyads nor in zigzag conformation; compare with *stichodyad*.

Stomatogenesis: new *mouth-formation*; in the broadest sense, this dynamic phenomenon embraces neoformation or replacement of *all* oral structures and infrastructures and any associated or attendant openings, depressions, or cavities in both the proter and opisthe during (sometimes including some time "before" and "after," as well) binary fission of the ciliate proper; a *morphogenetic process* or series of processes is involved, and patterns are discernible which are more or less unique for taxonomically different groups of ciliates; four major kinds or modes (with some inevitable overlapping, intermingling, or confounding: and many subcategories require future identification) may now be recognized from a descriptive "kineto-cortical" point of view – their definitions appear elsewhere under the following terms listed here in an order which roughly indicates an evolutionary sequence from "most primitive" to "most advanced": see **Telokinetal**, **Parakinetal**, **Buccokinetal**, and **Apokinetal**; names of major older descriptive categories are generally listed, more or less as synonyms, under the four preceding terms; *oral replacement*, a stomatogenic phenomenon which may occur periodically in some ciliates, refers to the *in situ* remolding of the old (parental) buccal structures (for the proter) or their total substitution by new organelles, because of the partial or complete dedifferentiation or resorption of the former ones; reversible *microstome-macrostome transformation* involves the growth and/or replacement of a small (the usual size in the organism) oral apparatus with a greatly enlarged one (or *vice versa*), a remarkable morphogenetic process which occurs, under appropriate conditions, in several ciliates (best known in species of *Tetrahymena*): it may be considered a special kind of oral replacement, and certainly stomatogenesis is involved. ★ ★

Stomatogenic Field: general term for the group of kinetosomes, nonciliferous throughout most of the process, actively involved – as the *anlage* – in the overall phenomenon of production of new mouthparts by any of the described modes (see **Stomatogenesis**, above); various "subcategories" or partial synonyms exist: see **Anarchic Field**, **Germinal Row**, **Scutica**, etc. ★ ★ [SF]

Stomatogenic Kinety: see **Kinety Number 1** and **Parakinetal** (*stomatogenesis*). ★ ★ [SK]

Stomatogenous Meridian: see **Stomatogenic Kinety**, for which this is an older term. ★ ★ [SM]

Striated Bands: name for a *(micro)fibrillar system* discovered to lie just below the *epiplasm* in some ciliates. ★ ★ [SBd]

Strobilation: kind of multiple *fission* in which successive *tomites* or *buds* are fully or partially separated or pinched off, sometimes within the confines of a cystic membrane and usually resulting in a (temporary) linear chain (a kind of *catenoid colony*) of small individuals requiring subsequent metamorphosis to regain the form typical of the normal *trophont* stage of the life cycle.

Structural Conservatism Hypothesis: maintenance (i.e., conservation) of a structure through time is inversely related to the level of its biological organization; in the evolution and phylogeny of ciliates, then, among the most stable and most conservative taxonomic characters would be those involving unitary infraciliary organelles, ultrastructures at a relatively low organizational level (e.g., the various microtubular ribbons associated with single somatic kinetosomes, even as contrasted with the only slightly more complex oral membranellar bases).

Structural Guidance Principle: positioning and orientation of newly arising organelles (e.g., ciliary rows on the surface of a holotrichous organism) under the localized influence of nearby preexisting structures; this may be considered as a restricted application of *cytotaxis*.

Style: see **Stylet**.

Stylet: variously used, but generally as a synonym of *podite*; also written by some workers as *style* or *stylus*.

Stylus: see **Stylet**.

Subkinetal Microtubules: one or more ribbons of *microtubules* coursing along under the proximal ends of kinetosomes in some kinetofragminophorans (e.g., *Brooklynella*); sometimes confounded with *basal microtubules*. ★ ★ [SkMt]

Sucker: variously used, but generally for the cup-shaped concavity forming the often nonhomologous *thigmotactic area* or *adhesive organelle* in scattered species belonging to quite different taxa (hypostomes, thigmotrichs, astomes, peritrichs, heterotrichs, etc.); some workers also use it to denote the *sucking tube* of the Rhynchodida; it may be rich in fibrils, polysaccharide plaques, thigmotactic cilia, etc.; a rare synonym, for protozoa, is *acetabulum*. ★ ★ [S]

Sucking Tentacle: see **Suctorial Tentacle**.

Sucking Tube: apically located, complex septate structure composed of microtubules which serves as the *ingestatory apparatus* of rhynchodid hypostomes; presumably homologous with the *cyrtos*, the cytopharyngeal apparatus characteristic of most other members of the kinetofragminophoran subclass Hypostomata.

Suctorial Organelle: see **Suctorial Tentacle**, of which it is a special (primitive?) type.

Suctorial Tentacle: tubular extension of the body of suctorians, extensible and retractable, containing a complex array (set or sets) of longitudinally arranged *microtubules* and equipped with (mature) *haptocysts* (containing proteolytic enzymes?) at its often capitate (knobbed or enlarged) tip and vesicles functioning in formation of food vacuolar membrane; the organelle serves for prey capture but is also the organism's *ingestatory apparatus*, analogous if not homologous with the *cytostome-cytopharyngeal complex* of neighboring kinetofragminophoran groups; the mechanism of feeding still not entirely elucidated; suctorial tentacles range from one (or even none) in number to many; their fascicular grouping, etc. on the body (whether involving *actinophores* or not) is often of taxonomic significance; the larval or *bud* stages in suctorian life cycles possess none, as a rule; a synonym is *sucking tentacle*; a type of extremely short, nonextensible tentacle is known in several families: it has been called an *endosprit* in *Cyathodinium* and a *suctorial organelle* in some other groups of suctorians. ★ ★ [ST]

Supernumerary Kinetosomes: existence of (what seem to be) extra *kinetosomes* or basal bodies: observed in various instances, in several different ciliates, in more than one stage in the life cycle, in differing but specific locations on the *body* or in the *oral area*, and with the kinetosomes either *ciliferous* or *barren*; significance not understood, and additional precise date highly desirable; overproduction during such morphogenetic processes as *stomatogenesis* appears to be a source of some of these supernumeraries (e.g., in the *parakinetal* stomatogenesis of *Tetrahymena*); in some cases, they may be *erratic kinetosomes* and/or parts of an *anlage* and/or parts of a *vestige*; the category might also include cases of intercalated *kineties*, whole or partial, which involve a line or file of several or even many additional somatic kinetosomes.

Suture Lines: sometimes may be simply folds or creases in the pellicle; but today they are generally associated with the important concept of the *système sécant*, the converging of kineties from different areas of the surface of the ciliate onto lines forming a pattern consistent within a given taxonomic group; see also **Preoral** and **Postoral Suture**. ★ ★

Swarmer: dispersive form in the life cycle of a number of ciliates; see **Larval Form**.

Symbiont: so-called dependent member or partner (except in cases of *mutualism*) of a pair of organisms exhibiting *symbiosis*, the other being the host; there may be endo- or ectosymbionts, which include endo- and ectocommensals and (less commonly in ciliates) true endo- and ectoparasites.

Symbiosis: the living together, more or less intimately and contiguously, of two organisms, the *host* and the *symbiont*; if the relationship is mutually beneficial (rare with ciliates, even as the host), it is *mutualism*; if beneficial to one with little effect on the other (a very widespread condition), it is *commensalism* (which includes *inquilism*); if beneficial to one and harmful (to varying degrees) to the other (not common with ciliates), it is *parasitism*; ciliates may serve as hosts or as symbionts (showing all degrees of beneficence, positive or negative), with the hosts in the latter case being other protozoa, vertebrate metazoa, or (principally) invertebrate metazoa; the ciliate may be an endosymbiont or an ecto- or episymbiont (or epibiont): the latter category embraces the widespread special type known as a *symphoriont*.

Symbiotic: see **Symbiosis**.

Symmetrogenic Fission: type of division (generally longitudinal) of a *parental organism* in such a manner that the two *filial products* are, in effect, mirror images of one another with respect to principal structures; typical of nonciliate protozoa; in opalinids the fission is, further, *interkinetal*; the mode is to be contrasted with the *homothetogenic fission* fundamentally characteristic of ciliates as a group. ★ ★

Symphoriont: episymbiont exhibiting a kind of *commensalism* in which the host (usually via its integument) appears to serve solely as a convenient substratum for attachment of the typically stalked sessile ciliate; not always clearly distinguishable from other degrees of intimacy between hosts and their associated ectocommensals, but it represents a convenient term with reference to many peritrich and suctorian species; not generally used, by convention, for parasitic ciliates exhibiting a *phoront* stage which, however, can really be very similar (see Phoront).

Synciliary Ciliature: see **Syncilium**.

Syncilium: group of closely packed cilia forming a special tuft exhibiting considerable internal coherence and arising from a packet of kinetosomes which, at their proximal ends, are interconnected with like packets in the vicinity; characteristic of entodiniomorphid vestibuliferans, syncilia were formerly called *membranelles*, with recognition of *adoral* and *dorsal zones*; they also occur as part of the *caudalia* present at the posterior end of the body of certain cycloposthiid species of the same group of vestibuliferans. ★ ★ [Syn]

Syngen: complex of two or more sexually compatible mating types (e.g., in *Paramecium* or *Tetrahymena*), formerly know as "*varieties*," long recognized as reproductively isolated units or "physiological" species, and now – very recently – beginning to be established as bonafide "taxonomic" species, uniquely named, etc.; thus "syngen," like "*variety*" (in the above sense) before it, will probably pass out of useful existence (the latter term has also been misused in a second way: see **Variety**).

Synhymenium: single apparent "membrane" resulting from an uninterrupted joining of parts of the hypostomial *frange*, coursing (in part) along the preoral suture in species of the several "lower" hypostome genera in which it is found.

Synkaryon: fusion nucleus; the product of fusion of two haploid "gametic" nuclei or pronuclei in the *sexual phenomena* of *conjugation* or *autogamy* in ciliates; its division products differentiate into the new diploid micronuclei and the (typically) polyploid macronuclei present in the usual sets in the lines of organisms arising subsequently by binary fissions of the exconjugants (or ex-autogamous individuals).

Synonym: one of two or more names applied to the same organism or taxon; the earlier or earliest published is the *senior* synonym (usually this name must prevail); the later (of two) is the *junior* synonym; an *objective* synonym is one based on (study of) the same material, whereas a *subjective* synonym is based on material which is different but alleged to represent the identical organism or taxon involved.

Système Sécant: various lines of convergence of (fields of) kineties over the surface of the body; *pre-* and *postoral sutures* and the convergence at the antapical pole are typical representatives of such systems, but *suture lines* may also occur consistently elsewhere, especially in heavily ciliated organisms which do not have regular rows of simply *bipolar kineties*; systèmes sécants are particularly striking in thigmotrichs, astomes, and heterotrichs (though also occurring in other groups), and such stabilized boundary lines or *aires sécantes* are of considerable taxonomic utility; an apt, if little-used, synonym is *kinetal suture system*. ★★ [SS]

Tactile Cilia: see **Sensory Bristles** and **Thigmotactic Ciliature**.

Tail: generalized term, variously used in nonspecific ways; such caudal appendages range from specialized cilia or mucous filaments (not to mention stalks) to narrow and lengthy extensions of the body proper.

Tangential Fibers: see **Transverse Microtubules**, the more acceptable term today for the structures involved.

Tastcilien: see **Sensory Bristles**.

Tectin Granules: small, subpellicularly located bodies involved in secretion of a substance, probably mucopolysaccharide in nature, comprising the *lorica* in a number of ciliates, especially among the sessiline peritrichs.

Teeth: nonspecific term; but also, perhaps unwisely, used to describe the nematodesmal *capitula* characteristic of some dysteriine hypostomes; see **Capitulum**.

Tela Corticalis: see **Lamina Corticalis**, essentially a synonymous term.

Telokinetal: type of *stomatogenesis* in which formation of the new oral area(s) occurs by direct (presumed or known) involvement either of kinetosomes at the anterior extremities of all or some of the encircling *somatic kineties* or of kinetosomes comprising the short *kinetofragments* available in the vicinity; in colpodids a *primordium* may be involved; the various subtypes recognizable (though, as yet, undescribed in the literature) in the modes manifest by different groups within the class Kinetofragminophora may not be homologous, but they are provisionally lumped together under telokinetal *sensu lato* for convenience; and they do seem to share more in common (from a descriptive-morphological point of view) with each other than with any of the three allegedly more advanced types of stomatogenesis known by the terms *parakinetal*, *buccokinetal*, and *apokinetal*; some of the (undescribed) telokinetal subtypes may also represent evolutionary experiments either leading to one or more of the other three major types or, by *convergent evolution*, coming to resemble them. ★★

Telotroch: free-swimming *migratory stage* in the life cycle of, especially, sessiline peritrichs; see **Larval Form**; *trophonts* of mobiline peritrichs are sometimes thought of as permanent telotrochs exhibiting *neoteny*. ★★ [Telo]

TEM: transmission electron microscopy, a technique becoming indispensable in certain aspects of comparative phylogenetics and systematics of ciliates.

Temporary Conjugation: fusion with subsequent separation of the members of the conjugating pair; the mode of *conjugation* shown by most ciliates (major exceptions, peritrichs, chonotrichs, and some suctorians); see **Conjugation**.

Tentacle: tubular extension of or projection from the surface of a ciliate, of several different and probably nonhomologous kinds: (1) *suctorial*, the (only) *ingestatory apparatus* in suctorians, complex, typically lengthy, extensible and retractable, and localized (often apically) on the body; (2) *prehensile*, a noningestatory organelle (additionally) present in some suctorians, solely for prey capture; (3) the short, nonextensible, apical *sucking tube* of rhynchodid hypostomes (called a tentacle by some workers); (4) the nonsuctorial but highly extensible and retractable prey-capturing organelle of such unusual haptorid gymnostomes as *Actinobolina*, composed of microtubular arrays often enclosing a prominent *toxicyst* and found in abundance, associated with clusters of cilia, nearly everywhere over the surface of the body; and (5) scattered other projections, lobes, or palps, and the like (but properly excluding any *proboscis*), which are or have been occasionally referred to by the term "tentacle"; first four types all possess arrays of microtubules in various patterns. ★★

Tentaculoid: small finger-like extensions of the cytoplasm found among the membranelles (*paramembranelles*) of the AZM of some tintinnine spirotrichs, contractile and containing curious, little understood "*capsules torquées*"; do they have a sensory function?

Terrestrial Biotopes: see **Edaphic** and **Xeric**.

Tertiary Meridian: see **Ciliary Meridian**.

Test: see **Lorica**, of which it is a synonym; but it is seldom used in reference to ciliates.

Tetrahymenal Buccal Apparatus: see **Buccal Apparatus**; "tetrahymenal" refers to the "four-membraned" nature of the ciliary organelles found in the oral area of many oligohymenophorans (cardinal example, members of the family Tetrahymenidae): *paroral* or *undulating membrane* on the right of the buccal cavity and the three *membranelles* comprising the "primitive" *AZM* more or less on the left. ★★

Tetrahymenium: see **Tetrahymenal Buccal Apparatus**, of which this is a little-used synonym.

Theca: see **Lorica**, though the terms are not generally considered synonymous; theca is thus inappropriate for description of the loricae of most ciliates, yet some peritrichologists have used the term in reference to the unusual envelope supporting certain operculariid species in particular. ★★ [Th]

Thecoplasm: see mention under **Spasmoneme**.

Theront: "hunter" stage in the polymorphic life cycle of a number of *parasitic* or *histophagous* ciliates (e.g., ophryoglenine hymenostomes); essentially a (more or less transformed) *tomite* searching for a new host or for a fresh source of food (on finding it, the organism becomes a *trophont*).

Thigmotactic Area or **Zone**: see mention under **Somatic Area**; see also **Thigmotactic Ciliature**.

Thigmotactic Ciliature: generally used to denote a patch, area, tuft, field, or zone of more or less specialized *somatic cilia* functionally modified to serve a presumed sensory-tactile or, more commonly, an adhering function (see **Holdfast Organelle**); often localized (e.g., as a group of contiguous portions or segments of kineties occurring on the anterodorsal surface of the body, as in many thigmotrichine scuticociliates); in certain astomes, and some other ciliates, the surface covered by the cilia may be concave and known as a *sucker*; the *scopula* of many sessiline peritrichs may, in a broad sense, be considered to possess thigmotactic cilia; single, scattered cilia are also sometimes called thigmotactic: see **Bristles**. ★★ [TC]

Tissue-eating: see **Histophagous**.

Tomite: one of two or more fission products of a *tomont* (or sometimes of a *protomite*), a stage in the polymorphic life cycle of a number of parasitic or histophagous ciliates in which the organism is small, free-swimming, and nonfeeding; it has usually emerged with numerous congeners from a cyst within which the divisions of the tomont have typically taken place; the next stage is the *theront* or *phoront* or *trophont*, depending on the species; the *filial products* of *any* binary or multiple fission could be called tomites, but generally – by convention – they are not. ★★ [Tom]

Tomitogenesis: production of tomites; see also **Palintomy**, which is sometimes the phenomenon invoked.

Tomont: prefission or dividing stage in the polymorphic life cycle of a number of parasitic or histophagous ciliates (e.g., apostomes and ophryoglenine hymenostomes); a large form, typically encysted; it may divide a number of times in quick succession: see **Tomitogenesis**.

Total Conjugation: complete fusion of the *micro-* with the *macroconjugant*; a phenomenon exhibited by *all* peritrichs and chonotrichs, a number of suctorians, and a scattered few other ciliates; (still) considered to be *syngamy* by some protozoologists; see **Conjugation**.

Toxicyst: slender tubular organelle, an *extrusome*, located subpellicularly in the cytoplasm of many gymnostomes, particularly the predaceous, carnivorous haptorids (e.g., *Didinium* and *Dileptus*), often concentrated in great numbers at or near the apical end of the organism and in the oral cytoplasm; also found in the nonsuctorial *tentacle* of *Actinobolina*; everting on discharge and apparently containing both paralytic and proteolytic enzymes, it penetrates, immobilizes, and commences to cytolyze the prey; it is the *Nesselkapseltrichocyste* and, less familiarly, the *cnidotrichocyst* and the *tubular trichocyst* of the older literature. ★★ [Txc]

Transverse Fibers: see **Transverse Microtubules**, the more widely used term today for the structures involved.

Transverse Fibrous Spur: dense *(micro)fibrillar* material found in a number of ciliates (some hypostomes, scuticociliates, etc.) associated with the proximal end of the kinetosome, arising near triplet number 3 (*Grain convention*) and extending a short distance to the left and upward into the nearby *pellicular crest*. ★★ [TFS]

Transverse Microtubules: ribbon or band of *microtubules* occurring widely throughout ciliate taxa, always in association with a kinetosome, arising tangentially to that organelle at its left anterior side close to triplets number 3, 4, and sometimes 5 (*Grain convention*); the ribbon, which may be composed of 4–6 (occasionally more?) cross-linked microtubules, first extends upward toward the pellicle and then continues across to the left, parallel to the nearby surface of the body and at right angles to the kineties, stopping just short of the next line of kinetosomes on the left; in the oral area of gymnostomes, extensions of transverse microtubules are involved in the composition of the *rhabdos*; called *tangential fibers* by some early workers. ★★ [TMt]

Trichite: term used in at least two senses: (1) as an older and once highly popular, but now preferably discarded, name for the *cytopharyngeal rod* (see **Nematodesma**) so prominent especially in the *rhabdos* of kinetofragminophorans; and (2) to describe the unique *skeletal structure*, hollow, rod-like, and of a proteinaceous nature, found in abundance in certain oligotrichs, radially arranged beneath the pellicle of the posterior hemisphere of the rounded body; in *no* sense is it related to any *extrusome* (trichocysts, etc.), as formerly believed.

Trichocyst: in the past, term used to embrace nearly all *extrusomes* found in ciliates; now properly limited to the rather prominent, spindle-shaped, nontoxic, explosive organelle located subpellicularly in such forms as the hymenostome *Paramecium*; it consists, in the mature stage, of an *apical tip* (shaped like an inverted golf tee) and a long, fusiform, *fibrous shaft*; on ejection, following an appropriate stimulus, it acquires a characteristic *periodic structure*; the function of such trichocysts is often considered as defensive, but this has never been adequately established, and other uses have also been suggested; the *fibrous trichocyst* of microthoracine hypostomes is considered a special case – see **Fibrocyst**; but *protrichocysts* (*mucocysts*), *toxicysts*, etc. (see **Extrusome**) are entirely different organelles; a "*trichite*" is even less related, the older literature notwithstanding. ★★ [Trc]

Trochal Band: see **Locomotor Fringe**; but the present term is perhaps the more popular synonym, judging by the usage of many peritrichologists. ★★ [TBd]

Trophic Nucleus: see **Macronucleus**.

Trophont: mature, vegetative, *adult*, interfissional or feeding or growing stage in the life cycle of any ciliate; the term is most often used, however, in reference to the specific stage between *tomite* (or *theront*) and *tomont* in the polymorphic life cycle of parasitic (*sensu lato*) or histophagous species (e.g., as found among apostomes and hymenostomes); a term with identical meaning is *trophozoite* (but see remarks under that word, below). ★★

Trophozoite: see **Trophont**, the synonym preferred by the great majority of ciliatologists for use with most taxonomic groups of ciliates (although the terms are fully identical in meaning); trophozoite seems to have become associated more with truly *parasitic* species of protozoa.

Tubercle: variously used; but see **Papilla**.

Tubicolous: tube-dwelling; in ciliatology, this term is used now and then with reference to loricate species (e.g., some folliculinids and a few hypotrichs) the members of which may only temporarily occupy their loosely fitting, tube-shaped, often gelatinous housing, in a manner reminiscent of some of the true tube-dwellers among the polychaete annelids. ★★

Tubular Trichocyst: see **Toxicyst**, for which this is a relatively unfamiliar earlier name.

Tubulin: specific class of globular protein serving as the principal macromolecular constituent (i.e., the basic unit) of all *microtubules* (e.g., as found in the kinetosome and the cilium).

Type-genus: nominal genus designated as the type of a *family-group* taxon and not to be removed from that taxon; the familial name must be formed from the stem of this generic name plus the appropriate suffix (-idae for family, -inae for subfamily).

Type-species: nominal species designated as the type of a *genus-group* taxon; it cannot be removed from that genus.

Type-specimen: single specimen (perhaps whole slide of cloned organisms will be acceptable for protozoological materials in the future) known as *the* type or type-material of a taxon in the *species-group*; major kinds include the *holotype* (first and most important), *lectotype* (named later if no holotype), and *neotype* (if all other material lost); *paratypes* and *syntypes* are the extra specimens in a series from which a holotype or lectotype has been chosen (see copy of the *International Code of Zoological Nomenclature* for detailed definitions).

Undulating Membrane: see **Paroral Membrane**; "undulating membrane" is a much older term but not as exact, since it implies a function not always realized (whereas "*paroral*" refers solely to the organelle's location, which is consistent throughout the phylum Ciliophora), and it is also widely used for a different structure in certain flagellate protozoa; it was made popular as the *UM* of the tetrahymenines in which its presence is so neatly revealed by *silver-impregnation techniques*, its base – on the right side of the buccal cavity – standing in bold contrast to the tripartite *AZM* (bases of the *membranelles*) on the left side (see **Tetrahymenal Buccal Apparatus**); all UM's (i.e., all *paroral membranes*) are very likely *not* homologous structures, though the idea that they might be was formerly proposed as a unifying phylogenetic hypothesis of considerable importance in ciliate systematics and classification. ★★ [UM]

Undulipodium: seldom used word which has been proposed to include both "cilium" and "flagellum" together under a single convenient (?!) term; see also **Pecilokont**.

Unit Membrane: differentially permeable, complex lipoprotein structure appearing under TEM as two dense but thin lines separated by a light space of a diameter up to twice the thickness of either line; the surface or *plasma membrane* of ciliates is such a membrane, although it may be elaborated, thickened, associated with extracellular secretions, etc.; all membrane-bound structures or organelles in ciliates basically involve one or more unit membranes, sometimes with associated ribosomes, vesicles, pores, etc.

Vacuoles: generalized term used for all sorts of sizable, fluid-filled, membrane-bound cavities or sacs in the cytoplasm; examples, which are specifically defined elsewhere, include *contractile vacuole*, *concrement vacuole*, *food vacuoles*, *receiving vacuole*, and *phagocytic vacuoles*; compare with *vesicles*, structures by convention of a smaller size.

Variety: see **Syngen**; also, in a second and inaccurate meaning of the term, it is considered by many workers as a formal taxonomic rank at an infraspecific level; but, actually, it – along with *forma* (very popular with specialists of some groups, such as the entodiniomorphids) – should not be so used in zoology (and ciliatology): such terminology as population, strain, race, *deme*, ecophenotype, culture (or possibly even subspecies) is, depending on the situation, preferable.

Vegetative Nucleus: see **Macronucleus**.

Veloid: see **Velum**.

Velum: term variously used by different workers for different structures: for example, for (1) the *paroral membrane* of some scuticociliates (sometimes termed a *veloid* rather than a velum), (2) the *extensor membrane* of peritrichs, (3) the *flange* of some forms, and (4) the skirt-like pellicular fold covering the *marginal cilia* in mobiline peritrichs.

Ventralization: presumed evolutionary process whereby the *oral structures* have come to be located anteriorly on the *ventral surface* rather than in a wholly apical (or near-apical) position, with interruption but not necessarily termination of the ventral *bipolar kineties*; position of cytostome *fundamentally* ventral, with no shift during fission, etc.; this condition is strikingly manifest in members of the kinetofragminophoran subclass Hypostomata.

Vesicles: membrane-bound cavities or sacs in the cytoplasm of a size usually much less than that of a typical *vacuole*; examples specifically defined elsewhere include *pinocytotic vesicles*, the *pellicular alveoli*, and (parts of) the *Golgi apparatus* and the *endoplasmic reticulum*; discoidal vesicles are involved in food-vacuolar membrane formation; *water expulsion "vesicle"* is a misnomer for the *contractile vacuole*.

Vestibular Ciliature: rows of cilia only slightly modified from (sometimes only extensions of) surrounding *somatic kineties*; but the cilia may be longer or closer together, etc., and there may be minor differences in the organization of the *kinetosomal territory* at the infraciliary level; the component parts could be considered, in effect, *kinetofragments* (at least from an evolutionary point of view); their location is characteristically in a cavity or depression (the *vestibulum*) which is reformed following binary fission of the organism; they have quite a complex appearance in the "*higher*" vestibuliferans (e.g., in colpodids, where they are sometimes called *cirromembranelles*), but the universally *telokinetal* origin of these organelles supports their relative primitiveness, phylogenetically, compared with the "true" *buccal* organelles of members of the two more highly evolved classes; the term (i.e., its definition or concept) no longer includes the *prebuccal ciliature* or the *ophryokinety* of the several hymenostome groups possessing such ciliature which was formerly considered to be "vestibular" in nature.

Vestibule: see **Vestibulum**.

Vestibulum: depression or invaginated area of body, at either pole, leading directly to the *cytostome-cytopharyngeal complex* and adorned with ciliature, more or less complex in appearance, which is predominantly *somatic* in both nature and origin, although possibly evolving to a state resembling – by convergence? – *buccal ciliature* in some species; the vestibulum is characteristic of and now restricted to organisms belonging to the subclass Vestibulifera, and thus it no longer includes the nonhomologous *prebuccal area* of certain hymenostomes; an old and now little-used synonym of vestibulum is *pseudoperistome*; another synonym, *vestibule*, is the (non-Latin) term preferred by some protozoologists. ★★ [V]

Vestige: term used in ciliate morphogenetic studies to mean a visible trace or part of a structure or organelle persisting, usually as a nonfunctional remnant, in one stage (typically the adult or mature form) as a carry-over from an earlier ontogenetic stage in which it was fully developed and functional; only occasionally used by ciliatologists in a phylogenetic sense, that is, to indicate a rudimentary structure carried over from a postulated ancestral form in which it was a fully formed organelle; curiously enough, what is essentially the opposite of "vestige" at the kinetosomal level, *viz.*, "anlage" (see definition on a preceding page), may *sometimes* turn out to be the same: that is, the remnant or *vestige* of an ontogenetic structure may serve as the *anlage* for production of that same structure in the next (repeated) stage in the life cycle (e.g., the *scutico-vestige* in the mature form of some scuticociliates is apparently a major source of the kinetosomes forming the *primordium* – which includes the *scutica* proper – of new mouthparts for the next generation, again being reduced to a vestige on completion of the morphogenesis of each daughter organism); see also **Erratic Kinetosomes**. ★★

Vierermembran: see **Quadrulus**.

Vierteilige Membran: see **Quadrulus**.

Watchglass Organelle: see **Lieberkühn's Organelle**.

Water Expulsion Vesicle: see **Contractile Vacuole**.

Xenodeme: see mention under **Deme**.

Xenosomes: "alien bodies," apparently of a bacterial nature, recently found in the cytoplasm of certain marine scuticociliates (e.g., *Parauronema*); these infectious particles are transmissible from ciliate to ciliate; the term – xenosome – may come to be considered more appropriate than *endosymbiont* for all such organisms; but see also **Endosymbiont** (*of* **Ciliates**).

Xeric: pertaining to a terrestrial habitat having a very low content of water (e.g., *desert* sands).

Xylophagous: wood-eating; capable of digesting cellulose; apparently true of a number of ciliate species, especially certain trichostomes and entodiniomorphids in the digestive tract of various artiodactylan ruminants.

Zeta Membranoid: see **Membranoid**, also **Haplokinety** and **Paroral Membrane**.

Zoochlorellae: endosymbiotic green algae (perhaps not all of the same species) found widely in the cytoplasm of ciliates belonging to nearly all major taxa; in some cases, they may be said to be exhibiting *mutualism*, holding an interdependent symbiotic relationship with their ciliate host; see also **Endosymbiont** (*of* **Ciliates**).

Zooid: term generally restricted in ciliatology to mean only the body proper of an attached sessile form (e.g., the *bell* of many peritrichs), minus the stalk; the term also refers to the individual members of a colony (free *or* attached), but usually (again) only of the *arboroid colony* so typical of peritrichs; *macro-* and *microzooids* are distinguishable by size and exhibition of certain functional differences (e.g., in *Zoothamnium* only macrozooids are capable of starting new colonies). ★★ [Z]

Zooplankton: see **Plankton**.

Zoopurpurin: see **Blepharismin**.

Zweigliedrige Kultur: see **Monoxenic Culture**.

EXPLANATION OF ACCOMPANYING FIGURES

In the following 14 pages of figures, comprising Plates I–V, an attempt has been made to illustrate the major morphological (including ultrastructural) features of ciliates – and even a few concepts – defined or discussed on preceding pages of this glossary. Labels used are abbreviated as indicated in boldface type at the ends of the above definitions: thus, no other "legend" is required. Many of the characteristics revealed in the drawings (and micrographs), however, really require no further specific labeling – beyond the verbal descriptions already given – for identification. Indeed, in such cases, superimposition of unnecessary label-lines, etc. would often be as discourteous to the organisms involved as displeasing to the eye of the beholder. It has been considered helpful to purposely associate a given figure with a particular genus, which is named, even though the feature(s) shown may be shared in common with numerous other ciliates. [See also the many figures, but *none* with labels, in Chapters 6–16 and especially 20.]

PLATE I, pp. 40, 41. Fig. 1. Rule of Desmodexy, and the individuality, integrity, and asymmetry of the bipolar kinety in ciliates (e.g., *Tetrahymena*): a, lateral views; b, from apical or anterior pole of body; c, from antapical or posterior pole. 2. Homothetogenic fission (ciliates – e.g., *Tetrahymena*). 3. Symmetrogenic fission (flagellates – idealized). 4–7 (also 24). Production of "larval" forms. 4 a,b. Adult and telotroch in peritrichs (*Epistylis*). 5. Endogenous budding in suctorians (*Tokophrya*). 6. Exogenous budding (*Ephelota*). 7. Evaginative budding (*Discophrya*). 8–13. Comparison of common external ciliary structures. 8. Scuticociliate (*Cyclidium*). 9. Gymnostome (*Didinium*). 10. Heterotrich (*Gruberia*). 11. Hypostome (*Nassulopsis*). 12. Hypotrich (*Euplotes*). 13. Entodiniomorphid (*Epidinium*). 14–23. Cysts. 14. *Didinium*. 15. *Podophrya*. 16. *Euplotes*. 17. *Colpoda* ("division" type). 18. *Nyctotherus*. 19. *Ophryoglena* (showing palintomy). 20. *Bursaria*. 21. *Vorticella*. 22. *Oxytricha*. 23. *Spirophrya* (with phoront). 24. Cryptogemmous budding in chonotrichs (*Cristichona*). 25–35. Loricae. 25. *Cyclodonta*. 26. *Cothurnia*. 27. *Eutintinnus*. 28. *Salpingella*. 29. *Dictyocysta*. 30. *Metacylis*. 31. *Tintinnopsis*. 32. *Metafolliculina*. 33. *Thecacineta*. 34. *Orbopercularia*. 35. *Pyxicola*. 36. *Maryna*. 37. *Stichotricha*. 36–41. Colonial organization (dendritic, unless otherwise stated). 36, 37. See generic names above. 38. *Cepedietta* (nascent catenoid colony). 39. *Epistylis*. 40. *Ophrydium* ("spherical" but also dendritic). 41. *Dendrosoma* (from Kent's classical portrayal).

PLATE II, p. 42. Figs. 1–8. Oral areas, arranged in postulated phylogenetic sequence. 1. Apical cytostome of prostome gymnostomes (e.g., *Holophrya*). 2, 3. Cytostome at base of vestibulum (*Coelosomides, Colpoda*). 4. Ventralization of oral area (hypostomes), with atrium possible (*Furgasonia*). 5, 6. Advent of buccal cavity (hymenostomes), sometimes with prebuccal "oral groove" (*Tetrahymena, Paramecium*). 7. Specialized infundibulum (peritrichs, e.g., *Vorticella*). 8. Prominent peristomial field (spirotrichs, e.g., *Euplotes*). 9–16. Major modes of stomatogenesis. 9, 10. Telokinetal (*Alloiozona, Colpoda*). 11, 12. Parakinetal (*Tetrahymena, Condylostoma*). 13, 14. Buccokinetal (*Pseudocohnilembus, Urocentrum*). 15, 16. Apokinetal (*Entodinium, Strombidium*).

PLATE III, p. 43. Figs. 1–32. Nuclei of diverse groups. Exact taxonomic positions ascertainable through use of Systematic Index, but it is clear that nuclei, in general, are *not* distinctive for whole groups of ciliates (in fact, all of the species belonging to any one of the genera included here do not necessarily show the same nuclear configuration). Outlines of organisms' bodies purposely shown (roughly) to scale, except for *ca.* 50% reduction in relative size in Figs. 10a, 20. Micronuclei, solid black; macronuclei, stippled; endosomes or nucleoli, clear; homokaryotic nucleus (*Stephanopogon*), cross-hatched. 1. *Vorticella*. 2. *Uroleptus*(?). 3a,b. *Stephanopogon*, and an enlarged nucleus. 4a,b. *Tracheloraphis*, partially contracted, and enlarged nuclear apparatus. 5. *Dileptus*. 6. *Paramecium*. 7. *Tetrahymena* (amicronucleate strain). 8. *Cyclidium*. 9. *Durchoniella*. 10a,b. *Loxodes*, and enlarged set of nuclei. 11. *Spathidium*. 12. *Plagiotoma*. 13. *Urotricha*. 14. *Schizocaryum*. 15. *Leiotrocha*. 16. *Didinium*. 17. *Tintinnopsis*. 18. *Ephelota*. 19. *Parahypocoma*. 20. *Stentor*. 21a,b. *Spirochona*, and enlarged macronucleus showing reorganization band with direction of its movement. 22. *Euplotes*, showing reorganization bands. 23. *Parastylonychia*. 24. *Deltopylum*. 25. *Aspidisca*, showing reorganization bands. 26. *Brachonella*. 27. *Insignicoma*. 28. *Remanella*. 29a,b. *Chilodonella*, and enlarged macronucleus. 30. *Epidinium*. 31. *Nyctotherus*. 32. *Protanoplophrya*.

PLATE IV, pp. 44–47. Figs. 1–10. Somatic and/or oral infraciliary patterns, particularly as revealed by use of the Chatton-Lwoff method of silver impregnation. 1. *Proboveria* (a, right-ventral surface; b, apical pole). 2. *Ancistrospira* (a, ventral; b, dorsal). 3. Mouthless *Curimostoma*, anterior pole. 4. *Tetrahymena*, anterior ventral surface. 5. *Tetrahymena*, polar views (a, apical, and b, antapical, *T. pyriformis*; c, antapical, *T. setosa*). 6. Late stage in stomatogenesis of *Tillina*, anterior end of organism. 7. *Frontonia* (left-ventral surface). 8. *Paranophrys* (ventral surface). 9. Cytopharyngeal apparatus of kinetofragminophorans (a, rhabdos of certain gymnostomes [*Prorodon*] ; b, cyrtos of nassulid hypostomes [*Nassula*] ; c, cyrtos of cyrtophorid hypostomes [*Chilodonella*]). 10. *Euplotes* (a, ventral; b, dorsal). 11–13. Systèmes sécants. 11. *Nyctotheroides* (a, left-ventral surface; b, right-dorsal). 12. *Paracoelophrya*. 13. *Prosicuophora*. Figs. 13–17. Holdfast organelles. 13, 14, 15c. Thigmotactic suckers (*Prosicuophora, Protoptychostomum, Steinella*). 15. Hooks or spines (a, *Metaradiophrya*; b, *Maupasella*; c, *Steinella*). 16. Stalks with eccentric or central spasmoneme (a, *Vorticella*; b, *Carchesium*). 17. Podite (*Dysteria*). 18. Cyrtos (cyrtophorid type), showing nematodesmal variation (at proximal end) within a single family: a, *Aegyriana*; b, *Brooklynella*; c, *Trochilioides*. 19. Peritrich infundibular structures (*Campanella*, at level *below* apical ciliary wreaths). 20. "Open" and "closed" systems of AZM in oligotrichs (a, *Halteria* or *Strombidium*; b, *Strobilidium* or *Tintinnopsis*). 21. Patterns of spiraling oral ciliature in mobiline peritrichs (a, *Trichodina* or *Urceolaria*; b, *Trichodinella* or *Tripartiella*; c, *Semitrichodina*; d, *Vauchomia*). 22. Aboral denticulate ring, extremes in composition (a, *Trichodina*; b, *Trichodinopsis*). [Explanations of Figs. 23–34 (drawings) and of 35–52 (photomicrographs) appear directly under the figures on pp. 46, 47.]

PLATE V, pp. 48–53. Fig. 1. Semi-diagrammatic representation of generalized cilium and associated kinetidal structures (modeled largely on *Paramecium*), with X-S's (a–e) at various levels as viewed from inside the organism looking out. 2. Bundle of microtubules (cross-linking not shown) comprising generalized nematodesma. 3–6 (also 10, 11). Various extrusomes. 3. Clathrocyst (*Didinium*). 4. Rhabdocyst (*Tracheloraphis*). 5a,b. Mucocyst, in place and discharging to exterior (*Tetrahymena*). 6a,b. Haptocyst of suctorians, generalized form and in position at distal end of tentacle (*Heliophrya, Acineta*, etc.). 7. Patterns of microtubules (cross-linking not shown), as seen in X-S, in suctorial (a–f) and prehensile (g) tentacles of suctorians and rhynchodids (f) and in nonsuctorial tentacles of certain gymnostomes (h): a, *Sphaerophrya*; b, *Loricodendron* (syn. *Ophryodendron*); c, *Acineta*; d, *Dendrocometes*; e, *Cyathodinium*; f, *Ignotocoma*; g, *Ephelota*; h, *Actinobolina*. 8. Illustration of fundamental differences between (a) *pair* of kinetosomes and (b) *dyad*, especially in orientation to body axis of organism. 9. X-S of generalized somatic kinetosome (modeled on *Paramecium*), near proximal (inner) end, as viewed from below (inside the organism) looking out, showing arrangement of microtubular triplets, numbering systems [Grain (*outer*) and Pitelka (*inner* numbers, in parentheses)], and position of the "landmark" postciliary ribbon or band. 10, 11. Extrusomes, discharged (10) and undischarged (11). 10a, 11a. Toxicyst (*Didinium*). 10b, 11b. Explosive trichocyst (*Paramecium*). 10c, 11c. Fibrocyst (*Pseudomicrothorax*). 12. Kinetosomal territories or kinetids (semi-diagrammatic and confined to somatic infraciliature) of diverse ciliates, showing kinetosomes in X-S (viewed from interior of cell looking out, with anterior end of organism's body toward top of page) and juxtaposition of some of the major associated fibers or microtubular ribbons [redrawn from various sources in the literature, with "i" from D. W. Coats, unpub.] : a, *Loxodes*; b, *Balantidium*; c, *Brooklynella*; d, *Ignotocoma*; e, *Trematosoma*; f, *Trichophrya*; g, *Espejoia*; h, *Paramecium*; i, *Porpostoma*; j, *Conchophthirus*; k, *Coelophrya*; l, *Spirostomum*; m, *Sicuophora*; n, *Plagiotoma*. 13. Conspicuous postciliodesma in *Stentor* (Huang & Pitelka). 14. Portion of rhabdos in *Urotricha*, showing circular arrangement of nematodesmata and lining of transverse microtubules (de Puytorac & Grain). 15. Oral infraciliature of *Tetrahymena* (Nilsson & Williams). 16. Oral area of *Frontonia*, showing particularly the nematodesmata (Didier). 17. Area around left lip of cytostome in *Paramecium* (buccal cavity in foreground), showing formation of (new) food-vacuolar membrane (on left) by involvement of cytopharyngeal ribbons of microtubules, membrane-limited discs (upper right and center), etc.; part of quadrulus visible at lower right (Allen). [Explanations of Figs. 18–22 (drawings) and of 23–58 (TEM and SEM micrographs) appear directly under the figures on pp. 50–53.]

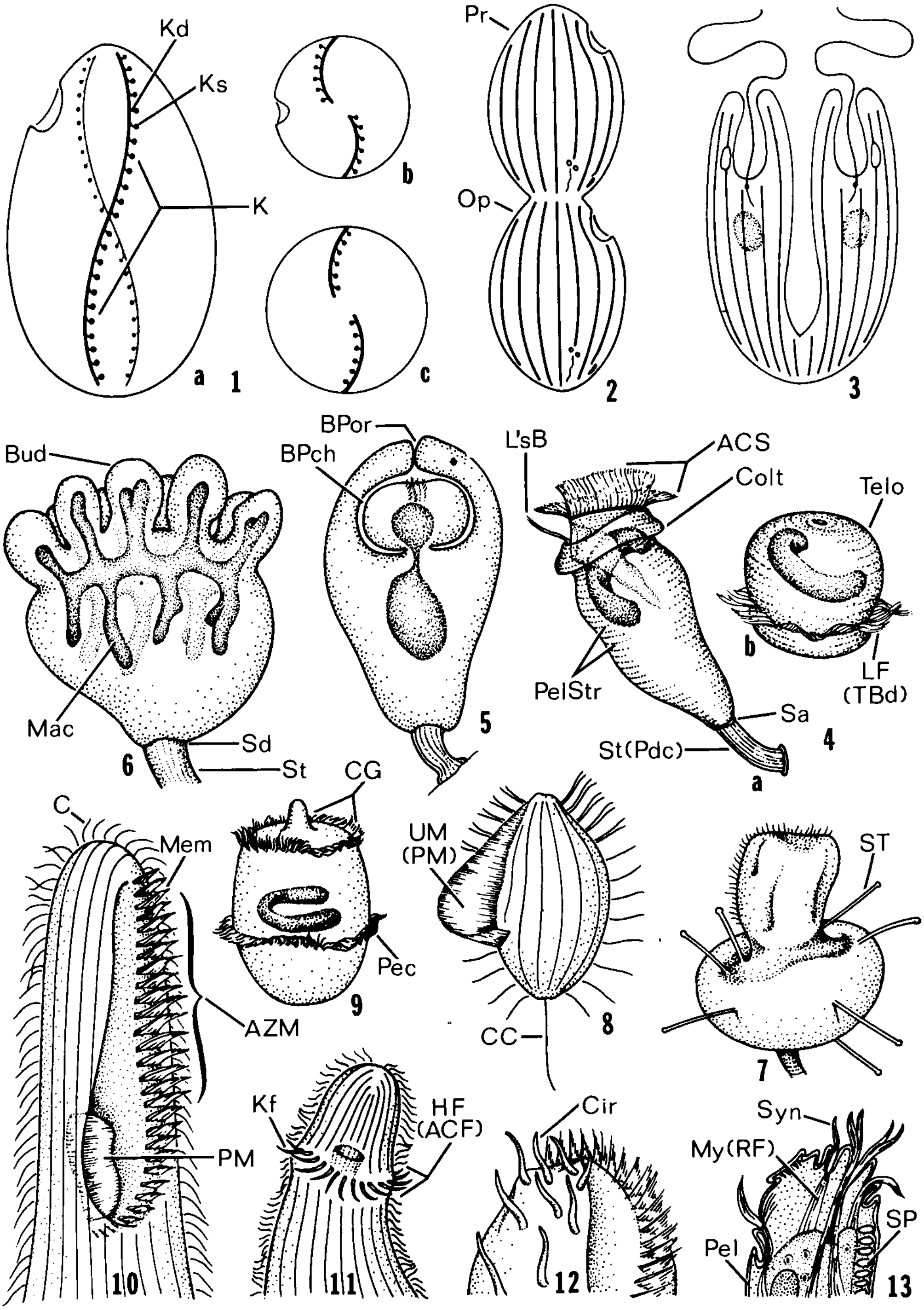


PLATE I. Structures and processes characteristic of ciliates. [See p. 38 for explanations.]

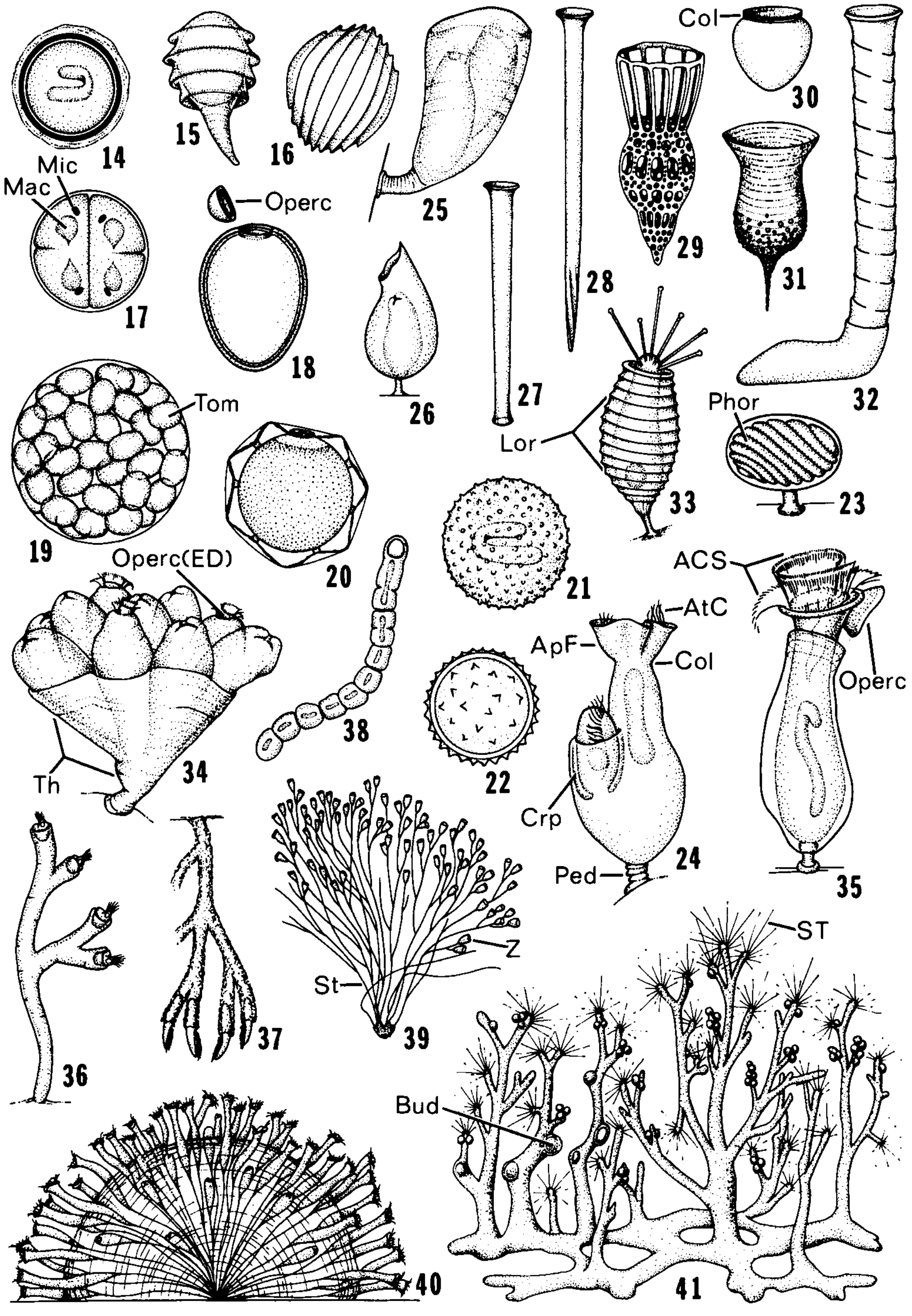


PLATE I, concluded. [See page 38 for figure explanations.]

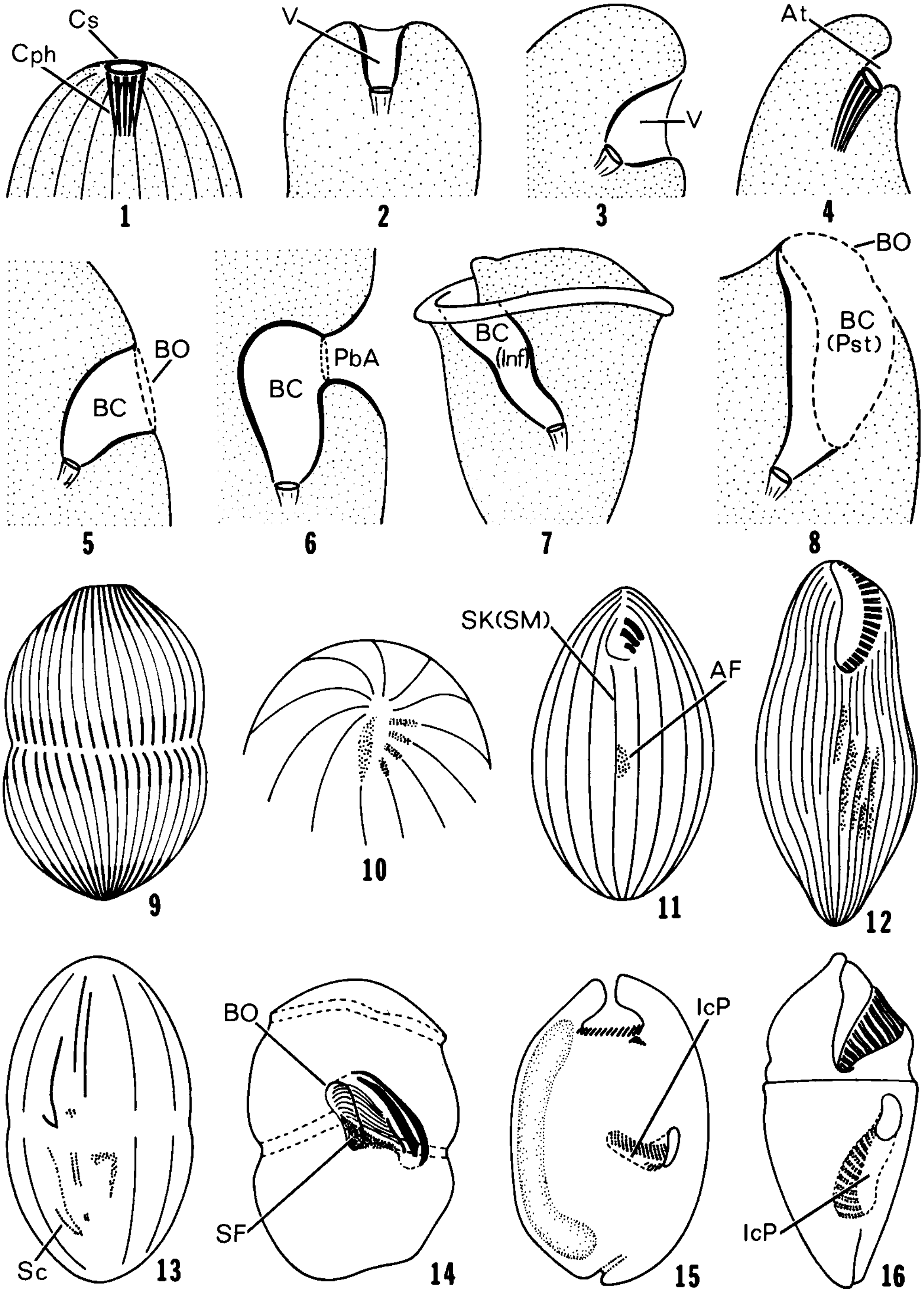


PLATE II. Noncilíary features of ciliate oral areas, and modes of stomatogenesis. [See page 39 for figure explanations.]

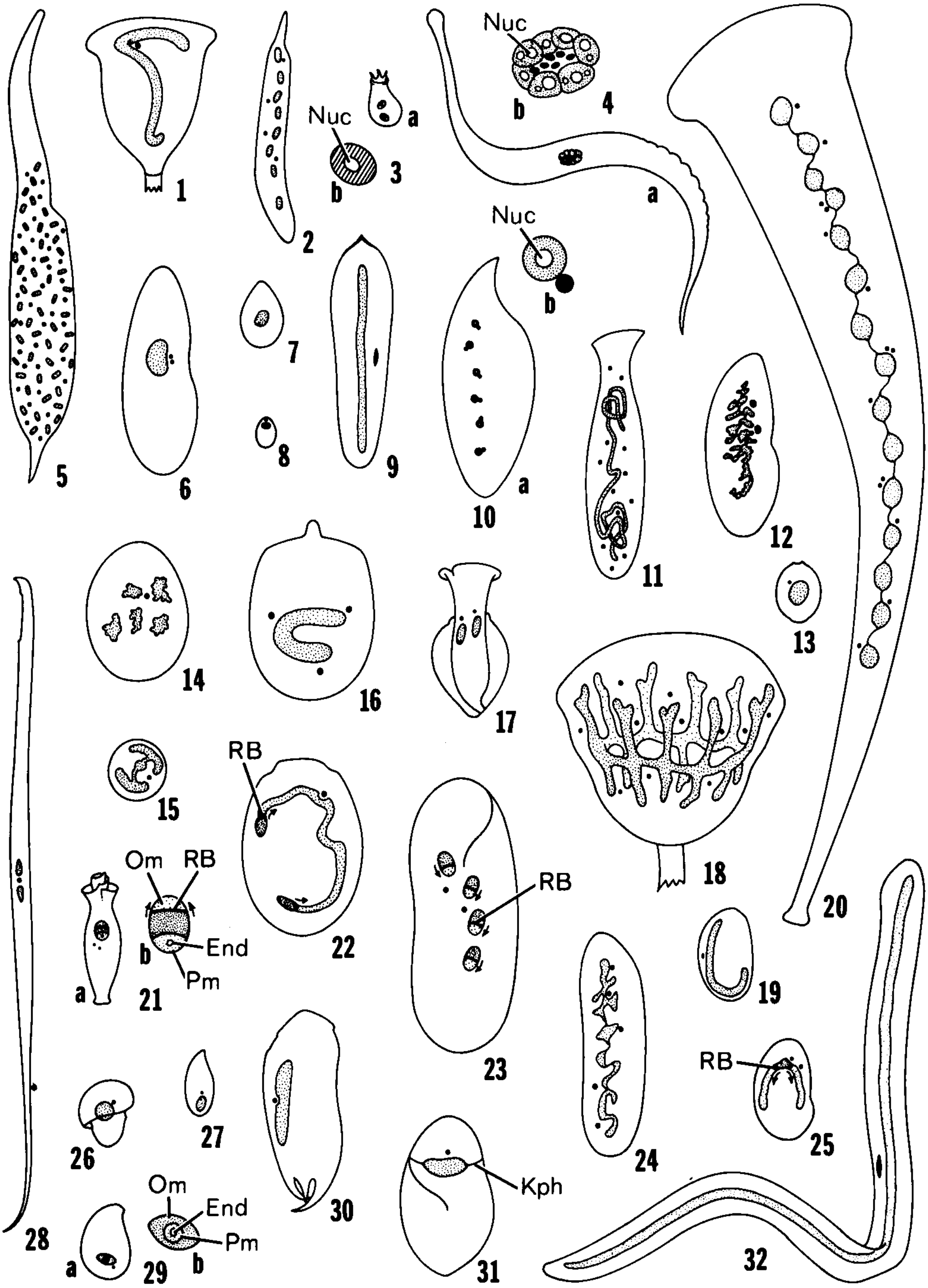


PLATE III. Kinds and diversity of ciliate nuclei. [See page 39 for figure explanations.]

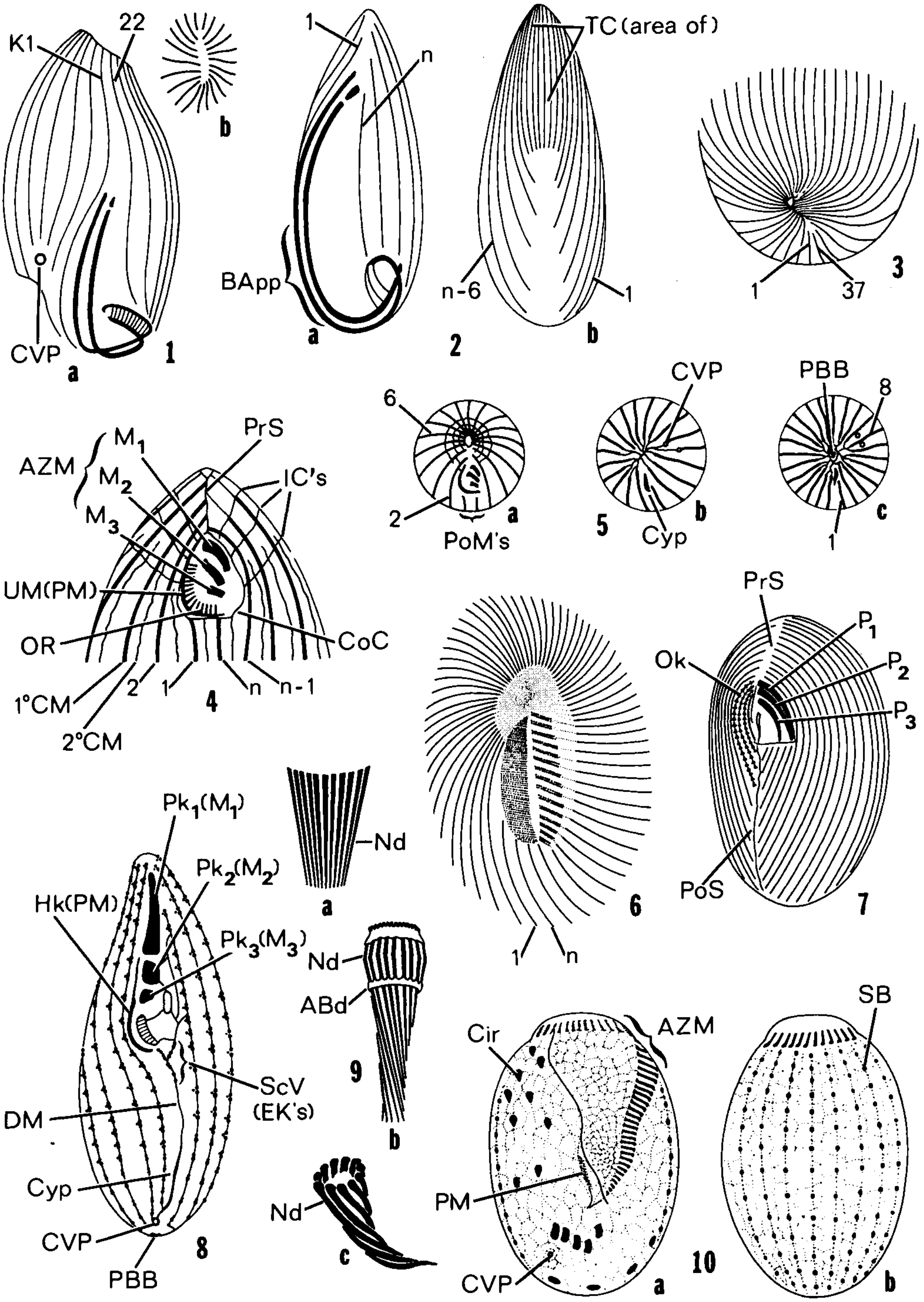


PLATE IV. Structures and features of ciliates revealable by use of silver-impregnation techniques. [See page 39 for figure explanations.]

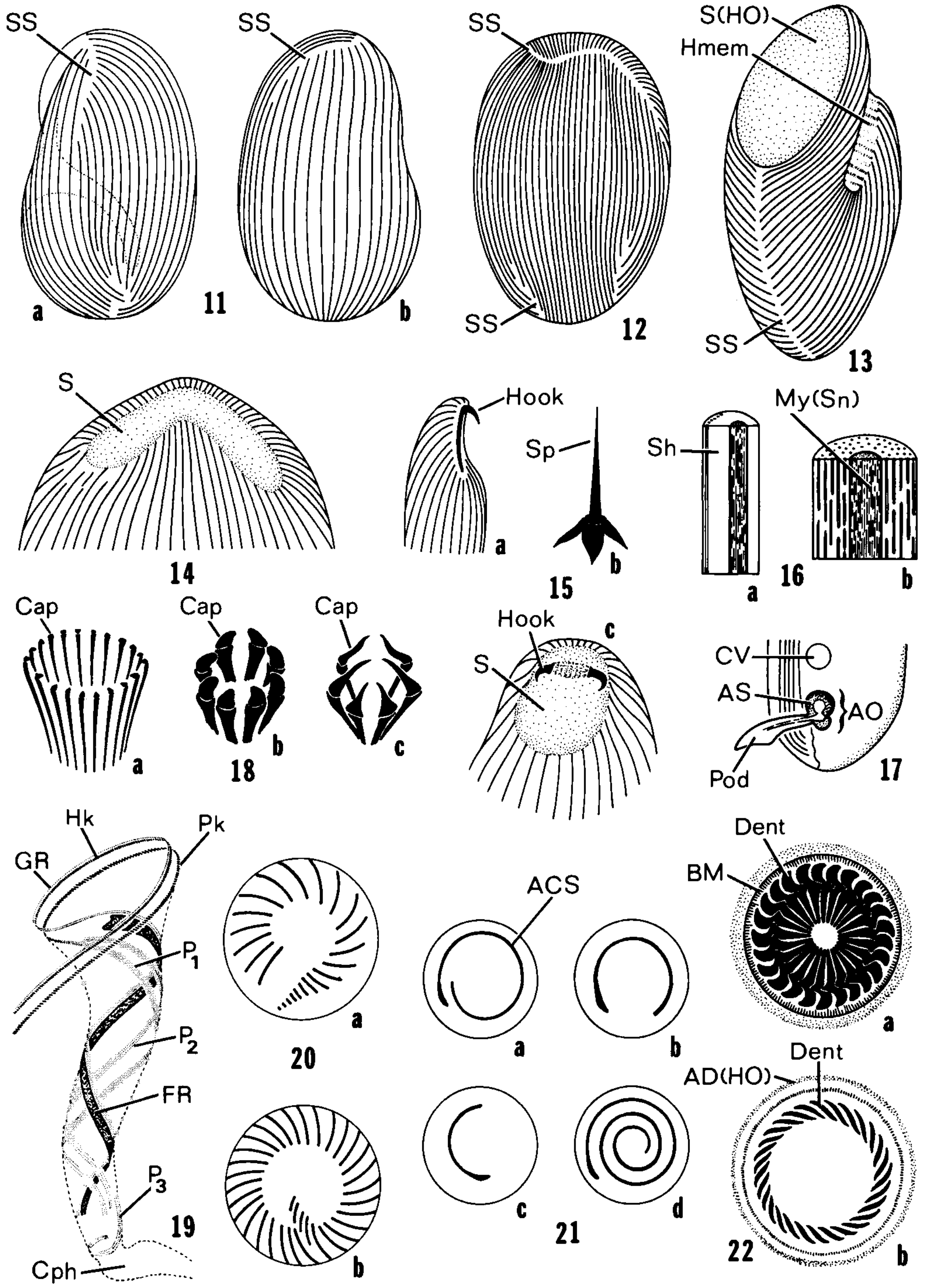


PLATE IV, continued. [See page 39 for figure explanations.]

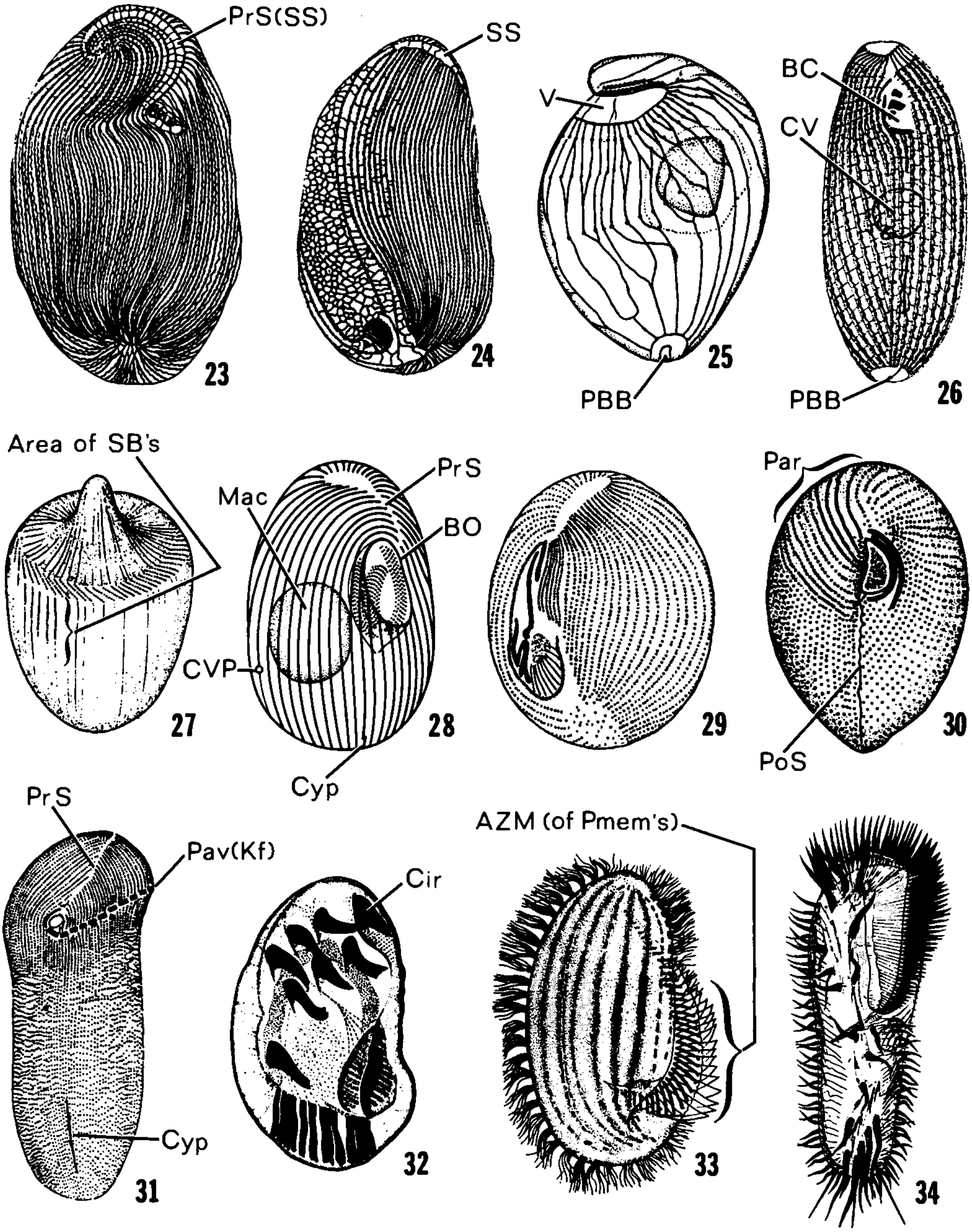


PLATE IV, continued. Drawings of specimens treated by various techniques of silver impregnation: Figs. 23—25, Klein "dry" technique; 26, von Gelei-Horváth method; 27—31, Chatton-Lwoff technique; 32—34, protargol stain. 23. *Colpidium* (Klein). 24. *Ancistrum* (Raabe). 25. *Trimyema* (Jankowski). 26. *Dexiotricha* (Jankowski). 27. *Monodinium* (Dragesco). 28. *Glaucoma* (Corliss). 29. *Pleurocoptes* (Fauré-Fremiet). 30. *Disematostoma* (Dragesco). 31. *Nassula* (Fauré-Fremiet). 32. *Aspidisca* (Tuffrau). 33. *Phacodinium* (Dragesco). 34. *Stylonychia* (Dragesco).

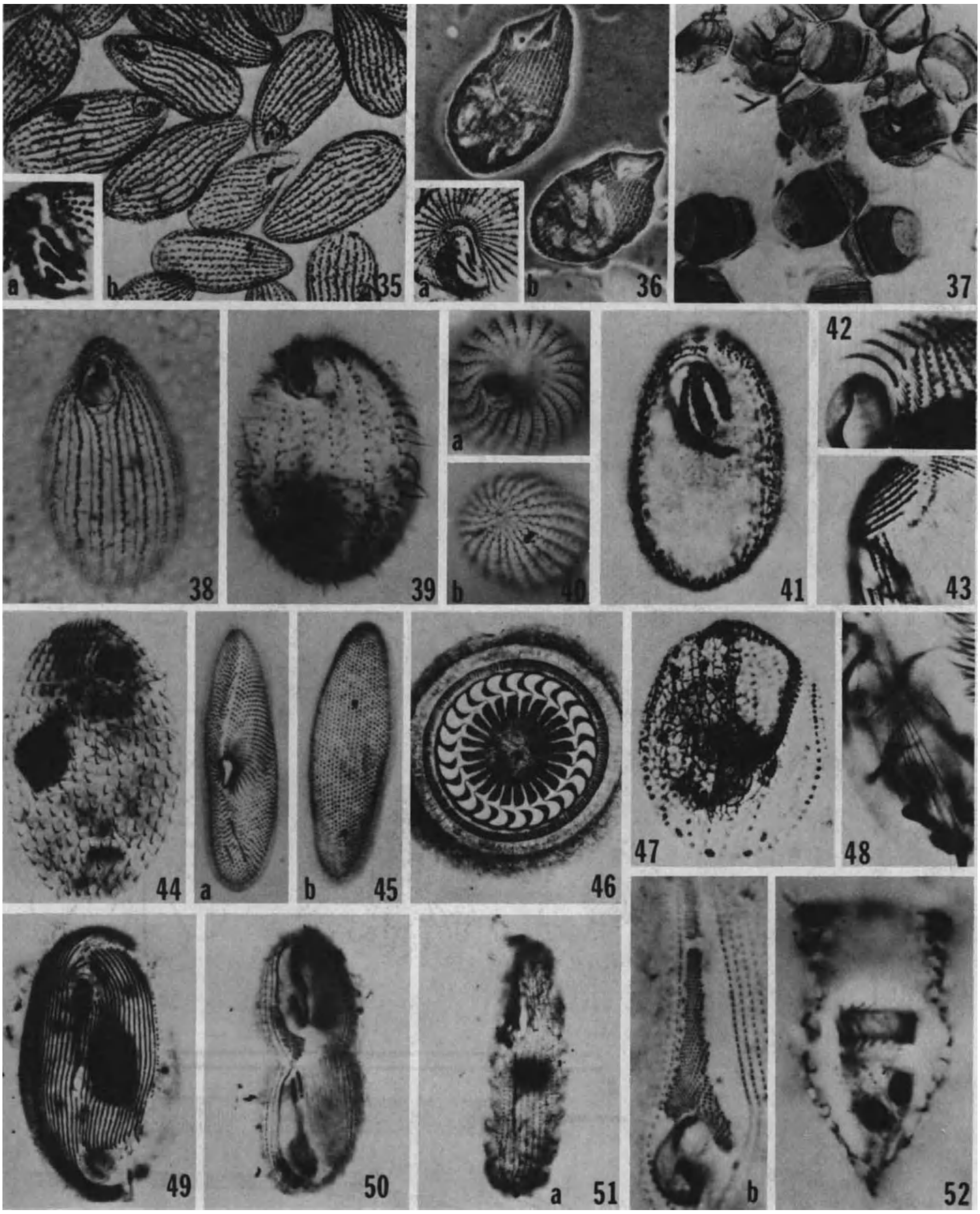


PLATE IV, concluded. Photomicrographs of specimens treated by various techniques of silver impregnation: Figs. 35–38, 40–43, 45–47, Chatton-Lwoff technique; 44, Rio-Hortega method; 39, 48–52, protargol. 35a,b. *Tetrahymena pyriformis.* 36a,b. *T. patula*, macrostome form. 37. *Urocentrum.* 38, 39. *Tetrahymena* sp. 40a,b. *T. setosa*, apical and antapical poles. 41, 42. *Glaucoma scintillans*, ventral, and preoral suture area. 43. *Colpidium*, preoral suture area. 44. *Dexiotricha* (Fernández-Galiano). 45a,b. *Paramecium*, ventral and dorsal (Dippell). 46. *Trichodina*, aboral pole with denticulate ring (Lom). 47, 48. *Euplotes*, ventral, and tract of cirral fibers (Tuffrau). 49. *Brooklynella* (Lom). 50. *Pleuronema* (Small). 51a,b. *Philaster*, left-ventral, and buccal area (Coats). 52. *Tintinnopsis*, contracted in lorica (Brownlee).

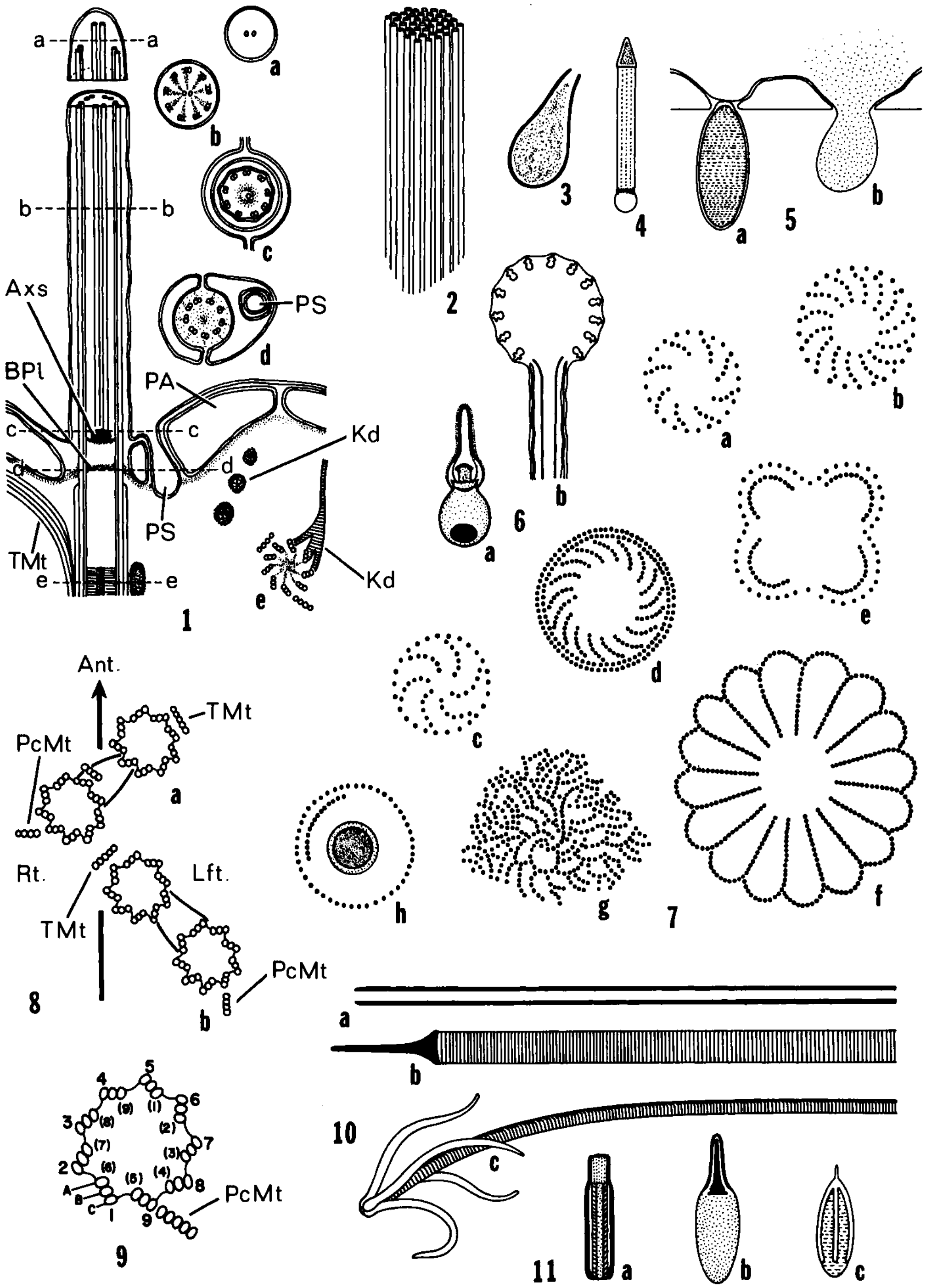


PLATE V. Structures and features of ciliates revealable by use of transmission and scanning electron microscopy. [See page 39 for figure explanations.]

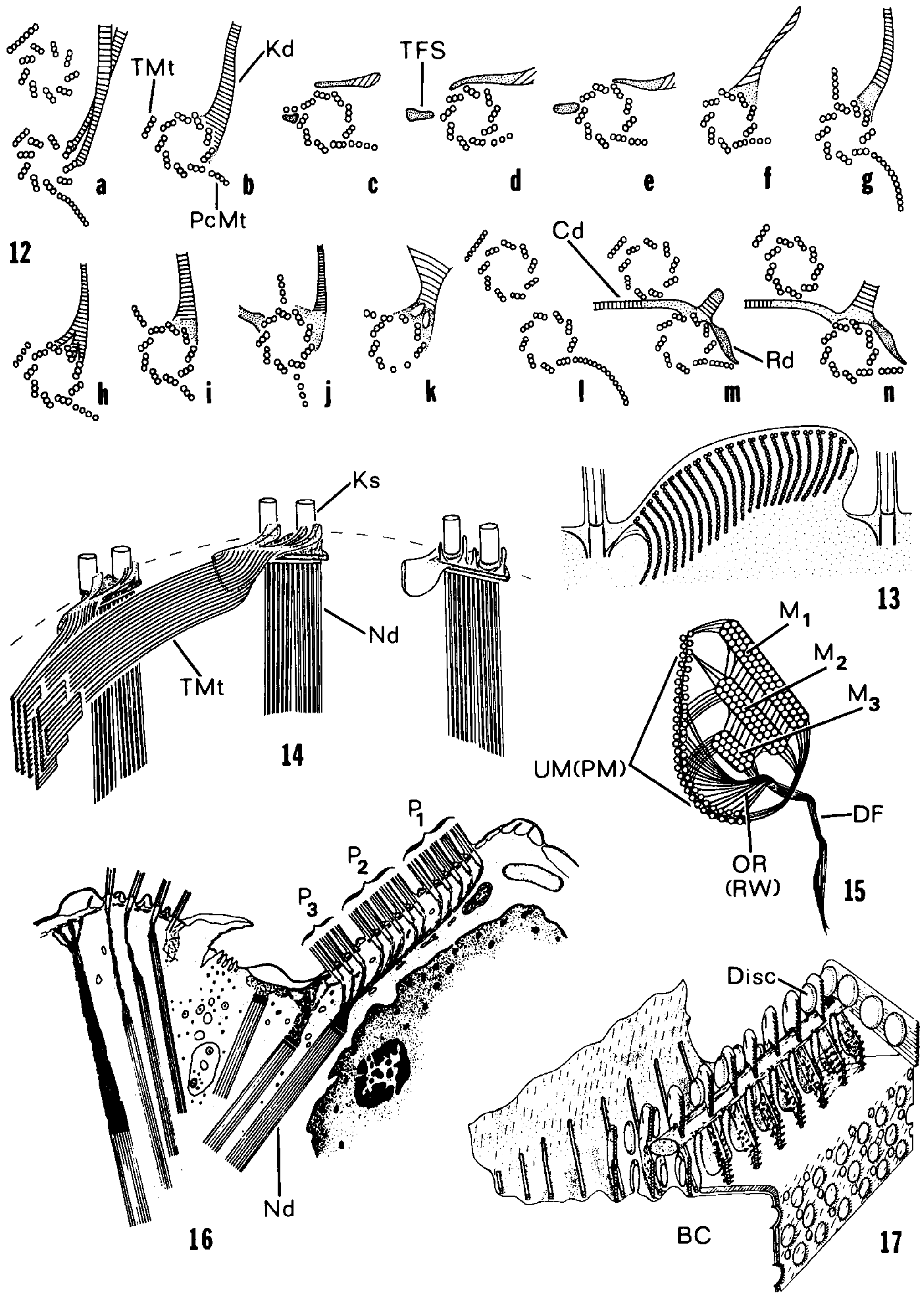


PLATE V, continued. [See page 39 for figure explanations.]

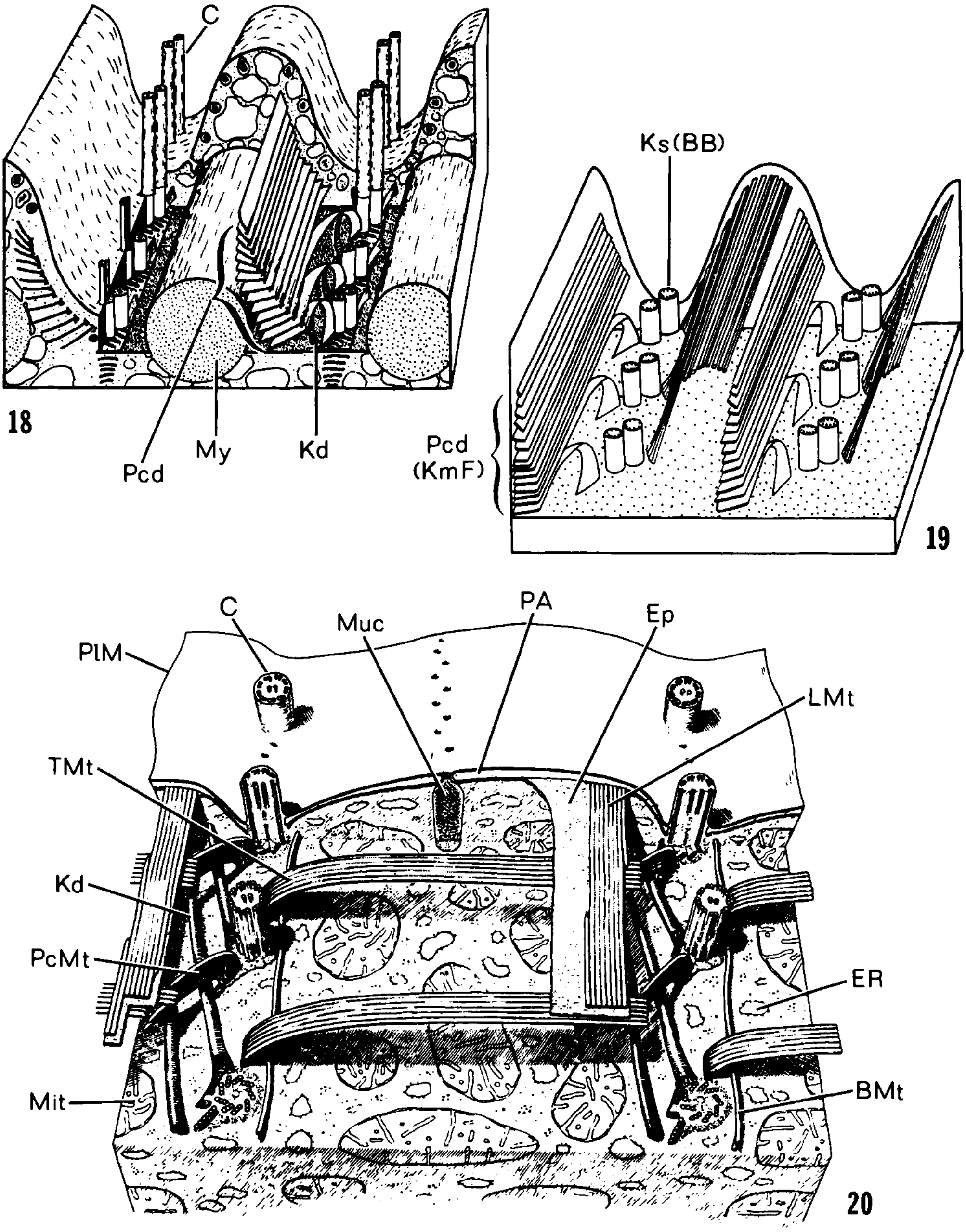
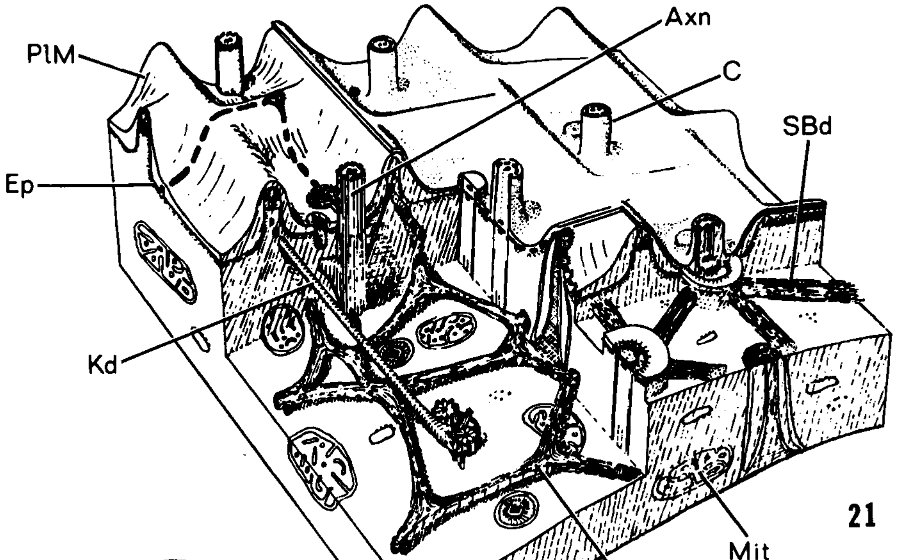


PLATE V, continued. "Cut-away" ultrastructural views of pellicular and subpellicular (somatic) organelles and structures in selected ciliates. Note well-developed postciliodesmata in first two organisms, forms traditionally very distant taxonomically. Fig. 18. *Tracheloraphis*, a "lower" gymnostome (Raikov et al.). 19. *Blepharisma*, a heterotrich (Gerassimova & Seravin). 20. *Tetrahymena*, a well-known tetrahymenine hymenostome (Allen).



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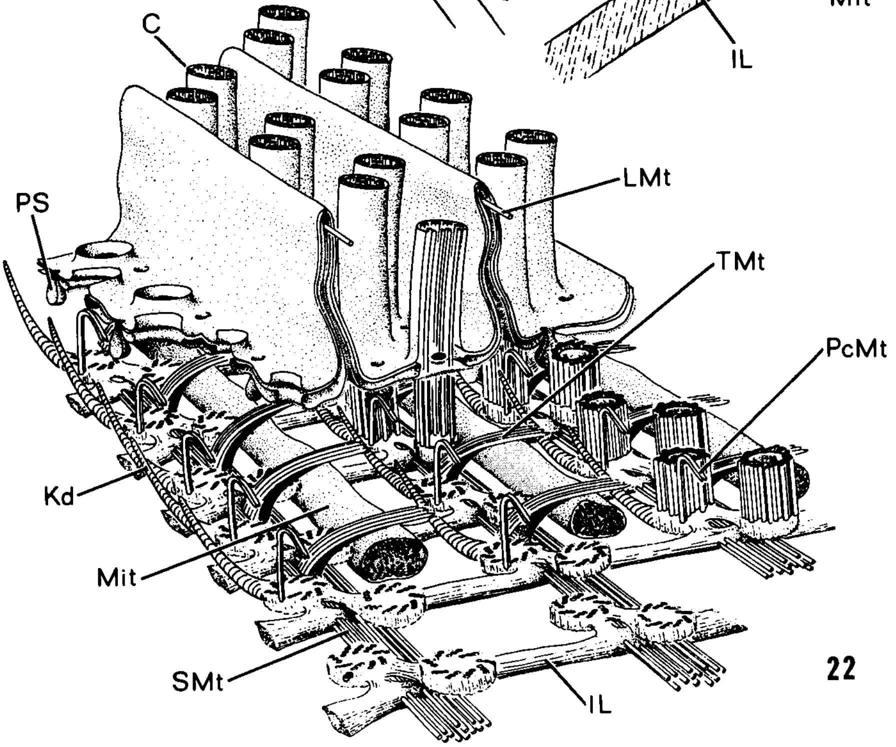

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PLATE V, continued. More "cut-away" ultrastructural views of pellicular and subpellicular (somatic) organelles and structures in selected ciliates (see also figures of preceding page). Specializations shown in some detail in a well-known peniculine hymenostome and a complex pleuronematine scuticociliate. Fig. 21. *Paramecium* (Allen). 22. *Conchophthirus* (Antipa).

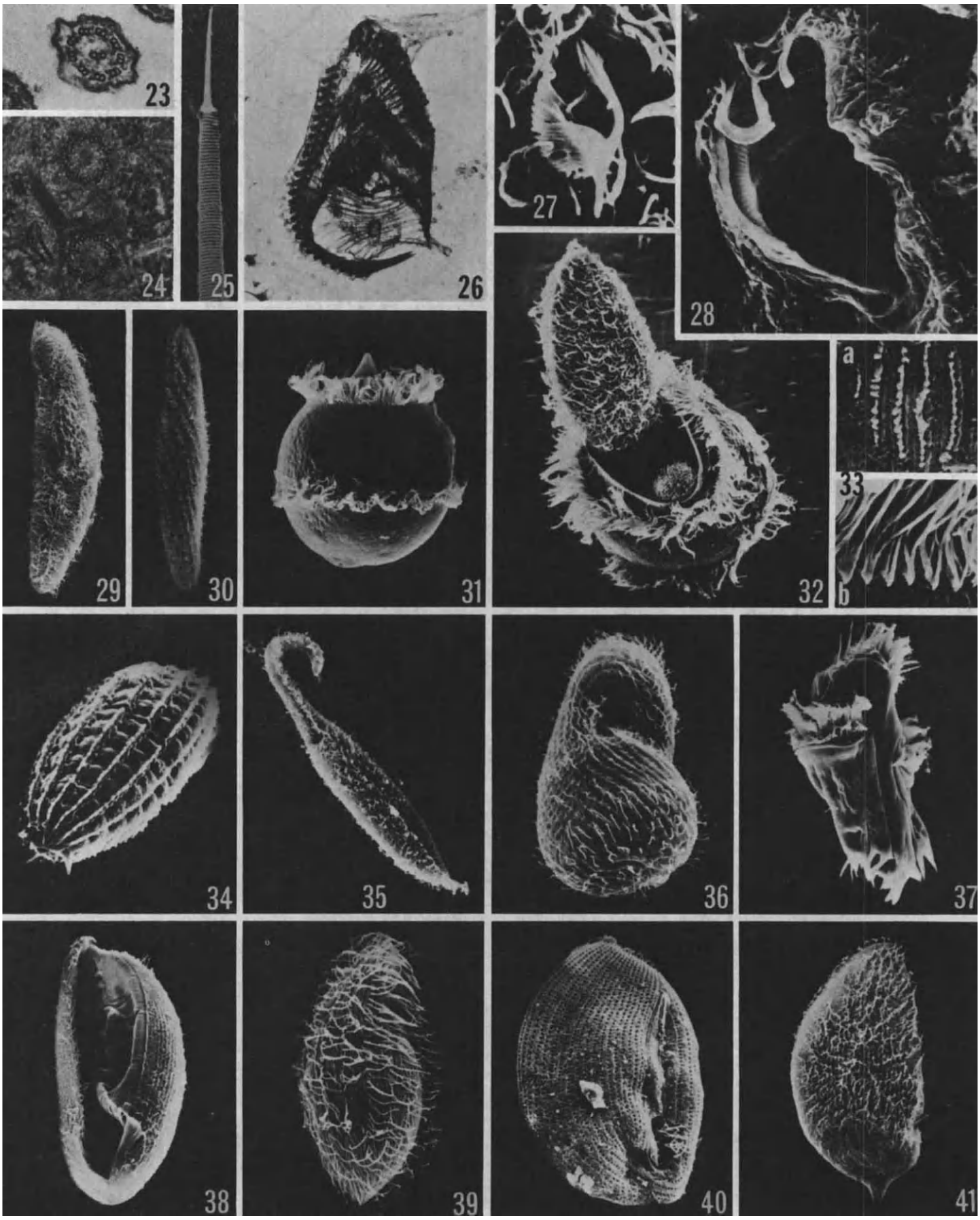

PLATE V, continued. Electronmicrographs of kinetofragminophoran and oligohymenophoran ciliates. Figs. 23–26. By TEM. 23–25. Cilium, and pair of kinetosomes (note kinetodesma), in X-S; trichocyst, shadow-cast by Dragesco 25 years ago (*Paramecium*). 26. Oral area of *Tetrahymena* (Langmuir trough critical-point drying technique, by T. K. Maugel). 27–41. By SEM (29–41 supplied by E. B. Small). 27, 28. Oral areas of *Tetrahymena pyriformis* and *T. vorax*. 29, 30. *Paramecium*, ventral and dorsal surfaces. 31–33. *Didinium*: trophont; individual engulfing *Paramecium*; "sensory-bristle" area, and pectinelles of ciliary girdle. 34. *Coleps*. 35. *Dileptus*. 36. *Colpoda*. 37. *Ophryoscolex*. 38. *Lembadion*. 39. Philasterine scuticociliate (from sea urchin; called "*Cyclidium*" in literature), with adherent bacteria. 40. *Pleurocoptes*. 41. *Biggaria*.

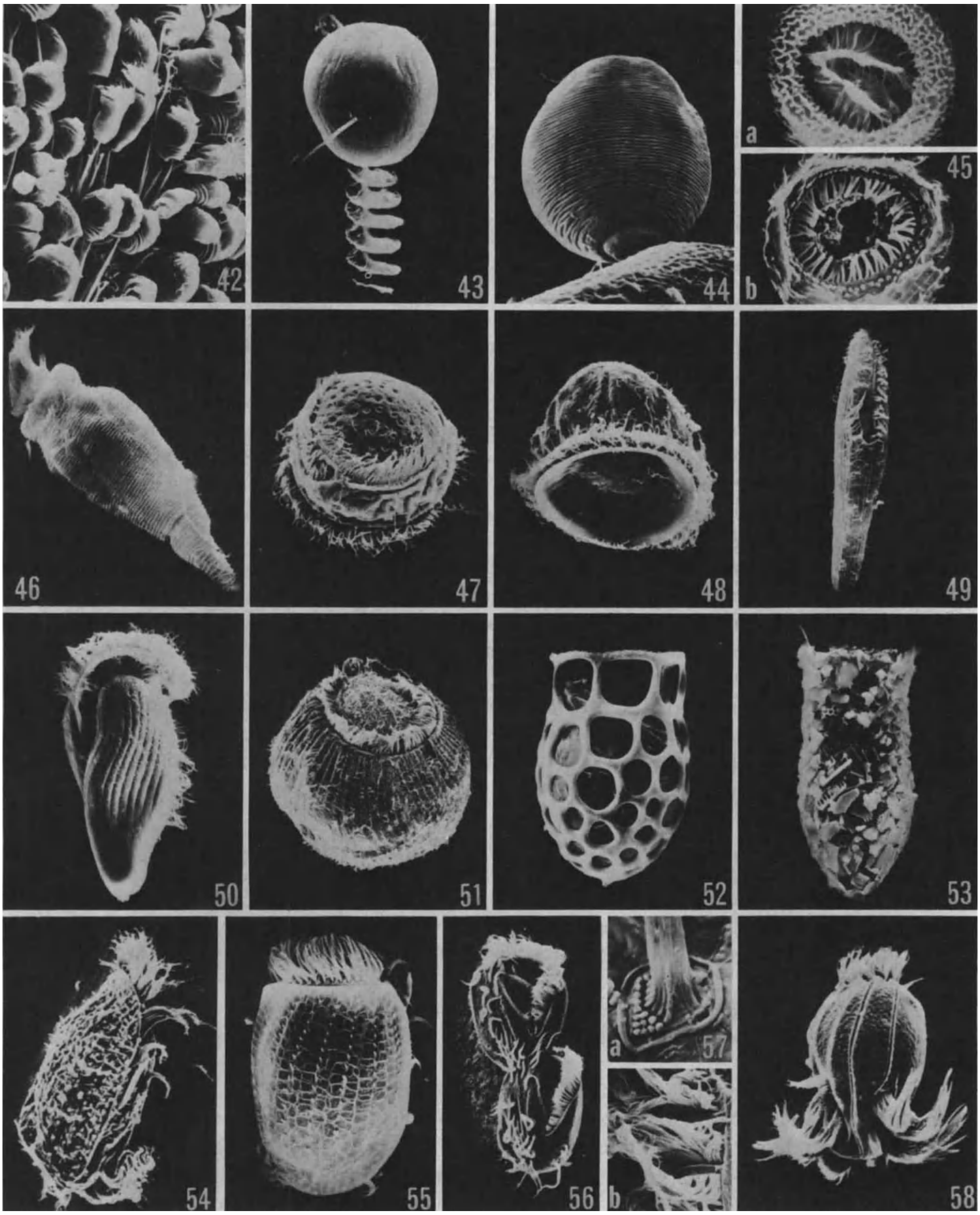

PLATE V, concluded. More scanning electronmicrographs: peritrichs and especially spirotrich (polyhymenophoran) ciliates. Figs. 42–45, 49–52, 57, 58 supplied by E. B. Small, 46, by the late H. E. Finley; 47, 48, 54, by J. Lom; 53, by K. Gold; 55, 56, by J. J. Ruffolo, Jr. 42. *Epistylis* (colony). 43. *Vorticella* (stalk partially contracted). 44. *Vorticella* (fully contracted). 45a,b. *Epistylis* (single zooid), oral and aboral poles (with latter at higher magnification). 46. *Rhabdostyla*. 47, 48. *Trichodina*, oral and aboral views. 49. *Blepharisma*. 50. *Metopus*. 51. *Stentor* (contracted). 52. *Dictyocysta* (lorica). 53. *Tintinnopsis* (lorica). 54–57. *Euplotes*, lateral, dorsal, and ventral (late stage of fission) views, plus enlargements of cirral base and membranelles of AZM (57a,b). 58. *Uronychia*, dorsal view.

Chapter 3

Sources and Use of Differentiating Characters, and the Rationale behind the New Classification

The difficulties and "pitfalls" besetting the worker in comparative ciliate systematics have been mentioned in Chapter 1 and treated in some detail in Corliss (1974c). Collecting numerous data from all possible fields, and treating them by proper quantitative methods, will overcome many of the problems involved; and it is perhaps surprising that there are really a goodly number of sources of characters of taxonomic value. In a full "check-off" list we might recognize some seven major classes or sources of helpful information, appreciating that overlapping is inevitable. The first two considered below require only light microscopy, and unstained living material will often suffice. The third demands the field and/or laboratory approaches standard in ecological research on protists in general. Use of one or more of the several techniques of silver impregnation is obviously highly desirable for category four, although combinations of (generally less satisfactory) other cytological staining methods could be substituted here. The fifth requires appropriate cytological (occasionally cytochemical) procedures, with preliminary fixation of material, etc. Category six, by definition, necessitates methods of electron microscopy (admittedly not available to every ciliatologist); and the seventh "class of information" demands experimental laboratory approaches often of considerable sophistication. Ideally, data for any ciliate – or group of ciliates – should be gathered from all sources. The glossary (Chapter 2) provides, among other terms, a listing (alphabetically) of the kinds of ciliate characters involved here, with definition and description, so they are purposely not enumerated below.

Sources of Taxonomic Characters

(1) *Gross morphological features.* Included here are facts about the body, the ciliation, and the oral area in general and at lower levels of magnification. Such observations can be of importance in overall "screening" or identification of the taxonomic group to which the organism(s) under study belong(s).

(2) *Gross physiological (including morphogenetic) features.* Data on life style, general functions and behavioral features, and the many morphogenetic phenomena involved in stages of the life cycle.

(3) *Ecological features.* Information about the general state of the organism (overlapping with "life style" above) and all sorts of features of the habitat – general, chemicophysical, biogeographical, its relation to food preferences, etc.

(4) *Cortical features (argyrome and infraciliature).* Perhaps the single most valuable source of data useful in ciliate systematics. In the present context, largely dependent on methods of silver impregnation; but, of course, the general category overlaps with number 6, below (ultrastructural approach). Here is the area concerned with the all-important kinetid ("kinetosomal territory") and all other somatic corticotypic features; but the oral infraciliary structures, in both "static" and "dynamic" (morphogenetic) states, are equally rich providers of data of great comparative value.

(5) *Endoplasmic and nuclear features.* Mitochondria, food reserves, endosymbionts, etc. are included here. And observations on the condition, numbers, kinds, shapes, sizes, locations, degree of ploidy, etc. of the nuclei are a must in a complete taxonomic study (again leaving ultrastructural and refined biophysical aspects for the following categories 6 and 7).

(6) *Ultrastructural features.* Essentially, many of the same structures or organelles included

in the preceding categories are implicated here, with the emphasis on descriptive information at the macromolecular level obtainable only by electron microscopy (SEM or TEM). Once again, dynamic states are to be investigated as well as the typical interfissional stages of the material under study.

(7) *Biochemical, genetic, or other molecular features.* Finally, not to be neglected are data available from sophisticated experimental treatment of ciliates: for example, in areas of metabolic pathways, ciliary movement, organellar template formation, chemical ecology, molecular ecology, chemical genetics, and molecular evolution.

Use of Appropriate Characters

It generally can be realized – intuitively – that some features are *qualitatively* more valuable (i.e., have a higher information content) than others in distinguishing a given ciliate from other ciliates belonging to different taxa. Even so-called "key" characteristics are obviously helpful, to a degree. Since it is widely agreed that the most trustworthy data are those which are evolutionarily the most conservative ("ancestral," "primitive," or "plesiomorphic" as opposed to "derived," "more highly evolved," or "apomorphic," though these are only relative terms), ciliatologists for some time have made general categorizations concerning the sources of features potentially most useful in comparative taxonomic studies. For example, the external ciliature, in close contact with environmental stimuli and thus subject to many selective pressures in an organism's adaptation to a new or changing habitat, is apt to be more variable and thus less reliable or less appropriate than the infraciliature, "protected" as it is in its subpellicular or cortical location. Organelles of fixation, much like those of feeding and locomotion, are generally subject to similar variation. Because of their location, the cytostome and cytopharynx, and certainly the nuclei, may not be so easily – or so rapidly – affected in the course of ciliate evolution. Of great value may be the larval or ontogenetic stages in a life cycle, although these, too, are subject to modification by selective pressure. But the morphogenetic processes taking place at the time of cytokinesis often may particularly represent a resource for conservative characteristics, since it is the mature "adult" stage which spends the greater amount of time "relating" (exposed) to its environment. (However, as noted above, this is not to imply that all ontogenetic features are of a less adaptive nature than other features.)

Following the tenets of the systematist of the better-known vertebrate and invertebrate groups, still other generalizations may be applied in deliberately "favoring" some kinds of characters over others in work in ciliate taxonomy. Widespread, universal features may be considered more stable and conservative than isolated ones or ones of scattered occurrence. Generalized characters are of more value than specialized; often, though with caution, simple is to be chosen over complex – and certainly homologous over convergent (i.e., as a basis for placing two forms showing the "same" trait close together). Knowing which features are truly homologous and which ones are not is the age-old difficulty here, of course. Characters exhibiting high degrees of constancy, consistency, and relative independence are generally reliable; ones which are highly variable or are of a highly redundant nature – that is, merely a necessary correlate of another character – are not good choices or are of lower information content. Differences (or similarities) due to reasonably obvious secondarily reduced ("regressive") states must also be kept in mind when dealing with some otherwise seemingly helpful traits. Hanson (1977) proposes the term "seme" for any unit character (ancestral or derived) of high information content.

In the case of the taxonomic level – suprafamilial – with which we are mainly concerned in this book, the time-tested and often well and widely studied morphological character is to be preferred, in general (but exceptions are welcomed!), over the less understood or more restricted physiological, ecological, biochemical, or genetic feature. At the present state of our knowledge in protozoology as a whole, this preference has to be acknowledged, nonideal though it may be even in matters of "organismic" (as opposed to "molecular") evolution. Finally, in a general way, characters about which we have more detailed or more broken-down-to-a-lower-level information ought to be chosen over broader, less specific characters of unknown detail. Thus, I enthusiastically endorse data from electron-microscopical studies, particularly when they furnish refinement of our knowledge concerning a structure, organelle, or organellar complex already believed to be of considerable value in comparative systematics and phylogenetics. And, in so doing, such investigations may also reveal completely new information (and have so done, abundantly: see especially Corliss, 1974a), data which may be as valuable as (or more valuable than) older information when applied to some particular taxonomic problem.

For the Ciliophora, I suggest that four broad sources of data should qualitatively be given greater weight or consideration and higher priority, overall and for application on an extensive scale, than any others (see also Corliss, 1976). These, the use of which is as appropriate in phylogenetic considerations (see Chapter 17) as it is in construction of a system of classification of suprafamilial groups, show obvious overlapping (but to no disadvantage). They are, briefly: the infraciliature, with emphasis (here) on the somatic structures involved; the oral area, including depressions and cavities, features of the cytopharynx, etc., as well as the oral or buccal infraciliature and ciliature; the mode of stomatogenesis, the explicit morphogenetic process of new mouth-formation which represents an ideal example of a dynamic feature in the life cycle holding rich clues to taxonomic (i.e., evolutionary) interrelationships; and the macronucleus, characteristics of which have been largely ignored to date in ciliate systematics and phylogenetics.

In application of data from the four principal "sources" mentioned briefly above to problems of comparative systematics, I suppose that the "number one" error would be to forget the possible effects of an organism's adaptation to a particular mode of life. Not only will such adaptations (e.g., sessility, to mention a common and very important one) alter significantly the appearance of structures in the particular species or group of species which may be under study but they will cause similarities, via convergence, in structures in what may be quite distantly related species, organisms likewise exhibiting the habit (such as sessility). An outstanding example may be found in ciliate organelles of fixation, structures studied individually by many ciliatologists but perhaps most thoroughly understood and appreciated from a comparative point of view by Fauré-Fremiet (see, for example, 1910a, 1969b, and many papers between those dates), whose passing precluded a planned definitive monograph on the subject. Another major peculiar mode of life manifest in many ciliates is an obvious one, *viz.*, exhibition of some kind of symbiotic association with other organisms (sessility, discussed above, is often involved, but so are many other morphological and physiological properties). Specific cases are rampant in the literature on many ciliate taxa; but two sources of excellent discussions are the aging but never "dated" collection of works by Chatton (1938) and the lengthy treatise on the subject by Z. Raabe (1947).

Relevant Hypotheses and Their Application

I have mentioned earlier (Chapter 1) that part of the reason for a new (and expanded) scheme of classification for the Ciliophora is to take advantage of and incorporate some of the fresh and stimulating ideas which have been proposed in relation to specific aspects of ciliate systematics and phylogenetics. In reviewing the overall situation, I should add two comments: all of the stimulating hypotheses are not necessarily "new" – some older ones appear to me to deserve "rejuvenation" – and certain of the canons and precepts of nonciliatologists are, obviously, also highly pertinent to many of the problems discussed in this book. [See particularly Hennig (1966), Mayr (1969), Remane (1956), Rensch (1959), and Simpson (1961); but citation of numerous references to other literature, with respect to important writings of the nonprotozoological evolutionary biologists, is reserved for a section of Chapter 21. My own recent past efforts and ideas are scattered through several papers (see Corliss, 1967a, 1968, 1972e, 1974a,c, 1975b,c, 1976; Corliss & Hartwig, 1977; Hutner & Corliss, 1976); and important concepts of other protozoologists referred to in my works (and described briefly in Chapter 2) embrace such topics as auxomorphy, cytotaxis, desmodexy, the kinetofragmon, oligo- and polymerization, parateny, the système sécant, and ventralization.]

General guidelines, not to be minimized, are to be found in the many "standard" tenets or hypotheses of the systematist of higher plant or animal groups; these must be mentioned (below), but very briefly. It also should be assumed that "cautions" exist for practically every criterion; but space simply does not permit reiteration of such dangers and "pitfalls" in application of time-worn taxonomic principles (but see Canella, 1964a, 1971; Canella & Rocchi-Canella, 1976; and Corliss, 1968, 1974c, 1976, for discussion of some of these).

A fundamental criterion for ranking groups is propinquity of descent. Equivalence of ranking in related taxa should be kept in mind, and even size of a taxon (creating too many "monotypic" groups is to be avoided). Parsimony – "Occam's Razor" – is always a guiding principle. There is a positive correspondence between degree of similarity of organisms and recency of their common ancestry. Simple *may* be ancestral to complex, *but beware*! Regressive characters are not primitive; nor are highly specialized, adaptive ones the most ancient. We are surrounded by examples of *convergence*: again, beware. Aspects of the Biogenetic Law, as understood in modern times, *can* be used in recognition of "fundamental" characters. Relevant when available are data on differential rates of evolution, branching, factors of dispersal, explosive radiation, and the like. The concept of monophyly should be adhered to. Occurrence of "mosaic" evolution must be appreciated. Only *a posteriori* judgment should be used in weighting characters. As a general rule, to be taken in context and applied judiciously, one ought to favor as diagnostic characters those exhibiting universality, constancy, consistency, homology, and independence; and one should eschew those which are highly variable, nonhomologous, regressive, or redundant. Finally, there is, still, some room for subjectivity in the art of taxonomy.

While not forgetting the importance of the principles alluded to above, there are several others (sometimes of overlapping content) which seem to me to be of particular relevancy for use in research on ciliate classification. Homologous characters *can* be identified without recourse to fossil material. Some groups of contemporary organisms have gone essentially unchanged in many characteristics for aeons of time, while others have not (attempting to assign members to either category is perfectly legitimate). Features of ontogeny (phylembryogenesis) can be of value in comparative systematics and evolution. A morphological character should not be utilized in isolation from functional and ecological considerations. Use of new techniques can produce new data which may be of an entirely different kind from facts or characters previously known. Characteristics "used up" in diagnoses of higher taxa should not be reemployed as "exclusive" also at a lower level (this may seem to be a petty point, but it is ignored with distressing frequency in taxonomic protozoology). One ought to avoid the temptation to elevate a group to a higher rank than formerly accorded it on the basis solely of (1) its "sudden" study after long neglect; or (2) its manifestation of a few seemingly "unique" characters discovered by means of a new technique which has not been concomitantly applied to members of neighboring groups (again, this has happened repeatedly in the recent past in protozoology).

A few more or less additional "hypotheses" or principles have been exposed in a recent paper of mine (Corliss, 1976) and need no lengthy treatment here. Generally they are not wholly original with the writer, although their usage in protozoology may be somewhat novel. *In toto*, they probably represent an expression of my own philosophy or rationale (as a compound "guiding principle") with respect to recognizing and using diagnostic characteristics and criteria in formulation of the scheme of ciliate classification endorsed in this book and in postulation of the phylogenetic group-interrelationships which are presented in Chapter 17.

Evolutionary Series. Recognition of (presumed) evolutionary trends among the ciliates, generally in the form of morphological series of (allegedly "representative" members of) genera or families (or even higher ranks), has long been practiced by ciliatologists (and other protozoologists: see Corliss, 1960a, 1962a, 1963a), although sometimes perhaps subconsciously. Arranging groups (i.e., in effect, subgroups) on the basis of increasing complexity in some set or sets of organelles (in recent years frequently infraciliary in nature) is a reasonable way to illustrate possible phylogenetic affinities, as long as care is taken with respect to the many "pitfalls" associated with the problem. Many characters or groups of characters are potentially usable in support of a given series, but identification of convergent as opposed to homologous characters is certainly the principal difficulty in attempting to establish the veracity of a proposed line. Scores of examples of application of this "hypothesis" exist in the following chapters; worthy of special mention are such works as those by Dogiel (1929), Fauré-Fremiet (1968), von Gelei (1950a), Jankowski (1972a), Poljansky & Raikov (1976), and Raabe (1971a).

Morphogenetic "Recapitulation." Even casual observations of "larval" forms of the several ciliate groups whose members have such clear-cut stages in their life cycles have long suggested that some of their characteristics might be of aid in proposing group affinities. With the advent of techniques of silver impregnation, and, more recently, of electron microscopy, it has become reasonable to suppose that certain structural similarities revealable in the ontogenies of ciliates from different taxa, to be noted even in cytokinesis without involvement of special "larval" stages, can be used – *with proper caution* – to throw light on the comparative phylogenetics of those groups. Involved may be such explicit phenomena as budding and stomatogenesis. To this extent, then, ontogeny *does* "recapitulate" phylogeny; and many examples are to be found (e.g., in Corliss, 1968; Jankowski, 1972a; Kormos & Kormos, 1957c; Raabe, 1971a; Small, 1967). [Sewertzoff (1931) laid the groundwork, with early ciliate applications by Dogiel (1951) and von Gelei (1950a).]

Constellation of Characters. It is obvious that at least a reasonable multiplicity of characters should be available for diagnostic separation of two suprafamilial groups, even if differential weighting is applied. And the combination or cluster of characteristics ought to include data from more than a single area or source. A singular advantage of adoption of the principle of a "constellation" of characters which is not always appreciated is the allowance of inclusion in a given taxon of an organism (or group) which is aberrant in certain ways and yet ought not be excluded or eliminated from the (larger) taxon. Even a startlingly different feature can be (judiciously) discounted if a goodly number of (other) important characteristics are possessed in common. Among pragmatic results of this broad-minded approach is the prevention of rampant "splitting" on the basis of isolated characters. It can also help substantially in alleviation of potentially polyphyletic situations (see below, as well). Examples are, once again, numerous and often obvious.

Karyological Relicts. As discussed adequately in recent papers (e.g., see Corliss, 1974b, 1975b,c, 1976; Corliss & Hartwig, 1977; Raikov, 1969), the evolution of the nuclei, particularly the macronucleus (as an organelle unique to ciliates), should not be disregarded in attempts to recognize discrete higher-level taxonomic groups within the phylum. If we do indeed have "relict" nuclei in several contemporary taxa, we must at least explore the possibility that those groups may represent remnants of "ancient" ancestral or primitive "eociliate" groups in the evolution of the whole organisms (see Chapters 5 and 17). My own direct application of this hypothesis has brought about proposal of major changes in the high-level classification of the groups of species affected.

Monophyletic Origin. This should really be considered more of a "dictum" than a hypothesis; but even as a "guiding principle" it has, curiously enough, been inadvertently neglected (or deliberately disregarded) on a wide scale in classificational work in protistology, as I pointed out several years ago (Corliss, 1972e). A *single* taxonomic group of *any* organisms simply cannot remain as such *if* various of its members are known (or overwhelmingly suspected) to have a phylogenetically different past history. That is, once a truly polyphyletic situation is widely recognized (e.g., by application of the other hypotheses discussed on these pages), steps should be taken to eliminate it. The stem members of, for example, a suborder must have had their origin in an immediately ancestral taxon of the same, or lower, rank: through one or more lineages, however, is acceptable. If the members of the suborder in question appear to have arisen from progenitors belonging to more than a single ancestral group (at the same or higher level in the hierarchy), then the taxon in question contains, itself, two or more groups so diverse that – by the concept of monophyly – they themselves have to be recognized as comprising separate high-level taxa (or as belonging to such distinct groups: more than one solution may exist for a given dilemma, and new taxa need not always be created to correct the problem).

Gap Size of Distinctness. For plant and animal groups in general, it has long been held that one should be able to recognize a gap of "sufficient" (how defined?!?) magnitude between any two groups of species before proposing their formal separation into different higher taxa. Since evolution is a continuous process, extinction of (intermediate) forms – verifiable in the fossil record for various metazoan groups, for example – aids in establishing a credible gap. We do not have any helpful fossil evidence for the ciliates, but discontinuities, whatever their nature or origin, appear to exist, and protozoologists have long been willing to split up the whole assemblage into varying numbers of sub-sets. That number, however, has grown mightily since the days of Bütschli, a century ago, as we have come to recognize and express the diversity of the (now) thousands of described species in a tangible taxonomic way (see Corliss, 1974a, for historical details). But I have a feeling that the "gap size of distinctness" (e.g., at the ordinal level), in the hands of some workers, has shrunken considerably and perhaps not always consistently nor justifiably. I have wondered (Corliss, 1976) if an attempt could be made to develop some sort of quantitative measure of the "uniqueness" of taxonomic groups at the various levels. That is, can we find – for the ciliates – a suitable method of quantifying "gaps," so that workers would uniformly be discouraged from proposing separation of any two groups of organisms unless their gap-size figure fell within some widely accepted range of values?

This last-mentioned principle or "hypothesis" is related to the mathematical, numerical, or "phenetic" approaches being applied increasingly frequently today – and with excellent results – to problems of (mainly morphological) "relationship" at the specific or infraspecific levels of all sorts of organisms (including ciliates: e.g., see Gates & Berger, 1974; Lynn & Berger, 1972; Powelson et al., 1975). Instructive books are appearing yearly; for example, see Blackith & Reyment (1971), on multivariate morphometrics, Clifford & Stephenson (1975), on numerical classification, and the latest edition of the "classic" in numerical taxonomy, Sneath & Sokal (1973). While not at all denying the tremendous impact such approaches are – and should be – having on parts of the field of ciliate systematics, I cannot but be wary of their direct extension and application to the somewhat different problems often encountered in *suprafamilial* classification (as opposed to demes, strains, subspecies, and the like). Here the very choice of sets of characters to measure or even to weight – out of innumerable possibilities, ranging from scores of ultrastructural aspects to similarly numerous (or potentially numerous) behavioral, ecological, nutritional, genetic, and biochemical parameters – may elicit the investigator's "built-in" bias or subjectivity from the very beginning, unless great care is exercised. To perhaps 95% of the protozoologists in the world, taxonomy seems to mean classification of *species*; thus, in short, entirely fresh "numerical" approaches may be required to grapple with the taxa at the "macrosystem" level. Factors of convergence, as stressed on earlier pages, and "mosaic" evolution, alone, may make the data-gathering and the subsequent analyses herculean tasks, with results ultimately obtained still subject to diverse interpretation.

Rationale for Present Classification

The rationale behind the systematic conclusions drawn in this book is not reducible to a single statement. Much of the material presented in preceding pages is an integral part of it. The "constellation of characters" principle has, it is true, served as a major guideline of mine; but the choice of (sources of) characters – not to mention their interpretation in some cases – and the emphases used in their application to any given (suprafamilial) problem (see following chapters) also involve all or parts of numerous other concepts (see definitions in Chapter 2), as discussed very briefly above. Unusual, perhaps, is my emphasis on the value of modes of stomatogenesis, the evolution of the macronucleus, and nonultrastructural (and even nonmorphological) features. I am well aware that mere availability of a greater number of characters (new or old) naturally is not, *per se*, proof of increased diversity which, in turn, would favor recognition of an increased number of taxa. Indeed, ultrastructural data (for example), on occasion, have clearly supported the amalgamation or "lumping" of taxa by their revelation of an underlying similarity in members of groups previously separated on the basis of more superficial characteristics. Nevertheless, it is my own belief (intuitive, in part, to be sure) that we are detecting – to date – only a very little of the great evolutionary gulf probably existing between groups of even "look-alike" ciliate assemblages and that, as our methods of investigation improve, we are bound to be astonished by the genuine separateness of many of the taxa comprising the phylum.

Addendum

In the work on this book, I have, when appropriate to any given problem, utilized recent ideas proposed by fellow ciliatologists as well as reviewed the great quantity of assorted and unsorted notions and data of the past literature, information representing an accumulation over the decades of diverse studies by hundreds of our predecessors. Unfortunately, some of the propositions from contemporary colleagues – the very hypotheses perhaps destined to be of the most importance in ciliate systematics, phylogenetics, and classification – are either still incomplete at this time or were suggested so very recently (e.g., during years 1976 and 1977) that I have not had an opportunity to test them out for possible extensive application in this book (mainly conceived in the period 1973–1975, with preparation of "final" drafts for the most part in late 1976). I am able to insert only a word about them here in this special addendum (and occasionally elsewhere), with references added to the bibliography or to *its* addendum.

In the category referred to above would particularly fall the latest works of four groups of people or "schools of thought" which show some interesting similarities – as well as differences – among themselves. Briefly, all are heavily, if not totally, dependent on the tool of electron microscopy, with little attention (with scattered important exceptions!) to ontogenetic features and practically none to nuclear or nonmorphological characteristics. Two groups emphasize mainly somatic infraciliary organelles, and the other two stress ultrastructural details of the oral region. For example, Gerassimova & Seravin (1976), in a very interesting approach, make much of the presence or absence of the somatic subpellicular kinetodesmata and postciliodesmata (their apt term) in diverse taxonomic groups; and Lynn (1976a–c, 1977), in his stimulating structural conservatism hypothesis, seems to favor (organelles of the) somatic kinetidal complex over mouth structures. On the other hand, Small (1976) focuses special attention on internal details of the fascinating cytostome-cytopharyngeal apparatus (particularly noting the presence or absence of either transverse or postciliary microtubules in or near that organelle); and the French school of Clermont-Ferrand (e.g., see Grain et al., 1976; Grain et al., 1973; de Puytorac & Grain, 1976; de Puytorac et al., 1976) relies almost exclusively on variation in the kinetosomal organization of the infraciliary bases of the oral ciliature, from the simple pairs in "lower" ciliates to the paroral and membranellar (*sensu lato*) structures of the "higher" forms.

Such a brief *exposé* hardly does credit to the significance or potential significance of these very recent proposals (and others have received no mention at all), but neither time nor space permits further coverage here. Not unexpectedly, there is some overlapping – especially in the data bases – of the ideas mentioned above. And I am not displeased to find that some of my own conclusions parallel certain of those of my experienced colleagues, or are at least partially supported by their perhaps novel data. In fact, the *similarities* in the resultant schemes of suprafamilial classifications merit our attention: they are many (see Chapter 18); and they may be considered to serve as evidence that diverse approaches and hypotheses can indeed lead to quite similar taxonomic arrangements of the numerous high-level taxa now endorsed as comprising a necessarily expanded phylum Ciliophora. The reader is advised to study first hand the original papers of such modern workers as those named above: references included in the bibliography of this book (see Chapter 22) represent a good starting place!

Chapter 4

Phylum Ciliophora: General Description and Overview of the Major Groups

> "Avec les Infusoires, nous entrons dans un monde nouveau; un monde immense, varié jusqu'à la limite du possible, étonnant dans la structure de ses représentants, dans leur activité physiologique et même les manifestations de leur psychologie; si bien qu'à les étudier l'observateur passe de la surprise à l'admiration." — Penard (1938)

The Ciliophora, with some 7,200 known species now on stage and with perhaps several times that number waiting in the wings, constitute a highly differentiated assemblage of forms which, despite considerable internal diversity, may well represent one of the most homogeneous groups within the entire kingdom Protista. The taxon clearly deserves the status of independent phylum which has been formally accorded it (Corliss, 1974a; Raabe, 1964a).

Extant species (as single individuals: a colony — as a collection of zooids — could be much larger) range in body length from 10 µm to 4,500 µm, and their body shapes run from near-spherical through ovoid to highly elongate, with laterally or dorsoventrally flattened, spiraled, or even more bizarre forms (e.g., with "tails" or "heads" and "necks") also numerous. The body form — at a given stage — is of some permanence or stability because of the presence of a distinct cortex, generally of a complex fibrillar nature. A cytostome is commonly present. Cilia, simple or organized into compound ciliary organelles and distributed — in greater or lesser abundance — in various patterns over the body and/or around the mouth (when the latter is present), are used in locomotion (swimming or crawling), feeding (generally of the filter type), or, less often, in a tactile manner or for attachment (usually temporary) to some substratum. An infraciliature is universal. The nuclei, except in one small primitive group, are of two kinds; that is, most ciliates possess a dual nuclear apparatus, often with more than one of each kind. The micronuclei undergo acentric mitoses, with intranuclear spindle apparatus and no dissolution of the nuclear envelope.

Habitat preferences extend from a wide variety of ecological niches for the free-living forms to an entire range of associations, involving both vertebrate and invertebrate hosts, for the symbiotic forms. Some species serve as hosts to either ecto- or endosymbionts of their own. A number of fossil forms — essentially all from marine habitats — are now known: the loricate tintinnines plus a few loricate heterotrichs (not to mention the dubious cases of a paramecium and several hypotrichs). Some ciliates show color: via cytoplasmic pigments, algal symbionts, freshly ingested food materials, or stored reserves.

Free-living groups, whether comprised predominantly of free-swimming, sedentary, or sessile forms, occupy the following kinds of habitats: fresh-water ponds, lakes, rivers, bays, estuaries, streams, reservoirs, temporary puddles, underground pools, and activated sludge; soil, desert sands, forest litter, and other edaphic biotopes; marshes, bogs, brackish waters, salt lakes, and briny pools; and marine locales ranging from rocky on-shore pools and mud or sands of intertidal zones to the open waters or depths of gulfs, seas, and oceans. Symbiotic forms, fewer in total numbers of species, are commonly found as harmless ectocommensals or epibionts or symphorionts, attached to the integument most often of invertebrates; but others occur as endocommensals, generally in parts of the body cavity or the digestive tract, in both vertebrates and invertebrates. Relatively few ciliates can be considered as true parasites, definitely harmful to their hosts; and only one genus (the trichostome *Balantidium*) is known to be parasitic in man. In all cases, hosts

— as a group, and with aquatic invertebrates particularly in mind — may have essentially the same ecological distribution as that of the free-living ciliates discussed above (not, of course, forgetting terrestrial organisms). For host taxa involved, see list appended to the Systematic Index.

The very wide geographic and climatic distribution of ciliates, and their plentifulness in many habitats, is influenced by their remarkable tolerance or adaptability to wide ranges in physicochemical conditions of the environment. Yet, as perceptively realized even in times well before the advent of the sophisticated methodologies utilizable today (e.g., see Noland, 1925, and Sandon, 1932), the single most important ecological factor controlling their distribution and abundance is undoubtedly — and simply — the availability of food.

All members of the phylum are heterotrophs, but modes of feeding and food preferences show a great range of variation: bactivorous, algivorous, fungivorous, herbivorous, carnivorous, omnivorous, microphagous, histophagous, cannibalistic, holozoic, phytophagous, phagotrophic, osmotrophic, pinocytotic, filter-feeders, particle-feeders, detritus-feeders, and scavengers (there is considerable overlapping among terms in this list, but, then, some ciliates have overlapping preferences!). Their metabolic sensitivities and their gustatory proclivities render some species valuable as assay organisms, pollution indicators, and pharmacological tools.

Some ciliated protozoa exhibit polymorphic life cycles, and many can form cysts of various kinds (Corliss & Esser, 1974; Poljansky & Cheissin, 1965). Reproduction (solely asexual in ciliates, strictly speaking) is by monotomy, palintomy, budding (of several types), or strobilation; it may be isotomic or anisotomic. Fission is commonly perkinetal. Stomatogenesis is basically of one of four major types: telokinetal, parakinetal, buccokinetal, or apokinetal (Corliss, 1973e). The sexual phenomenon of conjugation is either isogamontic or anisogamontic and temporary or total (Raikov, 1972a). Meiosis is "gametic" in its nature. Some species can produce loricae. In the mature state, a goodly number of ciliates are sessile or sedentary, solitary or in colonies, often attached to the substratum (living or inanimate) by a secreted stalk or peduncle. Colonial organization is of several distinct types; it appears to have reached its peak in evolutionary development in the complex arboroid system of zooids found among the sessiline peritrichs.

Ciliates possess or exhibit such an assortment of organelles and inclusions and extracorporeal structures, over and above the "normal" intra- or extracellular constituents or features of the usual (metazoan or metaphytan) cell — not to mention some of their amazing activities functioning as "whole organisms" — that there is little wonder why some biologists, even in modern times, have been tempted to call them acellular creatures (see Boyden, 1973, Corliss, 1957b, 1972e, and Tartar, 1961, and references therein, for further discussion of this fascinating and surely more than merely semantic topic). The cellular plan of organization, however, is (also) clearly evident. Perhaps the differences between the "free" ciliates ("pseudometazoa": Fauré-Fremiet, 1952) and metazoan cells, which are commonly prisoners of tissues and organs, justifies serious consideration of the former as *supercells* (Corliss, 1972e). But recall that ciliates have also been called "prisoners" — prisoners of their very unicellularity: Fauré-Fremiet (1953a).

Distinctiveness of the Phylum

A large yet compact group, the Ciliophora are readily distinguishable from members of any other eukaryotic protozoan or protistan assemblage. There are several major diagnostic features held in common (unless secondarily lost) by practically all species comprising the phylum; since these nearly unique properties have been well known, widely recognized, and generally accepted for many years (see Corliss, 1956, 1961, 1974a), they need to be treated here only very briefly (see also Corliss, 1978a).

1. *Manifestation of nuclear dualism.* With extremely rare exception (important though such cases are, from evolutionary and systematic points of view: see the following chapter), ciliates possess a uniquely — if we discount the unusual situation in certain foraminiferans (see Grell, 1973) — dual nuclear apparatus: one or more diploid (occasionally polyploid?) micronuclei and one or more polyploid or polygenomic (though diploid in a number of allegedly primitive

forms) macronuclei. Amicronucleate "races" have been discovered and may be produced experimentally, but they are "genetically dead" and certainly secondarily derived forms. The macronucleus, especially, may exhibit a variety of shapes or forms (see description in Chapter 2).

2. *Possession of simple cilia or compound ciliary organelles* (often in abundance or arranged in striking patterns, in at least one stage in the life cycle: absent entirely in very few species). Although cilia and flagella – together called pecilokonts in a short-lived neologism of Dougherty (1957) and undulipodia (term originally proposed by Smagina, 1948) by Raabe, on occasion, and by Jahn and a few other cell physiologists (e.g., see Jahn & Votta, 1972) – are essentially identical ultrastructurally and are probably homologous organelles, the species bearing them are seldom confused in nature. For example, the flagella of phyto- and zoomastigophorans are typically much longer, much fewer in number, and generally located solely at the apical pole of the organism. (Opalinid flagellates, however, must be – and are – distinguished from true ciliates on other bases: see Corliss, 1977b, and references in Chapter 1.)

3. *Presence, without exception, of an infraciliature located subpellicularly in the cortex.* "Once a ciliate, always an infraciliature" (Corliss, 1959). Consisting of the kinetosomes or basal bodies and a host of more or less closely associated microtubules and fibrils, all beautifully revealable today by electron microscopy, the kinetomal complex – as a whole – appears to be a very conservative and fundamental feature of ciliates. (Its temporary absence in the encysted stage of some species – e.g., see the precise studies by Grimes, 1973a–c, on *Oxytricha* – is baffling.)

4. *Exhibition of a basically homothetogenic mode of binary fission* (in contrast to the symmetrogenic type characteristic of other protozoan groups, especially the flagellates). In a typical case, this means that the plane of division in ciliate cytokinesis is perpendicular to the anteroposterior axis of the body, resulting in a *perkinetal fission*, often – but too loosely – described as transverse division. There are numerous exceptions, but nearly all are easily explicable as secondary acquisitions in the life cycle of the species involved. Stomatogenesis, of diverse types, essentially accompanies fission, although it may commence either before or after the beginning or the conclusion of division of the body of the organism.

5. *Absence of true syngamy.* Sexual phenomena in ciliates are represented solely by conjugation and autogamy (latter including cytogamy). In cases of total conjugation, the process is misleadingly considered as "true syngamy" by some protozoologists. It is true that in conjugation haploid gametic nuclei replace gametes, as it were, and the genetic outcome of the entire phenomenon is indeed the same as it is in syngamy of other protozoan and metazoan organisms.

6. *Presence, very commonly, of a cytostome* (associated, in many groups, with a more or less well-developed atrial, vestibular, or buccal cavity containing simple cilia or compound ciliary organelles, and always accompanied by a cytopharynx). Ciliates of some taxa, however, are completely astomatous; and members of a major group, the suctorians, possess sucking tentacles instead of a single oral opening and thus exhibit polystomy. But these are exceptional cases which do not detract from the commonness of a single well-defined mouth (typically permanently open) in ciliates in general, in contrast to the usual condition in species of other protozoan groups.

An additional half a dozen or so characteristics might be mentioned; but often they are features which have exceptions within the phylum itself or are paralleled by situations existing among certain nonciliate protozoan groups, such as the zooflagellates or opalinids. They may be listed briefly, without further comment, as follows: an axial symmetry and anteroposterior polarity; specific "systèmes sécants"; acentric mitoses (i.e., no centrioles involved in nuclear division), with intranuclear spindle and no dissolution of the nuclear envelope; "gametic" rather than zygotic or sporic reduction in meiosis; no micronuclear nucleoli; a contractile vacuolar system (contractile vacuoles or water expulsion vesicles), with permanent pores; a pellicular cytoproct; pellicular alveoli (a very significant feature, nearly unique to ciliates); and numerous specialized cytoplasmic organelles or bodies, such as extrusomes and various other microtubular or microfibrillar structures. (Descriptions or definitions of these – and many additional terms or structures – are to be found in Chapter 2.)

Major Included Groups

A few comments are in order concerning the composition and general characterization of the major groups (classes and subclasses) before presenting the more detailed accounts of the orders and suborders, and the pertinent literature on them, which form the substance of subsequent chapters (Chapters 5–16). I should also like to make an attempt, here especially, to relate the "new" groups – often, perhaps, with their unfamiliar and long latinized names, strange and a little foreboding – to the less complicated former classifications of the ciliates. So the nomenclature, past or present, for the major subdivisions of the phylum is purposely presented in a vernacular form below. At the end of the chapter, the new scheme is given in full, complete with all suprafamilial names and including their authorships and dates of origin (see Table III). This may serve as a convenient guide to the reader of any part of the book; it may be compared with Tables I and II in Chapter 1 and with the fuller comparative account of ciliate systematics, past and present, in Chapter 18; and it will serve as a very succinct summary or outline for the detailed taxonomic-nomenclatural treatment to be found in the large Chapter 20.

The three classes of the phylum which I recognize are the following:

1. *The kinetofragminophorans.* Essentially the "lower holotrichs" of the older literature, meaning the gymnostomes, trichostomes, chonotrichs, and apostomes (but now excluding the astomes), as these groups have been previously understood (see Corliss, 1961, and Kahl, 1930b, 1931c). But to these, I add the enigmatic suctorians, the equally curious entodiniomorphids (until very recently considered to be spirotrichs), and the small group of formerly rostrate-and-"suckered" thigmotrichs, the rhynchodids. There are numerous species – all told, more than in either of the following two classes – with great range in body size and often uniform ciliation; the majority are typified by the presence (unless secondarily absent) of "kinetofragments" in the oral area of the body and by exhibition of a broad type of stomatogenesis known as telokinetal (though apokinetal in one group).

2. *The oligohymenophorans.* The former "membranelle-bearing holotrichs" or "higher holotrichs" – the hymenostomes, thigmotrichs, and, controversially, the peritrichs (see Corliss, 1961). The astomes, presumably secondarily mouthless forms, have now been added to the assemblage. With the principal exception of the peritrichs, these ciliates possess only a modest buccal ciliature and generally show uniform body ciliation; stomatogenesis is of a more complicated type (parakinetal or buccokinetal); peritrich species (many of which are colonial) are very numerous; body sizes vary, but there are a good many small forms.

3. *The polyhymenophorans.* The old "spirotrichs," with little change in boundaries of the group (see Corliss, 1961, and Kahl, 1932b). The entodiniomorphids, as mentioned above, have been removed from the assemblage, however, and various internal taxonomic changes have been effected. The body size is often large, but the total number of species – if the enormous group of pelagic though loricate tintinnines is momentarily ignored – is relatively small; most species are free-living; overall morphology is dominated by the well-developed, conspicuous adoral zone of numerous buccal membranelles, often with concomitant reduction in somatic ciliation; stomatogenesis is either apokinetal or parakinetal.

The breakdown or subdivision of the three great classes very briefly described above is important in the new classification in that it suggests distinctive groupings not always recognized as such in the past, although these "subtaxa" – again using vernacular names, only, here – can be matched up quite easily with former groups of various sizes and positions in the taxonomic hierarchy. I am suggesting recognition of the following seven subclasses, with the first through the fourth (1–4, below) assignable to the kinetofragminophorans, the fifth and sixth to the oligohymenophorans, and the seventh, alone, to the polyhymenophorans.

(1) *The gymnostomes.* These may still – following tradition and preserving the time-honored name – be considered as the "naked-mouthed" ciliates, if one is willing (perhaps with tongue slightly in cheek) to go along with a rather unsophisticated understanding of "naked-mouthed"

with reference to the forms included here. Despite ultrastructural complexities now clearly known to exist in their oral area *sensu lato*, it must be acknowledged that gymnostomes by and large manifest no organized ciliature in the immediate vicinity of their cytostomal opening. The species placed here comprise essentially the *single suborder* of "rhabdophorine gymnostomes" of 25 years ago (Corliss, 1956; Fauré-Fremiet, 1950a), but some *five orders* are now required to represent them properly! Presumably extant representatives of the most primitive lines of ciliates, these forms have a mouth which is usually apically (or laterally) located, and the cytopharyngeal apparatus is of the rhabdos type.

(2) *The vestibuliferans.* The "trichostomes" of old are placed here, in an expanded form, plus the rather specialized entodiniomorphids which were formerly classified as "spirotrichs." Presence of a vestibulum, lined with ciliature derived from a somatic origin, is the principal distinguishing feature, although the cytopharyngeal apparatus is also considered to be relatively primitive; the subclass is believed to have arisen from a simple prostomatid (gymnostome) ancestry.

(3) *The hypostomes.* Here are the former "cyrtophorine gymnostomes." But that *single* old *subordinal* group has been tremendously expanded, even more so than the "rhabdophorines" (subclass 1, above), to include various formerly scattered other groups, such as the microthoracids, the rhynchodids, the curious apostomes, the hypocomids, and the amazing chonotrichs: *six orders* and *10 suborders*, all told! Species in these groups typically possess a ventrally located cytostome, often with nearby atrial ciliature, and a complex cytopharyngeal apparatus of the cyrtos type.

(4) *The suctorians.* Recognized as a discrete group of protozoa for some 125 years now, but with their closeness to (other) ciliates long disputed, the suctorians are characterized principally by their common possession of feeding tentacles and a noncontractile stalk in the cilia-less sedentary adult stage, and a partially ciliated body in the budded motile "larval" stage used for dispersal.

(5) *The hymenostomes.* These are the "membrane-mouthed" (but relatively inconspicuously) "holotrichs" of former classifications. Now, in an expanded diagnosis, the group, first of two subclasses of oligohymenophorans, embraces the mouthless astome ciliates as well as the "regular" hymenostomes and the scuticociliates (the latter group itself containing most of the former "thigmotrichs" of the literature).

(6) *The peritrichs.* A very long-known (more than 300 years!) group, the peritrichs still defy understanding with respect to their most likely phylogenetic relationship to other ciliates; but most workers recognize affinities with the hymenostomes *sensu lato*. Their morphology is dominated by development of structures at the two functional poles of the organism: the ciliary wreath of buccal organelles at one end and the stalk or adhesive disc at the other (aboral) end.

(7) *The spirotrichs.* The single subclass of my polyhymenophorans. The ciliates included here are clearly similar to the "spirotrich" assemblage of former classifications (minus the entodiniomorphids), as already mentioned, above. The four orders (plus numerous suborders) are still characterized, in general, by their common possession of a conspicuous adoral zone of buccal membranelles, restricted somatic ciliature (except among the heterotrichs), and essentially unique occurrence (especially manifest in the hypotrichs, which walk more than swim) of cirri. Some workers would separate the oligotrichs (including the tintinnines) off into a subclass of their own.

Numbers, Sizes, and "Utility" of Ciliates

Comprised of some 7,200 species described to date, the phylum Ciliophora is now of a very respectable size. In fact, it compares favorably with such well-known major animal groups as the annelids, the echinoderms, the nematodes, the parasitic helminths, and the birds. It contains a quantity of species which is more than (sometimes even double) the number comprising each of the following taxa: Porifera, Coelenterata, Bryozoa, Amphibia, Reptilia, and Mammalia (see Corliss, 1978a). It may be of historical interest to note that today we are able to recognize as distinct species of ciliate Protozoa about twice the total number of all animals known in the

Table III. Corlissian system, at suprafamilial levels, with authorships and dates of names

Phylum CILIOPHORA Doflein, 1901

Class I. Kinetofragminophora de Puytorac et al., 1974

- Subclass (1) *Gymnostomata* Bütschli, 1889
  - Order 1. Primociliatida Corliss, 1974
  - 2. Karyorelictida Corliss, 1974
  - 3. Prostomatida Schewiakoff, 1896
    - Suborder (1) Archistomatina de Puytorac et al., 1974
    - (2) Prostomatina Schewiakoff, 1896
    - (3) Prorodontina Corliss, 1974
  - 4. Haptorida Corliss, 1974
  - 5. Pleurostomatida Schewiakoff, 1896
- Subclass (2) *Vestibulifera* de Puytorac et al., 1974
  - Order 1. Trichostomatida Bütschli, 1889
    - Suborder (1) Trichostomatina Bütschli, 1889
    - (2) Blepharocorythina Wolska, 1971
  - 2. Entodiniomorphida Reichenow in Doflein & Reichenow, 1929
  - 3. Colpodida de Puytorac et al., 1974
- Subclass (3) *Hypostomata* Schewiakoff, 1896
  - Order 1. Synhymeniida de Puytorac et al., 1974
  - 2. Nassulida Jankowski, 1967
    - Suborder (1) Nassulina Jankowski, 1967
    - (2) Microthoracina Jankowski, 1967
  - 3. Cyrtophorida Fauré-Fremiet in Corliss, 1956
    - (1) Chlamydodontina Deroux, 1976
    - (2) Dysteriina Deroux, 1976
    - (3) Hypocomatina Deroux, 1976
  - 4. Chonotrichida Wallengren, 1895
    - (1) Exogemmina Jankowski, 1972
    - (2) Cryptogemmina Jankowski, 1975
  - 5. Rhynchodida Chatton & Lwoff, 1939
  - 6. Apostomatida Chatton & Lwoff, 1928
    - (1) Apostomatina Chatton & Lwoff, 1928
    - (2) Astomatophorina Jankowski, 1966
    - (3) Pilisuctorina Jankowski, 1966
- Subclass (4) *Suctoria* Claparède & Lachmann, 1858
  - Order Suctorida Claparède & Lachmann, 1858
    - Suborder (1) Exogenina Collin, 1912
    - (2) Endogenina Collin, 1912
    - (3) Evaginogenina Jankowski, n. subord.

continued

Table III. Corlissian system, at suprafamilial levels (continuation)

Class II. **Oligohymenophora** de Puytorac et al., 1974

Subclass (1) *Hymenostomata* Delage & Hérouard, 1896

Order 1. **Hymenostomatida** Delage & Hérouard, 1896
  Suborder (1) **Tetrahymenina** Fauré-Fremiet in Corliss, 1956
    (2) **Ophryoglenina** Canella, 1964
    (3) **Peniculina** Fauré-Fremiet in Corliss, 1956

2. **Scuticociliatida** Small, 1967
    (1) **Philasterina** Small, 1967
    (2) **Pleuronematina** Fauré-Fremiet in Corliss, 1956
    (3) **Thigmotrichina** Chatton & Lwoff, 1922

3. **Astomatida** Schewiakoff, 1896

Subclass (2) *Peritricha* Stein, 1859

Order **Peritrichida** Stein, 1859
  Suborder (1) **Sessilina** Kahl, 1933
    (2) **Mobilina** Kahl, 1933

Class III. **Polyhymenophora** Jankowski, 1967

Subclass *Spirotricha* Bütschli, 1889

Order 1. **Heterotrichida** Stein, 1859
  Suborder (1) **Heterotrichina** Stein, 1859
    (2) **Clevelandellina** de Puytorac & Grain, 1976
    (3) **Armophorina** Jankowski, 1964
    (4) **Coliphorina** Jankowski, 1967
    (5) **Plagiotomina** Albaret, 1974
    (6) **Licnophorina** Corliss, 1957

2. **Odontostomatida** Sawaya, 1940

3. **Oligotrichida** Bütschli, 1887
    (1) **Oligotrichina** Bütschli, 1887
    (2) **Tintinnina** Kofoid & Campbell, 1929

4. **Hypotrichida** Stein, 1859
    (1) **Stichotrichina** Fauré-Fremiet, 1961
    (2) **Sporadotrichina** Fauré-Fremiet, 1961

time of Linnaeus (e.g., 1758), some 220 years ago. [I should hastily add two comments. Of course the mid-18th century count of *scientifically named* beasts was a very scanty census of those available for binomina had the taxonomists of the times been numerous enough! Secondly – and less obviously – there are those workers today who would seriously be highly skeptical about accepting the figure of 7,200 species for the ciliates, claiming that many probably are not bonafide or, at least, have not been convincingly (= rigorously enough) described. In general, such an assertion is not refutable. Yet it is an interesting fact that nearly every careful modern study which "lumps" species of former workers includes descriptions of *new* ones itself, and with little hesitation. Furthermore, I believe that no one disputes the likelihood of vast numbers of yet-to-be-caught-and-described forms abounding in unexplored niches of less common habitats, free-living and symbiotic alike.]

The number of supraspecific taxa endorsed in this book may also be worth calling attention to briefly, especially from a comparative point of view: the growth of the phylum has been astounding. Considering only modern ciliate classifications (and rounding off the figures and lumping suborders with orders and subclasses with classes), we find that the numbers commonly recognized in the time of Kahl (some 40 years ago) were: 600 genera, 100 families, 18 orders, and 4 classes. By 1960 (see the first edition of this book), new descriptions had raised these figures to: 850, 130, 27, and 5, respectively. Now, only 16–17 years later (this book, and see Corliss, 1977a), we have: 1,125 genera, 204 families, 59 orders, and 10 classes. Yet some splitter-ciliatologists (e.g., Jankowski: see Chapter 18) would have us recognize even many more taxa, especially at the suprageneric levels; my system is thus rather conservative by comparison, avid lumper though I surely am not.

A word might be said here concerning the body size of ciliates. I have already mentioned, in an earlier section of this chapter, that the total range in the length of a ciliate (the independent "cell" or the zooid member of a colony) is roughly 10–4,500 μm. As proposed in Corliss (1975b), six categories of size (as reflected in body length) may be recognized (arbitrarily if unrealistically set up with nonoverlapping ranges), as follows: very small, 10–30 μm; small, 30–65 μm; average or medium or "common" (*for ciliates*) size, 65–150 μm; large, 150–600 μm; very large, 600–2,500 μm; and exceptionally large or, more accurately, lengthy, 2,500–4,500 μm. Differences in volume are, of course, much more striking to the eye than variations in length; but the above data may be helpful to the reader in a comparative way when the adjectival descriptors are used alone in the various group characterizations and diagnoses found in subsequent chapters. [Nothing new under the sun! After drafting the preceding "categories of size," I happened to be rereading Schewiakoff (1893) and discovered that that worthy ciliatologist had already proposed a set, some 85 years before me! It is interesting to note the coincidental similarities. Schewiakoff, without using ranges, had suggested: very small, < 40 μm; small, 70 μm; medium, 120 μm; large, 250 μm; and very large, > 250 μm.]

The abundance of ciliates, their great morphological and ecological diversity, their adaptability to laboratory as well as natural conditions, their size, their rate of reproduction, and their general ease in handling render them of considerable potential advantage as the experimental organism (indeed, often as a high precision tool) in many research problems of broadest biological and biomedical interest (Corliss, 1978a). Some idea of major areas of utility of these protists may be realized in the following very brief comments. The role of planktonic ciliates in the food web in lakes, streams, and oceans is yet to receive proper study, but there are indications that it is a significant one. The use of certain species as "pollution indicators" in general (not to mention their inclusion in ecological modeling work) and as principal components of the microcommunity in sewage treatment could also be cited. Members of the *Tetrahymena pyriformis* complex, culturable axenically on chemically defined media, are already widely employed as microassay organisms in detection of essential amino acids, vitamins, proteins, etc. and in testing the toxicity of various substances. *Tetrahymena, Paramecium*, and, increasingly today, additional ciliates are also considered as ideal study material in many other sophisticated investigations in cell biology, chemical genetics, biophysics, and similar areas.

Chapter 5

Class Kinetofragminophora: (1) The "Dawn" or Eociliates and the Problems they Pose

The first great class of the Ciliophora, the Kinetofragminophora, contains a myriad of species manifesting amazing diversity. Within its boundaries are not only those groups relatively easily recognized as "less advanced" (the "eociliates" proper) but also those many lines or assemblages of forms which may represent evolutionary experiments, yielding extant but surely dead-end groups showing secondarily derived specializations which are far from "primitive," ancient though the origins of the groups may have been. The task of determining the boundaries of this, perhaps more than of any other, class is thus extremely difficult – and not helped at all by our general ignorance of the organisms which we think should be included in it (see discussion in Corliss, 1974c, of the numerous obstacles confronting the student interested in the cytology, systematics, or evolution of any protozoan group). Nevertheless, I believe that we do have enough information to envision a separate "first class" in the phylum Ciliophora and that it may be identified by more than just the negative character of lacking the major features typical of the two more "advanced" classes, *viz.*, the widespread and uniform possession of highly organized buccal and somatic ciliature and infraciliature (see Chapters 10 and 14).

The salient distinguishing features of the kinetofragminophorans (comprising four large subclasses) may be appreciated in the following considerations of their many ordinal and subordinal groups (extending through Chapter 9). The remainder of the present chapter is devoted to the first two of the five orders which I assign to the first subclass (*viz.*, the Gymnostomata); the three other ordinal groups of this subclass are treated in Chapter 6. Representative genera are depicted, with other gymnostomes, in figures on page 78 (Plate VI) of the following chapter.

Order PRIMOCILIATIDA

At one time, there must have been a "dawn" or "eociliate." Unless it was derived secondarily from some multicellular metazoon or arose essentially full-blown from a prokaryotic (kingdom Monera) precursor, it must have had an ancestry among other protistan eukaryotic organisms, for example, from groups whose descendants are known today as flagellates (be they "algae" or "protozoa"). Since I have treated this matter in some detail in recent papers (Corliss, 1972e, 1975c, 1977b), I shall speculate no further on it here (but see also Orias, 1976, a stimulating work which has just appeared). The only advance of substance in our pertinent knowledge since the time of Minchin's (1912) wise words on the subject has been the recognition of truly homokaryotic forms among extant ciliates, although study of such "protociliates" (Corliss & Hartwig, 1977) seems to throw no light on precise identification of the guilty flagellate precursor.

Species of the single included genus *Stephanopogon* possess but one kind of nucleus, an exciting discovery made long ago by Lwoff (1923b) but largely ignored for the following 35–40 years. The evolutionary significance of having a ciliate which still retained the *pre-ciliate* homokaryotic condition – a single nucleus, neither micronucleus nor macronucleus in its properties – was finally appreciated by Raikov (see Poljansky & Raikov, 1961; Raikov, 1957, 1963a); and Corliss (1974a,b, 1975b) was the first to acknowledge its uniqueness taxonomically at a suprafamilial level.

In agreement with Raikov (see especially 1969), I believe that the diploid, RNA-rich, nucleolus-containing nuclei of *Stephanopogon* could hardly have been derived by a "degeneration" of either (or both) member(s) of the dual nuclear apparatus so dominant among ciliates today; *ipso facto*, it must represent retention of a truly primitive feature. And a "relict" nucleus must be in a "relict" species, which ought to occupy a "relict" taxon (Corliss, 1975c; Corliss & Hartwig, 1977). The *level* of the taxonomic separation is a subjective matter, admittedly, but proposal of the ordinal rank seems both daring enough and sufficiently conservative until we know more about the organisms involved.

The kind of nucleus in this sole occupant of my order Primociliatida – observed, at least in passing, now in some four species by a number of workers (e.g., Borror, 1965b; Dragesco, 1963a; Fenchel, 1968a; E. E. Jones, 1974a; Jones & Owen, 1974; Lwoff, 1923b, 1936; Raikov, 1963a, 1969) – provides reason enough for recognition of *Stephanopogon* as an eociliate descendant. But its other characteristics also support its placement among the gymnostomes, the location chosen for it by the original describer of the genus, Entz (1884), almost a century ago, and by Kahl (1930b, 1935b) and others, subsequently. The oral opening is apically located, slit-like, sometimes adorned with protoplasmic lips or protuberances but completely devoid, apparently, of any specialized ciliature. The cytopharyngeal complex may be considered to be of the *rhabdos* type (term proposed as new in this book: see Chapter 2), typical of gymnostomes and to be contrasted with the *cyrtos* type of members of the subclass Hypostomata. Multinucleate (2–16 nuclei, depending on the stage in the life cycle, but all of the same kind), the ciliate undergoes a multiple, but straightforward, type of cytokinesis within a reproductive cyst. Its feeding behavior is macrophagous (on diatoms of various sizes and small flagellates) and simple. No toxicysts have been reported. Although the process of conjugation has not been described, Lwoff (1936) suggested that he had seen one possible stage of it – a fusion of two individuals. This is an overlooked, exciting discovery, highly deserving of reconfirmation! Does it represent an early example of total conjugation (such as known today in peritrichs, chonotrichs, and some suctorians) or is it a residual example of a kind of hologamous fusion (= type of flagellate syngamy)? At least one contractile vacuole is present. Mucocysts abound. The organisms are all small, with bodies flattened dorsoventrally and with ciliation essentially only on the ventral surface.

The habitat of *Stephanopogon* is especially interesting. Reminiscent of the great bulk of the members of the order Karyorelictida, treated below, this eociliate is a marine benthic organism; though, unlike the other group, it is not strictly an interstitial form. What an ideal location for a slowly evolving ciliate! Certainly the interstitial (and nearby) ecosystem(s) would have provided the proper environment in the past, as they still do now, for primitive forms of this sort. So this relatively stable habitat may be added to the "relict" nucleus as another characteristic supporting my taxonomic and evolutionary conclusions (Corliss, 1974b, 1975b,c; Corliss & Hartwig, 1977). The prediction (Corliss, 1974b) that many more eociliates will be found if looked for among the teeming psammophilic (especially in marine intertidal zones) communities of micro- and meiofauna seems to be reasonable enough as well as challenging.

* * * * *

References to the scanty literature on the single genus comprising the order Primociliatida have been covered in the citations included in the preceding paragraphs describing this unique group.

Order KARYORELICTIDA

More than 150 species of a larger group of truly interstitial forms have been assigned to a second order of eociliates. The number of them and their considerable diversity, along with their advance in nuclear complexity, substantially compound the taxonomic and evolutionary problems involved. The stage of nuclear dualism has been reached, but the macronucleus is unique: a (usually) diploid nondividing form which, as in the case of the homokaryotic nuclei of *Stephanopogon*, causes the organism bearing it to be labeled a "karyological relict" (to use the apt term introduced by Grell, 1962, and publicized by Raikov, 1969). The diversity shown by these ciliates in some of their ciliary characteristics is particularly worrisome, because should they more properly be assigned to several different suprafamilial taxa (as has been concluded until very recently, following Kahl, 1930b, 1931c, 1935b; Dragesco, 1960; and others), then their nuclear properties would have to be not only treated as of minor significance but also considered as having arisen *repeatedly* and *independently* throughout early ciliophoran history, presumably by some kind of secondary simplification or degeneration.

I have provisionally concluded that the *ciliary* complexities alluded to above – but really much more needs to be learned about them, especially from an ultrastructural approach – are principally of one or the other kind (or some of both): either they are characteristics developed early in ciliate phylogeny in various evolutionary lines, *before* the origin of *any* polyploid-macronucleate forms; or they are later-arising characteristics similar by convergence and thus of a nonhomologous nature (Corliss, 1975b,c, 1977b; Corliss & Hartwig, 1977). With respect to the (macro)*nucleus*, the possibilities of either repeated polyploidization in separate lines of karyorelictid-like forms or repeated "depolyploidization" in lines following multiply-independent origin of the polyploid macronucleus are both unattractive from an evolutionary point of view (unless, perhaps, "repeated" is kept to a very small number of occurrences) and have few if any hard data in their behalf at the time of this writing. The idea once supported by Fauré-Fremiet (1954a, 1961a, 1970c), that the selection pressures exerted by the interstitial biotope might bring about a simplification of a formerly polyploid macronuclear condition, is not supported by the fact that many "advanced" ciliates (facultatively interstitial) are also to be found – quite unchanged – in the same ecological habitat. On the other hand, the likely presence of "relict" forms of various groups of small invertebrates in intertidal sands lends credence to the possibility that the karyorelictid ciliate species there are also of ancient vintage (Corliss, 1974b, 1975c; Raikov, 1969).

Taxonomically, the group(s) under discussion form a plausible link between the homokaryotic ciliates and the "typical" species with the usual nuclear complement; evolutionarily, they also fit perfectly the series of hypothetical forms postulated by Raikov (1957, 1963a, 1969, 1976b). Whether they – that is, *today's surviving representatives* – all belong to a single taxon or not is a question too difficult to answer with great confidence until we have more information of a comparative nature (e.g., few data on stomatogenesis have been made available to date). Despite the possible artificiality in setting up a single order (see Corliss, 1975b, and 1977a, in slight disagreement with my earlier, 1974b, more conservative proposal) to contain the diverse species which I assign to it, the value of recognizing their *phylogenetic* unity – if not also *present* affinities – is considerable, in my opinion. Very likely, many sublines have come and gone since the first diploid-macronucleate ciliate appeared, and equally likely a certain amount of evolutionary specialization has occurred over the aeons in the descendants which have survived.

Their nuclear condition clearly sets the members of the present order Karyorelictida apart from both the Primociliatida (above) and the Prostomatida, Haptorida, and Pleurostomatida (considered in Chapter 6). Though dual in nature, it is at an evolutionary stage of "primary differentiation" of the macronucleus. And while the micronucleus is diploid, rich in DNA, capable of mitosis, meiosis, etc., the macronuclei are (also) only diploid (or, at most, oligoploid), but rich in RNA, incapable of division, and periodically replaced by differentiation of specific products of micronuclear divisions. Both kinds of nuclei are small in size, typically spherical or ovoid in form, occur in small or large numbers throughout the cytoplasm, and may be present in curious clusters or nuclear complexes, with or without surrounding envelopes of some sort.

Studies of conjugation in the "lower ciliates" (see Dragesco & Raikov, 1966, Raikov, 1958a, and the comprehensive review in Raikov, 1972a), to date very few in number, may also cast light on their position in the ciliate evolutionary scale. It is already clear that there are differences of a significance which should not be overlooked.

Other salient features are not wholly unique to species of this order, but generally help establish their gymnostome affinities; and, taken along with the nuclear characteristics, serve well in recognition of the group as distinct within the subclass. The body is typically large – and especially lengthy (sometimes > 3,000 μm). It is also frequently flattened, sometimes with only the undersurface ciliated. Elongate, even vermiform, they may also be highly contractile, possessing longitudinally arranged myonemes; and nearly all are quite fragile outside their interstitial micro-environment. No cysts are known. In feeding, many are predaceous macrophages, carnivores or omnivores. Mucocysts and somatic toxicysts are present; a contractile vacuolar system often absent (replaced, as it were, by a kind of Müllerian vesicle in *Remanella, Loxodes,* and close relatives); and there may be other specialized cytoplasmic inclusions, including rhabdocysts (Raikov, 1974b; Raikov et al., 1976). Double somatic kinetosomes, with lengthy and overlapping postciliary microtubular ribbons (the postciliodesmata, as very recently named by Gerassimova & Seravin, 1976), are characteristic of all genera studied ultrastructurally to date.

The oral area, depending on the subgroup under consideration, is either strictly apical or subapical and ventral, in the latter case often appearing as an elongate slit on the concave surface of the body. The cytostome may be surrounded by cilia longer than found elsewhere on the body and, in some forms (e.g., *Geleia*), a complex ciliature exists on one or both borders. Simple bundles of nematodesmata reinforce the cytopharyngeal walls. Stomatogenesis is telokinetal, but perhaps sometimes of a type resembling buccokinetal (based on the few studies made to date).

Strikingly, with the principal exception of *Loxodes* (psammophilic but from *fresh*-water habitats), species of this order are found predominantly in brackish and marine sands or sediment as part of the fascinating interstitial microfauna so characteristic of intertidal zones and beaches. Adaptation to such a specialized, yet relatively ancient and stable, ecosystem is apparently responsible for many of the morphological and physiological similarities known in the diverse ciliate species found there, species not limited, either (if one includes the facultative forms), to members of the present order and class. Yet, despite similarities due to such factors of convergence, it is significant that distinctive infraciliary differences, as well as the profound nuclear distinctions already described, clearly persist in representatives of the separate higher taxa (now) living there side by side.

The distribution of these obligatorily psammobiotic species is global: they are therefore cosmopolitan forms, though "endemic" with respect to their biotype. Means of dispersal remain bafflingly unknown; Corliss & Hartwig (1977), somewhat in desperation, support the supposition that continental drift may have been partially responsible.

Several families have been assigned to the Karyorelictida (see Chapter 20); to me it seems premature to erect suborders, although this may ultimately need to be done (see remarks in Corliss, 1975b). The largest family, the Trachelocercidae, is comprised of such genera as *Trachelocerca*, *Trachelonema*, and *Tracheloraphis.* It appears to represent a natural unit and is probably the most primitive in the order: the exhaustive work of Dragesco (1960) did much to put this group "on the map." The family Loxodidae, with its fresh-water *Loxodes*, strikingly similar marine genus *Remanella*, marine *Kentrophoros* (mouthless and with prominent ectosymbiotic bacteria), and possibly others, forms a group very likely long separated from members of the preceding family. The quite different family Geleiidae (often in the past included with the trichostomes, though considered to be a gymnostome in Corliss, 1961), with numerous and huge species belonging to perhaps more than one genus, may well represent a third major group within the order. Some of its members have advanced even beyond the strictly diploid stage of macronuclear development, an important matter requiring careful investigation. Still other genera are (even more) difficult to place at this time. Based purely on infraciliary data (particularly of the oral area), the general French school of thought (see de Puytorac et al., 1974, and the very recent discussion in de Puytorac & Grain, 1976) insists that *Stephanopogon* and the Trachelocercidae are members of their order Prostomatida (which, for them, embraces only two suborders) and that the Geleiidae and the Loxodidae are bonafide families of the order Pleurostomatida. So resolution of the taxonomic problems raised by these intriguing "eociliates" remains controversial.

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The literature on the karyorelictids is scattered and often dated; a number of species have been known for a very long time (e.g., *Loxodes* and *Trachelocerca* were first described nearly 150 years ago). But it is now becoming quite voluminous, mostly because of the renewed ecological attention being given today to the interstitial meiofauna in general. And I expect that the enticing nuclear material available only in these ciliates will soon begin to excite cytologists and biochemical geneticists, as they come to appreciate its potential significance in problems of modern cell biology. Recent papers rich in citations to work, old and new, include particularly Corliss (1974b), Corliss & Hartwig (1977), Fenchel (1969), Hartwig (1973b), and Raikov (1969); also see the reviews, partially involving these organisms, by Borror (1973a), Canella (1971), Corliss (1975c), Dragesco (1974), Raikov (1972a, 1976b), and Raikov & Ammermann (1974). But some additional and specific citations must be made here to this fruitful area of ciliatological research, in proper acknowledgment of its growing attractiveness.

Most of the studies to date have been of an ecological nature, although, inevitably, taxonomy has been involved. The great series by Dragesco (1960, 1962b, 1963a,b, 1965b) – inspired by Fauré-Fremiet (1950c *et seq.*) and Remane (1952) – is a case in point. While monographing the ecology and systematics of psammophilic ciliates in general, many of which are obligatorily "endemic" forms, he offered excellent descriptions of some four new genera and over 60 new marine species in (what is now) the order Karyorelictida alone! Other series on marine forms which should be mentioned (with no attempt to cite every work, here, in each person's list) include those by Agamaliev (1966, 1967, 1968, 1971, 1972, 1973), Borror (1963a,b, 1965b, 1968, 1972b, 1973a,b), Burkovsky (1970a,b, 1971), Fenchel (1967, 1968a,b, 1969), Hartwig (1973a–c, 1974, 1977; Hartwig et al., 1977; Hartwig & Parker, 1977), Petran (1963, 1967, 1968), Raikov (1962a, 1963e; Raikov & Kovaleva, 1968), and Tucolesco (1962a,b). Scattered studies of importance also have been carried out by Elliott & Bamforth (1975), Fjeld (1955), E. E. Jones (1974a), Kattar (1970), Rao & Ganapati (1968), and Vacelet (1961a,b). (The older work of Delphy, 1939, remains taxonomically enigmatic.)

Additional cytological works have been published by some of the investigators listed above and by a few others; direct references may be handily found in Raikov (1969, 1972a, 1976b) and Raikov & Ammermann (1974). But some of the beautiful early publications of Raikov (e.g., 1958b, 1959b, 1963b–d) on the nuclear picture in species of *Trachelocerca*, *Remanella*, and *Geleia* must be recorded here. Electron-microscopical research results on sand ciliates are just beginning to appear, mostly – as might be expected – from the French and Russian schools, and generally with emphasis on the nuclei: see, for example, Kovaleva (1974), Kovaleva & Raikov (1973, 1974), Nouzarède (1975, 1977), de Puytorac, Raikov & Nouzarède (1973), Raikov (1972b, 1973a–c, 1974a–c, 1975a,b, 1976a). Raikov & Dragesco (1970), and Raikov et al. (1976); but Bedini et al. (1973) have studied the ultrastructure of Müller's vesicle in *Remanella*. The work by Gerassimova & Seravin (1976) on postciliodesmata has just appeared. A physiological investigation (on respiration in *Tracheloraphis*) has been carried out by Vernberg & Coull (1974).

The taxonomically enigmatic genus *Loxodes* has fascinated ciliatologists for decades, and its fresh-water species have now come under renewed scrutiny. Original observations or discussions on problems in its ecology, systematics, cytology (especially nuclear), morphogenesis (stomatogenesis), and ultrastructure are contained in the recent papers of Bick (1972), Canella (1971), Corliss (1974b), Dragesco (1966c, 1970, 1972b), Dragesco & Njiné (1971), Fauré-Fremiet (1954a, 1970c), Goulder (1971, 1972, 1974a,b, 1975), Jankowski (1973c), Mashansky et al. (1963), Njiné (1970), de Puytorac & Njiné (1971), Raikov (1959a, 1969, 1973b, 1975b, 1976a), Raikov et al. (1963), and Tuffrau (1963a).

Addendum. Belatedly available is the important monograph by Nouzarède (1977) on species of the Geleiidae: their cytology (including ultrastructure), ecology, physiology, regeneration, systematics. A separate atlas of 100 plates augments his text. The major taxonomic innovation is erection of a new order, the Protoheterotrichida (in the class Polyhymenophora!), to contain these particular psammophilic ciliates. I do not accept this proposal; my reasons are essentially stated on preceding pages. But the work underlines our need to continue to give attention to the possible systematic significance of the unusual characteristics of geleiids.

Chapter 6

Class Kinetofragminophora: (2) First of the "Typical" Ciliophorans, the Prostomatid, Haptorid, and Pleurostomatid Gymnostomes

Following the thorough and probably irreversible establishment (even if more than once) of the polyploid macronucleus, we must look to other characteristics for determination of the "next most primitive" group of ciliates. If such a phylogenetic decision can be reached, then it can be reflected in our classification. There is not likely to be disagreement that such a group is represented today by the so-called "prostome" forms, although exactly how to determine the boundaries of the group and arrange various subgroups within it remains controversial. The three orders discussed in the present chapter conclude my treatment of members of the first kinetofragminophoran subclass, the Gymnostomata. Representative genera, including gymnostomes of the preceding chapter, are depicted in the set of figures on page 78 (Plate VI).

Order PROSTOMATIDA

In general, the ciliates which I classify as "prostomes" *sensu stricto* may be characterized by having an apical or subapical cytostome; a near-spherical or cylindrical, often large, body, superficially exhibiting a kind of radial symmetry; uniform and holotrichous ciliation; a common absence of specialized oral ciliature, with simplest kinds of circumoral infraciliature, and a cytopharyngeal apparatus of the rhabdos type; a telokinetal mode of stomatogenesis; and a worldwide distribution, commonly as carnivores and mostly free-living. A number of species (in this and the following orders) are found as facultative inhabitants of the interstitial biotope. Toxicysts are sometimes present; mucocysts, always; and certain curious intracytoplasmic bodies or vesicles are known in a number of species. Endosymbiotic zoochlorellae occur in some genera.

The ciliates assigned to this order are commonly encountered in myriad habitats; thus they are often mentioned in ecological studies, many of which have – perhaps of necessity – taxonomic overtones. Dragesco et al. (1974) have started a series of comparative systematic and morphogenetic studies on free-living "prostomial rhabdophorine holotrichs" which will include a number of the genera mentioned on following pages. In these papers (the second one is now available: Fryd-Versavel et al., 1976), the French workers have assigned them all to one suborder in a single order (their Prostomatida), a group which I believe (Corliss, 1975b, 1977a) requires subdivision into *several* independent suprafamilial taxa (see below). Yet it is clear that, until we have sound ultrastructural data on many more forms than we do now, the exact placement of many species (some of which will even have to be moved out of their present genera, etc., with complex concomitant nomenclatural problems) will remain conjectural.

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A select group of recent "ecological" papers at least partially devoted to "prostome" (*sensu lato*) ciliates – usually rich themselves in references to shorter and earlier publications – includes the following: Bereczky (1975), Bick (1968, 1972), Bick & Kunze (1971), Borror (1972b, 1973a), Buitkamp & Wilbert (1974), Curds (1969), Czapik (1975: recalling Fauré-Fremiet, 1951, and Picken, 1937), Dingfelder (1962), Dragesco (1966a–c, 1970, 1972a,b), Dragesco & Njiné (1971), Fenchel (1968a, 1969), Fenchel & Lee (1972), Gittelson & Hoover (1969: cave ciliates), Grabacka (1971, 1973: most recent in a series started in the early 1960's), Grolière & Njiné (1973), E. E. Jones (1974a), López-Ochoterena (1966), Matthes & Wenzel (1966), Noland & Gojdics (1967), Spoon (1976), Stout & Heal (1967), J. C. Thompson (1972), Thompson & Croom (1977), Tucolesco (1962a–c), and Vuxanovici (1963a: preceded by others in this and in an earlier series which commenced with his 1960b paper).

Suborder (1) Archistomatina

This suborder was established by French workers (de Puytorac et al., 1974) as part of their recognition of the systematic significance of the ultrastructure and morphogenetics of the perioral or circumoral ciliature and infraciliature in species belonging to various gymnostome groups (Grain et al., 1973). I am now (contrary to Corliss, 1974b; but see Corliss, 1975b, 1977a) in accord with their views to the extent that I accept the Archistomatina as representing the most primitive prostomial group (evolutionarily advanced, however, over the homokaryotic and diploid-macronucleate forms treated in the preceding chapter). And I agree, at present, that the group should be represented by but a single family, the Buetschliidae. My previous hesitation (e.g., as expressed in Corliss, 1974b) was based on my concern over having a very primitive level represented by an assemblage of *totally endosymbiotic* species which, furthermore, possess a number of rather unique characteristics (such as concrement vacuoles) and a nonsimple nuclear apparatus (polyploid macronucleus). But I am willing to make what I believe to be two necessary assumptions: that other archistomatine lines, including simpler free-living forms, once existed but have become extinct or have had unrecognizable or undiscovered descendants; and that the specializations exhibited by the contemporary species of *Buetschlia* and related genera have developed subsequently to (and as a direct result of) their having adopted the symbiotic way of life maybe as long as 50–60 million years ago, early in the origin of their present-day ungulate mammalian hosts (or still earlier, when they may have first invaded host species lower on the vertebrate evolutionary scale).

Carefully studied species of this suborder – those belonging to such genera as *Alloiozona*, *Didesmis*, and *Polymorphella* – possess an apical cytostome, directly on the surface of the body (i.e., there is no oral depression). But more importantly, there is no special differentiation (e.g., pairing of kinetosomes at the anterior end of the body, other than their slightly more dense packing near the ends of the somatic kineties converging onto the cytostomal area. By means of electron microscopy, one may observe that these anteriorly located basal bodies sometimes bear long ribbons of transverse microtubules which are seen to line the walls of the cytopharynx. From both structural (including axial) and ultrastructural views, then, these organisms appear to represent the simplest extant ciliates we have among the heterokaryotic forms with polyploid macronuclei, despite their present symbiotic mode of existence.

The long evolutionary history of members of the large family Buetschliidae, including successful adaptation to existence in the digestive tract of camels and horses (with one report from mole rats: Sandon, 1941b), has witnessed what are apparently a number of important secondary acquisitions. The most noticeable of these is the curious concrement vacuole, with its dozen or so included calcium concretions, and the associated group of short rows of clavate cilia just above it on the dorsal surface of the body. Nematodesmal fibers from the kinetosomes of these somatic cilia participate in formation of the vacuolar membrane (Grain, 1966a). The concrement vacuole is also found in certain trichostomes living in the same hosts (see order Trichostomatida, Chapter 7). Concentration of somatic ciliature into tufts or bands in many archistomatine species appears to be another convergent characteristic which in the past has sometimes led to misclassification of these forms. It is interesting to note, however, that the body ciliation is quite uniform in species of the less well-known genera (e.g., *Blepharozoum* and *Holophryoides*).

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The older literature on the suborder – papers and monographs by such workers as Bundle, da Cunha, Gassovsky, Hsiung, Schuberg, and Strelkow – has been well covered by Corliss (1961); it is often the same as that on other ciliates from the same hosts (see Chapter 7). Few works on the group have appeared since 1960: outstanding are the series of notes by Grain culminating in

Grain (1966a), and the studies by Wolska (e.g., 1966a); but see also Thurston & Grain (1971). The more recent data and views of Corliss (1974a,b, 1975b), Grain et al. (1973), and de Puytorac et al. (1974) on the systematics and phylogenetics of this and other suborders in the order Prostomatida have already been mentioned in preceding paragraphs.

Suborder (2) Prostomatina

The "prostome" gymnostomes *sensu stricto* may turn out to be a rather small – but significant – group. The suborder is characterized in general by the properties assigned to representative or typical members of its higher taxa, the order Prostomatida and even the whole subclass Gymnomata, as enumerated on preceding pages. Notwithstanding the views of my French colleagues (e.g., see Dragesco et al., 1974; de Puytorac et al., 1974; and, now, Fryd-Versavel et al., 1976, and de Puytorac & Grain, 1976), I suggest (following Corliss, 1974b, 1975b, 1977a) recognition of a distinct "prostomatine" group which does *not* embrace the genera which I reserve for the following suborder (number 3) or for the following separate order (the Haptorida). More work needs to be done to determine if my decision is wholly justifiable.

The truly apical location of the cytostome, circular in outline, is judged to be a relatively primitive character; this simplicity is further supported by a simple axis of body symmetry and a generally uniform somatic ciliation. Toxicysts, interestingly enough, appear to be absent, although mucocysts are present. Feeding habits are generally microphagous. Stomatogenesis is strictly telokinetal and is completed following cytokinesis.

Ultrastructurally – in the few species carefully studied to date – a single pair of kinetosomes has been noted at the anterior extremity of each of the kineties surrounding the permanent cytostome, with both members of the pair bearing cilia. These basal bodies also produce the ribbons of transverse microtubules strengthening the nematodesmal walls of the cytopharynx (Grain et al., 1973; de Puytorac, 1965).

The most representative genus is *Holophrya*; but one of the taxonomically frustrating problems is that some "*Holophrya*" species surely belong in other genera. Schewiakoff's *H. simplex* may be one of the most primitive bonafide members of the genus (von Gelei, 1954). *Metacystis*, *Pelatractus*, and *Vasicola* are probably true prostomatine genera as well; fortunately, we have a recent fine study of some of their species by Dragesco et al. (1974). A number of them can produce loricae, often of a temporary pseudochitinous type; otherwise, they are quite nonspecialized and fit my concept of the suborder satisfactorily.

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The literature on the prostomatines is scattered. And, except for the observations of Dragesco (generally incorporated as minor sections of larger works: e.g., see Dragesco, 1960, 1965b, 1966a,c; and Dragesco et al., 1974), few major papers have appeared since 1960. Among older works not to be forgotten are the (appropriate parts of the) monographic efforts by Kahl (e.g., 1926, 1927b, 1930a,b, 1935b) and Penard (1922). Until a thorough and extensive taxonomic revision is undertaken (and the results published), preferably including ultrastructural data, the proper taxonomic location of a number of the genera formerly assigned to the over-large (see Corliss, 1961) gymnostome family Enchelyidae must remain undecided. In the present treatment, that family itself – in name and along with its type-genus *Enchelys* – is removed to the order Haptorida (below); and the "Holophryidae" are resurrected as one of the independent families of the suborder Prostomatina.

Suborder (3) Prorodontina

Gymnostomes which I include here have an apical or slightly subapical (and ventral) cytostome, permanently opened to the surface. In some species, the mouth opening, round or oval in outline, may be a little sunken, in a slight invagination or shallow atrium; or an unadorned oral groove may be present. A brosse is located anteriorly on the dorsal (or – perhaps temporarily? – on the ventral: a disputed point) surface of the body and may bear longer cilia. I consider that the brosse is unique to the prorodontines (but French workers are describing it also in haptorids and pleurostomatids: see Dragesco et al., 1974, and Fryd-Versavel et al., 1976). Toxicysts are generally present, but are considered somatic in nature – that is, they are seldom in direct association with the oral area *sensu stricto*. Mucocysts are common. The cytopharyngeal complex is still of the rhabdos type so typical of the subclass; but it may show a greater complexity than is found in species of the preceding suborders with respect to numbers and kinds-of-association of the constituent nematodesmal and other microtubules (particularly transverse) in the area.

Stomatogenesis is basically of the telokinetal type, and cytokinesis precedes its completion. The brosse is apparently reproduced at the same time (Dragesco et al., 1974), and formation of a primordium of some sort may be involved.

Electron-microscopical studies have shown that ciliated pairs of kinetosomes, arranged circumorally and derived from the anterior extremities of the (usually) bipolar kineties, contribute to the structure of the cytopharynx (via their transverse microtubules) and are active in stomatogenesis for the opisthe following cell division at the equatorial level of the body (Grain et al., 1973; de Puytorac & Grain, 1972). Fission may take place within a cyst, although this is never so for members of the somewhat individualistic *Coleps*. Species of the latter, incidentally, are well-known scavengers and also show a unique morphological characteristic in their possession of subpellicularly located skeletal plates, carefully studied by appropriate cytochemical techniques and, more recently, by methods of TEM and SEM (Fauré-Fremiet et al., 1968b; Fauré-Fremiet & Hamard, 1944, 1944; Fauré-Fremiet et al., 1948; Rodrigues de Santa Rosa, 1976; Schönfeld, 1974).

More representative of the suborder than *Coleps* are most of the other included genera (see Chapter 20). Studies in progress are showing that various species of "*Prorodon*" itself are, unfortunately, definitely *not* congeneric, and some possibly assignable to even different suborders! Fauré-Fremiet (1961c) perceptively sensed how taxonomically confusing the situation was here, long before any other worker in modern times.

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Although there are many older scattered papers on species which are, today, probably best assigned to this suborder Prorodontina, confusion will continue to reign until more studies are carried out using precise methods of silver impregnation, hopefully accompanied by ultrastructural investigation of the same organisms. The works already available which do include such observations are few in number but encouraging and taxonomically most helpful: for example, see André & Fauré-Fremiet (1967b), Dragesco et al. (1974), Fauré-Fremiet & André (1965b, 1968b), Fauré-Fremiet et al. (1968b), Kattar (1972), de Puytorac (1964), de Puytorac & Grain (1972), de Puytorac & Savoie (1968), and Seravin & Matvejeva (1972). Hausmann (1973a) has examined the fine structure of mucocysts in *Prorodon*. Some recent nonultrastructural works partially on prorodontine species are the papers by Borror (1975), Dingfelder (1962), Dragesco (1965b, 1966a–c, 1972a,b), Fenchel & Lee (1972), Foissner (1972b,d), Jordan (1974), Wilbert (1969), and Wilbert & Schmall (1976). The reader is also referred to the group of "ecological" citations included near the beginning of this chapter and the works on *Coleps* cited above.

Order HAPTORIDA

Rapacious carnivorous gymnostomes which seize their prey, often spectacularly, have long been known; and there are many of them. But never before the papers of Corliss (1974a,b, 1975b) have they been separated out at such a high level taxonomically. Like prostomatids, they possess apical (in a few species antapical!) or subapical cytostomes (sometimes at the distal end of a long neck), though the opening may be oval to slit-like in outline, and generally (except in such genera as *Didinium*) uniform and holotrichous ciliation. Mucocysts are present, and stomatogenesis is telokinetal. Some of the species have elaborate cystic membranes or walls; in *Didinium*, a newly

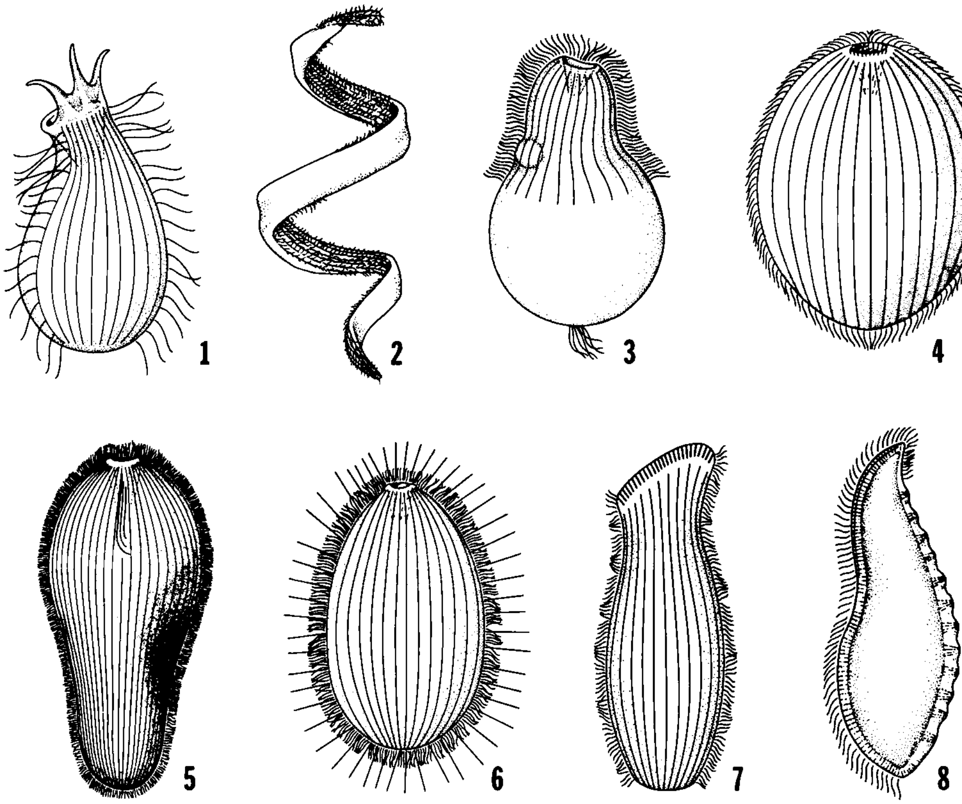

PLATE VI. Representative gymnostomes. Fig. 1. *Stephanopogon*, order Primociliatida. 2. *Kentrophoros*, order Karyorelictida. 3. *Blepharoprosthium*, order Prostomatida, suborder Archistomatina. 4. *Holophrya*, order Prostomatida, suborder Prostomatina. 5. *Prorodon*, order Prostomatida, suborder Prorodontina. 6. *Actinobolina*, order Haptorida. 7. *Spathidium*, order Haptorida. 8. *Loxophyllum*, order Pleurostomatida. [Additional figures appear in Chapter 20.]

discovered extrusive organelle, the clathrocyst, is involved in production of the mesocyst layer of the wall (Holt & Chapman, 1971). Kinetodesmata have been described in a number of genera.

Several characteristics set these gymnostomes distinctly apart from members of the preceding order. Toxicysts are often present in abundance, are of rather complex structure, sometimes serve a dual function (paralytic and proteolytic), are strongly localized, and are of at least two kinds (*Didinium* possesses three different types!). They occur either within the "oral cytoplasm" (of the cytopharynx) itself, or in the surrounding coronal area, or in a trunk or proboscis which may extend anteriad to the mouth for some distance, or, in certain cases, in nonsuctorial tentacles distributed over the body. The cytostome-cytopharyngeal complex may be permanent, often equipped with lips and extensible, even eversible. Coronal ciliature occurs at the anterior end of many of these organisms, in one or two rings around the body. Its cilia are longer than the regular somatic cilia; and its infraciliary kinetosomes usually occur in pairs, with the inner basal body nonciliferous but with both members of the pair associated with special fibers and microtubules and with nematodesmata of the cytopharyngeal area. The rhabdos itself is often relatively complex, with its microtubular components sometimes bound by a filamentous annulus of an elastic nature. Curiously enough, a cytoproct has never been described for members of the suborder.

Amicronucleate races have been reported (e.g., in *Didinium*: see references in Beers, 1946).

Finally, among other major distinctive characteristics, the fields or short longitudinal rows of clavate cilia which occur in many species should be mentioned. These "sensory bristles," as they were termed long ago in forms like *Didinium* by such keen observers as von Gelei (e.g., see 1933, 1934e), occur anteriad on the body, on the surface often labeled as dorsal: but they are *not* to be confused with the prorodontid brosse, in my comparative view of the structures involved.

Thus I cannot agree with my French colleagues that, today, this large assemblage of remarkably specialized ciliates – possibly separable into still additional independent suprafamilial groups, in fact – should be classified as merely "regular" prostomatids. Many of the genera assignable to this diverse order have long been known; very few new ones have been named since Kahl's (1930–1935) time (see Chapter 20). *Myriokaryon*, described recently by Jankowski (1973e), is one of the most interesting of such forms; Delphy's (1938) genera remain unconfirmed by subsequent workers. *Askenasia*, rarely studied outside of Europe, has recently been carefully observed in America by Tamar (1973).

Future research may justify recognition of separate suborders of haptorids, as hinted above. It is already evident that distinct groupings of genera may be made; but the usual problems present themselves, *viz.*, the placement of possibly "intermediate" forms (and, of course, the poorly known forms, most abundant of all) and the determination of the degree of impact of the "gap size of distinctness" (Corliss, 1972e, 1976; and see Chapter 3) on the level or rank within the classificational hierarchy. Some subgroup of the order, incidentally, with localized toxicysts and other specializations, may have given rise to the suctorians, if one believes in a gymnostome ancestry for that remarkable taxon (but see Chapters 9 and 17).

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The literature on members of this order is vast, but scattered and mostly of pre-1960 vintage (see Corliss, 1961). Species of two of the most popular ciliate genera, *Didinium* and *Dileptus* (haptorids but not at all closely related), have been intensively investigated in recent years as well as in the distant past (e.g., see the classics by Mast, 1909, and Thon, 1905). Important papers concerned with their behavior, ultrastructure, and comparative taxonomy appearing within the past 15–17 years include: Burbanck & Eisen (1960), Butzel & Bolten (1968), Butzel & Horwitz (1965), Dragesco (1962a, 1963c, 1966a,c, 1970, 1972b), Dragesco et al. (1965), Dumont (1961), Evans (1958), Golińska (1971, 1972, 1974), Golińska & Grain (1970), Grain & Golińska (1970), Holt & Chapman (1971), Karadzhan (1975), Kink (1973, 1976), Luckinbill (1973), Miller (1968), Rieder (1971, 1973), Schwartz (1965), Small et al. (1972), Vinnikova (1974), Wessenberg & Antipa (1969, 1970), and Yagiu & Shigenaka (1965). A major work on Wenrich's (1929b) related *Paradileptus* was carried out 25 years ago by Canella (1951b). And the remarkable "triple-*Paradileptus*," *Teuthophrys trisulca*, first described by Chatton & de Beauchamp (1923, 1924) but essentially independently by Mudrezowa-Wyss (1929) and Wenrich (1929a), has now recently been rediscovered in France (Clément-Iftode & Versavel, 1968) and in Africa (Dragesco, 1972a). But Weill's (1946) multi-tentacled *Ctenoctophrys* continues to baffle taxonomic ciliatologists.

Numerous ecological or taxonomic-ecological studies, post- as well as pre-1960 in date, which have included ciliates at all have seldom failed to implicate haptorids. It is not feasible to attempt direct citation of these many works here (*Enchelys* and *Spathidium* are two of the genera most frequently mentioned), but attention might be called to the often-overlooked papers of the early 1960's by such workers as Tucolesco (e.g., 1962a) and Vuxanovici (1959, 1962a–c, 1963a); and see the group of "ecological" citations near the beginning of this chapter (to which the generally neglected salt marsh papers by Kirby, 1932, 1934, might well have been added). Wang's (1930b) taxonomic paper on *Choanostoma* might be recalled; also see Czapik & Jordan's (1976, 1977b) works on the psammophilic *Plagiopogon*. *Spathidium* species have lent themselves to physiological research in recent years: the investigation by Williams (1966) represents an example.

Ultrastructural investigations of significance have been carried out very recently on several genera other than *Didinium* and *Dileptus*. For example, see the works by Bohatier (1971, 1973, 1975), Bohatier & Detcheva (1973), Fauré-Fremiet & André (1968b), Fauré-Fremiet & Ganier (1969, 1970a), Grain (1970), Grain et al. (1973), Hausmann (1973a), Holt et al. (1974), Kink (1972), Matvejeva (1973), Rodrigues de Santa Rosa & Didier (1976), and Taylor et al. (1971). Although not employing electron microscopy, Girgla's (1971) recent study of cortical structures and morphogenesis in *Homalozoon* warrants citation here: cytological studies of this genus have also been made by Diller (1964), Dragesco (1966c), and Fryd-Versavel et al. (1976).

The world-wide coastal marine organism *Mesodinium rubrum*, studied recently by Fenchel (1968c), McAlice (1968), Ryther (1967), Taylor (1974), Taylor et al. (1971), and Zimmerman et al. (1975), is of interest from several points of view. Ecologically, it is involved in red-water blooms, as noticed earlier by Bary (1953), Bary & Stuckey (1950), and Powers (1932). Evolutionarily, its "incomplete symbionts" – reminding one, in a way, of the classical earlier work by Fauré-Fremiet (1948f) on the oligotrich *Strombidium* (see also Blackbourn et al., 1973) – are of significance in their illustration of the feasibility of foreign chloroplast maintenance in "host" cytoplasm. Physiological aspects of this "symbiosis" are also intriguing.

Order PLEUROSTOMATIDA

Gymnostomes included here possess a number of traits in common, perhaps the most outstanding one being the truly lateral (= "edge") position of a vent- or slit-like mouth opening, as first clearly appreciated by Schewiakoff (1896) more than 80 years ago. The body is frequently large in size, elongate in form and laterally compressed (with ventral and dorsal surfaces thus becoming narrow "edges"), with somatic ciliature often mainly confined to the broad right surface. Toxicysts and mucocysts are present; and clavate cilia appear here and there on the broad left surface of the body (French workers have recently included these under their definition of brosse: see Fryd-Versavel et al., 1976). Division may take place within a cyst.

Although heterokaryotic and with their macronuclei beyond the diploid (primary differentiation: Raikov, 1969) stage, some of the species of this group may show a low ploidy number in their somatic nuclei. This – if it becomes a reconfirmed fact on a widespread basis – plus arrangement of the nuclear complex into sets of the two kinds of nuclei in some members of the order and, additionally, the frequent occurrence of pleurostomatids as facultative residents in marine interstitial habitats suggest strongly a karyorelictid ancestry for the group as a whole. In fact, many ciliatologists classify the two groups together, still (e.g., see Dragesco, 1970; and comments made earlier in this chapter).

The oral area often appears simpler than that known for some members of the Karyorelictida (e.g., the loxodids), interestingly enough. The explanation may be that, since their separation, the mouthparts of the nuclearly more primitive group have evolved to a more complex type or grade (via "mosaic" evolution: see Corliss, 1975c; Corliss & Hartwig, 1977) and that the structures involved are not strictly homologous. The cytostome of pleurostomatids is vent- or slit-like, as mentioned above, and is frequently on the narrow convex (ventral?) surface of the body. The cytopharynx is supported by seemingly uncomplicated arrays of nematodesmal microtubules (but we need more data on this matter). The perioral ciliature generally consists of pairs of kinetosomes (typically one ciliferous and one barren) along the right border (of the ventral(?) surface) – and no more than that, if that, along the left side of the area. Longer cilia may be present in the oral region itself. Stomatogenesis is typically telokinetal and is completed after cytokinesis.

The species are widely distributed in both fresh-water and marine biotopes, including interstitial zones. They are frequently voracious carnivores in their feeding habits, some having a predilection for grazing on colonial peritrichs and a few even tackling such metazoan prey as rotifers (see the comprehensive studies by Canella, 1951a, 1954). To what extent ciliate cysts – commonly ingested by *Loxophyllum* and relatives, as Webb (1956) and others have noted – may serve as a major part of their diet is one of many fascinating unanswered ecological questions: see Corliss & Esser (1974).

The only family which I include in the order is the long-known Amphileptidae; but French

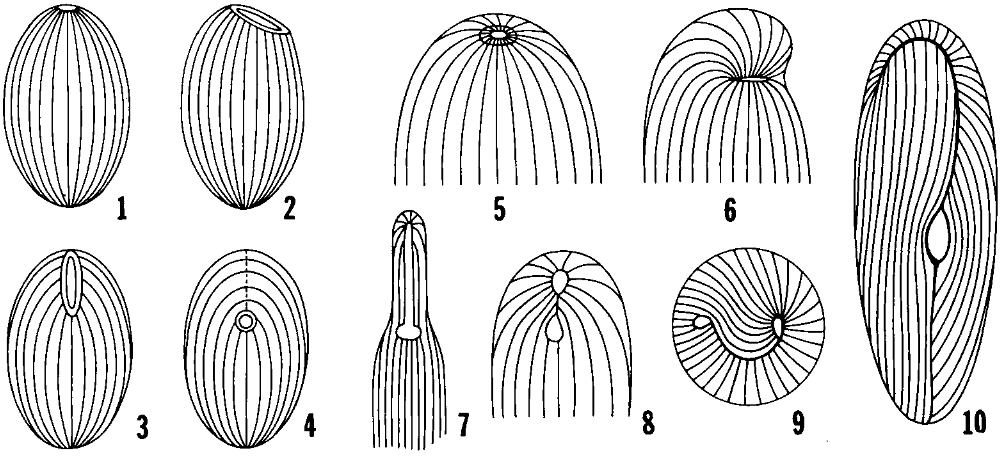

PLATE VII. Position of the oral area vis-à-vis the apical pole of the body in several groups of ciliates. (Figs. 1—4, after Bütschli; 5—10, after Klein.) Fig. 1. Mouth or cytostome terminal, directly at apical pole (*Holophrya*). 2. Mouth shifted eccentrically (*Enchelys*). 3, 4. Mouth on ventral surface, to different extents (*Spathidium, Glaucoma*). 5. Apically located (*Prorodon*). 6—10. Shifting, to various degrees, onto ventral surface (*Plagiopyla, Dileptus, Colpidium,* another *Colpidium, Paramecium*). See text and original accounts.

workers, as mentioned earlier, would place my karyorelictid Geleiidae and Loxodidae here also.

Recall that the "Pleurostomata" of old constituted the second of Schewiakoff's (1896) three tribes of Bütschli's suborder Gymnostomata: the first was the "Prostomata" (preceding pages), and the third the important "Hypostomata" (Chapter 8). Establishment of these three groups, expanded and altered though they are today, represented a highly significant taxonomic contribution by this astute Russian ciliatologist, one often not fully appreciated. After his "tribes" had finally become accepted (in the 1930's and 1940's), they then became (re-)eclipsed in the Faurean classification (see Corliss, 1961; Fauré-Fremiet, 1950a) by the latter's two gymnostome suborders "Rhabdophorina" and "Cyrtophorina." Only now are his views resurfacing. Plate VII illustrates postulated shifts in mouth areas, as figured by Bütschli (1887—1889) and Klein (1930): but the taxonomic significance of such shifts was perceived only by Schewiakoff. That is, Figures 3 and 7, for example, *could* represent his "pleurostomes," and 4 and 8, his "hypostomes," but were not so interpreted by early workers (an eventual exception: Calkins, 1933).

* * * * *

Many of the species included in the Pleurostomatida have been seen, if not studied in detail, by scores of protozoologists and ecologists over the past decades; thus the literature is voluminous, but highly scattered. Earlier papers have been cited in considerable numbers in Kahl (1931c, 1935b) and Corliss (1961), in the revision of several genera by Canella (1960), and in Vuxanovici (1960a). References to major ecological and/or taxonomic observations of the past 15—18 years may be found, directly or indirectly, in such recent comprehensive publications as those by Bick (1972), Borror (1972b, 1973a, 1975), Czapik (1975), Dragesco (1960, 1963a, 1965b, 1966a,c, 1970, 1972b), and Dragesco & Njiné (1971). The only taxonomic-ultrastructural studies published at the time of this writing (surely more are in the offing) are those by Bohatier & Njiné (1974) and de Puytorac & Rodrigues de Santa Rosa (1976), on species of *Litonotus* and *Loxophyllum*, respectively. Hausmann & Hausmann (1973) and Hausmann (1973a, 1977b) have examined the toxicysts, mucocysts, and — most recently — the curious conocysts of members of the latter genus by TEM; and Ruthmann (1963), some time ago, made a cytochemical study of their macronuclei.

Chapter 7

Class Kinetofragminophora: (3) The Vestibuliferans, from Trichostomes to Entodiniomorphids and Colpodids

The ciliates assigned to the subclass Vestibulifera exhibit quite a range of characteristics. Yet, on sum, it can be said that they are at a level of organization which represents an advance over the "typical" gymnostomes, on the one hand, and yet shows less complexity than that found in the hypostomes (or in the whole of the following classes of oligo- and polyhymenophorans), on the other. A vestibulum is commonly present, at one pole of the body or the other, giving the group its name. It is equipped with (vestibular) ciliature more or less distinctive; and it leads to a permanent cytostome. The cytopharyngeal apparatus is generally thought to be derived from the rhabdos type (though not so in the colpodids, according to Small, 1976). Toxicysts are rarely present. Geographical and ecological distributions are wide, with symbiotic forms occurring in the digestive tract of both vertebrate and invertebrate hosts.

The "trichostomes" *sensu lato* have long puzzled ciliatologists, often being – at one and the same time – considered polyphyletic and too heterogeneous and yet shy of additional forms which *should* be included within its boundaries (see Corliss, 1961; Fauré-Fremiet, 1950a,d, 1955, 1962b, 1963a,b; von Gelei, 1952). Although some problems undoubtedly still remain, many have finally been relieved through several recent major actions: (1) total removal of certain formerly included families, relocating them elsewhere (e.g., the Conidophryidae are transferred to the apostomes, the Cyathodiniidae to the suctorians, the Microthoracidae to the hypostomes, the Parameciidae to the peniculine hymenostomes, and the Entodiscidae, Entorhipidiidae, and Thyrophylacidae to the scuticociliates); but (2) inclusion of the formerly "spirotrich" groups of the entodiniomorphids and the balantidiids, and of certain former "gymnostomes" such as pycnotrichids; and (3) recognition of additional taxa at ordinal and subordinal ranks among the retained and augmented forms. Three orders, one conservatively with two suborders, are recognized and discussed below, arranged in a postulated phylogenetic sequence of sorts (i.e., the first order is considered ancestral separately to both the second and third). Representative genera are depicted in the set of figures on page 86 (Plate VIII).

Order TRICHOSTOMATIDA

Very likely evolved from a prostomatid gymnostome ancestry, the trichostomatids *sensu stricto* appear to have retained relative simplicity in body axes and overall morphology. Somatic ciliation is often uniform in nature, with derivation of vestibular ciliature from the terminal portions of a few to many body kineties. The cytostome is apical (or, curiously, antapical in several families), at the bottom of the vestibulum. During the morphogenetics of fission, especially if it occurs within a cystic membrane, an ontogenetic "recapitulation" of the presumed phylogenetic origin of the order from gymnostome progenitors may be demonstrable or so interpreted (Corliss, 1956; Fauré-Fremiet, 1963b). Stomatogenesis is thus basically telokinetal in nature; but few detailed studies have been carried out on the important process to date. Mucocysts are generally present, toxicysts typically absent. The cytopharynx is usually strengthened by nematodesmata. A cytoproct is in evidence, and contractile vacuole pores are lacking only in some endosymbiotic species (some of which do possess a concrement vacuole).

Suborder (1) Trichostomatina

Among the 10 rather heterogeneous families comprising this first (and much larger) suborder

– in effect, the Trichostomatida *sensu stricto* – one finds both free-living (mostly marine) and symbiotic forms, the latter in both vertebrate and invertebrate hosts. Distribution is widespread. Several genera are mentioned in illustration of the diversity of the group. *Balantidium*, the only ciliate genus with a species parasitic in man, embraces more than five dozen (mostly ill-defined) species which are endocommensals in many other – especially lower – vertebrates and a number of invertebrates (such as certain insects). Formerly classified as a spirotrich not too distant from (the now known to be totally different) *Nyctotherus*, many species of *Balantidium*, especially from amphibian and insect hosts, have been confused with nyctotherans *sensu lato* in bewildering taxonomic and nomenclatural tangles (see Chapter 14). *Coelosomides*, a free-living marine form, is diagrammatically representative of a typical primitive trichostome, with the exactly apical orifice of its vestibulum formerly misidentified as the organism's cytostome, the latter opening visible only in sagittal section. *Sonderia*, found in salt marshes and marine sands, has a cytoplasm which is full of what I suppose are toxicysts of some kind (called trichocysts by Fauré-Fremiet & Tuffrau, 1955). The curious fresh-water *Maryna*, attached, colonial, and producer of gelatinous loricae, is greatly in need of ultrastructural examination, as are many other species in this suborder.

Lechriopyla, some species of *Plagiopyla*, and *Schizocaryum* (a form taxonomically quite baffling) are found as inquilines in sea urchins, along with species of genera belonging to several other ciliate orders (especially the Scuticociliatida). A species of *Lechriopyla* is particularly exciting from an endosymbiotic-evolutionary point of view, in that its mitochondria appear to be composed of alternating segments or lamellae of true mitochondrial material and what is now thought to be an intricately embedded bacterium (see Lynch, 1930; and Lake & Berger, 1968, who have initiated an ultrastructural study the full results of which should throw considerable light on the problem). *Paraplagiopyla* is interesting in that it is found in the artiodactylan hippopotamus but resembles rather closely both the free-living and the echinoid inquiline members of the Plagiopylidae (Thurston & Grain, 1971).

Dasytricha, Isotricha, and relatives (with cytostomes at or near the posterior pole) are widely found in ungulate ruminants, with one species known from the cockroach – thus once considered (Weill, 1929) as possibly a former intermediate host or vector (but this seems unlikely: transfer is probably solely by contamination). *Paraisotricha*, from the digestive tract of horses, and with an apically placed mouth (and vestibulum, of course), possesses a concrement vacuole highly reminiscent of that found in the Buetschliidae of the prostomatid archistomatine gymnostomes. The curious *Pycnothrix, Collinina,* and *Nicollella* (plus other nearby genera), often neglected endocommensals in the digestive tracts of various mammals and with subequatorial or antapical cytostomes, presumably represent a special assemblage of forms which, nevertheless, belongs within this suborder, as I have envisioned its boundaries.

* * * * *

The literature on the Trichostomatina has not been extensive in recent decades and, except for works by Kahl, was generally widely scattered in still earlier years. The best older sources remain those of the great Hamburg monographer: see Kahl (1931c, 1935b), his summarizing treatise on free-living forms; and Kahl (1934a), for the endocommensal and parasitic species. But, for many ciliates of the latter group, Kirby (1941a) should also be consulted. Often omitted references on the paraisotrichids *sensu lato* are the papers by da Cunha (1915, 1917) and da Cunha & Muniz (1925) and the very brief but nomenclaturally important note by Hasselmann (1918). The classic on the Pycnotrichidae is the monograph by Chatton & Pérard (1921; see also 1919); but among the overlooked works are those by da Fonseca (1939); and Hegner & Rees (1933) – not to mention Schubotz (1909), who named the type-genus. Other neglected papers, this time on free-living forms, are von Gelei's (1950b, 1954) treatments of the intriguing colonial *Maryna*, the species of which were competently surveyed quite recently, however, by Dingfelder (1962).

For much of the interim 1930–1960, during which rather isolated papers (or sections within papers) on trichostomes of all kinds (exclusive of *Balantidium*) appeared by such leading workers as Beers, Fauré-Fremiet, von Gelei, Hsiung, Kirby, Klein, Lynch, Poljansky, Powers, and Wenzel, the most valuable source is the bibliography in Corliss (1961). Additionally, for the specialized literature on *Balantidium* up into the 1970's, mostly of a parasitic nature and by such authors as Auerbach, Cox, da Cunha, Grain, Hegner, Krascheninnikow, Kretschmar, Kudo, Levine, Meglitsch, Nie, Poljansky, Svensson, Wenrich, Westphal, and Young, see Levine (1961, 1973), who includes direct references to works by most of the researchers just named. Often missed, however, have been several major pre-1960 studies of the fibrillar system of *Balantidium*: McDonald (1922), only occasionally cited, and Fernândez-Galiano (1952, 1955b), rarely mentioned in the recent literature.

During the past 15 years or so, research on trichostomatines has been relatively scarce. Of course, a number of them are quite regularly included or mentioned in textbooks, ecological surveys, or parasitological reviews (including medical or veterinary works, with respect to *Balantidium*). But fewer than four dozen papers have appeared in which serious and substantial attention is given to their systematics or phylogenetics, and only those of Grain (alone or with colleagues) have utilized ultrastructural data in such a way to any extent to date. The cytological work on *Balantidium* of direct importance in medical research, however, should not be overlooked: for example, see Kan (1971).

If one excludes most of the important but more or less preliminary notices by Grain on the Isotrichidae and the Paraisotrichidae, well cited in Grain's (1966a) culminating monograph, and a number of the purely medical or parasitological notes on alleged species of *Balantidium*, practically the entire list (which includes descriptions of several new genera) of recent works would read as follows: Batisse (1965a, 1966b), Berger (1961), Bick (1972), Cox (1963), Dingfelder (1962), Dragesco (1968a), Fauré-Fremiet (1962b, 1963a,b, 1973), Fenchel (1968a), Grain (1964, 1966a,b, 1967, 1968b,c), Grain et al. (1973), Henriksen (1977), Jankowski (1964b, 1967a), Kaczanowski (1965), Krascheninnikow (1968), Krascheninnikow & Scholtyseck (1976), Kretschmar (1963), Ky (1971), Latteur (1967), Lee (1963), Lubinsky (1957d), Paulin & Krascheninnikow (1973), de Puytorac & Grain (1965), de Puytorac et al. (1974), Rao et al. (1976), Thurston & Grain (1971), and Wolska (1963, 1964a,b, 1965a,b).

Suborder (2) Blepharocorythina

Suggested as an independent order by Wolska (1971b) but reduced to a subordinal rank by Corliss (1974b, 1975b), who erroneously included it within the following instead of the present order (but see Corliss, 1977a), the group contains but a single family, the Blepharocorythidae, formerly classified with the trichostomes *sensu stricto*. Its characteristics are thus those of the family, which has now been expanded to contain some eight genera. The oral area is apical, its position marked by a prominent frontal lobe. Four or five tufts of cilia are usually present: two or three in anterior regions and one or two near the posterior end of the body. The vestibulum, with its ciliature, may penetrate quite deeply into the body, which is usually small in size and somewhat pliable. A simple, immobile apical process, corkscrew-like and rich in fibers, may project beyond the anterior end of the body.

These ciliates occur mostly in the intestine (colon or caecum) of horses, but some have been found in zebras, elephants, donkeys, hippopotami, and tapirs, and a few (*Charonina*) have been reported from the rumen of cattle. Unlike the situation for certain gymnostomes and trichostomatines found in some of the same hosts, no true concrement vacuoles have been developed in blepharocorythines. However, Wolska (1971b, and earlier papers) has suggested that a non-concretion-filled "rudimentary" vacuole with similarly associated somatic kinetosomes which does exist in a number of species is a homologous organelle; this proposal would support close phylogenetic relationship among the three groups. Furthermore, the special patch of kinetosomes continues to show up in members of a fourth group, the following order, even though no vacuole is present there – so possibly it is an evolutionary link of importance.

Species of the present suborder have been neglected: the family itself was not established until the work of Hsiung (1929, 1930); and the recent series of papers by Wolska (1966b, 1967a,b, 1968, 1970, 1971a–c) has quadrupled the original number of included genera. *Blepharocorys* itself contains a number of species (most commonly found in horses) and is the best known. Of the four genera described as new by Wolska, one – the amazing *Circodinium* with its seemingly close affinities with the ditoxid entodiniomorphid genus *Triadinium* – is from the horse; species of the others (*Raabena, Pararaabena, Spirocorys*) inhabit the intestine of the Indian elephant and, in the case of *Raabena*, also the African elephant.

The blepharocorythines quite likely had their ultimate origin from among archistomatine gymnostomes, possibly via some trichostomatine group now extinct. And it is not unreasonable to believe that, in turn, some of their own early members were ancestral to the now flourishing Entodiniomorphida.

* * * * *

The literature on blepharocorythines is not abundant. Papers subsequent to Hsiung (1930), which contains references to the older works, are generally to be found cited in the combination of bibliographies in Corliss (1961), Grain (1966a), Levine (1973), and Wolska (1971a–c); but see the recent note by Thurston & Grain (1971). Several older monographs deserve special citation, however: for example, Bundle's (1895) very early work, Hsiung's (1930) extensive treatment, and Strelkow's (1939) incomparable treatise. Grain (1966a), to my knowledge, has been the only investigator to employ electron microscopy in his study of a member of the suborder. In recent years, the most heuristic work on the overall group is certainly to be found in the fine series of papers by Wolska of Poland (references cited in preceding paragraphs).

Order ENTODINIOMORPHIDA

The single greatest – or, at least, most striking – change in the system of classification over that published in the first edition of this book (Corliss, 1961; and see the many subsequent adoptions, with little modification, including the celebrated "Honigberg Report," Honigberg et al., 1964) has been the total removal of this major order from among the allegedly highly evolved spirotrich ciliates with its reassignment to a position in the "holotrichs" alongside the so-called "lowly trichostomes" *sensu lato*. This taxonomic decision is reminiscent of others made recently or even some years ago; but these have involved only isolated genera (or occasionally families) – for example *Paramecium, Cyathodinium, Balantidium*, or *Neobursaridium* – and are dwarfed by the implications and magnitude of the present shift. (Admittedly, though, the change is not of any greater significance than the controversial "demotion" of chonotrichs, peritrichs, and suctorians in the Faurean scheme of a quarter century ago.)

The background or basis for the present move lies in the works of such investigators as Wolska, Noirot-Timothée, and Grain (see references below); the shift itself was formally – and with some variation – proposed essentially independently by Jankowski (1973c) and then by de Puytorac et al. (1974) and Corliss (1974a,b; and see 1975b). The history of the decision need not be retraced here: but see the preceding citations plus Canella (1971) and Wolska (1971b).

The entodiniomorphids are still – even as when they were considered to be spirotrichs – most easily recognized by their lack of uniform body ciliation, replaced, as it were, by isolated "tufts" of ciliature; by their firm pellicle, sometimes drawn out posteriorly into spines; by the presence of distinctive skeletal plates within their cytoplasm; by their laterally compressed bodies; by their "*de novo*" or apokinetic mode of stomatogenesis; and by their exclusive occurrence in the digestive tract of herbivorous mammals, mainly ruminants (but also elephants, horses and relatives, hippopotami, and certain anthropoid apes), where they thrive on cellulose and bacteria (though occasionally exhibiting cannibalism).

What has changed are not their characters but the interpretation of the nature of some of them, improved particularly by ultrastructural observations not widely available in pre-1960 years. Representing a principal example are the "ciliary tufts," long ago recognized as and named syncilia by von Gelei & Sebestyén (1932), now clearly exposed as *not* identical with membranelles

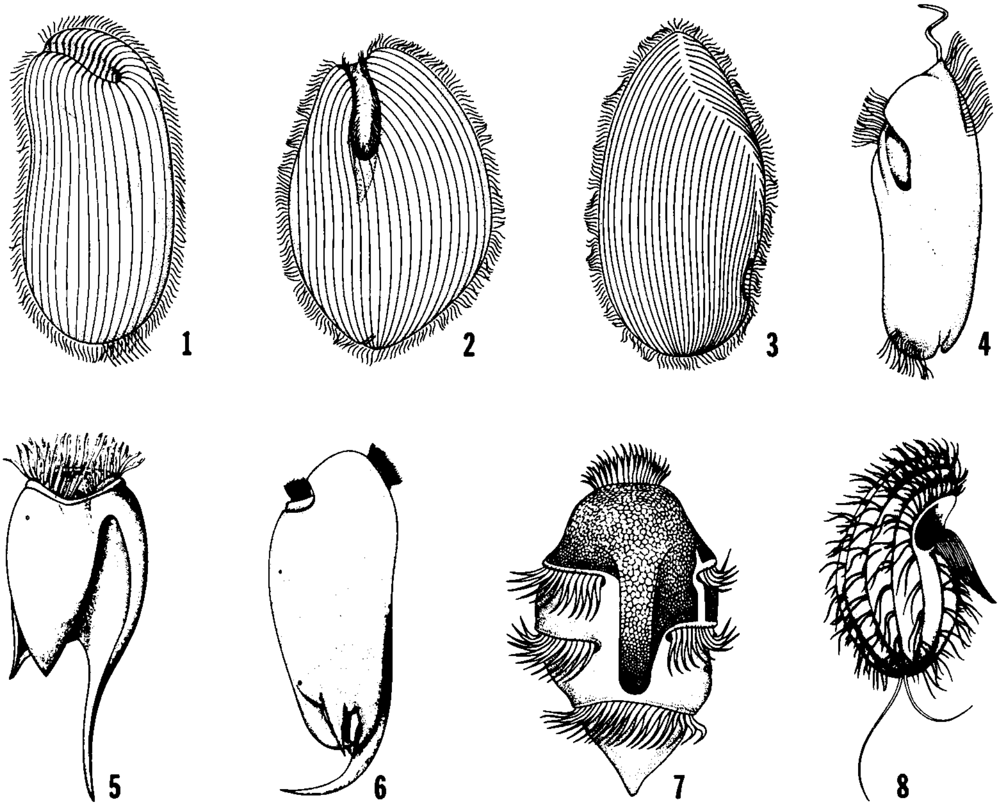

PLATE VIII. Representative vestibuliferans. Fig. 1. *Sonderia*, order Trichostomatida, suborder Trichostomatina. 2. *Balantidium*, order Trichostomatida, suborder Trichostomatina. 3. *Isotricha*, order Trichostomatida, suborder Trichostomatina. 4. *Blepharocorys*, order Trichostomatida, suborder Blepharocorythina. 5. *Entodinium*, order Entodiniomorphida. 6. *Epidinium*, order Entodiniomorphida. 7. *Troglodytella*, order Entodiniomorphida. 8. *Colpoda*, order Colpodida. [Additional figures appear in Chapter 20.]

so characteristic of bonafide spirotrich ciliates. Whether oral or somatic in location, their infraciliary organization is unique in comparison with that of any other compound ciliature – membranes, membranelles, cirri, etc. Those occurring in a circumoral depression are properly identified as a kind of vestibular ciliature, and the depression as a vestibulum. A cytopharyngeal apparatus of the rhabdos type is also now recognizable, confirmable by use of TEM. Its nematodesmata originate in the anteriad oral infraciliature, much as in gymnostomes and trichostomes. The cytostome, often retractable, is permanent. Mucocysts are present; but no toxicysts have been reported. Contractile vacuoles and pores are in evidence, notwithstanding the organisms' endocommensalistic existence in an anaerobic, highly specialized environment; but the "vacuous sac" appearance of their mitochondria does reflect the lack of oxygen in that habitat. In some forms, a special group of "free cilia" is present, reminiscent of the patch associated with the "rudimentary (concrement) vacuole" of the blepharocorythines of the preceding order.

The apokinetal mode of stomatogenesis exhibited is baffling ("de novo" appearance of kinetosomes subequatorially, sometimes in a pouch), at least from a phylogenetic point of view. Yet, subsequently, the entire process resembles that known in telokinetal stomatogenesis. And cytokinesis must be completed before finalization of new mouth-formation (for the opisthe: but the proter retains the parental oral apparatus), reminiscent, again, of the gymnostome pattern. The "uniqueness" of conjugation, on the other hand, has been exaggerated in the literature, due partly to misinterpretation of the precise observations made by Dogiel (1925) half a century ago. It is of the temporary type (Raikov, 1972a), with *no* total fusion (such fusion *is* characteristic of peritrichs, chonotrichs, and a few other ciliates). Even micro- and macroconjugants have been described in only one genus (*Opisthotrichum*). A "preconjugant" division does take place in many genera (but this is true in other ciliates as well), and the gametic or pronuclei – migratory ("male") and stationary ("female") – *are* morphologically distinguishable, but definitely *not* "cellularized."

There are further specializations underlining the distinctiveness of these particular vestibuliferans. The cytoproct is clearly in evidence and is surrounded by an array of microfilaments. There are often cytoplasmic lips around the oral area (and, in some species, a paralabial "sense" organ nearby); and the entire vestibulum is retractable, made possible by the presence of large tracts of contractile fibers. The skeletal plates of many species have already been mentioned above. Such features as these, made popular by the classical and still widely cited paper of Sharp (1914), clearly indicate a long evolutionary history apart from other members of the subclass and suggest that their restricted habitat has had a strong selective influence on their morphology and physiology. Little wonder that workers like Jankowski (1973c) and Wolska (1971b) have been tempted to accord them a separate subclass status!

Highly adapted to their endosymbiotic existence, most likely as commensals with limited – if any – value to the welfare of their hosts, species of the several families comprising this order occur in a number of the higher herbivorous mammals. The ophryoscolecids, for example, are widely found in cattle, sheep, oxen, goats, deer, caribou, related artiodactylan ruminants and even nonruminants (e.g., camels). The cycloposthiids, ditoxids, and several other groups dwell principally in the large intestine of horses or more or less related perissodactylans such as donkeys, zebras, tapirs, and rhinoceroses. The polydiniellids have all of their species in elephants, while the genus *Troglodytella* (for which I propose a separate family: see Chapter 20) occurs exclusively in anthropoid apes (gorillas and chimpanzees). Many likely hosts have yet to be systematically examined for presence of these obviously successful ciliates. The cattle-rumen forms are the best known and most widely studied, of course, with common genera including *Diplodinium, Entodinium, Eodinium, Epidinium, Epiplastron,* and *Ophryoscolex*; but even species of such genera are by no means limited to occurrence in cattle.

To my knowledge, bovine (or other) ophryoscolecids have seldom been reported from any other location than the rumen (or nearby parts of the digestive tract) and have never been implicated in any particular disease or "infection." Thus the claim by Rothenbacher (1964) of finding "rumen protozoa" (presumably *Ophryoscolex* or *Entodinium*, according to Levine, 1973) in sections of liver lesions in two cases of bovine hepatitis is of more than passing interest and worthy of further investigation.

The possibility that some of the numerous "morphological species" of entodiniomorphids described in the past are only "physiological races" or strains may be brought into perspective by modern-day observations on the range of morphological variability possible under differing (laboratory) environmental conditions. The same problem of proper recognition of bonafide species is paralleled in such other prolific ciliate groups as the peritrichs (Chapter 13) and the tintinnines (Chapter 15). But for the ophryoscolecids, such a problem – along with consideration of evolution within the group and its correlation with appearance of mammalian host-groups on the geological time-scale – was seriously treated by Dogiel (1927, 1946), among others, many years ago (see comprehensive review in Poljansky & Cheissin, 1965).

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The bulk of the taxonomic work on members of the Entodiniomorphida was carried out decades ago: references to most of the older monographs, surveys, and even isolated papers of importance may be found in Corliss (1961). Also, the reader may wish to consult Kirby (1941a), Levine (1961, 1973), Noirot-Timothée (1960), and Poljansky & Cheissin (1965) for such data. But a few of these works warrant special remention here, some because they have been widely overlooked by modern authors: for example, the papers of da Cunha (1914a,c, 1915, 1938), Davis (1941a,b), Dogiel (1927, 1946), Gassovsky (1919), Hasselmann (1918), Hoare (1937), Hsiung (1930, 1932, 1935, 1936), Kofoid (1935), Kofoid & Christenson (1934), Kofoid & MacLennan (1930, 1932, 1933), Lubinsky (1957a–c, 1958 a,b), Moriggi (1941, 1950), Poljansky & Strelkow (1938), Reichenow (1920), Strelkow (1929, 1931, 1939), Swezey (1934), and Wertheim (1935). And, of course, Stein (1859a,b) started it all, nearly 120 years ago! In cytological work of the pre-1960's, major papers were published by Bretschneider (1934, 1950, 1959), Dogiel (1925), Fernândez-Galiano (1949, 1955a, 1958, 1959), Latteur (1958), and, of course, Sharp (1914). Early comprehensive reviews on the physiology of host-parasite relationships of ophryoscolecids were those of Becker et al. (1930), Hungate (1950, 1955), and Oxford (1955).

Since 1959–1960, most of the works appearing have been brief and scattered descriptions of new species or new hosts. The greatest single contribution – in cytology and ultrastructure as well as taxonomy and phylogeny – has been the monograph by Noirot-Timothée (1960). The productive and continuing works, including major taxonomic revisions, emanating from the laboratory of Latteur warrant special citation as well: see Latteur (1966a–d, 1968, 1969, 1970), Latteur & Bousez (1970), Latteur & Dartevelle (1971), Latteur & Dufey (1967), and Latteur et al. (1971). Additional important taxonomic and cytological studies, sometimes including ultrastructural observations, have been carried out by Bretschneider (1960, 1962), Coleman & Hall (1971a,b), Gaumont & Grain (1967), Grain (1966a), Hollande & Batisse (1959), Roth & Shigenaka (1964), Senaud & Grain (1972), Thurston & Noirot-Timothée (1973), and Wolska (1970, 1971c). Raikov (1972a) has reviewed sexuality and conjugation in these ciliates, topics almost totally neglected ever since Dogiel's (1925) pioneering observations of more than 50 years ago. Zielyk (1961) reviewed *Entodinium* species from the white-tailed deer; Westerling (1970) carried out a survey of the reindeer in Finland; and van Hoven (1974, 1975) has recently studied ophryoscolecids of the hippopotamus and the tsessebe in South Africa. Canella (1964a, 1971), Corliss (1961, 1969a, 1974a,b, 1975b), Grain (1966a; and Senaud & Grain, 1972), Jankowski (1967a, 1973c), Noirot-Timothée (1969), de Puytorac et al. (1974), and Wolska (1971b,c) have treated the high-level systematic problems discussed above, including – in the works published since 1968 – the revolutionary shift of the entodiniomorphids out of the Spirotricha.

Several post-1961 studies on culturing and other nutritional aspects of these ciliates have been carried out – for example, by Coleman et al. (1972), Florentin (1965), Jouany et al. (1974), Mah (1964), Nouzarède (1965), and Senaud et al. (1973); and the recent major work by Bonhomme-Florentin (1974) should be added here. Modern reviews of physiological and biochemical findings in general are available in Bonhomme-Florentin (1974, 1975), Coleman (1963, 1971, 1975), Grain (1967), Howard (1967), Hungate (1966, 1975), and Levine (1973). No one has yet succeeded in culturing ophryoscolecids free from their hosts *and* without some rumen bacteria present in the medium. Although the host can live without its ciliates, the entodiniomorphids and the bacteria there have developed an interesting degree of beneficent mutualism – both within the rumen and in experimental *in vitro* culture.

Order COLPODIDA

This recently proposed order (de Puytorac et al., 1974) has been split off from the Trichostomatida proper on the basis, primarily, of the more highly organized nature or more complex morphogenetics of the vestibular (infra)ciliature in the species assigned to it. In fact, some ciliatologists (e.g., Bradbury & Outka, 1967, and, most recently, Lynn, 1976a–c) are proposing reacceptance of an older idea – to consider some of the oral ciliature in *Colpoda* and its relatives as representing true buccal *membranelles* (or "cirromembranelles," as suggested by Rudzinska et al., 1966) and to recognize a buccal (as opposed to vestibular) cavity in these organisms. From a comparative phylogenetic point of view, I am myself continuing – for the present, at least – to reserve the "buccal concept" for members of the allegedly more highly evolved classes, the Oligohymenophora and the Polyhymenophora. But French workers (e.g., Grolière, 1975b, and very recently de Puytorac & Grain, 1976) – now joined, to a degree, by Lynn (1976a–c) and Small (1976) who, however, reach similar conclusions via routes rather different from each other and from the French! – are tending to conclude that the colpodids (or perhaps only some of them) ultrastructurally manifest such infraciliary complexities that they cannot remain even in the same subclass with trichostomes. I believe that it is only fair to suggest that we await the results of additional and perhaps less restricted studies before attempting to settle these important issues.

Although the somatic ciliation is generally complete and the kineties essentially bipolar, a special property of most colpodids is their striking asymmetry. Yet – and this is still another special characteristic – such body torsion is lost during cytokinesis in those forms which undergo fission within a reproductive cyst, as beautifully shown years ago by Tuffrau (1952). This "recapitulation" may be considered to relate colpodids not only to the "simpler" trichostomes but also to prostomatid gymnostomes (Corliss, 1956; Fauré-Fremiet, 1950a, 1963b; Stout, 1960a).

The cytostome is permanent, and the cytopharynx is often supported by nematodesmata. In the case of *Colpoda*, it is now known that postciliary microtubules are associated with the cytopharnygeal complex: this is puzzling, since the gymnostome rhabdos is lined with transverse microtubules (Small, 1976, makes much of this difference in his high-level taxonomic separation of trichostomes and colpodids *sensu stricto*). Stomatogenesis is telokinetal, with a limited number of somatic kineties – via their anterior portions or fragments, evidence that we are, here, still dealing with members of the class Kinetofragminophora – involved in the proliferation of the infraciliary bases of the new vestibular ciliature (Hashimoto, 1966; Tuffrau, 1952). The apparent (but only additional?) formation of a primordium of sorts in *Colpoda* – considered very recently by some to render stomatogenesis parakinetal – admittedly complicates, once again, the picture of taxonomic interrelationships. Cytokinesis is completed well before stomatogenesis *sensu lato*. Palintomic divisions of the detorsioned encysted ciliates are reminiscent of the situation found in such trichostomes as *Schizocaryum* (e.g., see brief statement in Jankowski, 1964b), and are generally considered a rather primitive characteristic, since palintomy occurs less often among the "higher" ciliophorans.

Mucocysts are generally present; seldom – if ever – are toxicysts. Curiously enough, a permanent cytoproct seems to be lacking (although defecation has been mentioned by Rudzinska et al., 1966). The somatic kinetids typically show doublet kinetosomes, supposedly an evolutionary advance but one of unclear significance. It may be recalled that the enigmatic karyorelictids (Chapter 5) often show the same characteristic, but not the "regular" gymnostomes (Chapter 6). "True" kinetodesmal fibers are inconspicuous, even ultrastructurally (Lynn, 1975b). The single macronucleus of at least some colpodids contains a prominent RNA-containing nucleolus or endosome (Burt et al., 1941). There is growing evidence that *Colpoda* itself has a relatively primitive kind of polyploid or polygenomic macronucleus: one with a low ploidy number and well-defined subnuclei (Frenkel et al., 1973; Raikov & Ammermann, 1974). Amicronucleate races have been reported in *Tillina* by Beers (1946); nuclei of *Woodruffia* were studied by Evans (1944).

A number of members of the order are found abundantly in fresh-water habitats, and especially in moss and soil and other such edaphic biotopes and even on leaves of trees: thus the basis for their being called "terrestrial" protozoa. Important work on edaphic forms, aside from scattered still earlier observations, was carried out 20–25 years ago by such careful investigators as Gellért (e.g., 1950b, 1955, 1956, 1957), Gellért & Tamás (1958, 1959), and Wenzel (1953). Some colpodids occur as facultative parasites of certain invertebrates. Presumably, cysts are ingested along with litter or general detritus. *Colpoda* cysts are particularly widespread and are a frequent contaminant in field collections or even laboratory cultures of other protozoa. Curiously enough, conjugation has seldom been noted in this ubiquitous and well-known genus – "never," according to Raikov (1972a), but Klein (1930) shows pairs of *C. steinii* in one of his figures. *Woodruffia* has two cysts in its complex life cycle (Johnson & Evans, 1941; Johnson & Larson, 1938).

Taxonomically, the family Colpodidae is the principal group comprising the order. However, the controversial Woodruffiidae, which I am resurrecting as a family on the basis of recent reaffirmations of its uniqueness (Fauré-Fremiet, 1963b; Prelle, 1963a,b), is also included. One of its genera, *Platyophrya*, may have true fibrous trichocysts and may also possess oral ciliary organelles of too great a complexity to remain even in the subclass, let alone this order. The same taxonomic conclusion may need to be drawn for the nearby enigmatic *Cyrtolophosis*, member of the third family which I provisionally assign here (see Detcheva, 1976; Grolière, 1975b; McCoy, 1974a; de Puytorac & Grain, 1976). Once again, a state of "taxonomic unrest" is evident.

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Research on members of the order has been overwhelmingly devoted to the single genus *Colpoda*. Much of the resulting literature has been physiologically oriented, although there have also been classical studies carried out on the silverline system and taxonomy of several species in the genus. References to the extensive older works, on all members of the order, are well covered in such compendia as Kahl (1931c, 1935b) and Corliss (1961); and van Wagtendonk (1955) may be consulted for a concise review of physiological investigations – up to that time – related to en- and excystment in *Colpoda*. Often overlooked post-Kahlian papers of importance are those of Burt (1940), Taylor & Furgason (1938), and Taylor & Garnjobst (1939), on the taxonomy and silverline system of species of *Colpoda*; Gellért (1950a, 1955), on his new genus *Cirrophrya* and on two new species of *Woodruffia* (plus other diverse ciliates) from lichens; and Vörösváry (1950), on his new colpodid *Bursostoma*; also Claff et al. (1941) on physiology of *Bresslaua*. Even Kahl's (1931b) fine monograph on the Plagiopylidae is frequently forgotten.

Since 1960, full papers concerned specifically with members of genera *other* than *Colpoda* have been rare. One may cite nearly all of them, leaving aside ecological works which contain only brief accounts of various genera, with ease: Beers & Sherwood (1966), who watched a woodruffian devour fungal zoospores; Bramy (1962), who established *Kalometopia* as a new genus; Czapik (1971), who reexamined the little-known *Platyophrya*, a form now becoming highly controversial (see discussions in Dragesco et al., 1977; Grolière, 1975b); Dragesco (1972a), who described a new *Tillina* from Africa; Fauré-Fremiet & André (1965a) and Suhama (1969) – and now Lynn (1977) – who studied the ultrastructure of *Tillina*; Frenkel (1969, 1975), who analyzed the DNA of the macronucleus in trophonts and cysts of still another species of the same genus; Golder (1974) and Lynn (1975b), who argued over the obedience of species of *Woodruffia* to the important Rule of Desmodexy (Golder, 1976, has also very recently studied the nuclear complex of a species of this genus); Hashimoto (1966), who reexamined stomatogenesis in *Tillina*; McCoy (1974a), who rediscovered Stoke's amazing *Cyrtolophosis* (very recently examined ultrastructurally by Detcheva, 1976); Prelle (1963a,b), who, with reason, puzzled over the taxonomy of *Woodruffia* (never considered such a problem, perhaps, until von Gelei's, 1954, thought-provoking paper in which he elevated it to a position among the spirotrichs); and Stout (1960a), who investigated morphogenesis in *Bresslaua* and pondered over its phylogenetic significance.

The copious literature on species of *Colpoda* may be divided into several large areas, and no attempt can be made here either to mention them all or even to list completely all of the recent papers in any one given field of investigation. The most extensive area, from the point of view of multiplicity of references, is surely that concerned with ecological surveys, especially those involving soil, edaphic, or fresh-water systems. Selected works since 1960 include the following: Bamforth (1971, 1973), Bick (1972, 1973), Bick & Kunze (1971), Curds (1969, 1975b), Curds & Cockburn (1970a,b), Dingfelder (1962), Dragesco (1970), Gittleson & Hoover (1969: colpodids in caves, along with many other ciliates), Maguire (1963a,b), Mueller & Mueller (1970), Nikoljuk & Geltzer (1972), Stout (1960b, 1973), Stout & Heal (1967), Viswanath & Pillai (1968), and Wilbert (1969). Under the heading of ecology should also be included the occurrence of *Colpoda* as a facultative or accidental parasite (endosymbiont) in vertebrates as well as invertebrates. Since the early work of Reynolds (1936), scattered reconfirmations have been published: for example, note the relatively recent observations of Bradbury & Outka (1967), López-Ochoterena et al. (1966), and Rudzinska et al. (1966).

A second major area in which *Colpoda* has been quite intensively studied is that of physiology and biochemistry. Here most of the papers have dealt with nutritional problems under laboratory cultivation and/or the phenomena of en- and excystment. Many of these studies have been cited in Corliss & Esser (1974), a "cyst" review paper updating and extending the earlier one mentioned above (by van Wagtendonk, 1955; see also Flabi, 1965). Since the pioneering sophisticated work of 30–40 years ago by biochemical protozoologists at Stanford University and that of Pigón in Poland some 15 years ago, such research appears to be scattered and less frequent. But a Russian school is showing renewed interest in *Colpoda* in this area; for example, see Uspenskaja (1972). And note some of the recent work from other laboratories: Proper & Garber (1966), Tibbs (1966), Tibbs & Marshall (1969, 1970), and Wenzel & Meier-Tackmann (1975). *Colpoda* was often used in the studies of 40 years ago on tolerance to changed physicochemical conditions of a laboratory-controlled environment (e.g., see Finley, 1930; Lackey, 1938b; Loefer, 1939).

In recent decades, attention to the comparative systematics of *Colpoda* species has been woefully lacking (notable exception, Dragesco: e.g., 1970, 1972a,b). An ambitious undertaking, now appearing, by Lynn (1976a–c) includes an extensive, critical, statistically oriented review of the taxonomy of these organisms, with ultrastructural data – particularly of cortical organelles – playing a major role in the conclusions which he is drawing.

Finally, even in a very brief account, it is appropriate to give references to papers on *Colpoda* in the field of electron microscopy (in addition to those of Lynn, cited above), fully aware that much more work can be expected in this now flourishing area. A number of the investigations reported here are related to interest in cysts or cystic membranes, but this is not exclusively so: Didier & Chessa (1971), Frenkel et al. (1973), Hukui & Inoué (1965), Kawakami & Yagiu (1963a,b, 1964a–c), Rudzinska et al. (1966), and Tibbs (1968).

Addenda

1. To the cytological literature on entodiniomorphids (page 88), one should add the following recent references (belatedly brought to my attention): Ozeki et al. (1973), on distribution of ciliates in the large intestine of the horse; and Imai et al. (1977) plus Imai & Tsunoda (1972), on SEM of rumen forms in cattle and sheep, respectively. More papers may be expected from these productive workers. Two very recent additional works of interest may be cited here: Coleman et al. (1977), with the latest report on progress in laboratory cultivation of *Entodinium* species; and Kleynhans & van Hoven (1976), on rumen ciliates of the giraffe in East Africa.

2. To the ecological-taxonomic papers on *Colpoda* (page 90), the very recent work by Novotny et al. (1977) should be added. These investigators report a new species, found only in alkaline treeholes and uniquely possessing multiple micronuclei as well as exhibiting certain other morphological differences: in fact, the organism was first thought to represent a new genus. A further interesting recent series of investigations involving a species of *Colpoda* has been brought to my attention: the researches by Bader et al. (1976a,b) on grazing of ciliates on blue-green "algae."

3. To my brief discussion of the colpodid family Woodruffiidae (page 90), mention of the very recent work of Buitkamp (1977) on species of the family may be inserted here.

Chapter 8

Class Kinetofragminophora: (4) The Independent Hypostomes, in all their Intriguing Diversity

One of the most exciting changes in the ciliate classification system over that presented in the first edition of this book (Corliss, 1961) has involved the assembling of all "primitive" hypostome forms into one great subclass, with recognition of a number of more or less closely interrelated orders and suborders and with considerable shifting about of various families and genera within the now much expanded old "cyrtophorine gymnostome" group which had been originally conceptualized by Fauré-Fremiet (1950a).

The diversity represented by the new subclass is remarkable, and there will be ciliatologists who will want to press for even greater taxonomic separation of some of the contained groups: one finds an indication of this in the creation of superorders in the recent classification of de Puytorac et al. (1974). There is no doubt but that many "evolutionary experiments," confounded by factors of convergence, were undergone by the formerly scattered groups now placed together here. Thus exact relationships, both within the assemblage and between it and neighboring high-level taxa, are all the more difficult to work out. Yet the major feature shared in common by all hypostomes is their exhibition of what Deroux (Deroux et al., 1974) aptly terms "ventralization," a concept having its basis, first, in the 80-year-old work of Schewiakoff (1896) and, more recently, in Fauré-Fremiet's (1961c) insightful analysis.

Subclass Hypostomata is, as a whole, set apart from the other three *subclasses* within the class by several characteristics (see below). At the same time, it is separated from the other ciliate *classes* by the same kinetofragminophoran traits possessed in common with its neighboring subclasses, *viz.*, an oral ciliature basically derived from kinetosomes or kinetofragments originally associated with somatic kineties; a telokinetal mode of stomatogenesis, with rare exception; the presence of a conspicuous cytopharyngeal apparatus; and a general absence of the complex ciliature and infraciliature, buccal and somatic, so typical of members of the Oligohymenophora and the Polyhymenophora. Nevertheless, there will be those ciliatologists who may claim – with some justification, based in part on a differing interpretation of certain characteristics (especially at the ultrastructural level) – that the hypostomes (or, at least, many of them) are more like species of the other two classes than of the preceding kinetofragminophoran groups (e.g., this is the view espoused very recently in the important paper by Small, 1976).

The hypostomes, as main-line forms, do appear to be by far the most highly evolved group among the membership of the first class in general. Presumably arising evolutionarily from prostomatid gymnostomes, they appear to have given birth to the hymenostome and higher assemblages, thus occupying a pivotal spot on the proposed phylogenetic tree (see Chapter 17). They are distinguished by having a cytopharyngeal apparatus of the advanced cyrtos type, forming the principal element in their ventrally positioned oral area. It is typically composed of fewer but larger bundles of nematodesmata, strengthened by postciliary microtubules from perioral kinetosomes. In some species the body is pronouncedly flattened dorsoventrally, often asymmetrical in form, and shows a coverage of somatic cilia restricted to (all or only part of) the ventral surface; but in others, the body is nearly cylindrical, or only slightly flattened, and the ciliation is holotrichous. There appears to be greater independence of the kinetal fragments, in both structure and function, than was enjoyed by most ciliates assigned to the preceding subclasses. An atrium may be present; when so, the perioral cilia within it are properly referred to as atrial ciliature (though approaching buccal ciliature in their nature and organization in some species). Trichocysts and toxicysts are absent, with the important exception of the fibrocysts (a unique trichocyst) of the Microthoracina. But parasomal sacs, mucocysts, and contractile vacuole pores are typically present. Modes of stomatogenesis may tax my definition (Corliss, 1973e) of "telokinetal" (see comments in appropriate sections, below).

Six orders and 10 suborders comprise the subclass Hypostomata, as I presently envision it (this includes three cyrtophorid suborders not given by name in Corliss, 1975b: but see 1977a). These are considered briefly on the following pages, and representative genera are depicted in the set of figures on page 98 (Plate IX). For this subclass, more than for any other in the phylum, additional ultrastructural data are desperately needed before the tentativeness of any proposed classification scheme can be overcome. We are on the verge of learning much, and soon such information may oblige us to re-revise our ideas and thus our taxonomic arrangements – but, hopefully, not to an extent which will make the scheme endorsed here totally obsolete!

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The systematic, cytological, and evolutionary literature on the hypostomes is rich and widespread, and specific references are best left for consideration under the following discussions of included orders and suborders. Kahl (1931c, 1935b), and even Corliss (1961), are now completely out of date. Some of the predictably most significant monographs – by such systematists as Batisse, Deroux, and Grain – are yet to appear. Still, some of the most precise – if isolated – observations on hypostome species were actually carried out by pre-20th century researchers. The series of papers commenced by Fauré-Fremiet, cut off by his untimely passing, would have done much to stabilize our current thinking on the group overall. For example, see his often precocious and perceptive observations in the following works: Fauré-Fremiet (1959, 1961a, 1962a, 1965a, 1967a,b). Broader works by Canella (1971), Corliss (1974a, 1975b, 1977a), and de Puytorac & Grain (1976) contain analyses and numerous references of pertinence.

Order SYNHYMENIIDA

The perioral ciliature – or, as it has popularly been known in these and related ciliates, the hypostomial frange – is in the form of a very extensive band, even winding around helically onto part of the dorsal surface of the body and completely or almost completely traversing the ventral surface at a level slightly posterior to the oral area proper. Individual components of this kinetofragmental band are not separately differentiated, although the relatively long cilia arise from side-by-side kinetosomes in pairs. There is either no preoral suture or else it is confounded with (part of) the frange.

Somatic kineties are essentially bipolar, despite the ventrally located mouth. The body is cylindrical in shape (the body symmetry thus basically radial), and ciliation is holotrichous. These characteristics recall the prostomatid gymnostome.

Stomatogenesis appears to be parakinetal (Deroux et al., 1974), though I am currently willing to stretch the concept of the telokinetal mode and consider that "fragments of kineties" are involved in the process going on in the opisthe, whether arising "de novo" or derived from portions of kineties at that level. In view of the possibility that hypostomes gave rise to hymenostomes (Chapter 17), in some groups of which parakinetal stomatogenesis is typical, might it not be possible that the hymenostome (tetrahymenine) pattern was evolutionarily "tried out" first, and long ago, among various of the "lower" ancestral ciliate taxa (such as certain hypostome groups)? Note that this does not necessitate our calling *such* taxa hymenostomes.

The order now contains three families, the type-genera of two of which were placed in separate suborders by de Puytorac et al. (1974). A new one, the most primitive group, has been erected (see Chapter 20) to contain *Nassulopsis*; Jankowski's (1968d) Orthodonellidae includes his (Jankowski, 1967g) appropriately named *Synhymenia* plus *Orthodonella*, *Chilodontopsis*, and *Eucamptocerca* (a curiously long-tailed organism, as described by da Cunha, 1914b); finally, another new family is proposed for Stein's (1859b) long-known *Scaphidiodon*. All species are free-living, fresh-water forms.

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The literature on the order is sparse and generally recent. The most significant papers touching on the systematics and possible phylogeny of one or more of the included genera are those by Deroux et al. (1974), Fauré-Fremiet (1959, 1967a), and Jankowski (1968d). A few other references of pertinence have been given in preceding paragraphs; but special mention should also be made of Raikov's (1964) and Tuffrau's (1962) precise investigations of the nuclei of *Nassulopsis.*

Order NASSULIDA

In this group, the frange, on the ventral surface, never passes completely under or to the (organism's) right of the cytostomal area, although it varies from an extensive – but with periodic interruptions – band, even traversing around onto the dorsal surface, to three short "pseudomembranelles" located on the left very close to the mouth. When present, these three ciliary organelles, superficially so very reminiscent of the situation in certain hymenostomes, may even be located in an oral atrium, into which the cytostome-cytopharyngeal complex has also been sunken. In addition, a fourth or "paroral membrane" appears on the right in some of the included genera (Grolière, 1974). The cytopharyngeal cyrtos has been precisely and beautifully portrayed by Tucker (1968). It is not a "typical" cyrtos (as is found in the cyrtophorids, below).

Typically, the preoral suture has now become distinct and separate from the course of the frange. A large number of otherwise "bipolar" somatic kineties may converge anteriorly (and usually asymmetrically), from both left and right sides, onto this suture line. A (stomatogenic) meridian number 1 has even been identified in some genera; but it does not, in fact, play the straightforward role assigned to it in the case of "advanced" ciliates (i.e., certain hymenostomes and heterotrichs).

The atrium has been treated as either a vestibulum or a buccal cavity by some recent workers (but see definitions in Chapter 2). That it may be a forerunner of the "true" buccal cavity of hymenostome ciliates (for example) is a possibility. In the same vein, the mode of stomatogenesis – which I should like to suggest is a derivative from the fundamental telokinetal pattern – may be considered to be parallel (if not, indeed, coincidentally identical) to the modes labeled parakinetal and/or even buccokinetal. Nevertheless, and Jankowski (1967a, 1973c) notwithstanding, the order may be considered among the most primitive of hypostomes, as I visualize it; and it may include evolutionary lines leading to the cyrtophorids and also to groups beyond the present subclass.

Other remarks and literature citations are reserved for the following accounts of the two suborders which, in agreement with French workers (de Puytorac et al., 1974; de Puytorac & Grain, 1976), I now recognize (see also Corliss, 1975b, 1977a). Jankowski (1967a, 1973c) also placed them together, although at a level which would be included in my second class, the Oligohymenophora. Das et al. (1969) appear independently to be essentially in agreement with Jankowski, although their note leaves much to be desired.

Suborder (1) Nassulina

The whole gamut of variations mentioned above with respect to the hypostomial frange is exhibited among the many species and several genera included in this, the more plastic, suborder. *Enneameron* appears to have reached the extreme in reduction of the band: here it occurs in very short segments confined to a definitive oral atrium. Nassulines occur abundantly in freshwater ecosystems, and many characteristically feed on filamentous algae, drawing in long strands through the cytostome-cytopharyngeal apparatus in a seemingly effortless manner (Dragesco, 1962a). Body size is relatively large, the shape is cylindrical, and the organisms are typically fully clothed in cilia.

Three families are rather arbitrarily included here, and the position of the Furgasoniidae (new name for the Cyclogrammidae: see Chapter 20) is especially debatable. Perhaps *Furgasonia* (for preoccupied *Cyclogramma*) is truly some sort of primitive hymenostome, as Grain et al. (1976) and de Puytorac & Grain (1976) have very recently insisted in their proposal of a new oligohymenophoran order to contain it. The Paranassulidae are so different from the Nassulidae that I once proposed their separation at a subordinal level (see Corliss, 1974b); maybe this idea should be resurrected, with separation possible at even a higher level. The two genera comprising the Paranassulidae are also rather unlike, despite the fact that their species were originally set up as members of a single genus! Such problems are representative of the unsettled taxonomic situation obtaining in a number of the hypostome groups. Particularly lacking, to date, is a sufficiency of ultrastructural information; ultimately, such data should allow meaningful comparisons to be made.

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Aside from the older literature, which – though offering descriptions of numerous species (see Kahl, 1931c, 1935b) – mixed up many genera, families, and even orders (as now recognized), papers are few which bear directly on the systematics, comparative morphology, and morphogenetics of forms presently included in this suborder. Key recent works on species of nassuline genera are those by Beers (1966a), Dragesco (1962a, 1972a), Fauré-Fremiet (1959, 1961c,d, 1962a, 1967a,b), Grolière (1974), Jankowski (1967a, 1968d), Raikov (1962b, 1966), Raikov et al. (1963), Tucker (1968, 1970a,b, 1971), Tucker et al. (1975), and Vuxanovici (1962b). [Note: Batisse (1966b) placed da Cunha & Muniz's (1927) curious parasitic *Protohallia* among the nassulines, but I have removed it to an uncertain position in the subclass Gymnostomata (see its position in Chapter 20).]

Suborder (2) Microthoracina

The perioral ciliature (formerly frange, in origin) is reduced to only a few short kinetofragments (often three, on the left), sometimes set in a shallow atrium. The somatic ciliature may be reduced to fewer rows of cilia than typical of members of the preceding suborder; and the body is flattened laterally in many species. The cytopharyngeal apparatus is of the typical cyrtos type, but stomatogenesis is quite advanced, reminiscent of that found in the Hymenostomata. Body size is often small. Species are fresh-water or edaphic, with cystic stages common, and mainly bactivorous. Fusiform explosive trichocysts (fibrocysts), with a parachute- or umbrella-like tip after discharge and quadrangular in cross-section, are uniquely characteristic, as is a distinct and permanent vacuolar tube leading from the contractile vacuole to its conspicuous pore.

Two families are currently assigned to this suborder; one, the Leptopharyngidae, contains the well-known *Pseudomicrothorax*. The other, the Microthoracidae, embraces a number of genera, the better studied of which include *Drepanomonas* and *Microthorax*. The enigmatic *Discotricha* (a strange one, psammophilic, with "cirri," etc.: see Tuffrau, 1954; and, now, Wicklow & Borror, 1977) may well deserve separation into a family of its own.

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Modern literature (i.e., works employing silver-impregnation techniques and/or electron microscopy and generally carried out since the late 1950's) is scarce. Principal contributions, including careful investigations of the unique fibrocysts, are those by Corliss (1958a,b), Fauré-Fremiet (1967a), Fauré-Fremiet & André (1967), Hausmann (1974a, 1975, 1977a), Hausmann & Mignot (1975), Hovasse (1965), Jankowski (1967a, 1968d), Peck (1975, 1977b), Prelle (1961, 1966, 1968), Prelle & Aguesse (1968), and Thompson & Corliss (1958). Mostly edaphic forms, like the colpodids, these ciliates were and are often noted by ecologists working in such habitats.

Order CYRTOPHORIDA

Among all members of this large group, the frange, as such, has disappeared. The perioral ciliature is made up of several distinct kinetofragments derived from anterior extremities of left-hand kineties plus, on occasion, segments of right-hand kineties sweeping anteriad over the oral area to the very left-hand margin of the body. The "oral rows" (Lom & Corliss, 1971), in their definitive position, are never posterior to the cytostome-cytopharyngeal complex. They consist of double lines of kinetosomes in a zigzag pattern; only the outer are ciliferous.

Somatic ciliation is essentially restricted to the ventral surface of the body; the kineties are bipolar but converge onto a suture area which is bent or skewed far to the left. Generally flattened dorsoventrally and with a kind of beak-like tip or protruding edge in the antero-left-lateral "corner" and often a slight tail-like bulge posteriorly, many of these hypostomes superficially – and in "microsize," of course – resemble the form assumed in an early embryonic stage in the development of amphibian and fish larvae. An organelle of attachment (adhesive organelle) – known variously as a podite or stylet – is found at the posterior end of many species, developed to a greater degree in some than others; its base is surrounded by secretory ampullae (see Deroux, 1975). Thigmotactism is also strong throughout the order. The macronucleus is heteromerous, except in the suborder Hypocomatina.

The cyrtos, curved and often larger yet of fewer nematodesmata, is also more complex ultrastructurally than it is in the nassulids. The proximal (outermost) ends of the nematodesmata of some species are surmounted by capitula, sometimes taking the form of prominent "teeth" or "maxillae" (terms used in the literature). Stomatogenesis is of a telokinetal type which involves the anterior ends of only a small number of somatic kineties belonging to the left-hand sector or field on the ventral surface of the body, with subsequent extensive morphogenetic movements. But, in many ways, it is unique and complex and appears to involve even a "true" stomatogenic kinety (latest works: Deroux, 1976a,b; 1977). Stomatogenesis precedes cytokinesis.

Cyrtophorids feed mainly on bacteria, but some are histophagous, and many are found in nature in association – generally as ectosymbionts or epibionts – with a variety of vertebrates and invertebrates from both marine and fresh-water habitats. Several species may be harmful to fishes (Lom, 1970b; Lom & Nigrelli, 1970). More than 40 genera are assigned to this sizable order, falling into some eight families (see Chapter 20). The literature is considered at one time, following brief characterization of the three subordinal groups recognized in this book.

Suborder (1) Chlamydodontina

Here are to be found the "typical" cyrtophorids. The body is dorsoventrally flattened, the prominent cyrtos is slightly recurved as it plunges into the cytoplasm (thus resembling a "horn-of-plenty"), the macronucleus is clearly heteromerous, and the strong thigmotactic responses of the organism are mediated solely by the (ventral) ciliature. The species assignable here are widely distributed ecologically, in both fresh-water and marine habitats. In their ectosymbiotic associations with other organisms, they generally do not have a harmful effect on their hosts.

Three families are recognized: the ancient Chlamydodontidae (now reduced to two genera), the split-off Chilodonellidae, and the Lynchellidae (the latter two with some half dozen genera each).

Suborder (2) Dysteriina

The dysteriines, comprising the largest suborder by far, are particularly characterized by their usually prominent podite. Some of the most bizarre cyrtophorid body forms and the most conspicuous nematodesmal "maxillae" are also to be found among its diverse species. Widespread ecologically, a few species (e.g., *Brooklynella*) are known for their deleterious effect on their hosts (as gill and skin parasites of marine fishes). A number of dysteriines (e.g., the distinctive *Allosphaerium*) occur on the carapace and gills of amphipods. But some species of *Chilodonella* (preceding suborder) show the same kinds of host preference.

This suborder also contains three families: the long-known Dysteriidae, the now very large Hartmannulidae, and the very recently erected Plesiotrichopidae.

Suborder (3) Hypocomatina

Several curious genera of ciliates with a thigmotactic organelle in a depressed area on their flattened ventral surface, a convex dorsal surface, and a complex cytopharyngeal tube protruding from the body in a unique way have defied accurate classification since their early recognition as a separate family (the Hypocomidae) by Bütschli (1887–1889). Their occurrence as symbionts in or on a novel combination of hosts – tunicates, brittle-stars, barnacles, and peritrich protozoa – is of no help! Finally, unlike other cyrtophorids, the hypocomatines do not have heteromerous macronuclei.

Chatton & Lwoff (e.g., 1939b, 1950; and see Corliss, 1961) included species of this suborder among their "rhynchodid thigmotrichs." But, despite Canella's (1971) despair over our lack of knowledge and/or unity concerning their taxonomic position, it is clear that they are neither "rhynchodids" (see order Rhynchodida, this chapter) nor "thigmotrichs" (see scuticociliate suborder Thigmotrichina, Chapter 11). Earlier, in a review of the overall problem, I grouped them, under the name "Rhynchodina Chatton & Lwoff, 1939," as a suborder *near* the cyrtophorids (Corliss, 1974b); subsequently, along with Deroux (1975), I put the family Hypocomidae – plus Jankowski's (1967c, 1968b) relatively recent family Crateristomatidae – *within* the then suborderless Cyrtophorida (Corliss, 1975b). And here they are now (and see Corliss, 1977a; Deroux, 1976a), finally, in a separate cyrtophorid suborder of their own.

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Papers on species belonging to this long popular and now expanded hypostome order are numerous. Those published in early years may be found quite readily in such sources as Kahl (1931c, 1935b) and Corliss (1961), and in the bibliographies of many of the works cited below. Especially not to be forgotten are such classics as the works by Chatton et al. (1931) and Fauré-Fremiet (1950b) on the morphogenesis of cyrtophorids and the papers by MacDougall (e.g., 1925, 1936, and intermediate papers not cited) on their sexuality (including chromosome studies). Kidder & Summer's (1935) work on species associated with "sand-fleas" (beach amphipods) also merits attention, as well as Ozaki & Yagiu's (1941a,b) marine studies. The Hypocomidae are discussed in the great "thigmotrich" monograph by Chatton & Lwoff (1949, 1950). Huxley's (1857) perceptive paper establishing the genus *Dysteria*, 120 years ago, deserves special remembrance.

Works with some attention to the morphological, taxonomic, or phylogenetic significance of these ciliates which have been published in recent years, generally omitting shorter ecological-parasitological notes, include: Agamaliev (1974), Burreson (1973), Corliss (1975b, 1977a), Deroux (1965, 1970, 1975, 1976a,b, 1977), Deroux & Dragesco (1968), Dobrzańska-Kaczanowska (1963), Dragesco (1962a, 1966a, 1967), Fauré-Fremiet (1965c), Fauré-Fremiet et al. (1968a), Fenchel (1965a), Grain et al. (1973), Jankowski (1967a,c,d, 1968a,b), Janus (1972), Kaczanowska (1971a,b, 1974), Kaczanowska & Kowalska (1969), Kaneda (1960a–c), Kazubski & Migała (1974), Kowalska & Kaczanowska (1970), Lom & Corliss (1971), Lom & Nigrelli (1970), Pyne et al. (1974), Pyne & Tuffrau (1970), Radzikowski (1966, 1973), Radzikowski & Gołembiewska (1977), Sołtynska (1971), Tucker (1972), and Wilbert (1972a).

Order CHONOTRICHIDA

The vase-shaped, sparsely ciliated, sessile ciliates belonging to this unusual group have long been known, but poorly, although earliest studies of over a century ago correctly noted that they occurred as ectosymbionts on the appendages of certain crustaceans, were generally attached by a short noncontractile stalk, and reproduced by budding. In the first edition of this book (Corliss, 1961), the group was reported as containing only three families, eight genera, and some two dozen

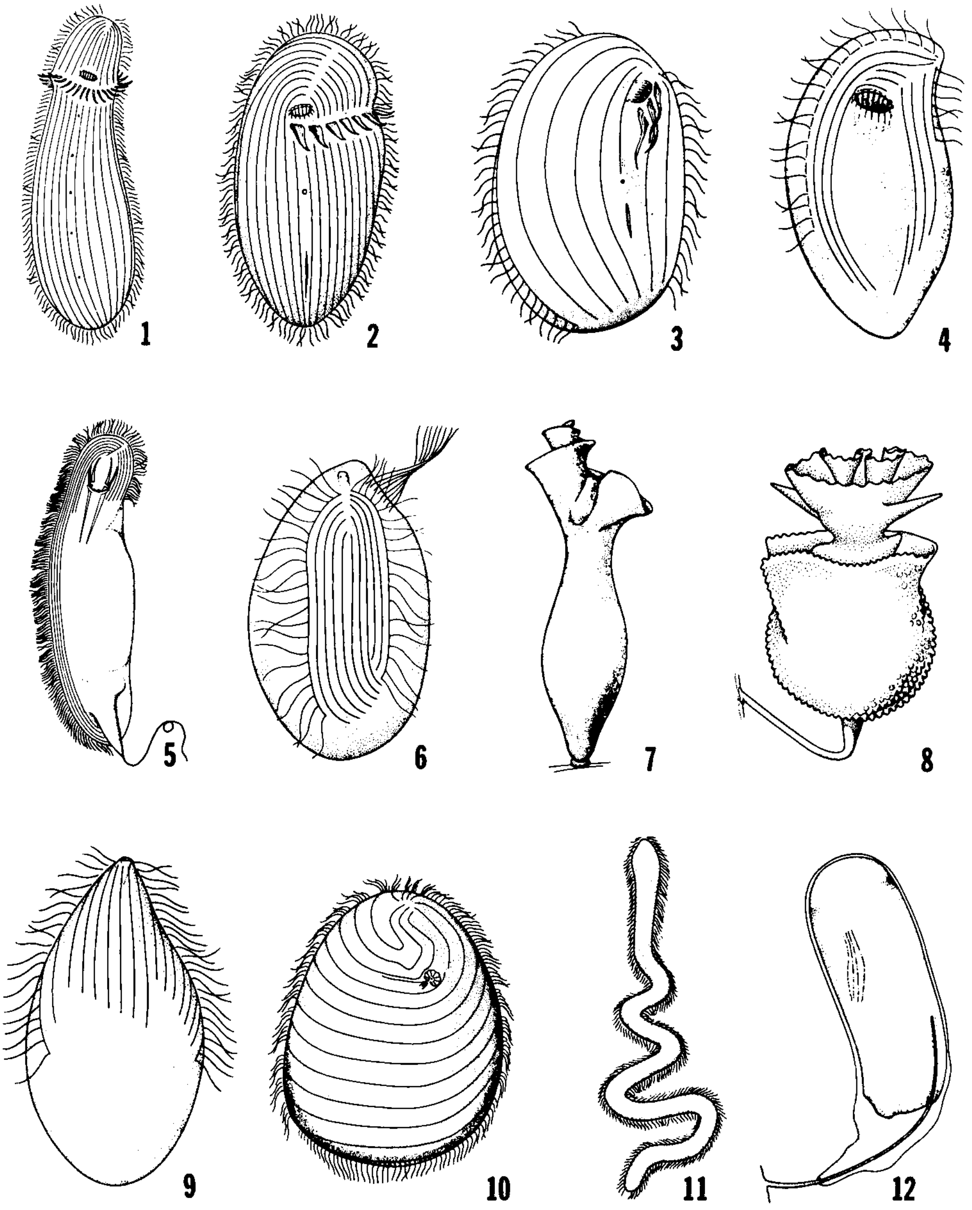

PLATE IX. Representative hypostomes. Fig. 1. *Nassulopsis*, order Synhymeniida. 2. *Nassula*, order Nassulida, suborder Nassulina. 3. *Pseudomicrothorax*, order Nassulida, suborder Microthoracina. 4. *Chilodonella*, order Cyrtophorida, suborder Chlamydodontina. 5. *Trochilia*, order Cyrtophorida, suborder Dysteriina. 6. *Hypocoma*, order Cyrtophorida, suborder Hypocomatina. 7. *Spirochona*, order Chonotrichida, suborder Exogemmina. 8. *Armichona*, order Chonotrichida, suborder Cryptogemmina. 9. *Raabella*, order Rhynchodida. 10. *Foettingeria*, order Apostomatida, suborder Apostomatina. 11. *Chromidina*, order Apostomatida, suborder Astomatophorina. 12. *Conidophrys*, order Apostomatida, suborder Pilisuctorina. [Additional figures appear in Chapter 20.]

species, little change over the situation in the times of Kahl (1935a). Today, due almost exclusively to the herculean efforts of Jankowski (e.g., see his fact-packed monograph, 1973b, and also his paper of 1971, not covered in the monograph), the numbers have risen to 11 families, some 45 genera, and more than 110 species, with clearly still more awaiting description. It is now a most respectable ordinal taxon indeed! In fact, some ciliatologists would separate them off at the higher taxonomic level of subclass (see Corliss, 1974a, and Chapter 18); yet others might feel that colleague Jankowski has been a bit too much of a "splitter" in his treatment of the internal taxonomy of the group.

Widespread throughout the oceans and in such fresh-water systems as Lake Baikal, these "collar ciliates" have a complex life cycle, have shown an explosive radiation in their morphological diversity, and have, in some cases, lost their stalks. In one very unusual case, the colonial state has been seen (unnamed blue-colored form from a bathypelagic host: see Mohr et al., 1970).

In addition to the general features mentioned above, chonotrichs are distinguished further by their lack of true somatic ciliature but the presence, in the adult forms, of a clearly disposed atrial ciliature within a deep and sometimes beautifully spiraled preoral funnel, at the bottom of which is found the cytostome proper. Perioral cilia, in a single row from paired kinetosomes with one member of each pair nonciliferous, comprise part of the atrial ciliature. Although the organisms are phagotrophic in their feeding, their cytopharyngeal apparatus is less developed than in most hypostomes: for example, no nematodesmata appear to be associated with it (Grain & Batisse, 1974; Karadzhan, 1976). Stomatogenesis may be considered to be telokinetal. No cytoproct has ever been described, and apparently contractile vacuoles are also absent. The pellicle is quite rigid, often adorned with lobes or spines. Stalked forms have a secretory ampulla involved in production of the attachment organelle, highly reminiscent of the condition found among cyrtophorids. Note that the preoral funnel represents essentially the entire ventral surface.

The macronucleus is heteromerous, as in the majority of the members of the preceding order. The life cycle is often correlatable with the exuvial cycle of the host species. Conjugants, whether of equal or unequal size, always, like peritrichs and some suctorians, exhibit total fusion (Mohr et al., 1970; Raikov, 1972a). Reproduction is by budding of two possible kinds, external or internal (cryptic), supplying the basis for Jankowski's (1972e, 1973c, 1975) taxonomic subdivisions of the group. The migratory bud or tomite shows a nonciliated convex dorsal surface and a slightly concave underside, the latter bearing two fields of cilia (left and right: fundamentally somatic, they become the atrial ciliature of the adult) and a posteriorly located adhesive gland.

Although most commonly found on gills and appendages of marine crustaceans, some (other) chonotrichs are attached to brackish- or fresh-water hosts. Several groups are on copepods infesting certain whales; and one – surely aberrant – species is associated with a marine alga.

The literature on the chonotrichs, cosmopolitan though the nature of these symphorionts is now known to be, is scattered, sparse, and predominantly ancient. It is considered below, following brief characterizations of the two included suborders.

Suborder (1) Exogemmina

Characterized by their mode of reproduction (i.e., the process of exogemmy or external budding only), the species assigned here occur on hosts (including the marine alga) from marine, brackish, and fresh-water habitats. The body is of "average" (see Chapter 4 for categorization of ciliate sizes) dimensions, with a usual range in length of 60–180 μm though occasionally up to 360 μm. The body form is long and cylindrical, not flattened; and, typically, there is a well-developed collar. Spines are poorly developed; true stalks are not common. The orthomerous part of the macronucleus is always oriented toward the oral area (in contrast to the situation in members of the second suborder). Few buds are produced at a time, generally only one.

The exogemmines are widely distributed on the bodies of cosmopolitan crustaceans. The most primitive chonotrichs are thought to be in this group. The suborder is comprised, according to Jankowski's (1973b) monograph, of some 6 families, 15 genera, and 54 species.

Suborder (2) Cryptogemmina

Budding here is internal, with the tomite's development taking place partially (or occasionally wholly) in a permanent "marsupium" or crypt. Species are found solely on marine hosts. The body is often flattened and angular, and the size small (usually 50–70 μm, maximum ca. 110 μm). The collar is reduced. Spines are common and sometimes strikingly developed; stalks are also generally present. In members of this suborder, the macronuclear orthomere is directed toward the attached pole of the organism. The life cycle is often quite complicated; and as many as eight tomites may be produced in or from a single brood pouch or crypt.

The cryptogemmines show a wide marine distribution, littoral and open ocean. One unusual group of hosts are the copepods, which infest many different species of whales. According to Jankowski's (1973b) exhaustive monograph, the present suborder is comprised of some five families, 26 genera, and 47 species; to these may be added the three new genera and eight new species described by Jankowski (1971) from "whale-lice" and, for some reason, not included in his monograph (apparently already in press). These "whale-lice" forms – exhibiting, in effect, hyperparasitism – are very widely distributed, their ultimate hosts (the whales) found in nearly all oceans and seas. Many, many species of cryptogemmines remain to be discovered. Mohr et al. (1970) tantalizingly make mention of several "undescribed forms" in their important review.

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Older references to the literature on members of the order Chonotrichida may be found in the bibliographies of Corliss (1961), Jankowski (1973b), and Mohr et al. (1970). Five classical pre-20th century papers deserve remention: Balbiani (1895), Hertwig (1877), Plate (1886), Stein (1851), and Wallengren (1895). To these must be added the heuristic monograph by Guilcher (1951), the first worker to point out and appreciate (the phylogenetic significance of) the striking similarities between members of this group, which she studied especially from a morphogenetic point of view, and those of the preceding order (the Cyrtophorida): in infraciliature, various organelles, life cycle, and macronuclear structure. Swarczewsky's (1928a,f) studies on spirochonids of Lake Baikal also ought to be cited here, and Gajewskaja's (1933) work as well.

In more recent years, there have been three principal groups of chonotrich-watchers: Mohr and associates in California (e.g., see Mohr, 1948, 1966; Mohr et al., 1963; Mohr et al., 1970; Matsudo, 1966; Matsudo & Mohr, 1964, 1965, 1968); French and Polish workers (Dobrzańska-Kaczanowska, 1963; Fauré-Fremiet, 1957b; Fauré-Fremiet et al., 1968a; Fauré-Fremiet & Guilcher, 1947b; Fauré-Fremiet et al., 1956a; Grain & Batisse, 1974; Guilcher, 1950, 1951; Tuffrau, 1953); and Jankowski, practically alone, in Russia (see 1967a, 1971, 1972e, 1973a–c, and shorter papers of pertinence cited in 1973b). However, the brief but excellent study by Fenchel (1965b) should be mentioned as well.

Published observations by electron microscopy (see Grain & Batisse, 1974, and, most recently, Karadzhan, 1976) may be interpreted as supporting a close relationship between chonotrichs and cyrtophorids (see also Chapters 17 and 18), although Russian protozoologists in particular (e.g., see Cheissin & Poljansky, 1963; Jankowski, 1973b,c; Poljansky & Cheissin, 1965) do not endorse the expression of such kinship which considers the two groups to be side-by-side orders within the subclass Hypostomata, the classification followed here. Mohr (1966) brings to bear on the argument his reasoning concerning the antiquity of the group (at least 225 million years old), based on the known evolution of their hosts: this, he claims, indicates the need for high-level taxonomic separateness, in agreement with the Russian view.

Order RHYNCHODIDA

Only two families of ciliates properly belong here, following the latest published arrangement (Corliss, 1975b, 1977a): the Ancistrocomidae and the Sphenophryidae. As the original rostrate "thigmotrich" forms of Chatton & Lwoff (1939a,b, 1949, 1950), they have been shifted about considerably and have had rather strange taxonomic "bedfellows" in past years, a story too detailed to review here (but see Corliss, 1974b, 1975b; and comments under suborder Hypocomatina, order Cyrtophorida, above).

The true rhynchodids, often of small or even very small body size (frequently only 20—50 µm in length), are characterized by the possession of a complex anteriorly located sucking tentacle, equipped with toxicysts, and by the location of their thigmotactic ciliature (when present at all in mature forms) on the anterior part of the flattened ventral surface. A few other somatic kineties may also be present (ancistrocomids); or the vegetative form may be completely devoid of cilia, though retaining kinetosomes which bear cilia in the larval (bud) stage (sphenophryids). Parasomal sacs are present.

The ciliates attach to host tissue by a knob at the enlarged end of the functional sucking tube which, according to some workers, represents the replacement of an "original mouth" presumed to have been located at the opposite end of the organism. Such an assumption (about the site of a former cytostome) is perhaps supported by the presence of an enigmatic kinetofragment in the lower right sector of the ventral surface and by the fact that conjugation involves fusion of the posterior parts of the ventral faces of the conjugants; but it is soundly contradicted by the ultrastructural evidence produced by Lom & Kozloff (1970).

Most species occur on the gills of marine bivalve molluscs (pelecypods); however, some are found on gastropods, both marine and fresh-water, one on a chiton (amphineuran mollusc), several, now, from various cirri of polychaete annelids, and one from a phoronid worm. Rhynchodids have even been found associated with a fresh-water oligochaete annelid, but the "host" was itself parasitizing a pulmonate gastropod which was (also) infected by the ciliates. *Lwoffia*, from marine bivalves, is unique to the family Sphenophryidae in its possession of cilia throughout its life cycle (Kozloff, 1955).

Electron-microscopical studies of the suctorial tube (Khan, 1969; Lom & Kozloff, 1968, 1970; de Puytorac, 1969c) reveal that it is reminiscent of the cytopharyngeal apparatus of nassulid and cyrtophorid hypostomes, though unique in some details. Microtubules are involved in its substructure, although no nematodesmata are present; and in its phagoplasm are toxicysts similar to those known especially well in haptorid gymnostomes (e.g., see Dragesco et al., 1965). The cytoplasm of host cells serves as food: thus rhynchodids are pathogenic parasites. Stomatogenesis, little studied with modern techniques, may be considered to be telokinetal.

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Papers on ciliates belonging to the Rhynchodida – reduced as it now is to two families – are not numerous. The pre-1960 literature of the early experts on the organisms – Chatton & Lwoff, Jarocki, Kozloff, and Raabe – is well documented in such works as Canella (1971), Corliss (1961), and, especially, Raabe (1970b). But it would be unconscionable to fail to remention the taxonomic monograph of Chatton & Lwoff (1950) or the excellent quartet of papers in the 1940's by Kozloff (1946d: last one). Little has appeared during the past five years (now Kozloff, 1976); however, a number of papers of the 1960's or very early 1970's deserve special citation and are listed without comment here: Antipa & Small (1971a), Dobrzańska (1961), Fenchel (1965a), Khan (1969), Kozloff (1961, 1965a), Lom & Kozloff (1968, 1970), de Puytorac (1969c). And Raabe's (1970b) comprehensive monograph should be consulted for references to a number of his own important papers of the 1960's (and earlier: e.g., Jarocki & Raabe, 1932).

Order APOSTOMATIDA

Among the most parasitic of symbiotic ciliates (some members of this curious order even show definite alternation of hosts, unique to the phylum), the apostomes *sensu lato* are associated with marine and fresh-water crustaceans, cephalopods, ophiurans, coelenterates, ctenophores, polychaete annelids, and possibly edaphic (terrestrial) acari. Some exhibit the phenomenon of hyperparasitism, being symbionts of other apostomes. The best-known species, the apostomes *sensu stricto*, however, are commonly found in such marine crustacean hosts as hermit crabs and copepods. Those with two known hosts have sea anemones as the second.

Apostomes are briefly characterized as possessing an inconspicuous or no cytostome, an organelle (when present) located ventrally and often accompanied by a unique rosette; by generally having, in the mature forms, a holotrichous – though sometimes sparse – covering of somatic ciliature typically arranged asymmetrically, in dextral spirals of fewer than 22 rows; and by exhibiting a complex polymorphic life cycle involving an orderly succession of distinguishable stages: phoront, trophont, protomont, tomont, protomite, and tomite (see definitions in the glossary of Chapter 2). A contractile vacuole, with pore, is present, despite the marine and parasitic existence of so many species; but no cytoproct has been reported. Mucocysts may be present. True kinetodesmata are in evidence, a characteristic thus shared with the hymenostomes (Chapter 10). Feeding is typically by osmotrophy or pinocytosis of the host's exuvial fluid, but phagotrophy is sometimes exhibited. The macronucleus, sometimes huge and/or reticulate, is homomerous in the trophont while heteromerous in the tomite of many species. A most striking attribute of certain trophonts is their coloration: apostomatines feeding on crab exuvial fluid, for example, may, while rapidly growing in size, become an intense sapphire blue in color.

The intimate structure, let alone the possible homologies with other ciliate groups, of the whole cytostome-cytopharyngeal-rosette area of apostomes *sensu lato* is yet to be completely resolved, although Bradbury (1966a,b, 1973), especially, has thrown considerable light on the enigma. There is certainly no cyrtos; yet the absence of such typical hypostome features is not, in my opinion, sufficient to rule out a cyrtophorid ancestry. By considering the classical x, y, z "buccal kineties" of Chatton and Lwoff to be perioral kinetofragments, one can conclude that stomatogenesis is of a telokinetal, albeit rather specialized, type. Other kinetal segments or fields, strongly thigmotactic in function, may also be implicated.

A good deal of variation exists with respect to patterns of life cycles exhibited by the traditional apostomes, and such differences may be of greater taxonomic significance than generally appreciated. Originally described in detail by Chatton & Lwoff (1935a) in their classical "first-of-three" (but, alas, the other two never appeared) monograph on the group, they have subsequently been reviewed with clarity by Kirby (1941a), Lwoff (1950), and, most recently, Bradbury (1966a). In addition to involvement of various hosts, cystic stages are also often part of the full life cycle. Perhaps most important, at least from morphogenetic and evolutionary points of view, is the occurrence of a detorsion of the spiraled kineties of the mature form, preceding the fission(s), often palintomic in nature, yielding the two to many tomites of the nonfeeding dispersal stage. Cytokinesis, stomatogenesis, and even conjugation may be spread across more than one phase in the life history.

The Apostomatida may merit a higher level in the classification system than that suggested here. In some major ways, its members seem to be distinct not only from all other hypostomes but even from the other taxa included within the entire class Kinetofragminophora. In any case, largely in agreement with Jankowski (1966a,c, 1967a, 1973c), I consider the group to contain three subdivisions, treated below as suborders. Principal references to the literature are reserved for inclusion under each subordinal section.

Suborder (1) Apostomatina

This large group is comprised of phagotrophic and osmotrophic forms which generally have a mouth in both trophont and tomite stages, typically bear a rosette, and commonly manifest palintomy within a cyst. Principal hosts are marine crustaceans. I include here two families (at most!), recognizing that the Foettingeriidae contain the bulk of the genera assignable to the order as a whole. Here are the "traditional" apostomes, the Apostomatida *sensu stricto*; thus its main distinguishing characteristics have been presented on preceding pages. On the basis of life cycle differences, Chatton & Lwoff (1935a) recognized some six subgroups or "sections" here; for three of these, Jankowski (1966c, 1975) created separate families, which I do not accept (see Chapter 20).

Reports of apostomatine ciliates from fresh-water hosts are rare, perhaps limited to the observations of Miyashita (1933a), who described a *Hyalospira* from shrimp; and Penard (1922), who noted a species (probably of *Gymnodinioides*) from gammarids, placing it at the time in the scuticociliate genus *Larvulina*. Among the least "representative" of the suborder (so perhaps it doesn't belong here?) is the genus *Cyrtocaryum*, described by Fauré-Fremiet & Mugard (1949b): it has no rosette, no mouth, and occurs in polychaete annelids (rather than crustaceans). Coincidental with Jankowski's (1975) recent and as yet unsubstantiated decision, I have also recognized the need for a separate family to contain it (Corliss, 1977a) and have erected it in this book (see Chapter 20). To this uncertain family I am provisionally assigning a second even more taxonomically enigmatic genus, Hovasse's (1950) *Spirobuetschliella*, a lengthy (up to 600 µm), heavily ciliated, mouthless form from the intestine of another polychaete; also studied by Fjeld (1956), it has generally been considered to be a species of the oligohymenophoran order Astomatida.

Until relatively recently, little work on host-parasite relationships had been carried out since the time of Chatton and Lwoff; yet the important papers of 20 years ago by Debaisieux (1957, 1960) and Trager (1957) should be cited. And, since then, the works of Fenchel (1965b), B. H. Grimes (1976), Jankowski (1967c), and Schauer (1972) have appeared. But the greatest "shot in the arm" for the apostomes has been the excellent series of investigations (principally on *Hyalophysa*, one of the three genera described as new within the past 10 years) – the latest ones involving electron microscopy – by Bradbury, working alone or with colleagues (e.g., see Bradbury, 1966a,b, 1973, 1974, 1975; Bradbury & Clamp, 1973; Bradbury et al., 1974; Bradbury & Goyal, 1976; Bradbury & Pitelka, 1965; Bradbury & Trager, 1967a,b; Johnson & Bradbury, 1976).

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Papers on species of this suborder are quite numerous but scattered and generally dated. Reference to practically all of the pre-1935 literature may be found in the fine bibliography of Chatton & Lwoff (1935a), including their own important notes appearing over a period of some years before the appearance of their culminating taxonomic monograph. Many of the earlier papers were brief, most of them by French workers, dating back 60–70 years ago (and a major one from the 19th century). Principal publications of the period 1935–1960 are referred to in Corliss (1961). Some such works are cited in preceding paragraphs where the emphasis, however, is on the modern literature. It may be noted, incidentally, that the celebrated (and sometimes controversial!) Rule of Desmodexy was formulated by Chatton and his young colleague Lwoff (see Chatton & Lwoff, 1935b) in the same year as that of the appearance of their incomparable apostome treatise.

Suborder (2) Astomatophorina

Here we find mouthless forms in the trophont stage, though rudiments of oral kinetofragments are detectable. Thigmotactism is marked. Methods of reproduction, for some species, include strobilation, as well as monotomy and palintomy. The body form is often elongate and worm-like. Hosts include cephalopods, coelenterates, and ctenophores from the marine environment and crayfishes, amphipods, and isopods from fresh-water biotopes. Two families may be recognized, one for *Opalinopsis* and the perhaps better-known *Chromidina*; the other for the enigmatic fresh-water genus *Collinia*, at first known only from the crayfish but now also identified with the sanguicolous "*Anoplophrya*" from the blood of certain amphipods and isopods (see de Puytorac, 1953; de Puytorac & Grain, 1975; de Puytorac & Lom, 1962). These false "anoplophryans," incidentally, unfortunately continue to be assigned to the order Astomatida by many workers and textbook writers. Some specialists might prefer transfer of the Colliniidae to the preceding suborder, maybe exchanging it (in effect) for the family there containing *Cyrtocaryum* and *Spirobuetschliella*? One more outstanding example of our need for more data.

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Little research has been carried out recently on these seemingly aberrant forms: almost none except for that of Jankowski (1966c, 1967c, 1972a) and of de Puytorac and colleagues (see above citations, the last two of which represent excellent ultrastructural studies). Aside from treatment in the monumental monograph by Chatton & Lwoff (1935a) and the interesting observations on *Collinia* (as "*Anoplophrya*") by Summers & Kidder (1936), the astomatophorines are principally mentioned only in the still earlier notes or papers by the original describers of the new species and genera involved (e.g., see the thorough work by Foettinger, 1881, of 96 years ago). Collin's (1909a) detailed account of conjugation in *Collinia* and Wermel's (1928) outstanding study of the morphology of *Chromidina*, however, deserve special mention. But the group as a whole has been neglected.

Suborder (3) Pilisuctorina

This is another fascinating but poorly known group of ciliates, possibly ancestral to the apostomes proper but still incompletely studied. Typically (genus *Conidophrys*), the mature "trophonts" (if that's what they truly are) are nonciliated and immobile, impaled (and encysted) on the setae of marine crustacean hosts (amphipods, isopods, and possibly others), producing ciliated migratory tomites by a strobilation type of budding. In such cases, the seta, or "exoskeletal hair," of the host appears to "pierce" the body of the parasite (through the cytostome-cytopharyngeal complex) and nourishment for the ciliate is the host fluid allegedly made available through pores in the seta. But the two atypical genera (*Ascophrys* and the very poorly known *Askoella*) included in the suborder attach directly to the cuticle of marine decapod or amphipod hosts, feed on the exoskeleton, and reproduce by repeated binary fissions (all within a cyst).

The tomites of all known pilisuctorine species possess sparse somatic ciliation, associated mainly with two groups of kineties. An attachment or thigmotactic area may be recognized. The "mature" forms of all genera are without cilia, though they retain a patterned infraciliature (comprised of nonciliferous kinetosomes).

Jankowski (1972a) has proposed that the trophont of *Conidophrys* is, in effect, a neotenous phoront of a "regular" apostomatine genus (e.g., *Gymnodinioides*) which has taken up both feeding and reproduction in the encysted state. Even the limited data available to date do seem to intriguingly support such an evolutionary relationship.

With respect to possible further extension of the host-list, it is exciting to learn (see Dindal, 1973) that what may be a conidophryan-like species has been observed in association with the cuticular setae of a mite, an edaphic, terrestrial arthropod far from the sea. Many species of litter-dwelling acari, according to Dindal, are apparently so infected with this curious microorganism, although its exact identity tantalizingly remains to be determined (it might even be a fungus).

Although the genus *Ascophrys* was included in this suborder in Corliss (1975b), the apparently similar *Askoella* was assigned to the Apostomatina. Despite our lack of detailed information, it now seems to me that these two recently described genera belong very close together in any classification. Here (and see Corliss, 1977a), I have chosen the present suborder as their common taxonomic home. Jankowski (1967c) proposed a separate family for *Askoella*, alongside the Conidophryidae. But, at this time, it may be wiser to retain solely the older family, placing all three genera tentatively together in it (see Chapter 20).

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The literature on the pilisuctorines is limited. Aside from the original monograph by Chatton & Lwoff (1936a; and see their preliminary note, 1934), the fine review by Kirby (1941a), and the brief note by Mohr & LeVeque (1948), nothing appeared again until Fenchel's (1965b) paper and the series of comments or observations by Jankowski (1966a,c, 1967c, 1972a). But now, very recently, interest has been revived, primarily through the activities of Deroux and colleagues (see Bradbury, 1976; Campillo & Deroux, 1974; Deroux et al., 1975); see also Jones & Khan (1970).

Chapter 9

Class Kinetofragminophora: (5) The Suctorians, a Most Singular Group

Among the most puzzling of ciliates, at least from the point of view of their possible affinities with other taxonomic groups within the phylum, have always been the suctorians or "tentaculiferans," as a number of their students still like to call them. Their seemingly unique characters – lack of ciliature (in adult stages); sessility, with usual attachment to the substratum by means of a stalk; reproduction by budding, external, internal, or evaginative; conjugation, often total and involving migration of a microconjugant; and, above all, possession of feeding tentacles, with replacement of a single mouth-opening of the conventional kind by such polystomy – have, especially in combination, long distinguished them from commonly known other ciliate groups whose species appeared to show few if any of the attributes just enumerated. Recall that Kahl (1930–1935) excluded them completely from his "Ciliata" series, a fact not often appreciated. Specialists in ciliatology, however, have long been aware that most of the characters briefly described above do occur or have their counterparts among various species of other ciliophoran taxa. In fact, many are shown, at least superficially, by numerous peritrichs and chonotrichs (though it should be pointed out that proponents for separation of the suctorians from all other ciliates use this as an argument for awarding similar taxonomic distinctiveness to these other two singular groups!). More significant, perhaps, is the "cropping up" of some of these "unique" features in still more "conventional" groups: for example, among gymnostomes and hypostomes, or even trichostomes, hymenostomes, and hypotrichs.

For all such reasons, Fauré-Fremiet (1950a) took the courageous step of suggesting that suctorians were (merely) another order of holotrich ciliates, albeit with specializations developed during a long evolutionary history of their own. Immediate support for this truly iconoclastic move came via data from study of silver-impregnated material and from comparative investigation of morphogenesis in a number of ciliates (see, for example, the comprehensive monographic work by Guilcher, 1951). There has followed additional evidence, interpretable as favorable, from subsequent investigations employing such refined cytological approaches as electron microscopy. Today, as a consequence, there is wide acceptance of a much closer relationship (as reflected in the schemes of classification adopted in many research papers, textbooks, etc.) between the hundreds of species of Suctorida and other "lower" ciliates than ever proposed or recognized before 1950 (see Chapter 18; and specific citations in the overall reviews by Corliss, 1961, 1968, 1974a). On the other hand, the view of workers such as Poljansky (e.g., see Cheissin & Poljansky, 1963; Poljansky & Cheissin, 1965), Jankowski (1967a, 1973c, 1975), and, to a lesser extent, Raabe (1964c) cannot be disregarded. In their support of the taxon rank of class for the group, they emphasize that knowledge of the probable phylogenetic ancestry of suctorians should not necessarily dictate their present position in the classificational hierarchy. They could have arisen, it is pointed out, from hypostomes or gymnostomes without having to be classified, today, as a closely neighboring taxon to either of those groups (see Chapter 17 for further discussion). Admittedly, there is certainly no problem in visualizing a high value for the group's "gap size of distinctness" with relation to most other ciliate taxa (see Chapter 3).

Therefore, I have taken somewhat of an intermediate or compromise position here. Along with many other ciliatologists, generalists and specialists alike, I no longer believe that the group should be considered "merely" another order of (the former) holotrichs. But I do think that it is appropriate to place it – as a separate and major subclass (in recognition of its combination of unusual characters) – within the class Kinetofragminophora (Corliss, 1974a, 1975b, 1977a).

This action is not too dissimilar from the recent conclusion reached by mainly French protistologists (de Puytorac et al., 1974), who used a superordinal rank for the group. In view of both its probable phylogeny and the fact that it possesses similar if not homologous ultrastructural characters in common with many other members of the phylum, setting it completely apart seems no longer defensible. Notwithstanding this overall conclusion, many suctorian species remain enigmatic, and the whole fascinating group is in need of sound taxonomic revisory study. Some further details in the characterization of the subclass follow.

As sedentary creatures, their attachment to the substratum (usually parts of the bodies of aquatic invertebrates) is, with rare exception, by means of a noncontractile stalk, of variable length, or a lorica. The stalk is produced by the scopuloid, to use Lom's (1971) appropriate term, and may have a specialized attachment disc at its distal end. Some species are colonial. A few are passive floaters in aqueous habitats, and some endoparasites are also stalkless. The body may be of odd shapes, caused mainly by protrusion of bundles of tentacles, etc. Sizes range from small or very small (e.g., *Podophrya* may have a diameter of only some 10–15 μm) to large or even very large (e.g., the stalkless "syncytial" *Dendrosoma* may stand well over 3 mm in height; and the common *Ephelota* may have a diameter of 250 μm, with a stalk 1.5 mm in length).

In the mature form, an infraciliature is present, comprising several rows (kinetofragments) of barren kinetosomes located near the contractile vacuole pore in most of the few species studied ultrastructurally to date, except for members of the third suborder. Parasomal sacs are present, associated with the kinetosomes. Kinetodesmata have been seen in some species. There is no cytoproct. The organisms are predators for the most part, the free-living ones feeding on other ciliates in particular.

The tomite or bud stage in the life history is often of very short duration. But it represents a very important form from the pragmatic point of view of dispersal and survival and from the theoretical point of view of possible "recapitulation" of the group's phylogenetic origin. It bears cilia (with rare exception), arising from an infraciliature received directly from the parental form; makes a new stalk, via secretions from the pores of the scopuloid; and produces new tentacles, possibly with some sort of kinetosomal involvement. The kinetids of the larvae have associated with them an array of basal bodies, fibers, and microtubules not unlike that now becoming known so well ultrastructurally in a great variety of ciliate groups. The infraciliary pattern appears to be a homologue of that shown by the ventral right-hand field of the cyrtophorid hypostomes. Mucocysts and parasomal sacs are also present in this migratory form which, sometimes within minutes, will commence metamorphosis into the sedentary, tentacle-bearing, nonciliated adult stage in the usual life cycle. (Even a long and complex stalk may be fully produced in one hour's time, according to Noble, 1932.) Some of the vermiform exogenine tomites look and act amazingly worm- or caterpillar-like, creeping over their substratum (e.g., host integument) like an inch-worm.

Understandably, the most studied part of the suctorian body has been the ingestatory (sucking) tentacle, especially since the advent of electron microscopy. Physiologists have long been fascinated with this complex and remarkable feeding organelle, and mysteries surrounding its exact mode of operation are yet to be solved. It may be thought of as a specialized cytostome-cytopharyngeal apparatus, and its substructure is rich in microtubular arrays distinctive for various taxonomic groups within the order. Enclosed in it (and becoming functional at its tip) are also the curious minute organelles now known as haptocysts, thought to be a kind of toxicyst or "microtoxicyst" by some protozoologists. At its distal end are also numerous vesicles apparently serving as a source of food vacuolar membranes. Recent papers and/or reviews of the combined problem of "micro-" form and function in these appendages are included in the suctorian literature cited at the end of this chapter. The number, arrangement, and distribution of tentacles (including the prehensile or nonsuctorial kind) are important diagnostic characters. In a few species, incidentally, all of the tentacles have been (secondarily) lost. Tentacles are often grouped into bundles, and sometimes (the bases of) these bundles, but not the microtubular arrays within a given "subsidiary" tentacle, are branched.

Conjugation in the Suctoria may be of any one of the three possible ciliate types (Raikov, 1972a): temporary, total with unequal conjugants, or total with equal conjugants. Curiously enough, all three kinds apparently may occur within a single family (or is such a family seriously in need of taxonomic attention?). Special conjugation tubes may be developed between members of a pair in temporary association (e.g., see Lanners, 1973a).

Species occur abundantly in fresh-water, brackish, and marine (majority here) ecosystems, typically attached to a substratum of one kind or another, including algae and other vegetation, other protozoa, and aquatic invertebrates of many groups (crustaceans, molluscs, insects, rotifers, coelenterates, annelids, arachnids, etc.), except echinoderms (on which no stalked ciliates of any group are apparently to be found). However, they also occur as symphorionts on semi-terrestrial organisms, such as turtles (Goodrich & Jahn, 1943). As endosymbionts, they have been reported from peritrich ciliates, other suctorians, the respiratory surfaces of invertebrates and fishes, and the intestinal tract of various animals, including such mammals as horses, elephants, and guinea pigs. Symbiotically, the Suctoria are the most widespread of all ciliate groups.

Despite the diversity shown within the subclass, I am maintaining a somewhat conservative approach to the grouping of the species at the next lower taxonomic levels, recognizing but a single order and three suborders (as opposed to the many of each proposed by Jankowski, 1967a, 1973c, 1975, and the multiple suborders endorsed by Batisse, 1975). The literature on the whole assemblage is treated at the end of this chapter, following brief consideration of the order and its suborders below. Representative genera are depicted in the set of figures on page 109 (Plate X).

Order SUCTORIDA

Characteristics may be found above (under subclass), since this is the only included order. The problem of how best to further subdivide the group is most difficult – perhaps the reason for ciliatologists' apparent satisfaction, down through the decades, with dropping down directly to families! The principal sets or groups of sources of characters available, as Collin (1912) recognized long ago, are: adult morphology, particularly features of the tentacles, stalk, and lorica; larval morphology, especially the pattern of ciliature and the body shape and size; mode of reproduction, that is, the type of budding process exhibited; and overall life cycle, including type of conjugation, colony-formation, mode of cystation, habitat preference, feeding habits, and association with other organisms. Even for the nonsuctorian specialist, it soon becomes clear that many genera within classically established families, and all too often even species within "well-known" genera, show diversity with respect to practically any single given character. Obviously, a thorough and very time-consuming systematic revision is called for, one well beyond the scope of the present treatise. In the authoritative paper by de Puytorac et al. (1974), no suborders were mentioned. In my own recent papers (Corliss, 1974a,b, 1975b), two suborders were adopted, essentially following Jankowski (1973b,c), with credit to Collin (1912) for the names: Endogenina and Exogenina. Now (and see Corliss, 1977a), I am adding a third one, the Evaginogenina, with name supplied by Jankowski (1975), the concept basically by Guilcher (1951), some new differentiating characters by Curry & Butler (1974), and the resulting overall characterization by me. Thus, I have made my choice, considering – even if rather conservatively (contrast the seven suborders proposed by Batisse, 1975, on the same basis) – the type of budding process to be of cardinal importance in the high-level taxonomy of the suctorians.

Suborder (1) Exogenina

As the name implies, species assignable to this suborder undergo a kind of budding in which no appreciable invagination of the parental cortex is involved. Basal bodies destined to provide the locomotor cilia on the body of the transient larval stage are present in subpellicular locations, typically near a contractile vacuole pore, and apparently undergo multiplication in the area before the actual budding-type of cell fission has commenced. Another characteristic of differential diagnostic value is the frequent occurrence of actinophores. A high level of morphological diversity is recognizable among exogenine groups in general.

Depending on the family (or sometimes the genus or even the species), budding may be monogemmic or polygemmic. In the second (rarer) case, the divisions are either "multiple-successive" or "multiple-simultaneous" (= essentially synchronous). A commonly cited example of the latter is found in *Ephelota*, a genus the species of which are also known for their exhibition of two kinds of tentacles, one prehensile and nonsuctorial. What might be considered an extreme in monogemmy, occurring in some *Podophrya*, results basically in a simple binary fission of the organism, both filial products being of practically the same size. The tomites or buds are typically large and possess a complex ventral ciliature, reminiscent of the pattern known in some groups (especially the cyrtophorids) of the preceding subclass of hypostomes. The larval forms produced by species in several families are of unusual shape, long and vermiform, and are practically naked of cilia, thus incapable of swimming. Are these regressive or primitive traits? Jankowski (1973c) considered suctorians with such buds, his "Vermigemmida," to comprise an entirely separate taxon: see Chapter 18. So did Batisse (1975), though only at the subordinal level; in fact, four of Batisse's suborders are included in my Exogenina, since I do not recognize minor refinements in methods of budding as constituting a broad enough basis for taxonomic separation at such a high level.

Although several well-known genera include fresh-water species, most of the many members of this suborder are marine forms, free-living or ectocommensal. A few are parasitic; a few produce loricae. I tentatively place Kozloff's (1966) amazing *Phalacrocleptes* here. It is a parasitic form (on a polychaete annelid) which has no cilia, even no infraciliature (i.e., kinetosomes); and no budding stage is present in the known life cycle; but the organism does possess very short tentacles (Lom & Kozloff, 1967). Another unusual form is the "two-generation" species of *Tachyblaston* which lives in and on another exogenine, *Ephelota* (see Grell, 1950). Perhaps the most polymorphic of all is the *Podophrya* species investigated so thoroughly by Fauré-Fremiet (1945a).

Suborder (2) Endogenina

The numerous species allocatable here manifest a type of budding accurately described as fully endogenous. The substance which will comprise the body of one or more larval tomites is produced below the surface of the adult form, in the brood pouch or embryo sac. Then the bud, having been pinched off internally and thus fully formed, emerges in due time through a birth pore, an opening which marks the site of original inpocketing of the parental cortex to form the pouch. "Marsupium" and pore are both temporary structures. Before the buds become fully differentiated, the reproductive process in endogeny is similar to that described above for members of the Exogenina; that is, a small but permanent field of nonciliferous kinetosomes located near a contractile vacuole of the parental organism is the ultimate source of the ciliature (and infraciliature) of the migratory form(s). The larval form here is typically small, with one or more bands of equatorial (encircling) ciliature. Since cytokinesis occurs within the brood pouch, the bud(s) may even move (swim) freely about within the body of the parental form before exiting to the outside for more or less wide dispersal. Both monogemmy and polygemmy (consecutive or synchronous) are exhibited.

Tentacles often occur in bundles, rather than singly; but actinophores are indistinct or absent. Loricae are produced by some species; and others can form colonies. Certain "ramified" forms (e.g., the incredible *Dendrosoma*) grow to an enormous size. The gamut is run with respect to kinds of habitats invaded: from fresh-water and marine ecosystems, free-living or ectosymbiotic, to existence as endocommensals in hosts ranging from other protozoa to metazoa (where the lining of the digestive tract is a common site of attachment). An amazing ecological diversity! This is probably the largest suborder (in species). A few (not the largest nor most common) genera of particular interest are *Anarma*, from the carapace of fresh-water turtles; *Allantosoma*, without stalk, in the caecum and colon of horses (possibly a most unique suctorian); *Endosphaera*, endosymbiont of peritrich ciliates, fresh-water and marine; *Choanophrya*, with its 10–12 tentacles

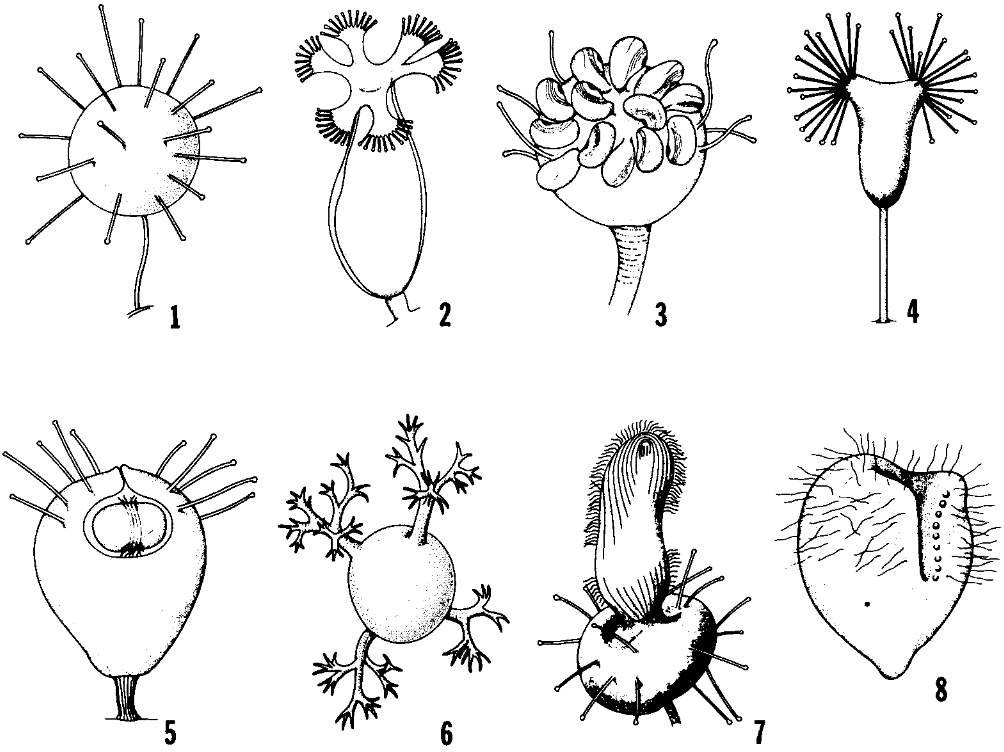

PLATE X. Representative suctorians (order Suctorida). Fig. 1. *Podophrya*, suborder Exogenina. 2. *Asterifer* (syn. *Ophryodendron* p.p.), suborder Exogenina. 3. *Ephelota* (with buds), suborder Exogenina. 4. *Acineta*, suborder Endogenina. 5. *Tokophrya* (with bud), suborder Endogenina. 6. *Dendrocometes*, suborder Evaginogenina. 7. *Discophrya* (with bud), suborder Evaginogenina. 8. *Cyathodinium*, suborder Evaginogenina. [Additional figures appear in Chapter 20.]

expansible at the distal end, enabling engulfment of large food particles; *Rhyncheta*, with a very short stalk and a single "primary" tentacle of great length and high mobility; and *Pottsiocles*, parasitic on marine *Cothurnia* and folliculinids, attached to host in the lorica by four delicate tentacles and possessing no stalk at all – the scantily ciliated "swarmer" precociously has (pair of) tentacles, also, and no "presumptive" stalk.

Suborder (3) Evaginogenina

The taxonomic significance of Guilcher's (1951) precise recognition of a third major mode of bud production in suctorians has long been overlooked. Perhaps the principal reason for this has been the lack of similar studies on other species which may well belong in the same category. Even now, from a pragmatic point of view, we do not know how many members of the large family "Discophryidae" resemble Guilcher's *Discophrya piriformis* in its remarkable kind of gemmation. At any rate, the principal distinguishing character of the present suborder is indeed the exhibition of an "evaginative" kind of tomite formation. A brood pouch is again formed (as in endogenous budding), but the larval form is not produced free within the body of the parental form. The entire "wall" of the pouch literally evaginates – turns inside out – to form the (usually single) tomite, with the process of cytokinesis finally taking place completely on the outside ("exogenously," in effect) of the body of the adult suctorian. No permanent field of nonciliferous kinetosomes is present in the vicinity of the contractile vacuole in the (few) suctorians showing this kind of budding which have been carefully examined to date. Brood-pouch formation is initiated almost anywhere on the surface of the parental organism, wherever a single presumptive(?) subcortical kinetosome may be located. Multiplication of basal bodies occurs, followed by their subsequent invagination. Later, evagination takes place as a rapid and continuous process (Dragesco produced a splendid film of this amazing phenomenon, years ago); and the pouch and the "birth pore" (not such an accurate term in this case) "disappear" as the large larval form, with its ventral surface bearing cilia, detaches and swims away.

The members of the old Discophryidae which I include with the known "evaginative" forms are not particularly spectacular in morphology or life cycles, in comparison with some members of the preceding suborders. Monogemmy seems to be the general rule; loricae are generally absent; habitats vary. In the family Dendrocometidae, however, one does find some unusual forms. For example, *Dendrocometes* itself – the "hatrack" suctorian so commonly found on fresh-water gammarids – has always been cited for its strikingly branched tentacular arms or trunks. And in another family we find the aberrant *Cyathodinium*, never properly classified in the literature (because only recently have we learned that it has rudiments of tentacles in its cytoplasm: Paulin & Corliss, 1969), an endocommensal in domestic and wild guinea pigs (see da Cunha, 1914c, and especially da Cunha & de Freitas, 1940). For *Heliophrya* (and two other genera), I am erecting a new family: the organisms involved show a number of special features (see Dragesco et al., 1955; Gönnert, 1935; Lanners, 1973a,b; Matthes, 1954a; Rieder, 1936b; Saedeleer & Tellier, 1930; Spoon et al., 1976; and Chapter 20). The evaginogenine group, very small at the moment, should grow with time, mainly by transfer of suctorians currently residing – without the benefit of knowledge to the contrary – in the other suborders, especially the Endogenina.

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The literature list on members of the Suctorida is a lengthy one and dates from the investigations of inquisitive protozoologists who were peering through their microscopes over 200 years ago. Reference to much of the earlier work may be found in Canella (1957), Collin (1912), Corliss (1961), Guilcher (1951), and Kahl (1934b). (The last-mentioned taxonomic monograph is much-neglected, considering its originality and its features of lasting value: at the same time, recall that its coverage was restricted to mostly marine species.) Major pre-1960 papers which should not be forgotten are Hadži (1940a,b); the several series by Matthes, including one on *Discophrya* (see Matthes, 1954b; last of that series) and the one in which the Thecacinetidae are described as a new family (Matthes, 1956); Nozawa (1938); Pestel (1932); the monographic works by Penard (1920), Rieder (1936a,b), and Wailes (1943); the several unusual earlier papers by Kormos (1958a,b) and Kormos & Kormos (1957a–c, 1958a,b); Swarczewsky's (1928b–e) valuable studies on symphoriontic species of Lake Baikal; and Lucas (1932a,b) and Nie (1950) on *Cyathodinium*.

Since 1960, the kinds of literature available fall roughly into three main categories: ecological (including parasitological) studies; (gross) morphological, morphogenetic, and taxonomic works; and research involving electron microscopy. Some important papers in these general areas are cited below; I am arbitrarily not placing any work in more than one category, even though the contents of a number of the publications contain data of an overlapping nature.

A sampling of recent papers in the area of general ecology or parasitology would include: Bick (1972), Borror (1973a), Clément (1967a; Clément-Iftode, 1967b), Fenchel (1965b), Gittleson & Hoover (1969), Jankowski (1963, 1973f), Kozloff (1966), López-Ochoterena (1966), Matthes (1971, 1973), Matthes & Stiebler (1970), and Wenzel (1961a). In many fresh-water habitat surveys, suctorians are nearly as commonly represented as any other free-living or epibiotic kinetofragminophoran group. Ball (1969) may be consulted for an up-to-date review of the "parasitic" association ("ecto-" and "endo-") of species with other ciliates. Some of the cases described before 1960 represent incredible adaptations to a truly unusual way of living (e.g., see

Chatton & Lwoff, 1927; Fauré-Fremiet, 1943a, 1945a, 1948e; Grell, 1950).

Studies on the general (nonultrastructural) morphology, morphogenetics, life cycles, and systematics of species of the Suctorida have not been especially plentiful during the past 15–20 years. However, the following papers serve as good examples, and some of their bibliographies represent convenient sources of many pre-1960 works of significance: Bowman (1977), Culbertson & Hull (1962), Curry & Butler (1974), Dragesco et al. (1955), Hitchen & Butler (1972), Hull (1961a,b), Jankowski (1967a,f, 1970, 1972a, 1973c,d, 1975), E. E. Jones (1974b), Kormos (1971a,b), Kormos & Kormos (1960a,b, 1961), Lanners (1973a,b), López-Ochoterena (1964), Matthes (1962, 1963, 1972b, 1974), Matthes & Gräf (1967), Matthes & Plachter (1974, 1975), and Wenzel (1961b). General accounts are given in textbooks of protozoology; Kudo (1966) probably represents the best overall coverage in English, brief and incomplete (and sometimes incorrect) though he actually is; Lepşi's (1965) often overlooked book includes some 28 pages on suctorian taxonomy – in Roumanian – and is relatively profusely illustrated. Batisse's (1975) very recent paper is of special importance in that it treats the taxonomy of the whole order, though necessarily very briefly, and it also merits attention as a precise review of the many types of budding recognizable.

The field of protozoan ultrastructural research is booming today and suctorians have been included in a number of significant investigations or continuing series of studies (particularly by such workers as Bardele, Batisse, Butler, Curry, Paulin, Rudzinska, and their associates). The following papers represent the modern literature (purposely no work predating 1965 is cited here) in this area reasonably well (although it is not intended to be exhaustive); topics covered are several, but the major one, not surprisingly, is concerned with the form and supposed function of the suctorial tentacle: André & Fauré-Fremiet (1967a), Bardele (1968, 1970, 1972, 1973), Bardele & Grell (1967), Batisse (1965b, 1966a, 1967, 1968, 1969a,b, 1970, 1973), Curry & Butler (1975, 1976), Hascall (1973), Hascall & Rudzinska (1970), Hauser (1970, 1972), Hauser & van Eys (1976), Henk & Paulin (1977), Hitchen & Butler (1973a,b, 1974), Jurand & Bomford (1965), Lom (1971), Lom & Kozloff (1967), Mignot & de Puytorac (1968a,b), Millecchia & Rudzinska (1968, 1970a,b, 1971, 1972), Paulin & Corliss (1969), Rudzinska (1965, 1967, 1970, 1973), Spoon et al. (1976), Tucker (1974), and Tucker & Mackie (1975). Grell's (1973) textbook deserves mention for its excellent coverage of ultrastructural aspects in the biology of the Suctorida.

Researches on the physiology of these fascinating organisms, incidentally – other than those covered directly or indirectly by various of the references given above – are not numerous. Kitching's (1967) review of contractile vacuolar function in protozoa includes treatment of some important experimental work, mostly carried out in his own laboratory, in which suctorian species were employed to advantage.

Chapter 10

Class Oligohymenophora: (1) The Hymenostomes *Sensu Lato* and *Sensu Stricto*

The hymenostome ciliates, as has been clearly recognized for some time (Corliss, 1961), stand neatly midway between the vast class of "lower" ciliates considered in preceding chapters and the compact but highly distinctive class of "higher" forms treated in Chapters 14–16. The intermediate position is particularly recognizable with respect to several general characteristics to be discussed immediately below. At the same time, I should stress not only that there may be important exceptions or even embarrassing discrepancies in such a sweeping claim but also that the long and independent evolutionary histories of the several groups involved have allowed appearance of complex and specialized features, have permitted convergent characters to emerge, etc., thus making any insistence on simplistic conclusions – for example, concerning phylogenetic interrelationships – highly unwise.

The class Oligohymenophora is composed of two large assemblages at the subclass level: the hymenostomes *sensu lato*, the Hymenostomata, and the peritrichs, the Peritricha, with one of the three orders of the former taxon set aside for the secondarily "simplified" astomes. Since astomes and peritrichs are considered in subsequent chapters, as specialized groups, most of the remarks made here treat the hymenostomes as reasonably representative of the whole class. This leaves us with two orders (comprised of a total of six suborders) – the Hymenostomatida and the Scuticociliatida – to contrast with the gymnostomes, vestibuliferans, hypostomes, and suctorians, on the one hand, and the polyhymenophorans (heterotrichs, odontostomes, oligotrichs, and hypotrichs), on the other. Following general discussion of the class (essentially via its first subclass, and that via the two orders), the order of hymenostomes *sensu stricto* is treated in more detail, reserving further consideration of the scuticociliates for the following chapter. A new "primitive" oligohymenophoran order, the Parahymenostomatida, incidentally, has very recently been proposed by Grain et al. (1976) to contain the controversial nassulid hypostome genus *Furgasonia* (formerly known as *Cyclogramma*); until additional data of a supporting nature are available, however, I am not accepting that proposal (see Chapter 20).

The oral ciliary apparatus of the hymenostomes *sensu lato* (as "typical" oligohymenophorans) illustrates their intermediate taxonomic position in the phylum. The kinetofragminophorans run the gamut from truly *no* oral ciliature to "franges" of various sorts and, rarely, to organized or semi-organized fields or tufts sometimes in a simple depression (see Chapters 5–9). The polyhymenophorans, on the other hand, are distinguished by their possession of highly distinct buccal membranelles organized as an adoral zone in a prominent buccal cavity of a broad and well-differentiated peristomial area (see Chapters 14–16). In the hymenostomes, we find that, while the oral ciliary apparatus is well defined, it is often inconspicuous and is composed of only three or four specialized membranes or membranelles. The latter are, however, located in a buccal cavity, a feature of the oral area which, as I define it, is absent from the "lower" ciliate groups. A common arrangement in the hymenostomes is an adoral zone of three membranelles *sensu lato* on the left and a single paroral membrane ("stichodyad" of de Puytorac & Grain, 1976) on the right; the infraciliature of such an apparatus is thrown into bold relief by silver-impregnation techniques.

The modes of stomatogenesis in the hymenostomes (following Corliss, 1973e) are parakinetal and buccokinetal, whereas the predominant pattern is telokinetal in the evolutionarily less advanced groups and apokinetal in the "higher" ciliate orders. The mouth area is seldom apical, in contrast with the typical situation in the gymnostomes, but the cytostome is permanent and open. Reproduction is commonly by isotomic binary fission, occasionally by palintomy within a reproductive cyst. Body ciliation is often, though not always, uniform and heavy (i.e., "holotrichous") in hymenostomes (including astomes); but it shows a great diversity among the kinetofragminophorans and distinct tendencies toward sparseness ("oligomerization") in many groups of the polyhymenophorans. Kinetodesmata, generally absent in spirotrichs and consistently present in perhaps only apostomes and haptorids (plus a few other scattered infraordinal groups) among the kinetofragminophorans, are typical of members of all three orders of the hymenostomes (and of peritrichs as well). Pellicular alveoli are well developed.

Body forms vary, and sizes of hymenostome and scuticociliate species cover a broad range, although a medium length (65–150 µm) is common; sessility, lorica- or colony-formation, and cystation are relatively rare. A wide diversity in ecosystem preference is also exhibited; a number of species enjoy symbiotic association with vertebrate or, more commonly, invertebrate hosts. Probably no conclusions of much taxonomic or evolutionary significance can be drawn from such general morphological or ecological considerations, including the additional observation that a majority of hymenostomes are free-living and free-swimming, are found predominantly in fresh-water habitats, and are microphagous filter-feeders. Furthermore, there are many – and important – exceptions; and one should recall that the marine environment, in particular, has been woefully neglected as the potentially rich source of ciliate species, for all taxonomic groups, which we are just now beginning to appreciate it to be.

Order HYMENOSTOMATIDA

A number of general characteristics have already been given above or are best considered comparatively in treatments of the suborders which follow. All members are "membrane-mouthed" (except for special cases involving supposed secondary loss) and possess a usually well-defined buccal cavity. Oral membranelles, few in number, have infraciliary bases typically three to eight rows of kinetosomes in width; the infraciliature of the single-pieced paroral membrane is comprised of two files of basal bodies, with the dyads arranged in a characteristic zigzag pattern.

In the kinetosomal territories, parasomal sacs are present, as is a wealth of associated fibers and microtubules. Nematodesmata, as such, however, are present only in species of the suborder Peniculina. No scutica is detectable during the morphogenetics of stomatogenesis. There are no toxicysts, and only the Peniculina exhibit explosive trichocysts; but mucocysts are common, and contractile vacuole pores are universally found. The cytostome (rarely absent) is on – but below – the ventral surface, usually in the anterior half of the body. Stomatogenesis is parakinetal or buccokinetal. The cytostome-cytopharyngeal complex is permanent; in a few tetrahymenine species a "receiving vacuole" is present in the macrostome form of the organism's life cycle. A primary ribbed wall of some complexity is located on the right side of the buccal cavity. Somatic kineties are essentially bipolar and ciliation uniform. Habitats are diverse, but fresh-water (and nonloricate) forms particularly predominate in this order. Of interest is thus the singular case of a possible "fossilized" paramecium: in amber, probably from the Cretaceous period, according to the very brief report in Wichterman (1953, p. 94).

The hymenostomes *sensu stricto* are now subdivided taxonomically into three suborders: the Tetrahymenina, the Ophryoglenina, and the Peniculina. One (the Ophryoglenina) is additional to the three recognized in the Faurean classification (see Corliss, 1961); but one of those former groups (the Pleuronematina) has now been removed *in toto* to the following order of scuticociliates. References to the literature are made following treatment of each suborder. But mention might be made here that two of the four best-known (= most popular) and most widely studied (= most often written about) genera in the whole phylum, which contains a total of over 1,100 bonafide genera, are to be found among the hymenostomes *sensu stricto*: *Paramecium* and *Tetrahymena*. (The third, *Vorticella*, belongs to the neighboring subclass of peritrichs; while the fourth, the heterotrich *Stentor*, is a member of the class Polyhymenophora.)

Representative members of the Hymenostomatida are depicted in the set of figures appearing on page 118 (Plate XI).

Suborder (1) Tetrahymenina

The species assigned here are the least highly differentiated among the hymenostomes, generally small in body size and with an inconspicuous buccal ciliary apparatus. Stomatogenesis is parakinetal; rarely more than one somatic kinety, the right-most of two or more postoral meridians, is involved in the production of the anlage for the mouthparts of the opisthe. The proter usually inherits the oral ciliature, with limited or partial dedifferentiation, directly from the parental cell, intact; or full resorption may occur, with reappearance via the phenomenon of *in situ* oral replacement. Experimentally, kineties other than "meridian number 1" have been observed to function in stomatogenesis (e.g., see Nanney, 1967); but this lability in the laboratory need not be considered to invalidate the taxonomic value of recognizing kinety number 1 as being normally associated with the important process of new-mouth formation in most tetrahymenines in nature.

Mucocysts are present; and there is a single contractile vacuole, with one to several pores. There is no area of specialized thigmotactic ciliature; caudal setae are rarely present, and, when so, are usually limited to a single lengthier but inconspicuous cilium. There is a preoral but no postoral suture. Amicronucleate races or strains are common in *Tetrahymena* (see Corliss, 1952a, 1953b, 1973b). Although cysts, loricae, etc. are commonly absent, a few species exhibit strikingly polymorphic life cycles which may include both resting and reproductive cystic stages. The occurrence of homopolar doublets, both naturally forming and experimentally inducible, should be noted. Most members of the suborder are bacteria-feeders, but a few are histophages; and the macrostome forms in polymorphic species may be carnivorous, even cannibalistic. Axenic cultivation is possible, and a few species have finally been established successfully on a chemically definable medium (most notably many strains of the *Tetrahymena pyriformis* complex): this is most convenient – and, of course, essential – for conducting "high-powered" experimental biochemical research. [More data on characteristics appear in the literature section, below.]

Included species are found primarily in fresh-water ecosystems (including caves) with a few in marine habitats; some are edaphic; and several exhibit symbiosis, to varying degrees, mainly with invertebrate hosts. The suborder is now comprised of four families: the Curimostomatidae, containing mouthless (presumably secondarily) forms obligately endoparasitic in various freshwater invertebrates (snails, limpets, clams, and turbellarians); the Glaucomidae, mostly fresh-water forms formerly assigned to the oversized Frontoniidae and then to the Tetrahymenidae; the Tetrahymenidae as presently recognized, containing, among other genera, the exceedingly well-known *Tetrahymena*; and, controversially, the Turaniellidae (see special treatment of this family in the "Addendum" at the end of this chapter, page 124).

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Papers published on the small family Curimostomatidae are so few in number that all of them which contain original cytological or parasitological observations may be listed: Kay (1946b), Kepner & Carroll (1923), Kozloff (1954), Lom (1961c), and Poljansky (1925, 1926). But credit for various decisions concerning its taxonomy – first, removing the group, all or partially, from the order Astomatida; next, erecting a new family to contain it; and, finally, consolidating its position within a revised suborder Tetrahymenina – should also be mentioned, by citing the following workers responsible for these actions: Kozloff (1954) and Corliss (1961); Jankowski (1968c); and Corliss (1971b). There are two genera: *Curimostoma* (often misspelled "*Curinostoma*") and *Dogielella*.

Members of the rather recently erected Glaucomidae have not received a great deal of attention in the modern literature, although *Glaucoma chattoni* was at one time becoming popular in experimental work (e.g., see Cho, 1971a,b; Erwin & Bloch, 1963; Frankel 1960a,b, 1961; Holz et al., 1961; Holz et al., 1962; Klug, 1968; Pitelka, 1961) and has very recently been studied from cytological and morphogenetic points of view by McCoy (1975a) and especially Peck (1975). Older sources of papers may be found in Corliss (1961) and Kahl (1926, 1931c, 1935b). In Corliss

(1971b), the publication in which the family was established, there are many references of pertinence to which should now be added Savoie & de Puytorac (1970) and de Puytorac, Savoie & Roque (1973) on the new species, *Glaucoma ferox*; and Grolière (1977) on a new genus, *Glaucomella*. *G. scintillans*, type-species of the genus, is a common, small, fresh-water ciliate seen by many protozoologists (and ecologists) over the past 150 years. Recently, attempts have been made to recognize mating types in it (Nakata, 1969; Phillips & Abraham, 1969). The organism labeled "*G. pyriformis*" off and on since the 1880's turns out to be a member of a different and very important genus (see below), *Tetrahymena*: so (but) one must (still) be very careful in reading the older (especially pre-1950) literature not to become confused by the nomenclature then often in vogue (the problem was finally officially resolved by the International Commission on Zoological Nomenclature, 1970, in approving a lengthy petition on the subject submitted by Corliss & Dougherty, 1967). *Epenardia* is definitely a member of the Glaucomidae; and *Espejoia* very likely belongs here (most recent studies are those by Didier et al., 1977, and Fryd-Versavel et al., 1975). Half a dozen additional genera require further study, though tentatively assigned here (see Chapter 20). Recent systematic reviews are to be found in Corliss (1971b), Czapik (1968b), Dragesco (1970), and McCoy (1975a); older works of importance include Bary (1950a), von Gelei (1936), Kahl (1926), and Penard (1922). [For family Turaniellidae: see "Addendum," end of chapter.]

The family which has really caused a boom in the literature – almost entirely via its type-genus – is the Tetrahymenidae. Of the other included genera, only *Colpidium* and perhaps *Deltopylum* are known at all outside a small circle of specialists; and it should be recalled that the once-popular *Leucophrys* has fallen as a synonym of *Tetrahymena*. The principal reason for *Tetrahymena*'s popularity is directly related to the ease with which its species can be cultured in the laboratory. Thus physiological, biochemical, biophysical, morphogenetic, ultrastructural, genetic, and all sorts of refined experimental researches using sophisticated instrumentation, etc. can be carried out most handily on such highly cooperative ciliates. Members of the *T. pyriformis* complex have been hailed as the "*Escherichia coli* of the nonphotosynthetic eukaryotes" (Hutner et al., 1972) and even as the "star performers" of the entire subkingdom Protozoa (Kidder in Hill, 1972) – accolades not easily won.

Czapik (1968b) has reviewed the Tetrahymenidae overall; Corliss (1971b), Jankowski (1964b,c, 1967b), and Thompson (1963) have also included observations on the taxonomy of the whole group. *Deltopylum* has been studied by Czapik (1968c), Dragesco & Njiné (1971), Fauré-Fremiet (1969a), and Mugard (1949); *Stegochilum* has been resurrected by Jankowski (1964b), and *Lambornella* by Corliss & Coats (1976). *Colpidium*, whose name was long embroiled in the taxonomic confusion over what are now recognized as species of *Tetrahymena*, is a genus with bonafide species of its own. Badly in need of the same kind of review which finally has been made of *Glaucoma* and *Tetrahymena* (see Corliss, 1971b, 1973b), *Colpidium* continues, nevertheless, to receive attention in the modern literature via isolated papers on the morphology and physiology of various of its members: for example, see Burbanck & Williams (1963), Cheissin & Mosevich (1962), Dive (1974), Dive et al. (1975), Fernândez-Galiano & Ruiz (1973), Foissner (1969a–c, 1970a,b, 1973), Foissner & Simonsberger (1975a,b), Jankowski (1967b), Laybourn (1975), McCoy (1974c), Morat (1970), and Mosevich (1963); and note the experimental ecological works by Dive & Leclerc (1977), Legner (1973), and Taylor & Berger (1976). The aging but unusual cytological study of chromosomes of *Colpidium* by Devidé (1951) warrants special citation.

With respect to the popular genus *Tetrahymena*, easily available recent sources serving as excellent references to the bulk of the more than 3,000 papers published on its species since 1940 (the year of the naming of the genus) are Corliss (1973c), Elliott (1973a), and Hill (1972). But readers here may wish to have immediately and directly available some additional specific citations; so a few are provided below under four major (but inevitably overlapping) categories of research in what one might call the field of "tetrahymenology."

(1) Systematics (including some corticotypic analyses), ecology, and general biology (including parasitism). Subsequent to the older works of the 1880's and scattered papers of the early 1900's, we reach the landmark paper of Furgason (1940); this was followed, in due time, by

contributions from Corliss, Czapik, Elliott, Fauré-Fremiet, Frankel, Kirby, Kozloff, Loefer, Mugard, Nanney, Njiné, Roque, J. C. Thompson, Jr., Williams, and others. A few of the major works, especially those of recent vintage and bibliographically rich or ones needing attention called to them or their topic, would include: Brooks (1968), Corliss (1965a, 1970, 1971a, 1973a), Corliss & Coats (1976), Czapik (1968b), Elliott (1973b), Frankel (1972), Gates & Berger (1974, 1976a), Gittleson & Hoover (1969), Hoffman et al. (1975), Loefer (1967), Loefer et al. (1966), Lynn (1975a), Lynn & Tucker (1976), McCoy (1974b, 1975b), Nanney (1972, 1975), Nanney et al. (1975), Njiné (1972), and Roque et al. (1971).

Species of *Tetrahymena* exhibit such a remarkable range in degrees of endoparasitism – from none to obligate, and amenable to experimental manipulation, as well – that the subject has merited special attention (see Corliss, 1972d, and references therein). Incidentally, the curious and poorly known cuticular-cyst-forming parasitic "*T. stegomyiae*" now turns out to be better considered as a species of *Lambornella* (Corliss & Coats, 1976). Available too late for detailed inclusion but most worthy of inserted mention is the very recent paper by Nanney & McCoy (1976) on characterization of some 14 separate species comprising the "*T. pyriformis* complex." The work parallels the taxonomic decision also made very recently by Sonneborn (1975a) with respect to the "*Paramecium aurelia* complex" (see a subsequent section of the present chapter) and helps set the stage for the future taxonomic-nomenclatural handling of syngens and/or other "genetic" or "physiological" groups now detectable within some of the other classical "morphological species" of ciliates. [Another relevant work, just out: Vaudaux et al., 1977.]

(2) Metabolism, growth, morphogenesis, and general physiology (more than two-thirds of all works on *Tetrahymena* to date have fallen into this category). The landmark paper was that of Lwoff (1923a); Kidder and Hall and their students, and their students' students, soon entered the field – and the mad rush into print was on! Shortly thereafter, the vast area of cell synchronization (with *Tetrahymena pyriformis* as the principal experimental organism) opened up, after the pioneering work of Zeuthen (e.g., 1953) and colleagues. Even all of the "principal investigators" are too numerous to mention here, but a short list should include the names of Buhse, Cameron, Conner, Elliott, Frankel, Holz, Hutner, Jahn, Loefer, Müller, Nilsson, Scherbaum, Seaman, Whitson, Williams, and Zeuthen.

Much of this "physiological-biochemical" literature (including, in a way, the following two categories as well) on *Tetrahymena* is not too difficult to find: the papers are many, the appropriate journals used as outlets are often very well known, etc. Nevertheless, a few of the major comprehensive reviews in the area under consideration may be cited as follows: Cameron (1973), Conner (1967), Conner & Koroly (1973), Dewey (1967), Everhart (1972), Frankel (1967), Frankel & Williams (1973), Hill (1972), Holz (1964, 1973, 1974), Hutner (1964a,b), Hutner et al. (1972, 1973), Kidder (1967b), Müller (1967), Nilsson (1976), Ryley (1967), Williams (1975), Zeuthen (1972), and Zeuthen & Rasmussen (1972). G. A. Thompson (1972) heuristically suggested *Tetrahymena*'s use as a model organism in the study of cell membrane phenomena (see also Baugh & Thompson, 1975; Csaba et al., 1977; Nozawa, 1975; Nozawa et al., 1975; Satir et al., 1973; Wunderlich et al., 1975; and others). The work by Organ et al. (1972) represented a significantly new way of viewing the "contractile vacuolar" system (CV's are termed water expulsion vesicles by these authors; but see also the very recent paper by Patterson & Sleigh, 1976). Gardonio et al. (1975) have developed a refined method of growing "colonies" of *T. pyriformis* on a solid (agar) substratum. Seaman & Reifel's (1963) review, often slighted, deserves inclusion here.

Recent papers of importance on a biochemical-morphogenetic approach to the study of *T. paravorax*, the most poorly known member of the *patula* complex (the three species which exhibit a striking reversible microstome-macrostome transformation in their polymorphic life cycles: see Williams, 1960, 1961, and references in Corliss, 1973b) are those by Didier & Metenier (1974), Dupy-Blanc & Metenier (1975), and Metenier (1975, 1977). Buhse's series on *T. vorax* (a species discovered and first studied nutritionally by Kidder et al., 1940), in which a combination of cytological, physiological, and ultrastructural techniques have been applied to a significant problem in morphogenesis, deserves at least partial citation here: see Buhse (1966a,b, 1967), Buhse &

Cameron (1968), Buhse et al. (1970), and Buhse & Rasmussen (1974). Some of the work by others on polymorphism has been cited in the preceding category; two papers on doublet formation should perhaps be singled out: Fauré-Fremiet (1948a) and Nanney et al. (1975). Seto & Tazaki (1971) have carried out an interesting but often overlooked study on carbon dynamics of *T. vorax* in monoxenic culture with *Escherichia coli.*

(3) Ultrastructural, biophysical, and other related molecular approaches. Here it is a little more difficult to single out tetrahymenological leadership in areas which are concerned with a diversity of cellular material and to cite convenient reviews of the literature which are limited principally to research on the ciliate *Tetrahymena*. But some of the protozoologically inclined cell biologists actively involved would include R. D. Allen, Child, Ehret, Gibson, Gorovsky, Hausmann, Munn, Murti, Pitelka, Ris, Satir, Swift, Wolfe, and Zimmerman. The overlapping with the categories treated above and below is so great that the general references given in those places, and in Corliss (1973c), Elliott (1973a), and Hill (1972), will suffice for an adequate coverage of the literature (which, however, continues to grow at a rapid pace). Nevertheless, the comprehensive ultrastructural works of R. D. Allen (1967, 1969), the chapter by Elliott & Kennedy (1973), the recent paper by Hartman et al. (1974) on RNA associated with *Tetrahymena*'s basal bodies, and the analyses of basal bodies by Wolfe (1970, 1972) ought to be specifically cited. An attempt to use SEM in analysis of a morphogenetic problem generally treated biochemically (stomatogenesis in *T. pyriformis*) is that by Buhse et al. (1973); and, more recently, Kolb-Bachofen & Vogell (1975) have carried out a morphometric ultrastructural study on mitochondrial biogenesis in the same species. Didier's (1976) important TEM study on membranellar cilia has just appeared.

In view of the significance of oral structures in ciliate systematics, the welcome confirmation of the tetrahymenal nature of the buccal apparatus in such small organisms as *Tetrahymena* – first determined long ago by light microscopy using silver-impregnated specimens – by electron microscopy (TEM and eventually SEM) is historically worth noting. Detailed references (to the earliest works, etc.) are available in Elliott (1973a), but the precise ultrastructural revelations by Williams and members of Zeuthen's group merit special citation: see Forer et al. (1970), Nilsson & Williams (1966), and Williams & Luft (1968). The more recent additional findings of Sattler & Staehelin (1974, 1976) and the very recent review by Nilsson (1976) ought to be mentioned, too.

(4) Genetics (chemical and otherwise), evolution, and nucleic acids. Although this, too, represents a conglomerate of separate "subfields," the breakthroughs in studies of sexuality in *T. pyriformis* have come with the discovery of mating types in 1952 (see Elliott & Hayes, 1953; Elliott & Nanney, 1952) and the report of linkage 12 years later (see S. L. Allen, 1964a,b). However, conjugation was beautifully described in *T. patula* (formerly *Leucophrys patula*) many many years earlier by Maupas (1889), reported in *T. chironomi* by Treillard & Lwoff (1924) and in *T. limacis* by Warren (1932) some 50 years ago, and first noted in *T. paravorax* by Elliott & Hayes (1954) over 20 years ago. The parallel phenomenon of autogamy was described in *T. rostrata* by Corliss in 1952 (Corliss, 1952b; and see especially Corliss, 1965b) in the very same year that Elliott and Nanney and students were discovering and exploiting conjugation in *T. pyriformis*. Numerous studies of considerable sophistication have now been carried out on the micronucleus (2N = 10; see Ray's, 1956, beautiful revelation of this) and the polyploid macronucleus of *T. pyriformis* (for recent examples, see Davidson & LaFountain, 1975; Murti, 1973; Orias & Flacks, 1975; Sugai & Hiwatashi, 1974; Vorob'ev et al., 1975; Yao & Gorovsky, 1974). [Most recent work on genetic organization of macronuclear subunits: Doerder et al., 1977.]

As approaches to the whole area represented by the above category become more and more chemical and molecular in nature, the leadership falls to such capable investigators as S. L. Allen, Bleyman, Byfield, Gorovsky, Leick, Mandel, Nanney, Phillips, Prescott, and their associates. The bulk of the literature published up to 1972 is covered, directly or indirectly, in Allen & Gibson (1973). Other reviews of pertinence include: S. L. Allen (1967), Borden et al. (1973a, b, 1977), Mandel (1967), McDonald (1973), Nanney (1974), Preer (1969), Prescott & Stone (1967), and Sonneborn (1974b). The papers by Gorovsky (1973; and Gorovsky et al., 1975) perhaps deserve special attention; and Allen & Li's (1974) work on nucleotide sequencing, Nyberg's (1974)

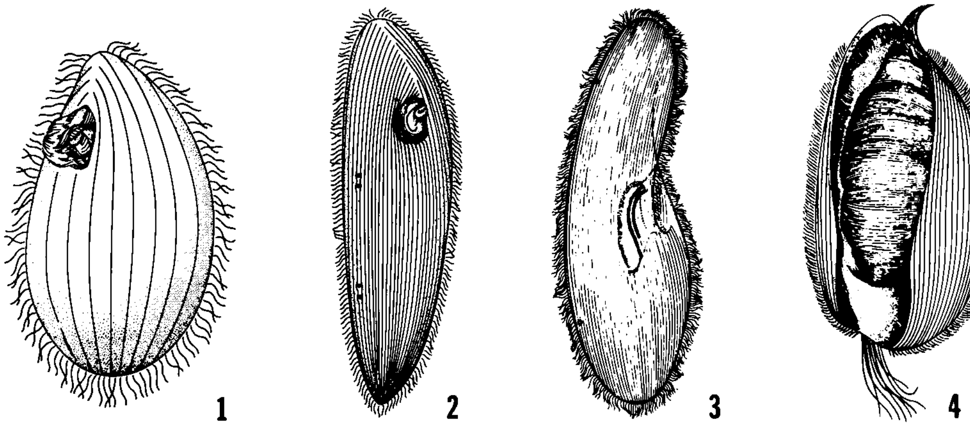

PLATE XI. Representative hymenostomes (order Hymenostomatida). Fig. 1. *Tetrahymena*, suborder Tetrahymenina. 2. *Ophryoglena*, suborder Ophryoglenina. 3. *Paramecium*, suborder Peniculina. 4. *Lembadion*, suborder Peniculina. [Additional figures appear in Chapter 20.]

observations on breeding systems and "stress," and Doerder et al.'s (1975) analysis of a genic mutant with altered cell shape also should be cited. What may be considered the "cytochrome *c*" breakthrough paper on *Tetrahymena* has very recently appeared: Tarr & Fitch (1976).

Suborder (2) Ophryoglenina

Large and common, yet forming a poorly known group, the ophryoglenines are primarily fresh-water, histophagous forms with dense somatic ciliation, swift swimmers in their "hunting" stage, and exhibitors of palintomy within a cyst in their reproductive phase. Were it not for the conscientious efforts, in relatively recent years, of the Canella family in Italy and a small group of Frenchmen in France, our knowledge would be even much more limited. Yet species of the group have been noted in the literature dating back nearly 150 years, and members of the included genus *Ichthyophthirius* have long been serious parasites (causative agent of "ich") of fresh-water fishes in home aquaria as well as in nature. This suborder is very likely phylogenetically closer to the preceding Tetrahymenina than to the Peniculina, the third hymenostomatid group which I recognize (see below).

Possessing a sunken and relatively inconspicuous buccal cavity of complex structure and organization, ophryoglenines have not only three membranelles *sensu lato*, with one attached to a kind of peniculus as well, but a pseudomembrane or ribbed wall, a triangular plate, a very long cytopharyngeal canal, two cytoplasmic bands, and – as long recognized – the unique organelle of Lieberkühn (see Canella, 1964b, and Canella & Rocchi-Canella, 1964, 1976, for details). The last-mentioned structure, lens-like and often but (according to Canella) improperly called the "watchglass organelle," remains functionally enigmatic. But the fact that it is associated with the buccal cavity of all members (except, apparently, *Ichthyophthirioides browni*) of the suborder and is intensely Feulgen positive makes it a most convenient "key" character for indisputable identification of these hymenostomes.

Mucocysts, parasomal sacs, and one or more contractile vacuoles, with pores, are present, but no nematodesmata or fibrous trichocysts. The somatic kineties are bipolar, except for several postoral meridians; at least one of the latter is involved in the complicated parakinetal stomatogenesis exhibited. A clearly defined preoral suture is always present. A number of closely packed kineties fill a depression, called a "vestibulum" by some but perhaps better identified as a prebuccal cavity, leading to the true buccal cavity. The oral apparatus in the proter as well as in the opisthe must be produced anew.

The typical life cycle of these polymorphic ciliates has been well illustrated in a comprehensive study by Mugard (1949). Reproduction within a thin-walled cyst may, in some species, involve as many as 10–11 palintomic divisions, thus yielding dozens to hundreds of tomites simultaneously. The released tomites commonly become theronts ("chasers") which, as histophages, search out a fresh source of food – sometimes another invertebrate or vertebrate host organism, in the case of parasitic forms. The resulting trophonts, engorged in a short time of feeding (with the intercalation of additional kineties over the body with concomitant expansion in size: Mugard, 1948), become tomonts which secrete their cystic covering and soon set about with another series of fissions to produce another population of tomites. Hosts, when involved, include dragonfly larvae, a number of turbellarians, and various fresh-water and marine fishes. Except for one species (brackish), the ophryoglenines which are scavengers are known from fresh-water sources only. Several such species have been cultivated axenically in the laboratory, opening the door for experimental research of a sophisticated nature.

Two families, both originally erected by Kent nearly 100 years ago, are recognized for the suborder, the Ichthyophthiriidae (resurrected) and the Ophryoglenidae. The genus with the most species, to date, is surely *Ophryoglena*; but the genera with possibly the most widely distributed and certainly the most destructive, though fewer, species are *Ichthyophthirius* (long considered a gymnostome!), the fresh-water fish parasite, and *Cryptocaryon*, its marine counterpart. Both of these last-mentioned organisms cause what is known as white spot disease.

* * * * *

The literature on members of the overall group, as mentioned above, is not extensive. Older works on the ophryoglenids proper are conveniently cited in Corliss (1961), Kahl (1931c), and Mugard (1949); for *Ichthyophthirius*, see Buschkiel (1936), Corliss (1961), MacLennan (1942), and Mugard (1949). Several of the rash of papers emanating in recent years from the laboratories of Canella and de Puytorac are given, along with scattered works from elsewhere, below; first, mention should be made of an excellent and very recent single bibliographic source of practically all of the pertinent literature of the 1960's (and much of the work before and since, as well) on the biology and cytoarchitecture of members of the entire suborder: the monograph by Canella & Rocchi-Canella (1976).

For the results of research on ophryoglenid taxonomy, morphology, and general biology, see Canella & Rocchi-Canella (1976), Rocchi-Canella & Trincas (1961), and the several works by Roque and colleagues, including the continuing series by Savoie (de Puytorac et al., 1969; Roque & de Puytorac, 1968; Roque et al., 1965; Roque & Savoie, 1966; Savoie, 1961, 1962a,b, 1968). Cytological work with emphasis on the knotty problem of stomatogenesis includes papers by Canella (1964b, 1971), Canella & Rocchi-Canella (1964, 1976), and Roque et al. (1965). Ultrastructural observations are found in Grassé & Mugard (1961), Hausmann (1974a), de Puytorac (1969d), de Puytorac et al. (1969), Roque & de Puytorac (1968), and Roque et al. (1965). Finally, recent physiological work (including refined culturing methods, etc.) appears in the publications of Albaret (1968a), Metenier (1971), Mugard & Rouyer (1967, 1968), de Puytorac & Paret (1965), Rouyer & Rouyer-Mugard (1967, 1969), Rouyer-Mugard & Renaud (1972), Rouyer-Mugard & Rouyer (1974), and Rouyer-Mugard et al. (1972).

Recent taxonomic or cytological investigations on *Ichthyophthirius* include papers by Canella & Rocchi-Canella (1976), Hauser (1972, 1973), Mosevich (1965), Nie & Lien-Siang (1960), Roque et al. (1967), and Uspenskaja & Ovchinnikova (1966). The allegedly very closely related *Ichthyophthirioides*, also a parasite of fresh-water fishes, was established as a new genus by Roque & de Puytorac (1968). An important series of studies on the physiology and pathology of ichthyophthiriasis, with a comprehensive review of the (sparse) literature in that field, has recently been carried out by Hines & Spira (1974: fifth in the series); the short overview by Nigrelli et al. (1976), which has just appeared, also should be consulted. Selected works on the enigmatic marine fish parasite properly known nomenclaturally as *Cryptocaryon irritans* (see Brown, 1951; Corliss, 1961) include the following: Brown (1963), Lom (1970b), Nigrelli & Ruggieri (1966), Nie & Lien-Siang (1960), and Sikama (1961, 1962; and earlier papers, predating Brown's first work, cited in these two). Canella (1972) offered a comprehensive review of the overall taxonomic-nomenclatural problem enmeshing *Cryptocaryon*; but his suggested "fair play" name for this controversial organism cannot, under rules of the Code, be accepted.

Suborder (3) Peniculina

Large, free-living, quite highly differentiated forms, usually with uniform ciliation over the body, the peniculines include some of the most common, most conspicuous, and best-known species of ciliates. Yet their principal characteristic of taxonomic value, their possession of several peniculi deep in a buccal cavity, went virtually unrecognized until the pioneering descriptive and taxonomic works of von Gelei (e.g., see 1952, and references therein) and the still fuller appreciation of their systematic and phylogenetic implications by Fauré-Fremiet (1950a,d) and, soon thereafter, by Corliss (1956, 1958a, 1959), Yusa (1957), and others. *Paramecium*, perhaps the single most popularly recognized of all ciliate genera, known for several centuries in the literature and the favorite experimental protozoon in many physiological and genetic laboratories for decades, was classified as a bonafide trichostome, rather than hymenostome, ciliate until about 25 years ago. But, now, perhaps the peniculines deserve separate *ordinal* status, even?

A second characteristic of great importance is the mode of stomatogenesis. Considered "autonomous" in nature (see above references plus Corliss, 1967a, and Evans & Corliss, 1964), although now better termed buccokinetal (Corliss, 1973e), it has been studied throughout the suborder by Roque (1961a, 1974). The earliest precise attention to the phenomenon in peniculines was given by Fauré-Fremiet (1954c), working on *Urocentrum*, and Yusa (1957), on *Paramecium*. The most recent thorough study on *Paramecium* is that by Jones (1976).

Mucocysts are not present in most peniculines; however, such genera as *Urocentrum* and probably *Lembadion* seem to have them (Didier, 1971). On the other hand, most of the group appear to be the only ciliates, except for members of the hypostome nassulid suborder Microthoracina, with true fibrous trichocysts, typically fusiform in shape. Many studies have been conducted over the decades (e.g., since Tönniges, 1914 and Krüger, 1936) on these so-called "explosive" organelles, including sophisticated work on their ultrastructure and morphogenesis (recent examples: Allen & Hausmann, 1976; Bannister, 1972; Didier, 1971; Dragesco, 1968c, Ehret & de Haller, 1963; Ehret & McArdle, 1974; Estève, 1975; de Haller, 1969; Hausmann, 1973c, 1978; Hausmann & Stockem, 1973; Hausmann et al., 1972a,b; Hovasse, 1965; Hovasse & Mignot, 1975; Pitelka, 1965; Pollack, 1974; Pollack & Steers, 1973; Rouiller & Fauré-Fremiet, 1957; Schuster et al., 1967; Steers et al., 1969; Stewart & Muir, 1963; Stockem & Wohlfarth-Bottermann, 1970; and Yusa, 1963, 1965). The pioneering electron-microscopic papers by Jakus (1945) and Pease (1947) deserve special citation. Interestingly enough, there are no such trichocysts in *Lembadion* and *Urocentrum*. In the enigmatic genera *Turaniella* and *Espejoia*, placed among the peniculines by some workers, there are neither trichocysts nor mucocysts.

There are often two contractile vacuoles per organism, each with a pore and typically with prominent collecting canals. The cytoproct, long visible in silver-impregnation preparations, has finally come to be recognized as a unique organelle (in other groups as well as here). Sophisticated studies of its ultrastructure and morphogenesis in *Paramecium* are now available (e.g., see Allen & Wolf, 1974; Chen-Shan, 1969, 1970; Estève, 1969; Jurand, 1961; Ng, 1976a–c; Schneider, 1964; and especially Ehret & McArdle, 1974). Food vacuolar formation has also been carefully investigated by TEM (Allen, 1974). Parasomal sacs are widely present, associated with ciliferous kinetosomes or with one of a pair in a somatic kinetid. The infraciliature of the endoral or paroral membrane, however, includes no parasomal sacs. Nematodesmata, contributing to the support of the cytopharynx, are present, in one form or another, in most species. Once again, aberrant forms include *Urocentrum* (and the controversial *Turaniella*), with no microtubular complexes identifiable as nematodesmata (Didier, 1971). Cortical alveoli are well developed. A postoral (as well as preoral) suture is typically present. The ventrally located buccal cavity (still called by various other names, such as "gullet"), which may or may not be preceded by an "oral-area depression" (which I have called a "vestibulum" in the past but which I am now naming the prebuccal cavity: see Chapter 2), contains the several peniculi, the organelles endowing the suborder with its name (Fauré-Fremiet, 1950a, and Fauré-Fremiet in Corliss, 1956). Described, though not properly identified, decades ago, and now well known from both light- and electron microscopical studies, there is little need to redescribe them here. In a "typical" situation, such as found in *Paramecium*, there are two peniculi of similar organization (four, or in some species more, closely aligned rows of cilia, etc.) and a third, a "polykinety" known as the quadrulus, of exactly four rows of cilia more widely spaced. Barely inside the buccal overture is the infraciliary base of the endoral (= paroral) membrane. In stomatogenesis, the organelles of the parental organism – the paroral membrane, ribbed wall, and even the buccal cavity itself, as well as the peniculi – are preserved intact for the proter, undergoing little or no dedifferentiation (this is not true, however, for the cytostome-cytopharyngeal complex). The opisthe has new structures and organelles formed or shaped for it during the morphogenetics of the process, the apparent origin of the new basal bodies being a field of kinetosomes arising near or from the parental endoral membrane. Sometimes "vestibular" (prebuccal) kineties or ophryokineties (e.g., in *Frontonia*) may also become involved in the overall process. Roque's (1974) review should be consulted for descriptive details of the phenomenon as it occurs throughout the Hymenostomatida; and Canella's (1971, 1972; see also Canella & Rocchi-Canella, 1976) papers should be perused for pertinent criticisms of recent works and for excellent bibliographies on the subject, still controversial in some of its details. See also Jones (1976), as mentioned above.

Although many other ciliates – and, indeed, many other protozoan species – are hosts to a variety of "endosymbionts" of numerous sorts (see Ball, 1969, for an excellent modern comprehensive review which updates the still-valuable Kirby, 1941b), the peniculines, particularly members of the genus *Paramecium*, have had such "cytoplasmic inclusions" or "plasmagenes" (or "xenosomes"?) mostly studied from the point of view of genetic intimacy with the host organism. Zoochlorellae, and, even more extensively, "kappa particles" and their (other) Greek-letter relatives (actually all gram-negative bacteria), have been investigated exhaustively by light and electron microscopy and by experimental and biochemical approaches of various kinds. The principal species involved have been (members of the) *P. aurelia* (complex) and the "green" *P. bursaria*. Recent sources of information on such work include Beale et al. (1969), Karakashian (1975), Karakashian & Siegel (1965), Preer et al. (1974), Soldo (1974), Sonneborn (1959), Vivier et al. (1967), and Weis (1969). Preer et al. (1974) even gave binomial names to *P. aurelia*'s endosymbionts, describing seven species in four distinct bacterial genera. Viral and other parasites have been detected in the nuclei of paramecia, too, but these have been less rigorously studied (Ball, 1969).

Peniculines are found primarily in fresh-water habitats; but a few enjoy brackish biotopes. One species is edaphic, and several are found in marine sands in the intertidal zone. Except for *Frontonia*, with some omnivorous species (one is even cannibalistic on occasion: Devi, 1964), and the carnivorous *Neobursaridium* and *Turaniella* (questionably a peniculine), feeding is typically microphagous, on bacteria (*Paramecium* highly prefers gram-negative over gram-positive forms) or algae: apparently rather aberrant is the case represented by the isolated observation by Diller (1958) of *Paramecium polycaryum* devouring *Tetrahymena pyriformis*. Axenic cultures have been established in the laboratory. All species of the suborder are free-living except one frontoniid, a commensal on the gills of *Amphioxus*. Perhaps the most curious ecological fact about the group is the general absence of cysts, although species of some genera, such as *Frontonia* and *Disematostoma*, do possess them. Distribution must be accomplished in other ways: Maguire & Belk (1967) have suggested one means. Swimming behavior (e.g., direction of spiraling) is another – this time physiological – baffling characteristic of perennial interest. Bullington (1939), nearly 40 years ago, carried out an exhaustive study on *Frontonia* with respect to such a trait (having still earlier investigated the phenomenon in *Paramecium* and other ciliates: see references in his 1939 paper or in Corliss, 1961).

Taxonomy within the suborder is still unsettled; for example, the number of "acceptable" peniculine families ranges from four to nine. Seven are tentatively endorsed in this book (see Chapter 20). I exclude the Turaniellidae, which more likely belongs near (or even in?) the tetrahymenine family Glaucomidae (as first suggested in Corliss, 1971b). *Turaniella*: the only certain genus in the family (although *Espejoia* has been claimed by some workers to be related), simultaneously possesses peniculine traits (e.g., peniculi) and tetrahymenine characters (particularly in its somatic infraciliature, mode of stomatogenesis, and exhibition of dimorphism: see page 124 for additional discussion). The group with most altered composition is the Frontoniidae, reduced from a taxonomic hodge-podge of the 35–40 genera (largely unrelated) at one time assigned to it (see especially Kahl, 1931c) to only 4–6 in this book. A lumper would probably put *Clathrostoma, Lembadion,* and possibly even *Urocentrum* back into it; but there are a number of family-level distinctions, from details of the oral area to ecological traits, among such genera.

* * * * *

The literature on members of the suborder Peniculina is enormous; no attempt to survey it all can be made here. Unfortunately, general, comprehensive works on the whole group (or on many of the genera together) are relatively rare: but post-1960 works which do fall into this category and are also usually rich in included bibliographic references are Canella (1971, 1972), Canella & Rocchi-Canella (1976), Corliss (1961), Didier (1971), Dingfelder (1962), Dragesco (1970), Roque (1961a, 1974), and Wilbert (1969).

Leaving to one side, for the moment, works primarily concerned with the "star" genus of the suborder, *Paramecium*, brief mention should be made of selected outstanding papers on some of the other 15 included genera, generally exclusive of the references cited in the preceding paragraph or earlier in this chapter.

On *Frontonia*, see Devi (1964, 1965), Didier (1970), Fenchel (1968a), Gerassimova (1976), Gil & Peréz-Silva (1964a–c), Hausmann (1973c), Roque (1961b,c), Roque & de Puytorac (1972), and Yusa (1965). Since the earlier work by von Gelei (1954) and the investigations, already cited above (by Didier and Dragesco and Roque), new studies on *Disematostoma* appear to be limited to the papers by Michiels & Wilbert (1974), Nair (1971), and Tuffrau & Savoie (1961); and those on *Stokesia*, to Dragesco (1966c). Wilbert (1972b) has offered a brief but excellent redescription of the curious *Marituja*. *Urocentrum* has been examined ultrastructurally by Didier & de Puytorac (1969) and Fernândez-Galiano & Guinea (1971); and *Lembadion*, by de Puytorac (1967). Species of the latter genus have also been studied by Dragesco (1965b, 1970) and Tuffrau (1963b); and Jankowski (1967a) suggested (but did not characterize) a family Lembadionidae. Small et al. (1971) have published scanning electronmicrographs of *Frontonia* and *Lembadion*.

The huge (up to 710 μm in length), *Paramecium*-like (though first classified as a spirotrich), pan-tropical *Neobursaridium* was named 35 years ago (Balech, 1941) but seldom seen again until the late 1950's and the 1960's, when suddenly "everyone" seemed to be sighting it! Although more papers are promised, already we have important descriptive data on this easily laboratory-grown ciliate in the works of Dragesco (1966b, 1968c, 1970), Dragesco & Tuffrau (1967: creators of the family), Nilsson (1962, 1969), and Thurston (1964). Another *Paramecium*-like organism, *Physanter* (formerly called *Faurella*, but this is a preoccupied name), was studied by Didier (1969) and Roque (1966). *Clathrostoma* has seldom been investigated since Penard (1922), Fauré-Fremiet (1924), and Kahl (1931c). Influenced by its prominent "cytopharyngeal basket," I once proposed its removal from among the "trichostomes" to the "cyrtophorine gymnostomes" (Corliss, 1958a, 1961); but, clearly, it is a peniculine hymenostome, taxonomically not far from *Frontonia*.

The situation with respect to the *Paramecium* literature is akin to that of *Tetrahymena*'s (see preceding section), except that it is probably even worse! Thousands of individual papers have been published on paramecia, and there appears to be no let-up. These organisms have been the object of intensive research from several points of view; perhaps the major ones, in recent years, have been and are genetics and ultrastructure. But fields of study often overlap a good deal today, so that biochemical and biophysical approaches may be simultaneously involved; and even the ecology and systematics of *Paramecium* have become more sophisticated. At least 150 papers on *Paramecium* were cited directly in Corliss (1961), mostly works published in the decade of the fifties. Here I am listing reviews or original investigations published principally in the 1960's and early 1970's; but space simply does not permit citation of a large number of isolated papers. Some references given in preceding pages have, of course, included findings on *Paramecium*, alone or along with other peniculine genera; and topics such as trichocysts and endosymbionts, with emphasis on ultrastructure and biochemistry, have already been treated above. Historically outstanding studies on the sexuality of *P. aurelia* (and other species) are referred to in appropriate sections of Chapter 21. Such important investigations gave respectability to the ciliate Protozoa as competitively useful experimental organisms in modern genetic research.

Books devoted entirely to *Paramecium* still represent a "number one" source of literature on this popular ciliate, although they can never keep up to date with the research literature which is continuously being poured out. Following the classics of old (Kalmus, 1931; Wichterman, 1953; Beale, 1954), we have today Jurand & Selman (1969) and now van Wagtendonk (1974), the latter containing several fine chapters by separate authors and a massive bibliography of the works published since 1953. Other key review works with significant data on *Paramecium* are Ehret & McArdle (1974), Jankowski (1972b), Kidder (1967a,b), Kimball (1964), Miyake (1974), Párducz (1967), Pitelka (1969), Preer (1969), Raikov (1972a), Seravin (1970), Sleigh (1974a), Sonneborn (1970a: updating his classical "methods" paper of 20 years earlier, Sonneborn, 1950), Sonneborn (1974c), Vivier (1974), van Wagtendonk & Soldo (1970a,b), and the chapters (rarely singled out for separate citation in the present book) in van Wagtendonk (1974). A few additional references, either too recent to be available in the works just cited or inadvertently omitted from them: Adoutte et al. (1972), Allen (1976), Cummings & Tait (1975), Golikova (1974), Hanson & Ungerleider (1973), Hausmann & Allen (1977), Jankowski (1960, 1972d), Just (1973), and Tamm (1972).

Very few modern works (up to 1973) of significance will have been missed in the combined bibliographies of the papers cited in the preceding paragraphs. Much of the important work of the present is being carried out by many of the same authors; so searching through current appropriate scientific journals for papers by such established investigators as those listed here should provide the reader, whether a budding student of *Paramecium*, or of genetics, or of cell biology in general, with more up-to-date material than I could possibly specifically cite: Adoutte, R. D. Allen, S. L. Allen, Andrivon, Bannister, Barnett, Beale, Beisson, J. D. Berger, Bick, Brittingham, Crippa-Francheschi, Diller, Dippell, Dragesco, Dryl, Dupy-Blanc, Eckert, Ehret, Estève, Finger, Génermont, Gibson, Gill, Gillies, Gilman, Golikova, de Haller, Hanson, Hausmann, Hiwatashi, Hufnagel, Inaba, Irlina, Jankowski, Jurand, Karakashian, Keeshan, Kennedy, Kimball, Koizumi, Kovaleva, Lewis, Lilly, Metz, Mitchell, Miyake, Mott, Mueller, Naitoh, Nanney, Ng, Nobili, Ossipov, Párducz, Pitelka, Plaut, Poljansky, Powelson, Preer, Prescott, Propper, de Puytorac, Raikov, Rao, Reilly, Roque, Satir, Schneider, Schwartz, Siegel, Smith-Sonneborn, Soldo, Sonneborn, Stevenson, Suyama, Swift, Tamm, Tartar, Tsujita, Vivier, van Wagtendonk, Watanabe, Weis, Wohlfarth-Bottermann, Wolf, Wolfe, Woodward, and Yusa.

Systematics and ecology might be singled out for special consideration, mainly because such a minute percentage of the research on *Paramecium* is directly concerned with these fields. Aside from the small amount of consideration typically given it in taxonomic works, rather little has been done in recent years in the area of ecology except for the series of "sensitivity" and "adaptation" studies being carried out principally in the U.S.S.R. For example, see Irlina (1963), Poljansky & Sukhanova (1963), and especially Poljansky (1973) and the references he cites; but also note the work of Propper (1965) and the unusual paper by Sorenson & Jackson (1968). The novel investigations of the (one-time) Michigan group on competition and other aspects of "community-ecology" in *Paramecium* deserve attention, too (e.g., see Gill, 1972a,b, 1974; Gill & Hairston, 1972; Hairston, 1958; Hairston et al., 1968; Vandermeer, 1969; and Vandermeer et al., 1972). Of course, "behavior" is often closely linked to genetics in work on species of this genus (see the recent paper by Kung et al., 1975, and recall Jensen's, 1959, work of 18 years ago).

In systematics, following the many papers of the pre-1950 era and the subsequent contributions of von Gelei, Fauré-Fremiet, Corliss, and Yusa, especially to problems at the higher taxonomic levels, there have been few publications in the field. New species have been added by Diller & Earl (1958) and Dragesco (1970, 1972a,b); and Vivier (1974) has reviewed the taxonomy of the whole genus. Jankowski (1969), who proposed recognition of three subgenera, has also carried out an extensive and often-overlooked study of conjugation in *P. putrinum*, a species long unrecognized (last of series: Jankowski, 1972b). Powelson et al. (1975; and see Gates & Berger, 1976b, and Gates et al., 1975) have used methods of multivariate morphometrics to confirm syngenic differences within several species. Sonneborn (1975a), in a bold but justified move predictable from his classic on "the species problem" in the protozoa (Sonneborn, 1957), has recently recognized and named 14 separate and bonafide new "taxonomic" species of the old and very well-known "*Paramecium aurelia*," a name which must now be abandoned (although we may continue to refer to the "*P. aurelia* complex" of species). At the "strain" level, many potentially exciting differences remain to be fully elucidated. One curious problem concerns chromosomal DNA and possible ploidy differences in the micronuclei; while recalling such a pioneering work as Dippell (1954), recent considerations include those of Jankowski (1972d) and Ossipov & Borchsenius (1973).

The cortex of *Paramecium* has been of such great interest to biologists from many points of view that the following references, representing major post-1961 works in several areas, should be mentioned: R. D. Allen (1971), Beisson & Sonneborn (1965), Didier (1971), Ehret (1967), Ehret & McArdle (1974), Hufnagel (1969), Jurand & Selman (1969), Miyake (1974), Ng (1976a–c), Párducz (1962, 1967), Pitelka (1963, 1965, 1969), Sibley & Hanson (1974), and Sonneborn (1963, 1970b, 1974a, 1975b). The relatively early electron-microscopic classic in the field remains the comprehensive review (yet containing many original observations as well) by Ehret & Powers (1959).

Addendum

Turaniella was assigned by Kahl (1931c), as *Turania* Brodsky, 1925, a name obliged to fall as a junior homonym, to his heterogeneous family Frontoniidae. In the first edition of this book (Corliss, 1961), I included it in a long list of "unassigned tetrahymenines." In my paper establishing the Glaucomidae as new (Corliss, 1971b), I placed it in that tetrahymenine family; at the time, Didier's (1971) masterful thesis on the cortical and buccal ultrastructure of peniculines, in which he erected a separate superfamily for *Turaniella*, was not yet available. In recent years, a number of additional works have appeared either involving (the cytology of) *Turaniella* directly or including critical comments on its taxonomy (see references, below).

Influenced particularly by French colleagues, I began to doubt my own earlier assignment of the organism. For a time (Corliss, 1975b), I placed the genus (with a remark on the somewhat similar *Espejoia*) in *both*(!) suborders, in effect; next, I decided to fully endorse Didier's view, allocating *Turaniella* to a family of its own in the suborder Peniculina (see Corliss, 1977a, a "preview" of the system in this book). Thus, in the pentultimate draft of the present chapter, I had included mention of it in the immediately preceding pages. Very recent *re*-review of all available data (alas, still scanty), however, has now "re-convinced" me that the genus, along with its family, should be returned – even if only tentatively – to a location in the Tetrahymenina. Various "in press" emendations (here, in Chapter 20, and including this Addendum) reflect this "11th-hour" decision.

Recent works on or related to the controversial *Turaniella* include the following: Canella (1971, 1972), Corliss (1971b, 1975b, 1977a), Didier (1971), Didier et al. (1977), Didier et al. (1970), Iftode & Grain (1975), Iftode & Versavel (1968), and Iftode et al. (1970).

A basic and most important paper in modern times on the biology of the genus *Espejoia*, incidentally, is the enlightened contribution by Fauré-Fremiet & Mugard (1949a), a work inadvertently omitted from citation on page 115.

Chapter 11

Class Oligohymenophora: (2) The Scuticociliates, an Integral Separate Assemblage

The Scuticociliatida represent the second of the three orders which I include in the subclass Hymenostomata. It contains three suborders, the third of which embraces the "mouthed" members of the formerly independent (see Corliss, 1961) order of thigmotrichs. Taxonomically a controversial group, it has never received proper overall attention since its establishment, a decade ago, by Small (1967). Thus, relatively more details may be warranted here than are supplied in many of the other chapters. Representative genera are depicted in the set of figures on page 130 (Plate XII).

Generally very small to medium in body size (with a few outstanding exceptions), scuticociliates are particularly abundant in marine habitats, free-living or as endosymbionts of various hosts, although some are found in fresh-water (free or in molluscs) or even in edaphic biotopes, including peat bogs. Body ciliature is usually uniform, though sometimes sparse, and typically one to several distinct caudal cilia are present. Areas of thigmotactic cilia are characteristic of many subgroups. The buccal ciliature consists of an often dominating paroral membrane on the right, a structure sometimes of multiple segments (most clearly recognized at the infraciliary level), and several (usually three) membranelles or "polykineties" of various conformations on the left. The buccal cavity may be clearly identifiable or shallow and indistinct. The ciliary organelles are very difficult to perceive as separate entities in living material; even methods of silver impregnation must be applied with care to reveal their infraciliary bases with accuracy. An argentophilic and generally kinetosome-less director-meridian, found in many scuticociliates, occupies the place in which a postoral suture or postoral meridians occur in hymenostome ciliates.

But the most outstanding and most characteristic feature of any and all members of the order is the appearance, during the morphogenetics of stomatogenesis (which is buccokinetal in nature), of a *scutica* (see glossary, Chapter 2), named for its hook-like or "whiplash" configuration at one stage in its fleeting existence. In nondividing stages of the organism the scutica, as such, is no longer present; a scutico-vestige may be detectable at or near the termination of the paroral membrane or as a small group of nonciliferous basal bodies near the anterior end of the director-meridian. The Scuticociliatida are probably the only ciliates defined and separated from other ordinal-level neighboring groups principally by a dynamic character, an essentially transient feature in their morphology. Of course, other differentiating features exist as well.

Kinetids often contain two kinetosomes, particularly on the anterior part of the body. This fact, and the spacing of the kineties and basal bodies in general in many of these ciliates, leads to the recognition here of the concept of parateny (Ehret, 1967); it is very clear in such a genus as *Loxocephalus*, for example. Interkinetal, rod-like mucocysts are present; "true" trichocysts (explosive fibrocysts) are apparently absent, although further investigation of the possibility of their occurrence is in order. The presence of longitudinally oriented, elongate mitochondria – large, numerous, sometimes fused (recognizable at times as a single "giant chondriome": see Kaneshiro & Holz, 1976, and Rodrigues de Santa Rosa & de Puytorac, 1976), and very close to the cortex – represents another distinguishing characteristic. Parasomal sacs are present, one to a pair in the case of somatic or buccal dyads of kinetosomes; two flank the single basal body of the caudal cilium, when the latter is present, forming with the kinetosome a tripartite polar basal body-complex. No nematodesmata are associated with the cytopharynx. Contractile vacuoles, with a single pore, are found in all species, marine as well as fresh-water, parasitic as well as free-living.

Although, as mentioned briefly above, distribution is widespread, some of the best-known subgroups are comprised solely of free-living marine forms (some in intertidal sands), commonly histophagous, or of endosymbionts in such marine hosts as bivalve molluscs, echinoids, crinoids, echiuroids, polychaete annelids, crustaceans, and sipunculids (and one species in the sea horse). But some of the thigmotrichine scuticociliates occur in fresh-water molluscs and terrestrial oligochaetes. A few well-known free-living species occur in edaphic habitats or in fresh-water biotopes; yet some others are found in locations of extremely high salt concentration, such as the Great Salt Lake in Utah. Cysts are commonly known. Life cycles do not appear to be complicated, although species of at least one genus (*Potomacus*) exhibit a reversible microstome-macrostome transformation reminiscent of *Tetrahymena* and *Espejoia* – and the taxonomically controversial *Turaniella* – among the tetrahymenines. Feeding preferences run the gamut, from bactivorous and algivorous to carnivorous, histophagous, and omnivorous. Fenchel (1968a) has made careful observations of the food-taking habits in a number of scuticociliates.

Suborder (1) Philasterina

Most of the salient features of this suborder have been described, or referred to, above, in discussion of the order itself. It is set apart from the following suborders primarily on the basis of the kinds, shapes, and infrastructure of its buccal organelles and on differences important in the morphogenetics of its stomatogenesis; such details cannot be treated *in extenso* here (but see literature citations, below, for reference to recent key papers containing most helpful accounts in this respect).

In the mature, nondividing ciliate, the paroral membrane, often known as the haplokinety, has a reduced "a" segment, a "b" segment with the typical zigzag arrangement of dyads (with only the outer basal bodies bearing cilia), and a reduced or even vestigial "c" segment, often represented by only a few nonciliferous kinetosomes (= the scutico-vestige). In stomatogenesis (see especially Coats & Small, 1976), kinetosomes of the anlagen of new oral ciliary organelles for the opisthe appear to be derived primarily from the "b" and "c" segments of the paroral. The scutica becomes prominently visible – as a curved line or hook of basal bodies – only at a late stage in the process, essentially either disappearing altogether following cytokinesis or detectable only as a scutico-vestige. Sometimes a "scutico-field" may implicate a goodly number of kinetosomes.

The polykineties (or membranelles *sensu lato*), characteristically on the left side of the buccal area, may appear simply as tufts or fields, or occasionally a single line, of cilia, rather than as the organized multiple-rowed organelles of the tetrahymenines, ophryoglenines, and peniculines. Thus, for some philasterines, Mugard's (1949) aptly descriptive names are still appropriate, reading from anterior to posterior: "le champ deltoide," "le champ trapézoide," and "le champ falciforme" (perceivable in the typical shapes of their argentophilic infraciliary bases). In some species, a few kinetosomes may be contributed from the (bases of the) membranelles to the various anlagen appearing during stomatogenesis. The first membranelle, or "M_1," incidentally, does not bear cilia in several genera. The histophagous *Porpostoma*, a baffling form taxonomically, is unique in its manifestation of multiple (up to 18!) polykinetal segments of M_1, at some stages in its life cycle.

Despite the complexities indicated above, stomatogenesis in this suborder may be termed buccokinetal (Corliss, 1973e), although it is obviously quite unlike the buccokinetal type shown by peniculines. The parakinetal modes of the tetrahymenines and ophryoglenines are different in still other ways. The oral area, though ventral, is seldom subequatorial in position. A director-meridian (in the sense of von Gelei, 1934b; see also Corliss, 1956; Mugard, 1949; and Chapter 2) is found in all philasterines. Other characteristics are the prominent rod-shaped mucocysts, often labeled "trichocysts" in the older and even some of the more recent literature, the caudal cilium with its polar basal body-complex, and the giant chondriome mentioned under the diagnosis of the order, above. Body sizes (lengths) range from as small as 15 μm (*Cinetochilum*) to 900 μm (*Thyrophylax*).

With respect to the ecology of members of the suborder, most of the species are found in brackish or marine habitats, including sands (a recent reference: Borror, 1973a). In addition to free-living forms, a number are found in association with various hosts, ranging from coelenterates and annelids to the sea horse. A large number of species (see Berger in Levine, 1972) live as endocommensals (obligatory inquilines) of echinoids, notably sea urchins: dwelling in specific parts of the gut, they survive mainly as either algivores or carnivores. About a dozen (a few rather controversial still) families may be considered to comprise this large suborder (see Chapter 20). Some of their principal genera are mentioned below, under consideration of sources of literature. The largest family, by number of genera, is the Philasteridae; but even here practically all of the ciliates are either poorly known, except for *Philaster* itself, and/or quite recently described as new. The small size of many philasterines, their generally unexplored habitats, and the absence (until very recently) of ways to correctly identify them have all been factors in their relatively high degree of "unpopularity" among protozoologists and ecologists as well as general zoologists, biochemists, and cell biologists. Many of them would make ideal experimental organisms, a fact just *beginning* to be appreciated (see several references below plus the very recent work by Berk et al., 1977).

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The literature on philasterines is scattered and/or uncoordinated. Kahl (1931c, 1934a, and earlier works) and even Corliss (1961) gave them no independent status, mixing them with trichostomes, tetrahymenines, and peniculines (or other hymenostomes), with individual genera often unassigned to any family or placed in the wrong family. Almost by chance, a considerable number of them were considered together in Mugard's (1949) thesis on histophagous hymenostomes. Berger's largely (to date) unpublished doctoral dissertation (but see Levine, 1972) and a number of papers from the 1930's (cited in Chapter 21) treated many of the echinophilic species. Thompson (see specific citations in subsequent paragraphs) has been the single most prolific worker in recent years with respect to describing new species, new genera, and even new families of free-living groups. Small (1967), in setting up the suborder, was the first to unite the (scattered) philasterines; but his emphasis was on the general systematic and phylogenetic significance of their morphogenesis, not on their detailed taxonomy or classification. Grolière (1975c) has recently created the Urozonidae as a philasterine family: Corliss (1961), Jankowski (1964b), and others had long mistakenly classified the puzzling *Urozona* among the hymenostomes.

Interstitial philasterines, representing some four or five genera, have been mentioned in larger works by such authors as Borror (1963b, 1973a) and Dragesco (1960, 1963a). Since 1959, a number of echinophilic species have been described or redescribed: for example, in papers by Beers (1961, 1963a), Berger (1963), Berger in Levine (1972), Berger & Profant (1961), Jankowski (1973g, and earlier notes), López-Ochoterena & López (1963), Lynn & Berger (1972, 1973), Poljansky & Golikova (1959: see also Poljansky, 1951b), Strelkow (1959a,b), and Urdaneta-Morales & McLure (1966). Wenzel (1961b) reported philasterines from sponges in the Gulf of Naples; Thompson & Berger (1965) described a *Paranophrys* associated with a hydroid coelenterate; and Didier & Wilbert (1976) have very recently presented an ultrastructural study of another presumed *Paranophrys* from gelatinous insect egg masses. Thompson & Moewus (1964) found *Miamiensis avidus* facultatively parasitic in the sea horse; this species has recently been used in physiological researches by Kaneshiro, Dunham & Holz (1969), Kaneshiro, Holz & Dunham (1969), and Soldo & Merlin (1972). Species of *Uronema* have also been successfully cultivated in the laboratory and their trophodynamics investigated by Hamilton & Preslan (1969, 1970) – stimulated by Johannes (1965) – and by Hanna & Lilly (1974), Parker (1976), and Soldo & Merlin (1972, 1977). The last two studies also included a species of *Parauronema*, a genus erected by Thompson (1967) and recently examined ultrastructurally by Rodrigues de Santa Rosa & de Puytorac (1976). Now identified as *Parauronema*, also, is the marine species with the fascinating endosymbiotic "xenosomes" in its cytoplasm (Soldo et al., 1974). Grolière (1975a) has made a comparative investigation of stomatogenesis in *Paralembus*, *Philaster*, and *Parauronema*, and Foissner (1972a) has studied morphogenesis of the cytoproct in *Uronema*.

The genus *Uronema* – a taxon many of the relatively numerous species of which have been long known and often observed (e.g., by Hoare, 1927b; Mugard, 1949; Noland, 1937, Párducz, 1939,

1958) in past decades – remains popular: see Bick (1972), Borror (1963a,b, 1965b), Curds (1969), Czapik (1968a), Dragesco (1960), Foissner (1971), Jankowski (1964b), Kaneshiro & Holz (1976), de Puytorac, Grolière, et al. (1974), Small (1967), Thompson (1964, 1972), Thompson & Evans (1968), Thompson & Kaneshiro (1968), and the physiological studies cited above. The related *Uropedalium* has (also) been found in Antarctica (J. C. Thompson, 1972). *Philaster* and *Loxocephalus*, too, have received renewed consideration in recent years, species of the first genus having been studied ultrastructurally by de Puytorac et al. (1967), and from other approaches by Coats & Small (1976), Small (1967), Thompson (1969), and Tucolesco (1962a). Species of the second genus, along with those of the neighboring auxomorphically related *Dexiotricha*, have been investigated recently by Bick (1973), Czapik (1968a), Fauré-Fremiet (1968), Jankowski (1964c), and Peck (1975, 1977a), the last-mentioned works (by Peck) including electron-microscopical observations. *Paradexiotricha* has been described as new quite recently (Grolière, 1975c); *Paratetrahymena*, 14 years ago (Thompson, 1963). The family Loxocephalidae, incidentally, appears to be quite different from the other familial groups in the suborder. The precise observations made on silver-impregnated specimens of *Loxocephalus* by J. von Gelei (1940), more than 35 years ago, deserve to be remembered here.

Sathrophilus has been studied by Czapik (1968b), Dragesco & Grolière (1969), Grolière (1973), J. C. Thompson (1972), Thompson & Cone (1963), and Vuxanovici (1962b); *Cinetochilum*, by Jankowski (1968c) – recalling the early excellent observations by G. von Gelei (1940) – and, most recently, by de Puytorac, Didier, et al. (1974); and *Thyrophylax* and *Plagiopyliella*, by Lynn & Berger (1972, 1973). The taxonomically difficult *Pseudocohnilembus* has been investigated by Evans & Corliss (1964), in the first thorough study of stomatogenesis in a philasterine; by Evans & Thompson (1964), who gave the organisms (more than half a dozen species) their new generic and familial names; and by Small (1967) and Wenzel (1961a). Thompson (1965, 1972) has described species of *Pseudocohnilembus* from the Antarctica. *Cohnilembus*, rather distantly related to the preceding genus despite the nomenclatural similarity, has been studied in recent times by Didier & Detcheva (1974), Evans & Thompson (1964), and Thompson (1968). Jankowski (1973g) has reviewed the family Entodiscidae, assigning nine genera to it (a taxonomic decision with which I am not in agreement: see Chapter 20). Evans (1969) included *Homalogastra* in his preliminary report on stomatogenesis in scuticociliates.

Three (more) relatively new genera (see also *Miamiensis*, *Paranophrys*, *Parauronema*, *Pseudocohnilembus*, and *Thyrophylax*, above) should be mentioned. But they have been little studied except in the papers in which they were established: *Glauconema* and *Potomacus*, in short notes by Thompson (1966a,b); and *Metanophrys*, in a work stressing stomatogenesis from a comparative point of view, by de Puytorac, Grolière, et al. (1974). The celebrated *Anophrys* of the literature (going back to Cohn, 1866) should, in my opinion, be restricted to its type-species, the marine scavenger *A. sarcophaga*; the crab-blood form and certain tubularian symbionts are quite likely better assigned to *Paranophrys*. Interest in the alleged *Paranophrys* ("*Anoplophrya*") which is pathogenic to crabs should be revived by the stimulating and relatively recent discussion offered by Bang (1970); his is the first major report since the classical and often overlooked observations of Poisson (1930), 40 years earlier. The symbiotic *Thigmophrya* have been investigated by Fenchel (1964a), studying stomatogenesis using the Chatton-Lwoff silver-impregnation technique; by Jankowski (1968f), briefly; and by Khan (1970b), in an ultrastructural investigation employing TEM. The genus *Cochliodomus*, a related form, has been described as new in Raabe's (1971b) thorough review of the family Thigmophryidae; and Kazubski (1973) has recently reexamined the enigmatic *Myxophyllum*. *Thigmozoon*, found in wood-boring molluscs, has been named and studied by Santhakumari & Nair (1973, 1975), who placed it near *Thigmophrya*, although it is probably more closely related to certain echinoid inquilines such as *Biggaria* (in fact, I suggest adding Tchang-Tso-Run's, 1958, mollusc-inhabiting "*Biggaria*" to this new genus).

Finally, at least brief mention ought to be made of some of the literature on several of the genera of uncertain taxonomic status which I have tentatively assigned to the Philasterina. *Gullmarella*, studied by Fenchel (1964b) and Jankowski (1973f), is tantalizingly one of these. Perhaps most baffling of all, however, is the enigmatic *Protocruzia*, long accepted (e.g., see Kahl, 1932b; Villeneuve-Brachon, 1940) as a polyhymenophoran heterotrich (recently so "reaffirmed" by Jankowski, 1964b), but "suspiciously" like a scuticociliate in a number of ways, including its "nonadvanced" nuclear apparatus, which has most recently been studied with precision by Ammermann (1968) and Ruthmann & Hauser (1974). Originally described by de Faria et al. (1922), the organism – in my belief – has come to be confused with superficially similar forms which *are* heterotrichs, species for which I suggest resurrection of Mansfeld's (1923) generic names *Diplogmus* and *Propygocirrus* (see Chapter 20). Fedele's (1927) "*Cryptostoma*" (preoccupied name he replaced with *Cryptostomina*) and Hentschel's (1927) *Ptyssostoma* are also "mysteries."

Suborder (2) Pleuronematina

Ciliates which I assign here can, in a general way, be distinguished from those of both the preceding and the following suborder by characteristics visible in the living organisms or in silver-impregnated specimens. Differences in the morphogenetics of stomatogenesis and in the ultrastructural composition of the infraciliature supply additional features of taxonomic value.

Often small to very small in size (with some exceptions, notably in *Histiobalantium* and species of *Schizocalyptra* which may reach 300 µm in length) and occurring principally as free-living and primarily marine forms, the pleuronematines are further distinguished by their typically hypertelic paroral membrane (sometimes a stiff velum), the equatorial or subequatorial location of their cytostome, and the possession of one or more prominent caudal cilia. Their somatic ciliation may be sparse, though basically bipolar, and a thigmotactic area, generally not well defined, may be present anteriorly. The body may be slightly flattened laterally. Membranelle number 1 is distinctly present; there is rarely a director-meridian; and the infraciliature of the lengthy paroral membrane has a very well-developed segment "b," with "c" (the scutico-vestige) also clearly in evidence. The oral area and the buccal infraciliature, often occupying much of the ventral surface, are conspicuous, but the buccal cavity itself may be very shallow. The scutico-hook is prominently visible during stomatogenesis. Membranelle 2, incidentally, is often highly conspicuous.

A (single) contractile vacuole is typically present, even in marine forms. Nematodesmata are absent. The macronucleus is generally single and compact, often located in the anterior half of the body. Mucocysts are common; cysts, uncommon. Some species of *Pleuronema* (and perhaps of *Cyclidium*) may have "true" trichocysts (see Hausmann, 1973b; Hausmann & Stockem, 1973). A few species are coprozoic in their habits and habitats (see review by Watson, 1946); others are edaphic or fresh-water forms; some important groups are commensals (or even parasites) in molluscs. But most pleuronematines, as mentioned above, are free-living marine species, including several psammophilic genera.

I tentatively recognize half a dozen families as comprising the suborder, with the realization that some taxonomic shifting at this level between the Pleuronematina and the Thigmotrichina is destined to occur as our knowledge, especially morphogenetic and ultrastructural, grows with respect to the species involved.

The long-known (in fact, oldest) family Cyclidiidae includes some of the smallest ciliates ever described, a common range in body length being only 15–40 µm. There are many species of *Cyclidium*, from diverse biotopes: edaphic, coprozoic, fresh-water, hot springs, marine, brackish, halophilic, sand; but the reports in the older literature that it has been found as an inquiline in echinoids may be cases of misidentification. Species in moss can form cysts. Whether in nature identical species of *Cyclidium* (and related genera) abound in *both* marine and fresh-water habitats remains an unresolved taxonomic (as well as ecological) problem demanding sophisticated restudy. Experimental observations of past decades (see references in Fauré-Fremiet, 1967d; Noland & Gojdics, 1967) suggest considerable tolerance to salinity changes on the part of a number of such ciliates. Kahan (1972) has the most recent paper on the subject.

The best-known group, the Pleuronematidae, shows most strikingly a large sail-like velum (paroral membrane), coursing from the anterior end of the body along the right side of a shallow

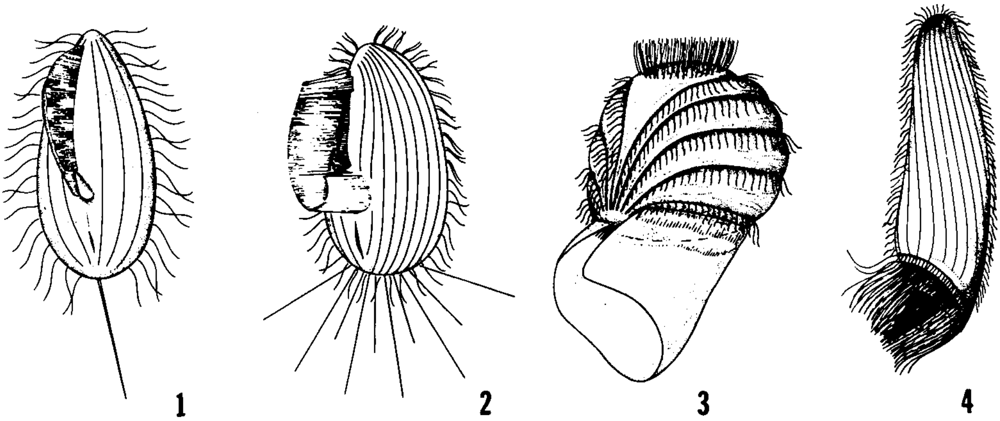

PLATE XII. Representative scuticociliates (order Scuticociliatida). Fig. 1. *Pseudocohnilembus*, suborder Philasterina. 2. *Pleuronema*, suborder Pleuronematina. 3. *Hemispeira*, suborder Thigmotrichina. 4. *Boveria*, suborder Thigmotrichina. [Additional figures appear in Chapter 20.]

buccal cavity and curling toward the left in a large semi-circle around the subequatorial cytostome. An array of long, stiff setae at the posterior pole of the body is also characteristic. *Pleurocoptes* is unusual in having a special area of thigmotactic ciliature: it is an ectocommensal on sea anemones. The species of *Pleuronema* are many and widespread; some are said to occur in both fresh- and salt-water ecosystems. Most of the species are marine, including some interstitial forms; but one is found as a commensal in the mantle cavity of fresh-water mussels. *Schizocalyptra*, a heavily ciliated marine interstitial sand form with a body size typically much greater than that of *Pleuronema*, is particularly characterized by the fragmentation of its segment "b" into nearly a dozen distinct parts.

Another family is the Conchophthiridae (still often misspelled "Conchophthiriidae"), long poorly understood though originally established nearly half a century ago and representing an important and sizable group of species. A highly significant investigation, involving both SEM and TEM, has been published recently by Antipa (1972); other references are given below. A distinctive feature of *Conchophthirus* is its relatively small buccal cavity occurring in a central or mid-location on the ventral surface. Some ciliatologists, not without reason, would separate this group from the other pleuronematines. In the relatively recently erected Thigmocomidae (see Kazubski, 1958; Raabe, 1970a) perhaps the most striking characteristic is the lack of somatic ciliature on the posterior part of the body. Some workers would place this family in the following suborder.

A new family is established (see Chapter 20) to embrace the genus *Histiobalantium*, studied in detail by Dragesco (1968b). Its buccal apparatus, its stomatogenesis (Grolière, 1973) – even its somatic ciliation, multiple contractile vacuoles, and body size – all support its high-level taxonomic separation from *Pleuronema*. Its species are found in fresh-water and marine sands. Finally, Fenchel's (1965a) Peniculistomatidae is also placed in this rather than the following suborder, although admittedly its position remains a controversial one. *Peniculistoma* was established by Jankowski (1964b), unfortunately with extreme brevity, for a former species of *Conchophthirus* described by Kidder (1933a) from marine mussels (see also Beers, 1959). Close to *Pleuronema*, and perhaps even closer to *Pleurocoptes*, it nevertheless appears to show differences justifying clear separation from such genera (Fenchel, 1965a; Jankowski, 1966b, 1972c; Raabe, 1967, 1971b), despite Canella's (1971) concern that this decision represents much too fine a splitting.

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The literature on pleuronematines goes back to at least O. F. Müller (1786); and no doubt Leeuwenhoek observed the antics of *Cyclidium* even 100 years earlier (see Corliss, 1975a; Dobell, 1932). Stein (1861) was the first to offer a recognizable description of a symbiotic member of the group (*Conchophthirus*). The classical works, up through Kahl's (1926, 1928, 1931c, 1933, 1934a) important contributions and beyond (into the 1950's), have been adequately covered in Corliss (1961): also consult the bibliography in Canella (1971) and, for certain of the symbiotic forms, Fenchel's (1965a) comprehensive treatise and Raabe's monographic series ending in Raabe (1972). But the following older papers deserve mention: De Morgan (1925, 1926), Hoare (1927b), Kidder (1933a,b), Miyashita (1929), Noland (1937), Párducz (1937, 1940), Penard (1922), Uyemura (1935), and Watson (1940). Recent papers of significance may be cited under three general headings, with occasional overlapping inevitable: those contributing to our taxonomic, morphological (primarily via light microscopy), and ecological knowledge of pleuronematines; those concerned mainly with morphogenesis (and its systematic implications); and, finally, ultrastructural studies.

The following papers may be listed in the first and largest category: Antipa & Small (1971a,b), Beers (1959, 1962, 1963b), Berger & Thompson (1960), Bick (1972), Borror (1963b, 1965b, 1973a), Chakravarty et al. (1960), Curds (1969), Czapik (1963), Czapik & Jordan (1977a), Dragesco (1960, 1963a, 1968b), Fauré-Fremiet (1961g), Fenchel (1965a), Gray (1974), Grolière (1973), Grolière & Detcheva (1974), Jankowski (1962, 1964b, 1968c), Legner (1973), Penn (1958), Raabe (1966, 1971b), Small (1967), and Wilbert & Buitkamp (1973). Not cited are most of the references given on immediately preceding pages and the published abstracts of several important research projects long in progress by Evans, Small, and their associates or students.

Works stressing morphogenesis, particularly stomatogenesis, are to date very few in number: Dragesco & Iftode (1973) and Grolière (1973), with limited data on *Histiobalantium*; Grolière & Detcheva (1974), a recent fine account of stomatogenesis in a new species of *Pleuronema*; Kazubski (1963) and Raabe (1963b, 1971b), using the Klein "dry" silver method on *Thigmocoma* and *Conchophthirus*, respectively; and Small (1967), both an overview and a preview of the process in *Cyclidium* and *Pleuronema*, but with details reserved for promised future publications. Additional full accounts may also be expected soon from the Evans group in Utah (e.g., see Evans, 1969), from Berger in Toronto, and from the busy center of ciliate research at Clermont-Ferrand.

Published full papers on the fine structure of pleuronematines are rare at the time of this writing although it is known that several investigators are working on species of the free-living genus *Pleuronema*, especially, with both SEM and TEM. Beams & Kessel (1973) have studied the cytoplasmic inclusions and the surface-associated bacteria of an alleged *Cyclidium* (but perhaps it is a philasterine scuticociliate?). The series of papers by Small and Antipa and colleagues (see Antipa, 1972; Antipa & Small, 1971a; Small & Marszalek, 1969; Small et al., 1971), often containing important data on the symbiotic *Conchophthirus*, deserves special citation.

Suborder (3) Thigmotrichina

Although taxonomically and phylogenetically this suborder is much more closely aligned to the pleuronematines than to the philasterines, it is, in my opinion, possible to separate it from each of the groups described on preceding pages (in disagreement with the view expressed very recently by de Puytorac & Grain, 1976). In so "re-recognizing" the taxonomic independence and integrity of the group, I am following the reasoning put forth recently in Corliss (1975b). Its most outstanding characteristic is the universal possession of thigmotactic ciliature, often localized in a distinct area on the left or dorsal surface near the anterior end of the body (typically the aboral pole). Coupled with the laterally compressed body form, the heavy, uniform somatic ciliation, and the frequently spiraled buccal ciliature located at or near the posterior pole, this feature appears to set the thigmotrichs apart from the other scuticociliates.

One need not even mention the ecological preference of the group, although it is also a "uniting" feature often cited in textbooks. The majority of thigmotrichine species occur in the mantle cavity of lamellibranch molluscs, fresh-water or marine. There are a few which prefer other hosts, terrestrial as well as aquatic (gastropod molluscs, oligochaete annelids, even echinoderms); and some are found in the host of their choice in locations other than the mantle cavity (body covering, posterior portion of intestine, liver, renal organ, etc.). Adaptation to the kinds of symbiotic life mentioned has, of course, influenced the development of specialized features at least some of which, then, are not of basic but only of convergent evolutionary importance in the comparative systematics of this and related scutico-, or even nonscutico-, ciliate groups. The anteriorly located sucker or adhesive disc of the hysterocinetids, sometimes quite prominent and complex, would fit into such a category. But basic differences (e.g., at the infraciliary level) are recognizable among the several additional characteristics considered briefly below.

The body size is often medium to large; there is seldom any tuft of caudal cilia; the small but distinct "M_1" membranelle of pleuronematines is missing, indistinct, or fused with M_2; the paroral membrane is never a stiff "velum"; and neither a director-meridian nor a postoral suture is known to be present; but there is a cytoproct. Although the scutico-hook stage has been noted in the few species studied carefully to date, a scutico-vestige may not be identifiable. Mucocysts, parasomal sacs, large and elongate cortical mitochondria (typical of all scuticociliates), and contractile vacuoles are present, but nematodesmata and trichocysts are absent; and encystment occurs rarely (reported once by Chatton & Lwoff, 1937).

Of the five families which I believe may justifiably be assigned to this suborder, the three largest are also the oldest and the best known: the Ancistridae, the Hemispeiridae, and the Hysterocinetidae. The first two of these (until now considered a single family) include such allegedly "primitive" genera as *Ancistrum*, much of the silverline system of which is, superficially at least, quite similar to that of free-living pleuronematine forms like the ubiquitous *Cyclidium*. The hysterocinetids (which may deserve a separate suborder of their own: see Jankowski, 1973b), are distinguished by their anteriorly developed sucker and their "degenerating" (i.e., sometimes nonfunctional) cytostome at the opposite pole. And their hosts are also atypical for the suborder: snails and especially oligochaetes (intestinal tracts). By convergent evolution these ciliates have come to resemble the Astomatida (see Chapter 12) in many respects, sometimes incredibly so (in body form and ciliation, etc., and even in the exhibition of catenoid colonies in some species).

The fourth family is comprised of another very "astome-looking" ciliate, Protanoplophryidae, with its single genus *Protanoplophrya* from the intestine of prosobranch snails (Miyashita, 1929; Raabe, 1972): a curious organism indeed! Incidentally, neither Corliss (1961) nor Raabe (1972) was justified in "correcting" the spelling of the name to read "*Protoanoplophrya.*" Finally, the fifth group, which I recognize only provisionally, the Nucleocorbulidae, was established as new only half a dozen years ago for a single species characterized by its possession of a huge ciliated posterior(?) sucker, somatic kineties appearing to run at right angles to the body axis, and a prominent basket-shaped macronucleus (Santhakumari & Nair, 1970, 1973, 1975). This allegedly highly unusual organism, found in the mantle cavity of shipworms, is avidly carnivorous, feeding indiscriminately on other ciliates (e.g., *Boveria* and *Trichodina*) present in the same habitat. But I wonder if it might not be (only) some kind of hysterocinetid?

* * * * *

The literature on thigmotrichines is extensive, even if we restrict the group to (only a part of) the old "arhynchodines" of Chatton & Lwoff (see Corliss, 1961), with the "rostrate" forms now dispersed among the Hypostomata (see Chapter 8). The earlier literature is quite easily available in such sources as Chatton & Lwoff (1949), Corliss (1961), Fenchel (1965a), Kahl (1934a), Kirby (1941a), de Puytorac (1968a), and Raabe (1949); see also Canella (1971) for selected citations. Of course, the best source of nearly all of the literature up into the early 1970's is the splendid monographic series completed by Raabe (1967, 1970a,b, 1971b, 1972) just before his passing: but we have to keep in mind that many of *his* "thigmotrichs" are not considered (by me) to be members of the Thigmotrichina of the present book. Older (pre-1960) papers on ancistrids sometimes overlooked include MacLennan & Connell (1931) and Uyemura (1937).

Except for the papers by Santhakumari & Nair (1970, 1973, 1975) involving *Nucleocorbula* – and the overall monographs by Fenchel and Raabe, cited above – much of the recent work on the group has concentrated on species of two well-known genera. Research on *Ancistrum* (and *Boveria* and occasionally other nearby genera) has been carried out by Fenchel (1964a), Khan (1970a), Lom et al. (1968), and Raabe (1959b); while papers on *Hysterocineta* (or closely related genera including the well-known *Ptychostomum* and some new forms), have been published by Kaczanowski (1961b, 1963), Kozloff (1960, 1965b), de Puytorac (1957c, 1963b, 1968a,b, 1969b), Raabe (1965), and Rees (1962). Also deserving of attention is Jankowski's (1974b) note on a new genus, *Dragescoa* (family Hemispeiridae), ectosymbiotic on an echinoid.

Unfortunately, stomatogenesis has been little studied since the pioneering work of Chatton & Lwoff (1936c) on *Proboveria*. Raabe (1949; and see 1972), long ago and using Klein's "dry" silver method, described some stages in *Hysterocineta*; and Small (1967) referred to occurrence of the phenomenon in species of several thigmotrich genera, but without details or figures. Equally unfortunate is the lack of published data of an ultrastructural nature on these important ciliates. Except for Lom et al. (1968), on *Ancistrum* and *Boveria*, Khan (1971), on *Ancistrumina*, and de Puytorac (1968b, 1969b), on hysterocinetids, all using only TEM, no further or more extensive papers have yet appeared at the time of this writing.

Addendum

Not available in time for consideration directly above or on preceding pages is the just-appearing light-microscopic work by Hatzidimitriou & Berger (1978) on the morphology and morphogenesis of a species of *Ancistrum*. The paper is particularly valuable for its detailed treatment of stomatogenesis, so rarely described in the literature on these ciliates (as mentioned above). In their discussion in which they compare aspects of the phenomenon as it occurs throughout the whole order Scuticociliatida, the authors suggest – among other conclusions drawn – that the separate subordinal status of the Thigmotrichina (first proposed by Corliss, 1975b) is justified.

Chapter 12

Class Oligohymenophora: (3) The Astomes, a Distinctive Group of Mouthless Hymenostomes

For some years, and into modern times, there has been concern over the fact that the mouthless condition of the symbiotic "astome" ciliates is perhaps given too much taxonomic weight in recognition of the order Astomatida as a high-level separate taxon. Their apparent origin from thigmotrichs raises the further question of how to reflect such a phylogeny taxonomically, keeping in mind the ever-present complication of convergent evolution. With absorption of the thigmotrichs into the hymenostome fold (certainly desirable: see Chapter 11), the question of the ultimate position (and rank) of the astomes may seem to have become even more knotty. But I submit that these problems can mostly be resolved without undue difficulty, primarily because of the expansion of the overall classification system on the basis of the revelation of greater diversity among groups than ever recognizable before (Corliss, 1974a). In brief, the subphylum Ciliophora has become a phylum; the hymenostomes have become a subclass containing separate orders, including the hymenostomes *sensu stricto* and the scuticociliates; and the scuticociliates have become an assemblage containing, as one of its suborders, the thigmotrichs (Corliss, 1975b, 1977a). Thus the astomes can remain an order within the new subclass, effectively being reduced to (just) another hymenostome group – and one which is conveniently a close neighbor to the thigmotrichs, their alleged ancestors.

There has had to be considerable "housecleaning" and reorganization within the order. Not only have certain species been shifted about to more appropriate locations within the assemblage but others have had to be excluded completely (e.g., the Curimostomatidae are now considered to be a tetrahymenine hymenostomatid family, a number of other "astome" genera have been transferred to the apostome kinetofragminophorans, etc.). Positions and characterizations of a number of families have been revised, largely on the basis of the comparative degree of evolution of their infraciliature and their specialized skeletal apparatus; at the same time, high regard has also been given such factors as the taxonomy, evolution, and distribution of host groups. The outstanding leader in all such recent works and revisions has been de Puytorac, with major papers dating essentially from his first monograph on the group (de Puytorac, 1954). Many questions which one could raise concerning the phylogeny as well as the taxonomy of the Astomatida have not yet been answered, naturally. A significant one is the relationship among what de Puytorac (see below) recognizes as superfamilies within the order: of the three groups represented by his superfamilies, the one containing the Haptophryidae is the most troublesome, from the point of view of (lack of) closeness to any families in the other two. There is a haunting possibility that the order is (still) polyphyletic, despite my own commitment to application of the concept of monophyly throughout the phylum whenever and wherever possible (Chapter 3).

From an overall approach, the astomes may continue to be characterized as relatively large, uniformly ciliated, mouthless ciliates found principally in the digestive tract of oligochaete annelids, although also in molluscs, leeches, polychaetes, turbellarians, and tailed amphibians. Unique characters include an almost universal infraciliary endoskeleton of varying complexity and, in many species, areas of thigmotactic ciliature or even elaborately developed holdfast organelles in the form of hooks, spines, spicules, or suckers. Fission is straightforward, particularly in that it is uncomplicated by stomatogenesis; but separation of the products is often incomplete, resulting in formation of catenoid colonies. The typical body form is ovoid to elongate, with a flattening apparently related to the habit of lying up against the intestinal epithelium of the host's digestive system. Some species, like some of their hosts, are virtually vermiform. Rows (numerous) of somatic cilia converge at the poles in characteristic patterns; the suture area or "aire sécante" at the anterior pole is of particular diagnostic importance. Contractile vacuoles, sometimes strung out in a long line, and mucocysts are present. Feeding is by osmotrophy.

Although not entirely unique, a curious feature of astomes is their widespread possession of facultatively symbiotic bacteria within their cytoplasm, often distinctive for a given species (Hovasse, 1946). A fact of perhaps similar interest is the presence of microsporidian protozoa in many species (de Puytorac, 1972a). Commonly present are a single compact macronucleus and a single lenticular micronucleus; but the former may be elongate and/or dentritic, and the latter – in one group – may be multiple. Conjugation has been but rarely observed. Encystment, also, seems to be rare; this is puzzling, since the mode of transfer to a fresh host, still unknown, conceivably could involve the phenomenon to considerable advantage.

Hosts may occur in the soil or in fresh, brackish, or marine waters. The taxonomic importance of astome distribution in various taxa of hosts (e.g., in families of annelids) has been thoroughly documented by de Puytorac, especially in his monograph on the family Hoplitophryidae *sensu lato*, an appendix to which includes host data on the Anoplophryidae as well (de Puytorac, 1972a). Often specific also is the particular sector of the intestinal tract of the host organism. It is unfortunate that no one has succeeded, to date, in culturing astomes free from their hosts. Of course, it is possible that some day a bonafide free-living member of the order will be found in nature. [Added note: in a very recent paper, Foissner (1976b) claims to have made just such a discovery! See Chapter 20.]

Fission has been mentioned above. More than one kind of strobilation or catenulation can be involved in the palintomy or tomitogenesis resulting in a chain-formation of the budded individuals in tandem; and the "chain" can be of different lengths. It is a curious fact that some of the hosts of these particular ciliates manifest analogous methods of asexual reproduction.

The endoskeleton so common to many astomes represents one of the most elaborate and specialized structures to be found in any group of ciliates in the entire phylum. Interestingly enough, though, the popularly known *Anoplophrya*, often labeled as a "typical astome," happens to possess neither skeletal parts nor attachment hooks. Electron-microscopical studies have revealed the principal origin of the endoskeleton from large, sometimes enormous, kinetodesmal fibers in specialized areas of the cytoplasm. These fibers become covered with a mucoproteinaceous material and are rigid; they are thus clearly visible in the organism, even at a low power level of light microscopy.

Anteriorly, many ciliates in families of this order develop one or more distinctive hooks or "crochets," scleroproteinaceous(?) attachment organelles often strengthened by an underlying ring of the same material. Others have single or multiple spines or spikes; still others a "mucron" reminiscent of that structure in gregarine protozoa. These cytoskeletal elements are presumably kinetosomal, ultimately, in origin. They serve as convenient features in taxonomic diagnoses at various levels in the classification scheme. Some species have a thigmotactic area or sucker (ciliated or bare) in addition to or instead of hooks. Certain members of the family Haptophryidae have highly developed suckers or acetabula, almost like those of trematode worms, with a pronouncedly thickened ecto-endoplasmic supporting area rich in fibrillar material. All such structures have evolved as adaptations to an endosymbiotic mode of life. The advantage of being able to cling successfully to the epithelial tissue of the host's intestinal tract (or, in one case, body cavity wall) is obvious.

Taxonomically, the Astomatida are easily divisible into three major groups, as mentioned above. These have recently been recognized as superfamilies by de Puytorac (1972a); since I have decided for this book not to use this taxonomic level (nor subfamilies, either: see Chapter 19), I am calling them merely "groups." Representative genera are depicted in the set of figures on page 136 (Plate XIII).

The first major group in my rearrangement (see Chapter 20) – leaving to one side the very new free-living Archiastomatidae of Foissner (1976b) which presumably should be placed as truly first of all – is represented principally by the family Anoplophryidae, plus a smaller separate

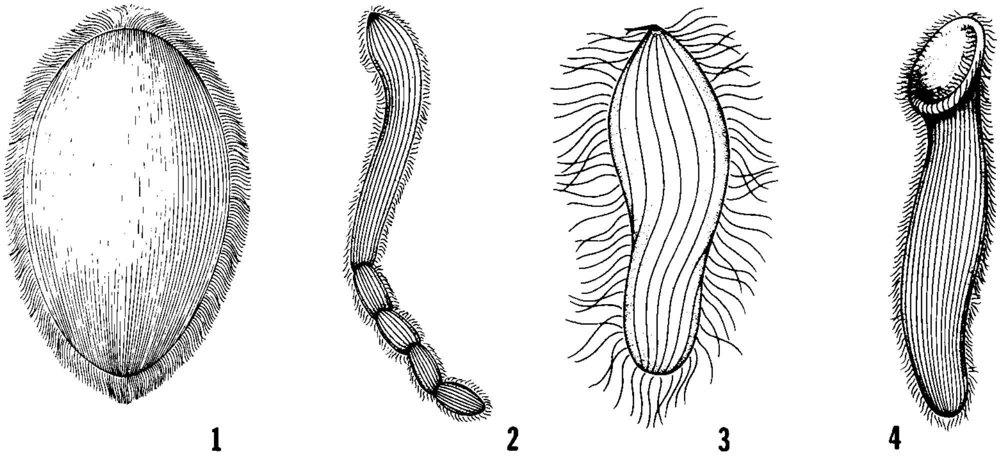

PLATE XIII. Representative astomes (order Astomatida). Fig. 1. *Anoplophrya*. 2. *Radiophrya* (with still-attached filial products forming catenoid colony). 3. *Maupasella*. 4. *Cepedietta* (often mistakenly called *Haptophrya*). [Additional figures appear in Chapter 20.]

assemblage centered around *Buetschliella*. Most of its known species are found in terrestrial oligochaetes (e.g., the common earthworm), although some also live in polychaetes and one has been reported from echinoderms. (The sanguicolous "*Anoplophrya*" of sandflea crustaceans is an apostome!) All are noted for their total lack of endoskeleton, hooks, and definitive suckers. However, a distinct anterior area of thigmotactic ciliature (said to be on the right side) is detectable in members of some of the genera, and it sometimes lies in a slight concavity of the body. The macronucleus is long and occasionally ribbon-like. There are usually two rows of contractile vacuoles, but sometimes contractile vacuole pores are absent. Chain-formation does not occur in the group. Conjugation has been seen but not studied in detail. The rows of somatic cilia are spiraled in a few species. With respect to size, many anoplophryid species are among the smaller astomes.

The second group contains the two large families Radiophryidae and Hoplitophryidae and three others, the well-known Intoshellinidae and Maupasellidae and the recently erected Contophryidae. The greatest diversity in cytoskeletal structure is seen here. Also characteristic is the widespread presence of a heavy inverted "V"-like structure at the apical end of the body, onto which the skeletal fibers converge (or, if you will, from which the fibers appear to arise). Hosts for species of the first two families include fresh-water and terrestrial oligochaetes, polychaetes, and molluscs. The distribution for species of the other families is more limited: terrestrial oligochaetes and leeches for the Maupasellidae; principally tubificids and lumbriculids for the Intoshellinidae; and tropical oligochaetes of the annelid family Glossoscolecidae for members of the small Contophryidae (see de Puytorac, 1972a, and references therein). The ciliary rows may be spiraled in some species of this assemblage, especially in the Intoshellinidae. Long-bodied ciliates in general, some may reach a length of nearly 2,000 µm. The bulk of all astome genera are assignable to these families (but note that I have removed the curious *Spirobuetschliella*, found in polychaete annelids, to the apostomes).

The third group, the most uncertain in both its relationship to other astomes and its internal taxonomy, is best known via the Haptophryidae. Unfortunately, taxonomic-nomenclatural confusion has long plagued this time-honored family and there has been much misunderstanding of what genera it includes, which ones are in which hosts, etc. Most of the problems involved were resolved a dozen years ago (see Corliss et al., 1965), but a number of astome workers still seem to be unaware of that paper. The haptophryids *sensu stricto* are heavily ciliated, large organisms, some reaching an individual length of as great as 2,000 μm; and they are equipped anteriorly with a generally conspicuous thigmotactic area or adhesive sucker, which, in turn, is provided with two or more hooks in some genera. The contractile vacuolar system is represented by a long canal with several pores. Binary fission is unequal, with chain formation common but not universal. The ciliary rows converge anteriorly onto a horseshoe-shaped suture line. The macronucleus is oval in shape or elongate, with the single micronucleus nearby. Hosts include marine and fresh-water planarian worms and tailless and (especially) tailed amphibians. A second family is proposed (see Chapter 20) to include several species of mouthless ciliates described from the body cavity of certain land snails (Lom, 1959c) and originally placed within a subgroup of the Haptophryidae containing the long-known fresh-water planarian intestinal symbionts. In general agreement with de Puytorac (1963a; and unpublished), I am here removing them (*Clausilocola* and relatives) from that taxonomic location to a nearby family of their own. Briefly, the forms involved may be said to be characterized by their lack of a clearly defined sucker (although there is a depressed area of thigmotactic ciliature), by differences in the pattern of their infraciliature and in the shape of the macronucleus, by their scattered multiple contractile vacuoles, and by their greater overall resemblance to *Anoplophrya*-like astomes than to typical haptophryans, even if much of this has been brought about by convergence. Their hosts are totally different as well.

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The more classical literature on the astomes – going back nearly 150 years – need not be repeated directly here (see Corliss, 1961; and the bibliographies in the more recent papers cited above and below), although at least the names of the half-dozen outstanding authorities on the various groups during the first part of the present century should be mentioned, *viz.*, Bush, Cépède, Cheissin, Georgévitch, Heidenreich, and Rossolimo, some of whose monographic works are cited in Chapter 21. Key papers, particularly those concerned with astome systematics and generally published within the past 15–20 years, are listed below, roughly arranged by the three taxonomic groups discussed on preceding pages. Two points may be noted first. The bulk of the modern work is coming from the laboratory of de Puytorac; and, with the sole exception of Cheissin (1963b), the only ultrastructural observations available to date (to my knowledge) are those of Grain & de Puytorac (1974) and de Puytorac (1959c, 1960b, 1961a–c, 1963a, 1970a).

Important recent papers concerning my group one, the Anoplophryidae *sensu lato*, include several of the works already cited above (see especially de Puytorac, 1972a) and, in addition, de Puytorac (1961b,c). See also the note by Hartwig & Jelinek (1974).

Results of most of the relatively recent research on the Hoplitophryidae and close relatives may be found in the works of Georgévitch (1941), Kaczanowski (1961a), Lom (1956, 1957, 1959b, 1961a), Meier (1954), Morat (1965), Sukhanova (1963), Williams (1942), and the following continuing series by de Puytorac, alone or with colleagues: Grain & de Puytorac (1974), de Puytorac (1957b, 1959a,b, 1960a,b, 1961a, 1963a, 1969a, 1970a, 1971, 1972a), de Puytorac & Dragesco (1969a,b), de Puytorac & Rakotoarivelo (1965), and de Puytorac & Schrevel (1965).

For the last group, comprised of organisms belonging to the Haptophryidae and alleged relatives (perhaps the whole assemblage should be separated from all other astomes at a subordinal level?), most of the literature is well covered in Corliss et al. (1965). But the following works, four since that date, deserve mention here: Bush (1934), Kay (1942), Lom (1959c), MacLennan (1944), Powders (1970: an interesting ecological study of *Cepedietta* in salamanders), de Puytorac (1957a, 1963a, 1969a, 1971), Rankin (1937), Sikora (1963), and van der Velde (1975). The last two papers cited deal with the long-neglected *Steinella*, symbiotic in marine triclad turbellarians.

Addendum

An ultrastructural paper just out, by Gerassimova (1977), briefly treats the cortical fibrillar system of species of *Anoplophrya* and *Mesnilella*.

Chapter 13

Class Oligohymenophora: (4) The Peritrichs, Taxonomically a Perennial Puzzle

Long considered an independent group at a very high taxonomic level (e.g., see Kahl's, 1935a, still authoritative monograph), the Peritricha and their hierarchical position have been the center of a widely ranging controversy ever since Fauré-Fremiet (1950a), supported by Corliss (1956, 1961), proposed that their presumable ancestry among the hymenstomes *sensu lato* would also suggest close taxonomic ties with that group. Recent research with electron microscopy (e.g., see Lom et al., 1968, and references therein; and additional citations below) seems to lend credence to such a hypothesis. Yet some peritrichologists (e.g., see Finley, 1974) have felt that the uniquenesses of their group demand taxonomic exclusiveness, placing, or keeping, them at a rank roughly equivalent to the (formerly) two great assemblages of "holotrich" and "spirotrich" ciliates. This view was strongly supported by Cheissin & Poljansky (1963), Finley (1969a), Hyman (1959), and Raabe (1964a) and partially accepted by Honigberg et al. (1964) and Jankowski (1973c). On the other hand, the "descentation" stand, as Finley (1974) wittingly termed it, has been favored by Fauré-Fremiet (1965b), Jankowski (1967a), Lom et al. (1968), de Puytorac et al. (1974), de Puytorac & Grain (1976), Small (1976), several recent textbook writers, and the author, who has defended it on a number of occasions (e.g., Corliss, 1960a, 1961, 1968, 1974a,c, 1975b).

For me, two questions (i.e., answers to them) are most significant in this continuing debate. Does not the generally accepted ancestry of peritrichs from hymenostome scuticociliates (via the suborder of thigmotrichs) justify a reasonable closeness in taxonomic (classificational) position? And, secondly, are the distinctive characters of peritrichs truly completely exclusive or are not their "equivalents" (e.g., see lists of samples in Corliss, 1960a, 1974c) found among many (other) ordinal taxa belonging to various other high-level groups within the phylum? I believe that data exist showing that even some of the "most unique" features of peritrichs – be they morphological, physiological, morphogenetic, ecological, behavioral, cytogenetic, biochemical, or genetic – do appear to have their homologues or analogues in scattered species belonging to various other taxa of ciliates. It should also be kept in mind that the sedentary state of (most) peritrichs has surely had a profound effect on the secondary development of all sorts of adaptive characters, physiological as well as morphological. Such considerations, combined with the possible phylogenetic "evidence" referred to above, lead me to persist in the conclusion that peritrichs belong *among* – not separate from – the oligohymenophorans. But I concede that the level of subclass may be appropriate, in view of the sum total of their specialized attributes. It is likely that this taxonomic problem, overall, will continue to remain a controversial one.

Order PERITRICHIDA

Despite the arguments made above for "taking the peritrichs into the fold," the subclass Peritricha with its single order does exhibit a number of distinguishing characters; and its numerous and diverse species still maintain a homogeneity which sets the group as a whole apart from even its nearest taxonomic neighbors. Over a decade ago, Fauré-Fremiet (1965b), very concisely, and Raabe (1964a), more extensively, offered valuable discussion of many of the peritrich features considered below. I am supplementing their data with appropriate material or observations from the more recent studies of these taxonomically perennially puzzling but adorably fascinating creatures, curiosity-arousers since their first detection and delightful accounting by Leeuwenhoek nearly three centuries ago (see historical notes in Corliss, 1975a; Dobell, 1932; Finley, 1974).

With an oral field covering the entire apical end (ventral surface?) of the body, a greatly reduced somatic ciliature, often a stalk or holdfast organelle plus a locomotor fringe of cilia at the aboral pole, and an unusual arrangement of prominent peristomial ciliature circling in a counterclockwise sense the oral end of the organism and then plunging deep into an infundibular cavity at the bottom of which is found the cytostome, the peritrichs are easily superficially distinguishable from practically all other ciliates. When one adds the presence of curious pellicular pores, highly developed myonemes, a specialized buccokinetal mode of stomatogenesis, a division plane during fission which is parallel to the major axis of the body, the common production of arboroid colonies, and the dimorphism exhibited not only in production of the migratory telotrochs but also often in the differentiation of both macro- and microzooids and macro- and microconjugants (the latter fusing in total conjugation), then it is not difficult to understand why specialists on the group ("familiarity breeds respect": Corliss, 1976) insist that it is a very distinct one indeed.

There is still one more major distinctive character, probably the most important of all, although its homologue certainly occurs among other taxonomic groups, particularly the thigmotrichine scuticociliates. It is the scopula, the function of which – in the majority of peritrichs – is to participate in production of the stalk attaching the organism to the substratum. The stalk is a complicated and complex structure, contractile or noncontractile and single or ramified by successive dichotomies (in colonial forms). Its relationship to the group of scopulary kinetosomes had been suspected long ago, following the early discovery of the latter by Fauré-Fremiet (1904a,b, 1905), the same worker who much later was also the first to investigate the scopula so thoroughly ultrastructurally (see references on a subsequent page).

Additional features of taxonomic value may be listed briefly. The body form of stalked peritrichs is commonly bell-shaped, with the apex at the scopular pole; the form of motile species is generally disc- or goblet-shaped. Sedentary forms may be solitary or colonial; colonial forms may be contractile or noncontractile, with respect to individual zooids. Cysts are characteristic of many groups, though never reported for the Mobilina. Solitary species include a number which produce loricae. Endosymbiotic zoochlorellae are common in several peritrichs. Free-living forms are filter-feeding bactivores or, occasionally, algivores. Although some ectosymbiotic groups have essentially become parasitic in their habits, they continue to feed on bacteria (or debris) in the area, with rare exception, only directly utilizing host tissue. Endosymbionts presumably nourish themselves, in large measure, by osmotrophy. Contractility is not limited to spasmoneme-containing stalks: for example, other sets of myonemes function in a sphincter-like closure of the oral or epistomial disc of the organism or in contracting the body proper, independent of the stalk. The basal disc of mobiline species is also under control of a separate set of myonemes.

Mucocysts are present; but presumably more important are the still-enigmatic pellicular pores covering the body so noticeably in many species. Parasomal sacs are associated with kinetosomes of the oral ciliature. The contractile vacuole (occasionally multiple) empties into the infundibulum of the oral apparatus rather than directly to the outside, as is typical of other ciliate groups. There may be no true cytoproct (controversial in the literature). The single homomerous macronucleus is generally sausage-, horseshoe-, or "C"-shaped and accompanied by a single micronucleus.

Much attention, in recent years as well as in past decades and centuries, has been given to the scopula, the stalk, and the contractility of (many of) the latter; but a similar interest has always been maintained in the ciliary organelles at the other end of the peritrich body. However, not until the availability of techniques of silver impregnation and electron microscopy have investigators been able to begin to understand not only the structural intricacies involved but the possible homologies with elements of the oral ciliature and infraciliature of ciliates belonging to other taxonomic groups. Dynamic aspects of the process of stomatogenesis had to be elucidated as well as the static structural picture seen in the nondividing organism; and tracing the organelles involved all the way down to the cytostome had to be carried out. Although earlier works of Fauré-Fremiet, Raabe, and others had cast considerable light on the organization of the outer part of the oral apparatus, Lom's (1964) already classical monograph of 14 years ago presented the first thorough study of the *infundibular* part of the buccal apparatus and of the overall phenomenon of stomatogenesis, the latter complex process having been reported only once before (in a note on a mobiline species by Chatton & Villeneuve, 1937) and the inner oral ciliature of the infundibulum having been detected only partially (by Schröder, 1906c; later by Kofoid & Rosenberg, 1940).

Peritrichs possess a paroral membrane (or "haplokinety" or "stichodyad") with both ciliature and infraciliature similar in some detail to those encountered throughout many ciliate groups: see especially preceding accounts on other members of the class Oligohymenophora. The "polykineties" are conspicuous and/but possibly homologous with those of hymenostomes (see most recent discussion on this complex topic in de Puytorac & Grain, 1976, and de Puytorac et al., 1976). The cytostome-cytopharyngeal complex is located at the inner or lower end of the infundibular "funnel." No nematodesmata are present, although there are microtubules in the area and great masses of fibers known as the filamentous reticulum are present in the cytoplasm adjacent to the buccal cavity throughout its extent (first beautifully described by Rouiller & Fauré-Fremiet, 1957). Stomatogenesis may be considered to be buccokinetal (Corliss, 1973e), but of a subtype not yet defined. Particularly involved is the so-called "germinal row," a line of nonciliferous kinetosomes associated with the terminal portion of the (infraciliary base of the) paroral membrane and considered a homologue of the scutica by many workers.

Conjugation is total, as mentioned above. Sexual differentiation in these ciliates represents a field of study of great interest, although it has generally been neglected. The heroic efforts of Finley (e.g., see Finley, 1939, 1943, 1946, 1952, 1969a; Finley & Nicholas, 1950; Finley & Williams, 1955) are finally being recognized (e.g., see Raikov, 1972a). Few other protozoologists, with the principal exception of Dass (1953, 1954a,b) and Mügge (1957), have worked in the field within the past 25 years.

Peritrichs have become adapted to a wide range of habitats; several fresh-water species can even tolerate a dilute saline milieu. Sedentary forms are abundant in marine, brackish, and fresh-water habitats, attaching to a variety of available substrata, plant, animal, and inanimate. The potential use of many such species as biological indicators (e.g., of pollution) is now being clearly realized. Some sessiline species, interestingly enough, are known to live within the loricae of closely related peritrichs which, in turn, are regular symphorionts on aquatic coleopterans (Matthes & Guhl, 1975). Stalked solitary species (loricate and nonloricate) and colonial species abound, making the order – on the basis of its first suborder (the Sessilina) alone – easily the second largest (oligotrichs are first, just barely!) of all taxa within the phylum. More than 1,000 species have been described in the literature to date; scores of these are of dubious distinctness, however, as we begin to learn – or suspect – more about the great variability possible within single bonafide species under differing environmental conditions (but this is a problem which confronts us in the case of various other ciliate groups as well, including the allegedly more abundant oligotrichs). Permanently mobile forms (i.e., ignoring the free-swimming telotroch stage and the infrequent secondarily free-swimming species of "sedentary" peritrichs) occur as ectosymbionts, or occasionally endosymbionts, in association with a number of different kinds of marine or fresh-water hosts, ranging from other protozoa and the coelenterate *Hydra* to fishes and amphibians. A heavy trichodinid population on the gills of certain (particularly fresh-water) fishes has been known to contribute to the ultimate death of the host.

I recognize two suborders in this (single) order. Jankowski (1967a, 1973c, 1975) regards these as separate *orders* of the subclass Peritricha, and then recognizes some four suborders within the first one. The matter is considered further below. There are 17 families of peritrichs, in my scheme, some containing a number of genera and several very rich in species. But the number of new genera proposed since 1960 is not especially high: fewer than 15, and over half of these may not survive as separate taxa (I have placed five into synonymy myself: see Chapter 20), considering the traditional conservatism of specialists on this group of ciliates. A tremendous quantity of literature exists on the peritrichs. Significant monographs and papers, stressing those of recent vintage, are cited in appropriate places either in or at the end of the following taxonomic sections. Representative genera are depicted in the set of figures on page 144 (Plate XIV).

Suborder (1) Sessilina

Sedentary forms, rarely secondarily "remobilized," and typified by the widely- and long-known *Vorticella* (with its many and seemingly ubiquitous species), the sessiline peritrichs have been generally characterized adequately on preceding pages. Their morphology is dominated by the extensive oral ciliature at one pole and the scopula (with or without stalk) at the other. Pellicular ridges or "annulations" encircling the bell-shaped body, more distinct in some species than others, may be regularly accompanied by nearby pores similarly arranged circumferentially. The aborally located ciliary band of the telotroch, the cylindrical migratory "larval" form which arises via an anisotomic fission (or total conversion) of the attached form, typically does not bear cilia in the nondividing sedentary stage of the organism: only the kinetosomal infraciliature is then present. Species are free-living or epibiotic (ectocommensal "symphorionts" on a wide range of hosts), solitary or colonial. Colonial forms, basically with dichotomously branching stalks, manifest considerable diversity in size, structure, patterns of organization, modes of reproduction, etc., thus serving as ideal organisms in "cell lineage" studies at the protistan level.

Jankowski (1967a, 1973c) based his four suborders (of his "order Sessilida") on their differing means of (in one case, absence of) attachment to the substratum. I do not believe that such diversity is major enough, alone, to warrant such high-level taxonomic separation of the groups involved; further, there are important exceptions to his arbitrary arrangement. Nevertheless, his divisions do recognize some differences valuable in keys and similar sorting-out processes. They are essentially used below as a convenient way to discuss the kinds of forms embraced by my single large suborder Sessilina; and I include comments on the taxonomic unity (or lack thereof) in each case.

1. *Forms without stalks.* A number of sessiline peritrichs adhere to the substratum without the help of any – or of an identifiable, well-developed and "typical" – stalk. Their scopulae may be strongly thigmotactic, and the posterior pole of the body may be broadened or spread out to increase the area of surface contact, or only slender fibers may be produced. Species of *Scyphidia*, for example, occur on the gills or body surfaces of both fresh-water and marine vertebrates and invertebrates. One is even an ectosymbiont on another peritrich; another, an endoparasite of a polychaete annelid. In another group, colonial forms of *Ophrydium* exhibit the following unusual combination of characters: production of a seemingly nonarboroid colony (but slender branching fibers do unite individual zooids) embedded in a common gelatinous matrix; exhibition of a (colony) size as great as six inches (15 centimeters) in diameter; and presence of zooids with highly contractile bodies and containing green symbiotic zoochlorellae, the latter giving color to the whole colony. *Ellobiophrya* grasps host gill filaments with a pair of remarkable aboral "arms."

2. *Prominently stalked forms.* Four very common genera – among many others in Jankowski's overall group – may be distinguished on the basis of a number of characteristics, but most obviously by the few considered here. *Vorticella*, by its solitariness (though often occurring in large groups or masses) and its highly contractile and often very lengthy stalk; *Carchesium*, by its colonies of independently contractile zooids (i.e., the spasmonemes are not continuous throughout the branched stalks of the colony, as they are in most colonial peritrichs which are contractile at all); *Zoothamnium*, by its colonies with continuous spasmonemes, so that the entire group of zooids, numbering into the hundreds (thus easily visible to the naked eye), contracts or expands simultaneously; and *Epistylis*, by its colonies with totally noncontractile stalks and by its almost indiscriminate attachment (as a *generic* character: but some of its species are highly host-specific) to a great variety of living substrata. The acontractility of the stalk of the last genus (and its close relatives) sets them quite clearly apart from the other groups represented by the three immediately preceding genera. Epistylidids may also hold the record for size among peritrichs: some zooids are as large as 600 µm (length), with stalks extending 5-6,000 µm above the substratum! [The familial name Epistylididae is, alas, so *very* commonly misspelled.]

3. *Loricate forms.* Jankowski's third group is perhaps taxonomically the most artificial of

all, although it echoes the separation represented by the tribes espoused by Kahl (1935a) and is certainly set up on an easily discernible basis: the presence (or absence) of a lorica. All peritrichs *except* members of this group would have to be aloricate, according to Jankowski's system. But he excludes such forms as some of the epistylidids and operculariids which possess elaborate "thecae," extensions of the outer sheath of the stalk which may grow up to form a large cup or saucer-like structure enveloping a whole group of zooids (e.g., see illustrations in Matthes & Guhl, 1973b; Vávra, 1962). On the other hand, studies of ultrastructural properties of the intended membership of Jankowski's group may reveal some additional common attributes (beyond presence of a lorica) which might turn out to be at least partially supportive of Jankowski's recognition of a separate taxonomic group here. For example, the included *Lagenophrys* is not only loricate but has no stalk and apparently has, at most, a vestigial scopulary field (Couch, 1973). Representatives of a second family, however, the well-known genera *Cothurnia* and *Vaginicola*, do have stalks or, at least, scopulae. The stalks are used – in these and related genera – either to attach the organism to the inside wall of their own lorica or, in species in which the stalk protrudes through the ciliate's housing, to affix the whole complex to the substratum. Often the lorica itself is apparently "gluable" to a surface, essentially independently of the living body it houses. An amazing ability of many of these peritrichs is their sensing of the onset of cuticular molting by the arthropod to which they may be attached and their subsequent action: in brief, they manage to abandon such a substratum (and their attached loricae) "in the nick of time," later resettling on appropriate surfaces of the freshly emerged host organism and forming new loricae.

4. *Secondarily mobile forms*. The stalkless fresh-water species which swim about freely throughout their life cycle are also set apart in a separate suborder by Jankowski. However, somewhat paralleling the situation described in preceding cases, there are two groups lumped together here by Jankowski which basically may have little in common. One, represented by *Astylozoon* and *Hastatella*, has no visible posterior ciliary girdle, has a reduced scopula with one or two stiff bristles protruding from the area, and characteristically swims with the oral end of the body directed forward, propulsion being provided by the oral ciliature. The second, represented by *Opisthonecta* and *Telotrochidium*, has a permanently ciliated and highly visible trochal band, can attach to the substratum temporarily by strands of mucus secreted from the scopular area (but also so can *Astylozoon* on occasion), and always swims with its aboral end forward, as does the telotroch in the life cycle of all peritrichs with such a stage. One may ask whether any of these forms is a "permanent telotroch," thus serving as an example of neoteny at the unicellular level. Or – though probably much less likely – has a stalked sessile stage gone undetected? In a very recent paper by Foissner (1976a), another suggestion is made: that the Opisthonectidae may be ancestral to the stalked peritrichs (rather that *vice versa*).

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The literature on sessiline peritrichs is prodigious! The very widespread distribution of many of its hundreds of individual species has brought members of the suborder to the attention of biologists from a number of disciplines; and peritrichs are mentioned, at least in passing, in numerous works not solely protozoological in nature. From Leeuwenhoek and Linnaeus to Lom and Laird, these puzzling protozoa – and their relatives among the Mobilina – have been studied and recorded and written about: one can hardly expect to find an adequate digest of all such literature in any one publication. Most pre-1960 papers are deliberately omitted in subsequent pages, because the bulk of them are included in the bibliographies of the more modern sources of reference which are cited. But a group of earlier papers or monographs – from the 1880's through 1959 (occasionally more recent) and mainly taxonomic in nature – are submitted here because of their lasting value (the topics they cover can mostly be gleaned from perusal of their titles in the bibliography of Chapter 22 – some of the larger works are not devoted exclusively to the sessiline peritrichs, however, as will be noted): Baer (1952), Biegel (1954), Bütschli (1887-1889), Chatton (1936), Chatton & Lwoff (1929), Dons (1922), Entz (1892), Fauré-Fremiet (1905, 1910a, 1922, 1930, 1943b, 1948c,d), Gajewskaja (1933), Hammann (1953), Kahl (1933, 1935a,c), Kent (1880-

1882), Kitching (1938, 1956), Koltzoff (1912), Lust (1950), Matthes (1950a,b, 1955, 1958), Nenninger (1948), Noland (1959), Noland & Finley (1931), Penard (1914, 1922), Precht (1935), Schröder (1906a–c), Sommer (1951), Stammer (1955, 1963), Stiller (1941, 1960), Stokes (1888), Summers (1941), and Swarczewsky (1930).

Four arbitrarily chosen major areas of research on these peritrichs are treated below, with references limited to selected studies from the relatively recent literature and with mention of the principal organisms involved. I am deliberately avoiding citation, with rare exception, of a given paper in more than one category.

(1) The broad, combined area of systematics, morphology, and ecology. A "representative" few works from the fields of morphology and taxonomy are the following: Banina (1976), on aloricate sessiline families; Bock (1963), on *Thuricola*; Corliss & Brough (1965), Couch (1967, 1973), Debaisieux (1959), and Kane (1965, 1969), on species of the loricate and ectosymbiotic *Lagenophrys*; Dingfelder (1962), on *Astylozoon* and *Hastatella*; Dragesco (1972a) and Foissner (1976a), on *Telotrochidium*; Felinska (1965) and Kralik (1961a,b), on several loricate vaginicolids; Jankowski (1967e), Matthes & Guhl (extensive series: see, for example, 1973a,b, 1974a–d, 1975, and references therein), Matthes & Scheubel (1970, 1971), Noirot & Noirot-Timothée (1959), and Vávra (1962), on *Epistylis*, *Opercularia*, and relatives; Laval (1968), on a species of *Zoothamnium* which is the only marine pelagic vorticellid; López-Ochoterena (1963), on *Systylis*; Piesik (1975), on a new vorticellid genus, *Parazoothamnium*; Sugi (1960, 1961), Zagon (1970, 1971), Zagon & Small (1970), and Zagon et al. (1970), on *Carchesium*; and Willey & Walkosz (1975), Wilbert (1977a), and Winkler & Corliss (1965), on *Ophrydium*. One of the few new sessiline peritrich families erected during the past 40 years is the Rovinjellidae, described by Matthes (1972a). Taxonomic use of the annularly arranged silver-impregnable pellicular pores and/or striae has become popular in recent years for various species from the vorticellid, opisthonectid, operculariid, and astylozoid families. Stemming from the work of the Finley school of peritrichology (Barlow & Finley, 1976a; Davidson & Finley, 1972; Finley & Bacon, 1965; Hobbs & Lang, 1964; Reid, 1967), it is now heartily relied on in the prolific investigations of Foissner (e.g., Foissner, 1975, 1976a, 1977; Foissner & Schiffmann, 1975, 1976; Foissner & Schubert, 1977).

Finally, mention should be made here of two important monographs involving genera of both the Sessilina and the Mobilina: the first, by Lom (1964), a landmark in the comparative study of the buccal ciliature and infraciliature in these ciliates; the second, by Stiller (1971), a key to the peritrich fauna of Hungary with individual illustrations of some 416 species. Jankowski's (1967a, 1973c, 1975) important ideas on a new classification of the sessilines have already been discussed on preceding pages.

In ecology (see also the fourth "area," below), the excellent – though now aging – reviews by Fauré-Fremiet (1967d) and Noland & Gojdics (1967) contain many references of pertinence. Since that year (occasionally earlier), examples of research in the area which have often involved new approaches in both field and laboratory work are the following: Bick (1972), Bierhof & Roos (1976), Burbanck & Spoon (1967), Cela (1972), Curds (1969, 1975b), Curds & Cockburn (1970a,b), Curds et al. (1968), Detcheva (1972), Dietz (1964), Finley (1969b), Finley & McLaughlin (1963), Gittleson & Hoover (1969), Laval (1968), López-Ochoterena (1966), Morishita (1968, 1970, 1976), Nusch (1970), Persoone (1968), Roos & Trueba (1977), Ruthven & Cairns (1973), Sartory & Lloyd (1976), Small (1973), Spoon (1976), Stiller (1968), and Wilbert (1969).

(2) Ultrastructural investigations. TEM and SEM have been used increasingly ever since the pioneering works of Fauré-Fremiet and colleagues in the mid-fifties (principally on the stalk and scopula: see Rouiller & Fauré-Fremiet, 1957, 1958; Rouiller et al., 1956). The following are recent references to TEM work on various groups of sessilines: R. D. Allen (1973a,b), Amos (1972, 1975), Foissner (1975), Laval (1968), and McKanna (1973, 1974), on vorticellids; Baudoin & de Puytorac (1969), Bradbury (1965), Fauré-Fremiet et al. (1962), Favard & Carasso (1965), Lom (1973a), Noirot-Timothée & Lom (1965), and Rosenberg & Grim (1966), on epistylidids and opisthonectids; Couch (1973), on *Lagenophrys*; Lom & Corliss (1968), and Noirot-Timothée & Lom (1965), on *Scyphidia* and *Termitophrya*, respectively; and Willey & Walkosz (1975), on the

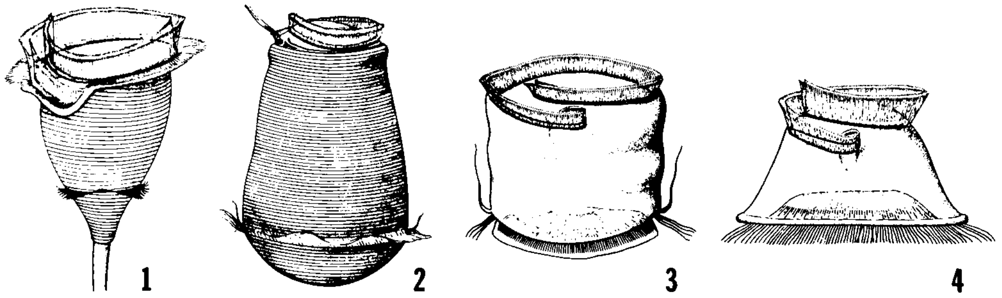

PLATE XIV. Representative peritrichs (order Peritrichida). Fig. 1. *Vorticella*, suborder Sessilina. 2. *Opisthonecta*, suborder Sessilina. 3. *Urceolaria*, suborder Mobilina. 4. *Trichodina*, suborder Mobilina. [Additional figures appear in Chapter 20.]

scopula of *Ophrydium*. Randall & Hopkins (1962), in an early important comparative study, examined the ultrastructure of stalks of species belonging to several genera: a significant and sometimes overlooked painstaking investigation. Pitelka's (1963, 1969) reviews remain a valuable source of information. Work by SEM is still in its infancy; but note the beautiful results obtained on *Carchesium, Telotrochidium, Vorticella,* and related forms by Barlow & Finley (1976b), Finley et al. (1972), Small & Ranganathan (1970), and Zagon (1971).

(3) Physiological or biochemical research. Because of the difficulty in culturing peritrichs profusely and in a simplified axenic medium, the amount of work involving sophisticated physiological or biochemical approaches – especially in the field of nutrition *sensu lato* – has been greatly restricted. Should that barrier ever be overcome, one might expect a burgeoning of the literature in the area comparable to that witnessed for the hymenostome *Tetrahymena* during the past three or four decades. Improvements in culture techniques have been particularly sought by Finley and his students (e.g., see Finley, 1966; Finley & McLaughlin, 1963, 1965; Finley et al., 1959; McLaughlin et al., 1974); and they have been utilized in chromatographic studies of sexuality (Finley & Williams, 1955), in physiological work on en- and excystation (Finley & Lewis, 1960), and in the taxonomic studies from his laboratory which were cited in a preceding paragraph. Vorticellids, epistylidids, and opisthonectids have served as favorite experimental organisms both in Finley's institution and in most of the other laboratories in which the following recent works (purposely omitting papers given on preceding pages) have been carried out, investigations mainly concerned with the biochemistry of contraction or the cytochemistry of nuclei or of various cytoplasmic inclusions: Carasso & Favard (1965, 1966), Carasso et al. (1970), Chattopadhyay et al. (1972), Goldfischer et al. (1963), Rahat et al. (1969), Thiery (1967), and Townes & Brown (1965). Jones et al. (1970b) undertook a novel investigation of contractility of stalks in species of several genera by use of precise microcinematographic techniques; and Jahn & Hendrix (1971) have studied locomotion in *Opisthonecta*.

(4) "Host-parasite" relationships. The whole area of "symbiology" needs – in the case of the peritrichs and of many other mostly "nonparasitic" *sensu stricto* ciliates (which includes the bulk of the taxa treated in this book, since few embrace truly parasitic forms) – to be developed using the modern technologies and sophisticated approaches of today's physiologically-biochemically oriented parasitologist of the sporozoa (among the protozoa) and the helminth groups (among the lower metazoa). For the large number of species under consideration in the present chapter, most papers have been limited to merely descriptive accounts of the occurrence of peritrich symphorionts on a great variety of living substrata. Often there may be rather strong host specificity; and the adaptability of the ciliate to habits or habitat of the host organism may be quite remarkable, involving pronounced morphological as well as physiological changes. Hosts may come from diverse taxa, but the main

groups involved in the following selected recent researches are as follows: crustaceans, salt- and fresh-water decapods and amphipods – Arvy et al. (1969), Clamp (1973), Fenchel (1965b), Kane (1965), Matthes & Guhl (1974c), and Sprague & Couch (1971); water-beetles – Baudoin (1964), Matthes & Guhl (1973a,b, 1975), Matthes & Scheubel (1971); and earlier papers by the Erlangen group; marine and fresh-water molluscs – Lom & Corliss (1968); and fresh-water fishes – Banina (1968), Chernyshova (1976), Lom (1966, 1973a), and Scheubel (1973). An old but unsurpassed account is that by Chatton & Lwoff (1929), who described the unique adaptation of the incredible *Ellobiophrya* to the gill filaments of a marine lamellibranch mollusc. The organism makes a closed ring around the host tissue by amazing embracing movements of two posterior outgrowths of its body. More recently, Laird (1959) and Naidenova & Zaika (1969) have described species in genera closely related to *Ellobiophrya*: the group deserves familial status.

Suborder (2) Mobilina

Comprising a much smaller though important and widespread group, the mobiline peritrichs possess many characteristics in common with the sessilines, particularly in their oral ciliature and infraciliature, their trochal band (permanently ciliated, however), their nuclear apparatus, and aspects of their general behavior and ecology. They even swim with disc-end (aboral pole) forward, like sessiline telotrochs. Conjugation again involves total fusion of conjugants. On the other hand, mobiline species are stalkless, conical or cylindrical or goblet-shaped (though often orally-aborally flattened), small, free-swimming forms characterized by the complex thigmotactic apparatus so commonly present at the aboral pole of the body; and they all have a strong affinity for very close association with some vertebrate or invertebrate organism as a host. Such living substrata occur in both fresh-water and marine habitats and involve diverse groups: coelenterates, turbellarians, molluscs, echinoderms, crustaceans, amphibians, and various fishes – not to mention many potential hosts yet to be searched for mobiline peritrich riders. Even other ciliates may serve as a substratum.

Ultrastructural, as well as silver-impregnation, studies carried out to date indicate that infraciliary structures, cytoplasmic and pellicular organelles, etc. bear, in general, close resemblance to their counterparts present in members of the preceding suborder. It should be emphasized, however, that differences *in detail* do exist and that such variations are of considerable taxonomic and evolutionary significance within the order.

The adhesive apparatus of the mobiline peritrichs, as mentioned above, is their most distinctive feature. The basal disc is typically broad and flat (or slightly concave) and is in very close association, both structurally and functionally, with the permanent locomotor fringe. In addition, there may be other concentric rings of posterior ciliature, of mysterious origin and function, in the vicinity: in some species certain of these – the marginal cilia – are so prominent that they have been referred to as cirri. Finally, other (or the same) species may possess a well-developed velum in the area.

The disc proper is reinforced by a band of radially arranged ribs which, in turn, are associated with a system of radiating myonemes. There are several of these elements for each part of the skeletal or denticulate ring which represents the "core" of the disc – a most striking and elaborate organelle. Exceedingly reminiscent of metazoan vertebrae (on a micro-scale!), two or three dozen articulated skeletal denticles, composed of a scleroprotein, form a nearly perfect circle. Details in their number, organization, and substructure are taxonomically of great diagnostic importance, especially when coupled with differences in composition and dimensions of component parts of the buccal apparatus at the other pole. Despite its "hard" appearance and remarks in the older literature about its probable abrasive usage in "boring" or cutting into host epithelium, the denticulate ring does not so behave. The whole disc is smooth and flexible; yet it is true that its rim may serve to constrict some of the underlying cells of the host's epithelial tissue, causing a localized lesion if the ciliates are present in great enough abundance.

There are about a dozen genera acceptably included in the suborder today, but long the best known and with species the most widely distributed is *Trichodina*. Trichodinids, which have all of the elaborate structures briefly described above except for the strong marginal cilia, are commensals on or in many species of aquatic animals, fresh-water and marine. Hosts range from *Hydra* to *Hyla*; and several species are common as endoparasites in the urinary bladder of fishes and amphibians. Some are themselves infected with parasites – for example, with the suctorian *Endosphaera*. Over 60 species of trichodinids have been recovered from gills of marine fishes alone (Lom & Laird, 1969); but the disease called trichodiniasis is known principally from invasions in fishes from fresh-water habitats, curiously enough (Lom, 1970a). Species of several genera have now been studied by TEM: citations to that literature are included below.

There are enough measurable characters, especially considering the ones revealed with such clarity in specimens impregnated with silver, to make possible a refined morphometric approach to the comparative taxonomy of trichodinids and their relatives. It has not been appropriate to attempt the undertaking of such a major task here; I can only hope that the classification tentatively proposed in Chapter 20 is a reasonable approximation to that which might result from such a detailed revision. My own taxonomic conclusions, though rather less conservative, are in large measure based on the important observations and ideas of Lom (1963c, 1975) and Raabe (1963a), to whom I am thus greatly indebted. I recognize five families within the suborder, groups separated on differences in characteristics associated with the following: (1) the skeletal ring at the aboral pole (e.g., attributes of the denticles there – number, structure, composition, etc.); (2) the buccal ciliature at the oral pole (including the number of turns of the apical ciliary wreath); (3) a complex of additional morphological-cytoplasmic features – body shape, cortical rings (pellicular striae?) on the body surface, form of the macronucleus, shape of the infundibulum, presence or absence of specialized structures or cytoplasmic inclusions; and (4) the host involved – kind(s), site(s) occupied by the symbiont, etc.

Species of the time-honored *Urceolaria* (alas, a preoccupied name: but see nomenclatural remarks at the end of this chapter) occur on fresh-water planarians and marine polychaete annelids and in the mantle cavity of certain marine molluscs (Fenchel, 1965a; Zick, 1928). *Leiotrocha*, which I am more or less resurrecting and whose family name I have essentially rediscovered, contains forms found on the gills of marine molluscs, on the spines of sea urchins, and on a few other invertebrates (Beers, 1964; Fenchel, 1965a; Johnston, 1938). *Polycycla*, for which a family was once erected (by Poljansky, 1951a), then neglected, but subsequently supported by Fauré-Fremiet (see Fauré-Fremiet & Czapik, 1966), lives primarily in the intestinal tract of holothurian echinoderms. The single species *Trichodinopsis paradoxica*, from the intestine of a terrestrial mollusc (see Grassé & Mugard, 1963; Issel, 1905–1906) is the sole occupant of a fourth family; known for 120 years, it has recently been studied ultrastructurally (see references below). Finally, we have the Trichodinidae, by far the largest mobiline group with its seven or eight presumably bonafide genera. Species of *Trichodina* itself show the greatest diversity and widest distribution of all. Members of the family overall are found to occur on a variety of vertebrate, invertebrate, and even protozoan hosts or within the urogenital tract of lower vertebrates (fishes and amphibians). As mentioned above, the fish-gill parasites may have a truly deleterious effect on their hosts.

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Papers on mobiline peritrichs are numerous, though far fewer than those on the sessilines. Once again, many works not primarily concerned with peritrichs contain mention – or occasionally treatments of some substance – of selected species: this is particularly true of certain ecological studies and taxonomic surveys (e.g., by ichthyoparasitologists). Such papers are not commonly cited here. Most of the following references are of research results published within the past 15 years. Still older literature, much of which is indeed important, extending back some 200 years, can be found either in the bibliographies of works cited below or in such sources as Corliss (1961) and Kahl (1933, 1935a,c). Furthermore, some of the older peritrich works already listed under the preceding section on the Sessilina are of value for the Mobilina as well. An isolated late 19th century treatise of considerable systematic significance but often overlooked is Wallengren (1897).

The majority of pre-1960 papers are taxonomic or morphological, though Colwin (1944), as an example of an exception, studied conjugation in a polycyclid. Dogiel (1940, 1948), and Fauré-Fremiet (1943c; Fauré-Fremiet & Thaureaux, 1944) laid a lasting foundation for the comparative taxonomy of many genera, with emphasis on kinds of characters to use and on a biometric approach to their treatment. Brouardel (1951) and Hirshfield (1949) produced substantial works on species from marine limpets; Davis (1947) offered an early comprehensive review of mobilines found associated with fresh-water fishes; Poljansky (1951a) gave the name *Polycycla* to species in holothurian echinoderms; Šrámek-Hušek (1953) discussed the problem of pathogenicity of trichodinids; and Uzmann & Stickney (1954) carried out a superb study of a trichodinid from a marine bivalve mollusc, pioneering in post-Chattonian usage of the French silver technique with these ciliates. I am not citing here the additional works of such astute investigators as Chatton, da Cunha, Fauré-Fremiet, Hirshfield, Jackson, Laird, MacLennan, Mueller, Nigrelli, Noble, Padnos, Pai, Poljansky, Raabe, Šrámek-Hušek, Suzuki, Tripathi, and Vojtek. Organisms most frequently studied have belonged to the widespread genus *Trichodina*, whose 175–200 (all bonafide?) species occur in association with a great range of hosts, as already mentioned. [Some of these papers *do* now appear, in a special addendum to the bibliography.]

In more recent times, new investigations and fresh ideas on mobiline peritrich morphology, systematics, and ecology (plus occasionally physiology) are to be found in the substantial papers of Beers (1964, 1966b), Beinbrech (1967), Bradbury (1970), Fauré-Fremiet & Czapik (1966), Fenchel (1965a), Grassé & Mugard (1963), Jankowski (1968f, 1974b), Kashkovsky (1974), Kazubski (1958, 1971), Kazubski & Migała (1968), Khan (1972), Laird (1961a,b), Nobel et al. (1963), Richards (1971), Sandon (1965), Stein (1961, 1967, 1968, 1974, 1976), Wellborn (1967), Zaika (1966), and Zhukov (1964). Also reference should be made to the large, but taxonomically conservative, monograph by Haider (1964); and, above all, to the indispensable series both by Lom and by Raabe (e.g., see Lom, 1958, 1959a, 1960, 1961b, 1963a–c, 1964, 1970a,c, 1973b; Lom & Haldar, 1976, 1977; Lom & Hoffman, 1964; Lom & Laird, 1969; Lom & Stein, 1966; and Raabe, 1958, 1959a,c, 1961, 1963a, 1964b; Raabe & Raabe, 1959). New genera within the past 20 years have been described by Kazubski (1958), Lom (1959a, 1963c), Raabe (1963a), Stein (1961).

Published data on the ultrastructrual nature of these peritrichs are rather rare, to date. The principal genus so investigated has been the curious *Trichodinopsis*. Fauré-Fremiet et al. (1956b) made an early study of its sole species (found in a terrestrial snail) with TEM; later Favard et al. (1963) reexamined its aboral disc in some detail; and Noirot-Timothée, with Lom, made an extensive ultrastructural investigation not yet published in full (but see Noirot-Timothée, 1968; and Noirot-Timothée & Lom in Grain, 1969). Favard et al. (1963) also studied a *Trichodina* (from the urinary bladder of the frog) with TEM; the basal disc of this organism is more elaborate, the linked skeletal denticles possessing very strong spines and blades. Finally, Lom (1973b) has studied *Trichodinella* (from the gills of fresh-water fishes) ultrastructurally from the point of view of effect on the host tissue at the surface of contact.

Nomenclatural Remark on *Urceolaria*

As Johnston (1938) – in a totally overlooked paper – has pointed out, protozoologists have been unaware that Lamarck's (1801) original *Urceolaria* contained but a single species, an organism subsequently identified as a rotifer! No ciliates were included until Lamarck (1815); thus, strictly, the name is not available for use with protozoa. In the meantime, Dujardin (1840) had erected the family; and Stein (1854, 1867) had (re)established the genus, though ignoring Lamarck and choosing as type-species a form described by von Siebold (1850). For the past 110 years, many have credited Stein with descriptions and even names of both family and genus. Rejecting, now, my own very recently suggested solution (Corliss, 1977a) – replacement of the name *Urceolaria* because of its junior homonym status – I intend to petition the International Commission on Zoological Nomenclature as Kirby (1954) did for *Stentor*, for preservation of the time-honored names (generic and familial) with dates and authorships as shown in Chapter 20.

Chapter 14

Class Polyhymenophora: (1) The Heterotrichs, Base Group of the Spirotrichs, and the Odontostomes

Commonly large, widely distributed, free-swimming forms, with ciliation ranging from a uniform and holotrichous coverage to a sparse arrangement of only compound ciliary organelles, members of the well-known "spirotrich" assemblage of ciliates recently (re)named the Polyhymenophora represent, on the whole, a much more compact taxonomic group of species than those comprising the two preceding classes. This results primarily from the fact that their morphology is dominated by their conspicuous and well-developed oral ciliature: they all share in possession of a prominent, regularly organized adoral zone of multiple membranelles (AZM) – better termed "paramembranelles" for the typical polyhymenophorans, according to the very recent work of de Puytorac & Grain (1976) and de Puytorac et al. (1976) – which occupies the left side of the buccal cavity or peristomial field and often extends out onto and/or around the anterior end of the organism. On the right are usually one or more paroral membranes (not necessarily homologues of the same-named structure in the Oligohymenophora). There are no mouthless members of the class. Stomatogenesis is parakinetal or apokinetal (Corliss, 1973e). A second widely shared major characteristic is the paucity of simple somatic ciliation, although this is not the condition found in many members of the first large order, the heterotrichs. Diversity among polyhymenophorans is manifest in variation in arrangement, location, density, etc. of parts of the compound somatic and buccal ciliature and/or in development of unique structures adaptively related to the differing ecological or physiological conditions characteristic of the several taxonomic subgroups comprising the class.

Except for the modern important systematic works of such prolific ciliatologists as Balech, Borror, Dragesco, Earl, Hirshfield and associates, Jankowski, Laval-Peuto, Loeblich, Radoičić, Tappan, and Tuffrau, and very recently Albaret, most of the monographs on major groups of the Polyhymenophora date back well before the middle of the present century. But the publications of Kahl (1926, 1927a, 1928, 1929, 1932a,b, 1933, 1935b) and of such workers as Chatton & Séguéla (1940), Fauré-Fremiet (1924, 1936, 1945b, 1948b), von Gelei (1954), Hadži (1951), Jörgensen (1927), Kofoid & Campbell (1929, 1939), Penard (1922), and Villeneuve-Brachon (1940) will always remain invaluable papers to consult. They, plus Corliss (1961), also supply direct references to the great bulk of the literature which appeared in even earlier years. Among the growing number of books dedicated to treatment of single genera, two have appeared on polyhymenophorans: *Stentor*, majestic "king of ciliates," has been monographed, principally from a morphogenetic-experimental approach, by Tartar (1961); and *Blepharisma*, another well-known and often-pigmented ("pink") genus, has been treated more recently – primarily from a physiological point of view – by Giese (1973) and collaborators.

The Spirotricha is the only subclass included in the class; thus the class and subclass characterizations are identical, and the traditional name for the group has (also) been preserved! Of the four orders which I recognize, the first (the Heterotrichida), with its (now) six suborders, and the Odontostomatida are treated here (below); the other two are considered in following chapters. The general taxonomic conservativeness or noncontroversial nature of the whole group may be realized by comparison of the scheme of classification endorsed here with that supported by Corliss (1961) some 15–16 years ago. The most highly significant high-level change (while not disregarding the importance of the establishment of several new suborders and new families) has been the total ejection of the order Entodiniomorphida, now universally recognized as having much closer affinities with the vestibuliferan trichostomes (see Chapters 7, 17, 20). As essentially the only major change in the case of the spirotrichs, it is to be contrasted with the multiple and drastic reorganization proposed at class and subclass, as well as ordinal and familial, levels within the former "holotrich" assemblage of the Faurean system of classification (see Chapters 1, 5–13, 20).

Order HETEROTRICHIDA

Large in size, of common occurrence, sometimes highly contractile, and possessing amazing regenerative powers, many heterotrichs could nonetheless superficially be easily mistaken for certain gymnostome or hymenostome ciliates – because of their uniform and holotrichous body ciliation and anterior location of the mouth – were it not for the dominating, extensive AZM originating on the left side of the buccal area. That the group demonstrates lability and plasticity, evolutionarily speaking; that it arose from some kind of hymenostome (or "prehymenostome," such as gymnostome) ancestry; and that it gave rise – via its several suborders – to the "more advanced" spirotrich taxa are conclusions generally – rightly or wrongly – little disputed. In this respect, then, the heterotrichs phylogenetically may be considered a pivotal group of importance (see also Chapter 17).

The paroral membrane appears to occur as one or two separate lines of ciliature: much more work needs to be carried out at the ultrastructural level to determine the possible infraciliary (and phylogenetic!) significance of such apparent differences. Available too late for detailed analysis are the very recent papers of pertinence by de Puytorac & Grain (1976) and de Puytorac et al. (1976), comparative studies in which the infraciliature of the typical heterotrich (exclusive of the armophorines, clevelandellines, and plagiotomines) paroral membrane is described as a "stichomonad," with a pair of these characteristic only of the heterotrichines (see glossary, Chapter 2). Kineties are usually numerous and bipolar; true kinetodesmata (as I define the organelle) are generally absent (except among the clevelandellines). Pigment vesicles are present in a number of species, often visible *en masse* as longitudinal stripes in the pellicle. One or more contractile vacuoles are always present, and encystment is common. Nematodesmata of relatively small numbers of microtubules contribute to the support of the cytopharyngeal apparatus in the species studied ultrastructurally to date. Extensive systems of postciliodesmata (Km fibers) and myonemes (M-bands) appear to be involved in contraction, extension, and elongation of the body in species exhibiting such phenomena. Feeding methods and preferences are diverse. Distribution is widespread in fresh-water, brackish, interstitial and marine habitats; and some species are ecto- or endosymbionts on or in various invertebrate or vertebrate hosts.

The literature on the heterotrichs is considered in place for each of its six suborders, treated below. Representative genera are depicted in the set of figures on page 154 (Plate XV).

Suborder (1) Heterotrichina

Comprising some 9–10 recognized families, the heterotrichines constitute the largest subdivision of the order and contain some of the best-known and most common ciliates of the whole phylum. Species belonging here possess most of the characteristics described in a general way in preceding paragraphs. Somatic ciliation is well developed; the body generally has simple axes of symmetry and, in many (but far from all) species, is highly contractile; there are no kinetodesmata; loricae are absent, but cysts are common. Stomatogenesis appears to include both parakinetal and apokinetal modes, depending on the organism. Macronuclei are compact or beaded. Practically all species are free-living (a few are echinophilic inquilines), free-swimming (some attach temporarily) forms, and habitats are diverse.

Except for segregating out several "atypical" families into new suborders (see below), the taxonomic composition of the heterotrichines has not been greatly altered over that recognized years ago by Kahl (1932b) and Corliss (1961). New genera have been added (and many new species) and two or three new families have been proposed. The removal to new suborders of several distinctive groups parallels my own treatment, two decades ago (Corliss, 1957a), of the Licnophoridae. Now, based on the work of Jankowski (1964a,b), the resurrected Caenomorphidae has become the suborder Armophorina; and the Folliculinidae, the Coliphorina. Albaret (1974, 1975) has proposed Plagiotomina to contain the (now) small symbiotic family Plagiotomidae; and, very recently, de Puytorac & Grain (1976) have established the Clevelandellina for other families of endocommensalistic heterotrichs, basing their decision primarily on the masterful study by Albaret (1975).

To conserve space, further treatment of characteristics distinctive of various of the heterotrichines and mention of some of the principal genera are considered together, below, along with reference to the copious literature on the group.

* * * * *

Papers on members of the Heterotrichina are very numerous and extend back at least 200 years. If I were to be limited to citing the single pre-20th century work of the most outstanding quality and lasting value, I should submit reference to Stein (1867), without hesitation. What an admirable and beautiful production! Other early publications cannot, for the usual reason of space restriction, be listed here: but the combined bibliographies of Corliss (1961), Dragesco (1970), Giese (1973), Jankowski (1964b), Kahl (1932b + 1935c), Pitelka (1969), Sleigh (1974a), Tartar (1961), Taylor (1941), and Villeneuve-Brachon (1940) should lead the interested reader to the bulk of such important literature – not only to systematic works but also to the results of research in such areas as cytology, physiology, and morphogenetics. Even the post-1960 literature of importance is too vast to be totally referred to here. Major subjects covered range from ecological and taxonomic considerations to physiological (e.g., contractility) and ultrastructural studies. Rather than list or discuss works in these areas which have been concerned specifically with a great number of the included genera and species of each of the 10 families I recognize (see Chapter 20), I am, first, giving rather cursory consideration to some dozen genera; this is followed by citation of results of selected but more numerous investigations on three of the best-known and most frequently studied genera of the suborder – *viz.*, *Stentor*, *Blepharisma*, and *Spirostomum*.

Metopus (a unique polyhymenophoran genus, incidentally, in its exhibition of total conjugation: see Noland, 1927) and relatives have been intensively studied by Jankowski (1964b); Dragesco (1968b) has described a new species with typical care; Schulze's (1959) and Villeneuve-Brachon's (1940) older works should be cited; and Tuffrau (1968) has carried out a thorough investigation of the fibrillar system in these ciliates. Many metopids (and some genera from nearby families) are polysaprobic forms; thus protozoan ecologists have frequently encountered them. Such works are too numerous for complete citation here, but papers with comprehensive treatments include Buitkamp & Wilbert (1974, on *Bryometopus*), Dingfelder (1962), Dragesco (1960, 1963b, on marine forms; 1966a, 1968a, 1970, on fresh-water forms), Fenchel et al. (1977), Schulze (1959), Tucolesco (1962a), Vuxanovici (1962b,c, 1963a), and Wilbert (1969). Among marine forms are the interesting cases of *Metopus* species living as obligate inquilines in certain echinoids (see Berger in Levine, 1972; Lucas, 1934, 1940; and references therein). Kirby's (1934) aging but excellent description of the very closely related *Spirorhynchus*, free-living in salt marshes, should be recalled.

Bursaria is often seen. In recent years, Dragesco (1972a) has described a new species of it; Ruthmann (1964) and Ruthmann & Heckmann (1961) have investigated its macronucleus; and Tuffrau (1968), its fibrillar system. Jankowski (1973f) has reported a suctorian parasite which kills its bursarian host. Intensive study of this genus may reveal unsuspected taxonomic differences in comparison with other heterotrichine genera (personal communication from Dr. Dimas Fernândez-Galiano). Marine species of *Peritromus* have been studied by Borror (1963b) and Tuffrau (1968); the totally marine *Anigsteinia*, comprised of a group of species formerly in either *Blepharisma* or *Spirostomum*, has been treated recently by Isquith & Repak (1974). Didier & Dragesco (1978), Dragesco (1970), and Roque (1971) have published on the morphology of the intriguing *Phacodinium metchnicoffi*, a neglected ciliate which I studied some years ago (unpublished) and which I now (inspired by Dragesco) place in a family of its own (see Chapter 20): Gellert's (1950b) fine study of it, incidentally, has been universally overlooked.

Three other genera long known (generally as inhabitants of marine ecosystems yet also with some notable fresh-water forms) but little studied during the past 25–35 years – although their species would appear to be attractive for experimental work – are *Climacostomum*, *Condylostoma*, and *Fabrea*. Repak (1972) united the first and third in a new family, the Climacostomidae; and *Condylostoma* is the type-genus of a neighboring family. Corliss (1961), Kahl (1932b + 1935c), and Villeneuve-Brachon (1940) cite most of the significant older literature. Aside from Borror's (1963b), Dragesco's (e.g., 1963b, 1970), and a few other workers' modern taxonomic-ecological observations and Repak's (1972) systematic and morphogenetic paper, only a handful of additional post-1960 papers have appeared on these genera. *Fabrea* has been studied from the point of view of its encystment process (Demar-Gervais & Génermont, 1972; Génermont, 1964; Génermont & Gervais, 1967; Génermont & Wright, 1965), its conjugation (Demar-Gervais, 1971; and recall Ellis, 1937), and its fibrillar systems (Tuffrau, 1968). *Condylostoma* has been investigated by Bohatier et al. (1976), Tartar (1965), Tartar & Pitelka (1969), Tuffrau (1968), and Yagiu & Shigenaka (1960); Fauré-Fremiet (1958) studied a psammophilic species possessing symbiotic chlamydomonads. The noncontractile (like *Blepharisma*) *Climacostomum* has recently been thoroughly examined, using both light and electron microscopy, by Peck et al. (1975).

Now we come to that regal genus *Stentor*, species of which have so long attracted the attention of protozoologists and cell biologists because of their size, ubiquity, ease of general laboratory culture and study under low powers of magnification, contractility, regenerative powers, and amenableness to experimental manipulation. Fortunately, the long and often colorful past history of work on *Stentor* has been competently and elegantly presented in the monograph by Tartar (1961; see also 1962). Morphogenetic aspects have been brought up closer to date in Tartar's (1967) review chapter, a good source of reference to his own post-1960 investigations (but also see Tartar, 1968a,b, 1970, 1972) as well as those of other workers. Much of the experimental research (including what one might call "experimental embryology at the protozoan level") on *Stentor* and other heterotrichs, however fascinating and important from other points of view, has had limited impact on the principal themes of the present book, systematics, comparative taxonomy, and phylogenetics. Setting the stage, incidentally, for many of the fine 20th-century studies of this nature on such ciliates by Fauré-Fremiet, Schwartz, Tartar, Uhlig, Weisz, and others were the classical researches of patient and perceptive "old-timers" like Balbiani (1888, 1892-1893), Johnson (1893), Lillie (1896), Morgan (1901), Moxon (1869), Schuberg (1890), Stein (1867), and Stevens (1903).

Selected recent investigations on contractility, ciliary movements, morphogenesis, conjugation, learning, nucleic acids, and other physiological or biochemical approaches to the biology of *Stentor*, beyond any already cited or referred to and exclusive of the ultrastructural papers cited below, include: Banerjee et al. (1975), Banerjee et al. (1972), Bannister & Tatchell (1968, 1972), Bennett & Francis (1972), Blumberg et al. (1973), Burchill (1967, 1968), Burchill & Rustal (1969), De Terra (1967, 1969a,b, 1970, 1971, 1972), Frazier (1973), Haight & Burchill (1970), Harden & Holland (1968), Huang & Mazia (1975), Hyvert et al. (1972), Jones et al. (1970a), König (1967), Makrides et al. (1970), Mandel & Muzyka (1971), Margulis et al. (1975), Margulis et al. (1969), Meister (1970), Neviackas & Margulis (1969), Pelvat & de Haller (1976), Pelvat et al. (1973), Plapp & Burchill (1972), Preece (1969), Sarras & Burchill (1975), Schulte & Schwartz (1970), Schweikhardt (1966), Sleigh (1962, 1966, 1968, 1969, 1974a,b), Tuffrau (1968), Uhlig (1960), Webb & Francis (1969), Wenzel & Liebsch (1975), Whiteley (1960), Whitson (1965), Younger et al. (1972), and Zech (1966).

Sometimes electron microscopy (both TEM and SEM) has been employed as one of the tools of study in the works cited above. In the following references, the main emphasis has been on ultrastructure, although the research may be in such areas as contractility or morphogenesis. Pioneering works on the fine structure of *Stentor* date from the publications of Fauré-Fremiet &

Rouiller (1958a,b), Inaba (1959), and especially Randall & Jackson (1958): see the early review by Pitelka (1963). Some modern papers include: Grain (1968a), Huang & Pitelka (1973), Newman (1974), Paulin & Brooks (1975), Paulin & Bussey (1971); and see Pitelka (1969).

A number of species of *Stentor* show hues of blue, green, blue-green, rose, red, yellow, brown, or black; others are colorless: see Tartar (1961) for discussion of pigmentation in the genus in general, and Møller (1962) for a chemical analysis of stentorin. A note on the seasonal blooms of a red form (a new species, the latest – but also see Kumazawa, 1974 – to be added to the genus: see Murthy & Bai, 1974) has recently been published (Bai & Murthy, 1975). No attempt is made here to list general ecological works on this genus (and other heterotrichs), because they are so numerous: Bick (1972), Borror (1973a), and the several modern textbooks of protozoology (see Chapter 21), however, may be consulted as guides to many such references. But the recent and extensive taxonomic-ecological observations of Dragesco (1966b, 1970), including a major treatment of *Stentor*, warrant special consideration. And Vuxanovici (1961b) might be mentioned.

A genus at times seeming to rival *Stentor* in attention these days is the noncontractile *Blepharisma*. In fact, direct or indirect reference to much of the literature on this taxonomically neighboring ciliate may be found in the many publications cited on immediately preceding pages, including "reviews" like Corliss (1961), Giese (1973), and Pitelka (1969). Giese (1973) is especially helpful, not only because of its recency but also because some of the book's 12 principal chapters are authored by appropriate invited specialists and each has its own bibliography. Although most of the volume is concerned with physiological topics, the chapter entitled "Classification, Distribution, and Evolution," authored by Hirshfield et al. (1973) contains information of particular pertinence to the present book: so the reader is especially referred to it.

Recent contributions to our knowledge of *Blepharisma* in areas of cytology, cytochemistry, comparative morphology, and systematics are: Bai & Tara (1974), Bhandary (1962), Dragesco (1970), Foissner (1972c), Hirshfield et al. (1965), Jankowski (1964b), Kattar (1965), Nilsson (1967), Parker & Giese (1971), Repak et al. (1977), Smith & Hirshfield (1976), Tuffrau (1968), Wilfert (1972); and see Giese's (1973) book. Pigment has been restudied by Kennedy (1966) and Sevenants (1965). One of the most interesting, as well as most diagnostic, properties of the "pink" *Blepharisma* is its possession of blepharismin (formerly known as "zoopurpurin"), a photosensitizing pigment which, under strong light, becomes lethal to its bearer. Morphogenesis, following the important work in modern times of Suzuki (1957c: and see 1970), has been investigated further by Eberhardt (1962), Isquith & Hirshfield (1968), Janisch (1969, 1970), Pohlídal & Janisch (1971), and Sawyer & Jenkins (1977); and cysts have been studied by Repak (1968). Cannibalism, another common characteristic, is treated in a chapter of its own in Giese (1973). The DNA cycle and RNA synthesis have been looked into by Bhandary & Hirshfield (1964), Minutoli & Hirshfield (1968), and Seshachar & Saxena (1968a). Patterson (1976) has just completed a novel study of the contractile vacuolar cycle in *Blepharisma*. Except for the outstanding 20-year-old investigations by Suzuki (1957a,b), conjugation – and sexuality in general – have not been much studied in species of this genus. Miyake and colleagues, however, have very recently reopened the field with a series of exciting papers (e.g., Honda & Miyake, 1976; Miyake, 1975; Miyake & Beyer, 1974; Miyake & Bleyman, 1976) emphasizing biochemistry of the phenomenon. A conjugation-inducing glycoprotein named blepharmone (originally, by coincidence, called "blepharismin," the term coined a few months earlier by Giese for the "pink" pigment of some species: see above) has been discovered – and now a second gamone, blepharismone, as well.

Comprehensive surveys of the ultrastructure of *Blepharisma* may be found in Kennedy (1965) and in the 39 micrographs appended to the chapter in Giese (1973) which was written by Jenkins. Selected papers published in the interim include: Dembitzer & Hirshfield (1966), Inaba & Sotokawa (1968), Jenkins (1967), Kurita (1969), Repak & Pfister (1967), Shigmatsu (1967), and Small et al. (1971: a survey by SEM of various ciliates, including several heterotrichs). Work of note since 1973 should include the paper, in press at this time, by Jenkins (1977) on macronuclear division; and the recent work by Gerassimova & Seravin (1976), in which the concept of postciliodesmata was developed, should also be appended here. *Blepharisma* was one of the many genera investigated (also see, now, Seravin & Gerassimova, 1977).

Finally, in this brief treatment of heterotrichine genera of special importance, I must mention *Spirostomum*, an impressive ciliate of great length (up to 4,000 µm) and amazing contractility. Common forms are found primarily in fresh-water habitats. Repak & Isquith (1974), in a recent paper on the overall systematics of this old and well-known genus, reduced the number of bona-fide species to nine. *Spirostomum*, like the genera of preceding paragraphs, has been subjected to many kinds of study – morphological, cytological, taxonomic, physiological, morphogenetic, etc. – over a period of nearly 150 years. Older works of significance may, once again, be located through direct or indirect reference in the bibliographies of many of the major books or treatises already cited.

Recent papers on contraction, morphogenesis, nuclear cytology, general physiology and biochemistry, comparative morphology, and on the interesting phenomenon of calcification in this unusual ciliate include: Bien & Preston (1968), Boggs (1965), Eberhardt (1962), Fabczak et al. (1973), Grim (1968), Hawkes & Holberton (1975), Jones (1967), Jones & Jahn (1965), Jones et al. (1966, 1970a), Legrand (1971), Lehman & Rebhun (1971), Osborn & Hamilton (1977), Pautard (1959), Rao (1968a), Repak & Isquith (1974), Schwartz (1967), Seshachar (1965), Seshachar & Saxena (1968b), Sleigh (1970), Struttmann (1973), Tuffrau (1968), and Vuxanovici (1961a). TEM work on *Spirostomum* was first carried out in the 1950's in the laboratories of Finley, Inaba, Randall, and Yagiu. In more recent years, ultrastructural studies have been published by Burton (1970), Daniel & Mattern (1965), Finley et al. (1964), Grain (1968a), Vivier et al. (1969), Winet & Jones (1975), and Yagiu & Shigenaka (1963). Research with SEM has been reported by Legrand (1972) in connection with his investigation of contraction.

Suborder (2) Clevelandellina

In his monographic doctoral dissertation, Albaret (1975) established two great superfamilies, one to contain what are essentially the (free-living) heterotrichines of the preceding pages and a second to comprise the bulk of the so-called endocommensalistic heterotrichs. Very recently, de Puytorac & Grain (1976), briefly making a taxonomic decision with which I am in full accord, in effect raised these two superfamilies to subordinal rank: thus was created the suborder here under consideration. Although the trait of being "symbiotic" as opposed to "free-living" may serve as a convenient "key" character, there are other more basic differences between members of the two groups (and still more will surely be revealed with additional study); nevertheless, a number of the clevelandelline characteristics of differential value are obviously related to the organisms having adapted, long ago, to an existence in intimate association with (in fact, in the hind gut or colon of) some metazoan host, vertebrate or invertebrate.

Ultrastructural uniquenesses are yet to be fully understood, but there appear to be significant differences, according to the very recent observations of de Puytorac & Grain (1976), in the organization and arrangement of infraciliary structures of both the prominent AZM ("heteromembranelles") and the paroral membranes ("diplostichomonads"). In the somatic kinetids, there are true (though short) kinetodesmata, organelles lacking in all other spirotrich groups; furthermore, from a nearby site, cathetodesmal fibers also arise: these periodically striated structures appear to be unique in the whole phylum. Somatic kinetosomes appear in pairs. Mucocysts are abundant. The système sécant is complex in most species; such complexity is related, in part, to the location of the buccal apparatus which, in some families, is at or near the posterior pole of the body. An extremely conspicuous and fiber-rich polysaccharide-impregnated sucker or holdfast organelle is present in a number of clevelandellines, usually located anterodorsally or on the right side of the organism and sometimes accompanied by a flattening of the body proper. Many species exhibit a karyophore supporting a massive macronucleus; and some possess a cilia-lined cytoproct. Stomatogenesis, though a complicated process, is probably classifiable as parakinetal; the buccal anlage is typically either obliquely or transversely positioned with respect to the longitudinal axis of the body.

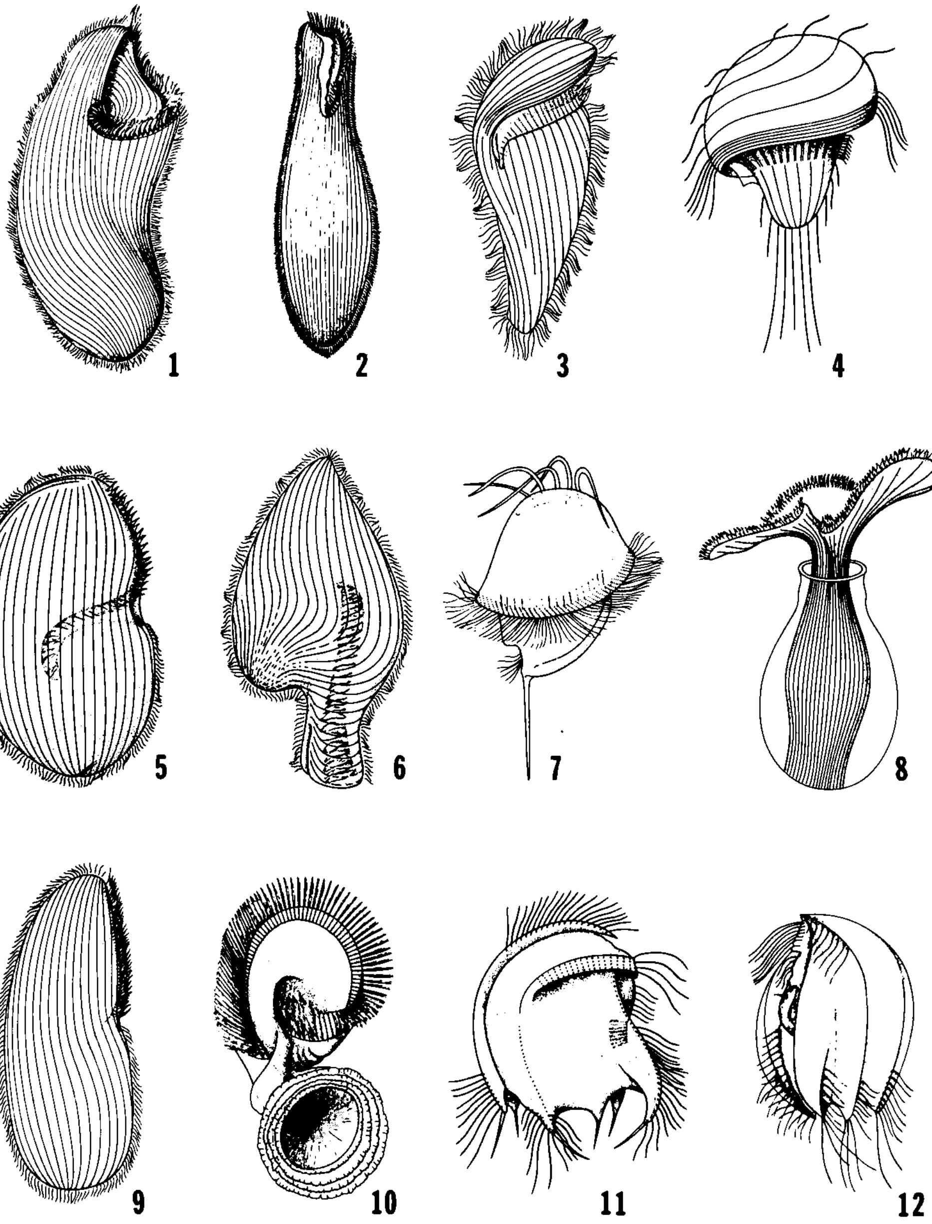

PLATE XV. Representative heterotrichs and odontostomes (order Heterotrichida, with six suborders; order Odontostomatida, last two figures). Fig. 1. *Climacostomum*, suborder Heterotrichina. 2. *Condylostoma*, suborder Heterotrichina. 3. *Metopus*, suborder Heterotrichina. 4. *Brachonella*, suborder Heterotrichina. 5. *Nyctotheroides*, suborder Clevelandellina. 6. *Clevelandella*, suborder Clevelandellina. 7. *Caenomorpha*, suborder Armophorina. 8. *Ascobius* (misidentified in past as *Folliculina*), suborder Coliphorina. 9. *Plagiotoma*, suborder Plagiotomina. 10. *Licnophora*, suborder Licnophorina. 11. *Saprodinium*. 12. *Epalxella*. [Additional figures appear in Chapter 20.]

Hosts range from terrestrial arthropods to fresh-water lower vertebrates. Some of the particular groups of such hosts are mentioned below in the brief discussion of various clevelandelline genera. Of the five families (one uncertain) and 15 genera which I recognize (see Chapter 20), more than two-thirds represent taxa described as new within the past 10, often only five, years! I predict even greater expansion in forthcoming years – probably a number of such taxonomic works are in preparation at this very time. The phylogenetic origin of these curious endocommensals is very likely from some group, such as the plastic metopids, among the heterotrichines, as both Albaret (1975) and Jankowski (1968e) have suggested.

The old genus *Nyctotherus*, established by Leidy (1849, 1853) long ago, now reduced in size and probably deserving even further reduction in numbers of bonafide species, exhibits a strong karyophore, has a buccal apparatus extending only part way down the length of the body from the apical pole, and occurs primarily in invertebrates (oligochaetes and especially insects and other terrestrial arthropods) but also in certain reptiles. In many of the invertebrate hosts, it is sometimes most confusingly accompanied by valid species of the superficially "look-alike" trichostome *Balantidium* and of other clevelandelline genera! *Nyctotherus ovalis*, the well-known species from cockroaches, remains a bonafide member of this genus. *Nyctotheroides*, with reduced karyophore, occurs mostly in anuran hosts (along with species of some of the newer genera in the suborder) and questionably in certain fishes. The popular "*Nyctotherus cordiformis*," from the colon of frogs and toads, is more properly assigned to this second genus in the family Nyctotheridae. Species of related genera (see Chapter 20) are found in myriapods (centipedes, millipedes, etc.), shipworms (molluscs), and certain (e.g., African) oligochaetes. But Sandon's (1941a) genus *Paranyctotherus* may be considered to be a *Balantidium* species; and Earl's (1970, 1972) *Kudoella* and *Pseudonyctotherus* probably belong in some earlier-named nyctotherid genus.

Members of the family Sicuophoridae, often with a well-developed sucker (see above), are widely distributed in anuran hosts, but *Geimania* is found in reptiles and Jankowski's (1974a) *Ichthyonyctus* (if it belongs here) was discovered in certain herbivorous tropical fishes. Earl's (1972) *Wichtermania* is a name which should probably fall as a synonym of de Puytorac & Grain's (1969) *Sicuophora*. The sole genera in two other families, Ky's (1971) *Inferostoma*, with its gigantic sucker and posteriorly located oral area, and Singh's (1953) curious *Nathella*, are also endocommensals of fresh-water fishes. The last-named taxonomically enigmatic form reminds one of the equally mysterious *Stentoropsis*, the alleged *Stentor*-like parasite of fishes originally described by Dogiel & Bychowsky (1934) and seen only once since then (by Gavrilova, 1969).

Perhaps among the most bizarre of all in body form are the three genera of clevelandellids (oral opening at antapical pole, contorted kineties, etc.). First discovered in xylophagous roaches and termites some 40 years ago (see Kidder, 1937, 1938; Yamasaki, 1939), they are considered by Albaret (1975) to have rather close affinities with the nyctotherids. Uttangi & Desai (1963) added a third genus to Kidder's family.

* * * * *

The literature here is nearly as confusing and confused as is the taxonomy of the involved ciliates themselves. For many many decades the situation seemed relatively simple: the alleged "spirotrich" species found in the hosts mentioned above were essentially all assigned to two genera, *Balantidium* or *Nyctotherus*, both old and venerable groups established well over a century ago. *Plagiotoma*, another ancient genus, was the principal nominal vehicle for the very few spirotrichs from annelids. (It was largely implicated because the family based on its name, the Plagiotomidae, embraced the popular *Nyctotherus*.) With the realization that *Balantidium* was a trichostome genus, not a spirotrich at all (Fauré-Fremiet, 1955; and see Corliss, 1961, and Chapter 7), the problem need not have become confused, but it apparently did. The difficulties may actually have started, however, with Grassé's (1928) erection of a subgenus of *Nyctotherus*, named *Nyctotheroides*. When that became elevated to generic status (first suggested in Corliss, 1961; and see Albaret, 1972), an immediate problem was to sort out practically all past-described symbiotic heterotrich species – dozens of them, unfortunately – into one or other of these two major "competing" genera, *Balantidium* being no longer available within the order. Then, suddenly, within the past decade, the number of genera comprising the overall group began to mushroom. Still further confusion was caused in the recent complete separation of *Plagiotoma* from all the other heterotrichines (and clevelandellines). Taxonomically, this was a commendable idea; but recall that, originally, all "nyctotherans" *sensu lato* had been assigned to the single family Plagiotomidae. With its removal, but accompanied by *only its type-genus*, to the separate suborder Plagiotomina, the vacuum for familial vehicles filled quickly. The resulting nomenclatural entanglements may require years for ultimate resolution.

Thus today – and, as predicted above, the end is far from being in sight – we have some four or five families embracing at least thrice that number of different genera, with a good many of the type-species involved being based on erstwhile *Nyctotherus* (or even *Balantidium*) species. Such organisms were either rediscovered and restudied or simply arbitrarily reassigned, based on use of improved techniques and/or better understanding of structural characteristics judged to be of diagnostic value in comparative systematics of the implicated groups. The expanded "new classification," with all of its unresolved ramifications, is, as Earl (1972) has wryly pointed out in his own work on some of the forms involved, the price we pay for progress!

Principal papers, many of which have been published within the past 10 years and some of which have already been cited above, are given without particular explanation or discussion, except to point out that the most helpful and/or most important systematically are the works by Albaret (1975 – monographic in scope), Amaro (1972), and Earl (1972). Others in the recent literature concerned with the taxonomy, light-microscopic morphology, or general biology of species of the several families currently identifiable as the "endocommensalistic heterotrichs" are the following: Albaret (1968b, 1969, 1970b, 1972, 1973a), Albaret & Njiné (1976), Amaro & Sena (1968a,b), Earl (1969, 1970), Earl & Jiménez (1969); Gisler (1967), Golikova (1965), Jankowski (1968e, 1974a), Ky (1971), Laval & Tuffrau (1973), Lee (1963), Poljansky & Sukhanova (1963), Rao (1969), Santhakumari & Nair (1973, 1975 – with description of the first alleged marine *Nyctotherus*), and Uttangi & Desai (1963). Works in which techniques of electron microscopy have (also) been employed include: Albaret (1970a), King et al. (1961), Oktem (1966), Paulin (1967), de Puytorac & Grain (1969), de Puytorac & Oktem (1967), and Stahlmann (1962).

Suborder (3) Armophorina

Jankowski (1964a,b) has boldly separated off from the metopid-type of heterotrichines the family of caenomorphids, a group of predominantly fresh-water polysaprobic ciliates which resemble some species of *Metopus* but only superficially, placing them into this independent suborder. Unfortunately, Corliss (1961), Kahl (1932b), and many other workers of the pre-1960's were not – in retrospect – as perceptive as they might have been concerning the genuine differences shown by these forms, considering them all as taxonomically very close to *Metopus*. Armophorine heterotrichs exhibit no ordinary somatic ciliature (except for a tuft of caudal cilia) but bear one or two unique series of cirri at the anterior end of the body (which has developed into a huge lobe) and a "ciliary stripe" which accompanies the winding oral ciliature and participates in both feeding and locomotion. The pellicle is often rigid and armor-like and may show one or more folds as it covers the body proper. Several posterior spines, sometimes quite lengthy, are typically present. The AZM (of "paramembranelles") commonly encircles the body, spiraling one or more times, ending up near the antapical pole, the location (also) of the cytostome. The paroral membrane is a "diplostichomonad," according to the very recent terminology of de Puytorac et al. (1976). Stomatogenesis, still to be studied with care, is very likely of an apokinetal nature.

The possibility of a fairly extensive somatic infraciliature (i.e., in this case, rows of nonciliferous basal bodies spiraling around the body, never producing cilia), as suggested in the observations of Villeneuve-Brachon (1940) and, later, Jankowski (1967a), needs confirmation by electron microscopy. If true, the finding could be of considerable phylogenetic importance: at the very least, it would offer support to the suspected metopid ancestry (from *Brachonella* via

Cirranter to *Caenomorpha*) for these armophorines.

Bactivorous and occasionally algivorous, the species assigned here are typically found in fresh-water habitats; but a few forms have been recorded from saline biotopes. Taxonomically, this small suborder contains but a single family, with three included genera: *Caenomorpha*, with perhaps a dozen species, and *Cirranter* and *Ludio*, each with only one species.

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The recent literature on members of the Armophorina is very scant, the comprehensive work by Jankowski (1964b) being the only publication of substance since the days of Kahl (1927a, 1932b), Lackey (1932), Penard (1922), Villeneuve-Brachon (1940), and Wetzel (1928). Dragesco (1960) mentions a *Caenomorpha* from the sands of Lake Geneva, and the ecology of several armophorine species is treated briefly in Bick (1957, 1972, and several intervening papers not cited here), Noland & Gojdics (1967), and Wilbert (1969).

Suborder (4) Coliphorina

This is the second Jankowskian heterotrich suborder, erected to contain members of the large and essentially marine family of folliculinids (Jankowski, 1967a). The coliphorines are set apart by their universal production of loricae and their unique development of a pair of "peristomial wings," anterior extensions of the body normally protruding from the lorica and bearing the prominent AZM. Somatic ciliation is holotrichous. In division, a vermiform migratory "larval form" – the anterior daughter or proter – is commonly produced; it is mouthless until it has settled and secreted a new lorica. Stomatogenesis is apparently parakinetal. Like *Stentor* and various other heterotrichines, the folliculinids are often pigmented and also highly contractile.

Almost without exception, coliphorines are marine, with their rigid loricae attached to such common substrata as strands of certain algae or the integument of various invertebrates. Distribution is world-wide, probably principally via the "normal" migrations of the host organism. In an interesting case, a folliculinid and the shell of its host have been reported as being "rafted" across the Atlantic Ocean: see Scheltema (1973). However, the "larval" form also provides a means of convenient dispersal (for short distances). One exceptional species, but possibly only a race of *Folliculina boltoni*, has long been known to be a bonafide *fresh*-water form, attached to rocks or plants, although the earliest reports on it were received with some skepticism. Penard (1919) offered an excellent account of it; and, more recently, Hamilton (1952b) described the same organism from a lake in northwestern Iowa – the first unquestionable case of a fresh-water folliculinid from North America and definitely a record for distance inland from a seacoast. In recent years, Dioni (1972) has found the same form in Argentina and has also described a new fresh-water species (in a new genus, *Botticula*) from the same river. Since 1957, following their discovery – as a new genus, *Priscofolliculina* – by Deflandre & Deunff (1957), fossilized (loricae of) coliphorines have been found by several workers. Occurring in rocks of the Mesozoic era, they are never more than 100–200 million years old. Loricae of tintinnine ciliates (Chapter 15), on the other hand, have been discovered in geological material dating back well over 400 million years.

As is equally true for members of the oligotrich suborder Tintinnina, the lorica is the single most distinguishing feature of the present group. It offers a most convenient feature for further taxonomic subdivision: differences in the size, shape, color, sculpturing, etc. of these "houses" are of consistent diagnostic value. It is the "pseudochitinous" loricae, only, which are preserved as fossils – again paralleling the situation in the tintinnines. Andrews (1923) and Hadži (1951) have particularly treated the fascinating subject of case-making in folliculinids. Uhlig (1964a,b, (1965; Uhlig et al., 1965), a modern authority on their morphogenesis, systematics, and ecology (including culturing methods), has described a very large form (up to 1,000 μm), *Magnifolliculina*, with a peculiarly sculptured double-lorica and with a dimorphic (i.e., differing in the adult and larval stages of the organism) macronucleus. Half of the 22 genera assignable to this suborder were described some 25 years ago by Hadži (1951). Only two were known before the turn of the century; and two have been erected as new within the past dozen years (see Chapter 20).

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Large and common forms, the coliphorine heterotrichs have been studied by many workers in past decades. Guides to the older literature in general may be found in Corliss (1961), Hadži (1951), and Kahl (1932b). O. F. Müller (1786) described the first species, as a vorticellid peritrich, and Lamarck (1815) erected the first genus in the family. Wright's (1858, 1859, 1861) early observations should also be noted. Post-1900 but pre-1960 works of importance need to be mentioned. In the combined areas of morphology, taxonomy, and ecology, see Andrews (1914, 1921, 1923, 1953), Das (1949, 1953), Dons (1913–1914, 1948), Fauré-Fremiet (1936), Kahl (1932b), Ringuelet (1955, 1959), Silén (1947), and especially the comprehensive monograph by Hadži (1951). In the area of morphogenesis (as related to binary fission and stomatogenesis), one finds essentially only the works of Fauré-Fremiet (1932a) and Villeneuve-Brachon (1940). Post-1960 papers, except for marine ecological surveys (and the like) in which folliculinids are usually mentioned only in passing, are exceedingly rare. The important recent contributions by Uhlig have been been cited above, as has Dioni's discovery of a fully fresh-water genus. Matthews' (1968) observations on the association of folliculinids with pearl oysters in Japan could be added to the short list.

Suborder (5) Plagiotomina

One of the most recently erected of all heterotrich suborders, the Plagiotomina was established by Albaret (1974) for a single family containing a single genus with, at that time, but a single species, the time-honored *Plagiotoma lumbrici* of Dujardin: but now see Albaret & Njiné (1976) and Mandal & Nair (1975) for very recent descriptions of additional species. The organisms do appear to possess characteristics which separate them from ciliates belonging to either the Heterotrichina or the Clevelandellina, notwithstanding former classifications (see the monographic treatment by Albaret, 1975).

Characters held in common with many free-living heterotrichs include the lateral flattening of the body, the holotrichous somatic ciliation, the extensive AZM (of "paramembranelles"), a cytostome slightly subequatorial in location, a parakinetal mode of stomatogenesis, and the absence of a macronuclear karyophore. The presence and disposition of the "diplostichomonad" type of paroral membrane and occurrence in the digestive tract of an invertebrate (lumbricid oligochaetes) resemble features known for various of the symbiotic clevelandellines. Mucocysts, curiously enough, appear to be totally absent. The macronucleus is dendritic, but in a rather globular way (reminding one of a bunch of grapes).

Several unique (or nearly unique) characters are strongly reminiscent of structures known for certain hypotrich ciliates (Chapter 16). These include the presence of minute groups of 2–9 somatic cilia arising from basal plaques, arranged in longitudinal lines, strikingly like the cirri of the so-called primitive hypotrichs; the cortical organization and fibrillar system, including disposition of certain tracts of microtubules; and the infrastructure of the paroral membrane, which is (also) a "diplostichomonad" in many hypotrichs (see de Puytorac et al., 1976). Whether these latter similarities are due to factors of convergent evolution or not, the point remains that they endow the plagiotomines with a distinctness which deserves to be reflected at a relatively high level taxonomically.

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The entire literature directly concerned with the small family comprising this suborder is scanty. *Plagiotoma* is mentioned, in passing, in many textbooks and the like; its name has been known for nearly 150 years. Numerous oligochaete-watching protozoologists have probably seen its species (e.g., see Heidenreich, 1935). It has seldom been investigated in any depth, however, since the comprehensive paper by Pertzewa (1929), half a century ago, until the work by Dworakowska (1966) and, most recently, the series by Albaret (see Albaret, 1973b, 1975; Albaret &

Grain, 1973; Albaret & Njiné, 1976).

The family Plagiotomidae itself has been best known for its numerous species of the genus *Nyctotherus* (and relatives): but such ciliates are now completely excluded from it (see suborder Clevelandellina, above). Therefore, some of the literature cited in a preceding section of this chapter – for example, Earl (1972) – may include some reference to *Plagiotoma*, since the separation has been effected so very recently. Amaro (1972) was the person to take the first step in recognizing taxonomically some of the differences between *Plagiotoma* and *Nyctotherus*-and-relatives; he established the family Nyctotheridae to contain all of the genera of the old family Plagiotomidae except *Plagiotoma* itself. Shortly thereafter, Albaret (1974), who had already been studying the non-*Plagiotoma* groups (erecting new genera among them, etc., paralleling similar work by colleagues de Puytorac, Oktem, and Grain), as well as *Plagiotoma*, increased the separation still further by erection of the present suborder. As already mentioned, Mandal & Nair (1975) have recently described another new species.

In the several modern studies carried out by Albaret and colleagues (cited above), a thorough examination of the structure, ultrastructure, and morphogenesis of *Plagiotoma* species has been carried out. These very recent works must be consulted by any student seriously desiring to enter the field of "plagiotominology."

Suborder (6) Licnophorina

The fourth suborder of heterotrichs to be established for a single "aberrant" family and the second for a group devoid of ordinary somatic ciliature, the licnophorines exhibit a body form which is, at one and the same time, both top-heavy and bottom-heavy. That is, their hourglass-like figure bears a very prominent oral disc at the apical pole and an equally conspicuous basal disc at the posterior end of the body. The oral disc bears a massive wreath of buccal organelles, the AZM, winding clockwise down (posteriad) toward a sunken cytostome. The basal disc is a complex, fiber-rich organelle of attachment, and includes a ventral palette, several concentric ciliary rings, and a flexible flange or velum. Practically all licnophorines are ectocommensals on predominantly marine hosts belonging to such groups as holothurian, asteroid, and other echinoderms, polychaete annelids, anthozoan and hydrozoan coelenterates, opisthobranch and prosobranch molluscs, ascidian tunicates, and even a cyanophycean alga. Conjugation has been noted, and cysts observed. The macronucleus is long and beaded or sometimes fragmented; the micronucleus is often inconspicuous.

Reminiscent of the situation in the armophorines, nonciliferous somatic basal bodies are also claimed to be present in *Licnophora* (Villeneuve-Brachon, 1940). They appear to occur in a short line or in rows around the "neck" (middle third) of the body, although somewhat erratically in some species. Again, ultrastructural studies are badly needed: it may be recalled that the "naked kinetosomes" of vorticellid peritrichs, rather similarly arranged and described, turned out to be (merely) pellicular pores when investigated with electron microscopy. Stomatogenesis appears to fall clearly into the category which I have termed apokinetal (Corliss, 1973e).

Although there are fewer than a dozen species of *Licnophora*, the only genus currently assigned to the suborder, they are widespread in marine habitats (see list of hosts, above). Food preferences seem to be bacteria and algae, occasionally a phytoflagellate protozoon (also = an alga, of course!) or another ciliate (if nearby), and sometimes host tissue – shed epithelial cells, mucus, etc. There is no evidence, however, that the host organism suffers from the presence of these ectocommensals.

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Modern literature on the licnophorines is essentially nonexistent, if one here uses the term "modern" to mean since the 1940's. Corliss' (1957a, 1961) presentation of the suborder as "new" was very brief and based on earlier findings of other workers. Balamuth (1941, 1942) and Villeneuve-Brachon (1940), unfortunately publishing practically simultaneously so that neither author could offer critical comment on the other's findings, each offered excellent and thorough treatments of *Licnophora*, but more than 35 years ago. Balamuth concentrated principally on the cytology and morphogenesis of a single species, while Villeneuve-Brachon reported on the infraciliature, comparative taxonomy, and morphogenesis of a number of species (fortunately including the one studied independently by Balamuth). Still earlier papers are scattered and often short or are limited to the taxonomic description of a new species. The combined bibliographies of Balamuth and Villeneuve-Brachon, plus Kahl (1932b, 1933), cover the "ancient" literature well. The often-overlooked notice of a species uniquely found on the filaments of alga of the Cyanophyceae group was published by Fauré-Fremiet (1937). Three of the best *and* earliest works on *Licnophora* were those by Stevens (1901, 1904) and Wallengren (1894).

Order ODONTOSTOMATIDA

Leaving the vast assemblage of heterotrichs, we come to a modest group of small, laterally compressed, wedge-shaped ciliates with a rigid and often ribbed armor-like pellicle, the odontostomes. These spirotrichs show a reduction in somatic ciliature to a few short kineties located on either anterior or posterior ridges of the body (though possibly an infraciliature persists in between), with a few posterior cirri also present in some species. The pellicle itself is frequently drawn out into spines, particularly at the posterior end of the organism. The body size is typically small (e.g., 45 x 30 µm): in fact, the greatest length ever reported to date is well under 100 µm. The nuclear apparatus is composed of a single micronucleus and one or a few (up to four) rounded macronuclei. A contractile vacuole is present, located posteriorly; no cytoproct has been described. The buccal apparatus, located just supra-equatorially on the narrow ventral surface, is much reduced (oligomerized): only eight or nine membranelles comprise its AZM, which does not extend out onto the body surface. There is apparently no paroral membrane. The common presence of a single "tooth-like" spine often overhanging the buccal cavity was the inspiration for the originally proposed name, the "ctenostomes," for this group of ciliates (Kahl, 1932a). Fortunately, the replacement name, odontostomes, fits as well: preoccupation made the change of name necessary (see Corliss, 1957a). Representative genera are depicted, along with several heterotrichs, in the set of figures on page 154.

In a number of characteristics, the odontostomes are very similar to the (larger-sized) armophorine heterotrichs. The principal difference lies in the striking contrast between the AZM's, long and spiraling and conspicuous in armophorine genera like *Caenomorpha* and greatly reduced and hidden in odontostomatid forms such as *Saprodinium*. Jankowski (1964a,b, 1967a) – in postulating a similar phylogenetic origin from heterotrichine metopids for both groups – suggested that their differences can be accounted for by implicating diverse genera within the family Metopidae, *Brachonella* serving as the ancestral group for the armophorines and *Metopus* itself for the odontostomes. Any resemblance between the Odontostomatida and the "true" oligotrichs (see Chapter 15) may now be considered largely superficial or due to convergence, although formerly many authors placed the two orders closely together.

Polysaprobic forms, the odontostomes occur primarily in fresh-water habitats rich in putrefying organic material. Some genera, such as *Saprodinium*, have species very commonly and widely found in such ecosystems. Kahl (1932a) has recorded the existence of a few species in marine biotopes, but such reports are apparently rare. The organisms are bactivorous, with often a preference for sulfur bacteria. Potentially of considerable value as biological indicators of pollution, various odontostomes have been fitted into a "saprobity system" (see Bick, 1972; Curds, 1969; Lackey, 1938a,b; Liebmann, 1962; Noland & Gojdics, 1967; Sladeček, 1973; and also others) of some ecological interest and utility. Taxonomically the Odontostomatida are divisible into three families, six genera, and some three dozen bonafide species. It is one of the smaller ordinal groups in the phylum. Its two oldest genera, the first of which contains a third of all the species in the order, are *Epalxella* (originally named *Epalxis*) and *Discomorphella* (originally *Discomorpha*), type-genera of two of the included families.

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With the important exception of Jankowski's (1964b) fine overall and quite detailed treatment of the comparative morphology, phylogenetics, and classification of the odontostomes in his "polysaprobic heterotrich" monograph, and their inclusion in such ecological works as Bick (1972) and Wilbert (1969), there have been practically no new papers of substance on these potentially important organisms since the times of Kahl (1932a,b), Lackey (1925, 1932, 1938b), Lauterborn (1908, 1916), Penard (1922), and Wetzel (1928). Klein (1930) depicted the silverline system of several species. Sawaya (1940), in a paper "rediscovered" by Corliss (1957a), proposed the change in the ordinal (subordinal at that time) name alluded to above. References to the few additional older papers on the ecology and/or taxonomy of the Odontostomatida are available in the combined bibliographies of Bick (1972), Corliss (1961), Jankowski (1964b), and Kahl (1932b + 1935c); an extensive ecological survey including species of *Epalxella* which is sometimes overlooked is Šrámek-Hušek (1957). By the date of this writing, no work – to my knowledge – has been carried out on the ultrastructure of any member of this interesting group.

Chapter 15

Class Polyhymenophora: (2) The Oligotrichs, Specialized Forms Often Neglected

If the heterotrichs are considered a taxonomically rather conservative or closely interrelated group among themselves (Chapter 14), the organisms treated in the present chapter, the oligotrichs, may be thought of in a similar way. Their loss of the old entodiniomorphids to the class Kinetofragminophora and of the odontostomes to a location closer to the Heterotrichida, plus the decision to reduce the tintinnids to the rank of suborder, have made their unity closer than ever before. And this seems to have strengthened their taxonomic distinctness from other polyhymenophorans (see below). The Oligotrichida show considerable diversity at lower taxonomic levels, occupy a number of interesting ecosystems, and contribute most substantially to the total number of ciliophoran species known to date. They share in common with all previously treated taxa – and maybe show it even more so – a pressing need for more extensive and more thorough study, from ecological, physiological, genetic, ultrastructural, etc. approaches as well as from systematic, classificational, and – discouragingly enough – even nomenclatural points of view. The widening recognition today that a considerable number of their species are organisms which play significant roles in plankton productivity, food chains, energy cycles, and the like – and are potentially valuable as pollution-indicators as well – clearly underlines the critical necessity of our knowing more about them.

Members of the order represent a large but unified and distinctly different group of polyhymenophorans. Perhaps, as Corliss (1975b) has suggested, they are deserving of a separate subclass standing, alongside the Spirotricha (from which possibly the hypotrichs, with their oligotrich similarities, should also be removed). In recent decades, their species have often been distributed between two independent orders; but, today, differences formerly used in making such a division are considered by many ciliatologists to support a separation no higher than at the level of suborder. Some workers might even suggest that relationships are so close that the oligotrichs *sensu stricto* and the tintinnines, the two groups involved, might well be included as only a collection of separate families within the order, recognizing no suborders. But considerable evolution has taken place within the two assemblages, I believe, and their separation at the rank of suborder does not seem out of place when compared with (the bases for) similar decisions proposed or defended in preceding chapters of this book for other ordinal/subordinal situations. Representative genera are depicted in the set of figures on page 165 (Plate XVI).

Key features of this specialized if neglected group include an extensive AZM, often with two distinguishable parts, one within the buccal cavity and one out onto the body surface in the area of the anterior pole of the organism; a paroral membrane composed of cilia arising from a single and nonzigzag row of infraciliary kinetosomes (= a "stichomonad," according to de Puytorac & Grain, 1976); a somatic ciliature often reduced to a few widely spaced and shortened rows of specialized cilia or bristles; and an ovoid to elongate noncompressed body, enclosed in a thickened pellicle and sometimes tailed. All members of the second, and much larger, suborder are loricate. Stomatogenesis is apokinetal, with the *de novo* anlagen of the buccal organelles for the opisthe occurring within a temporarily appearing pouch located subequatorially below the surface of the body. Other characteristics of diagnostic importance include the absence of kinetodesmata and of a cytoproct and the presence of reorganization bands in the macronuclei preceding cytokinesis. All species are free-swimming forms, even when loricate, and microphagous in feeding preference; and most oligotrichs occur in marine habitats, especially the open seas. However, some well-known species are found in fresh-water ecosystems, and marine forms have been observed in symbiotic association with echinoids. A number of the loricate oligotrichs have been described from their fossilized loricae (see Tintinnina, below).

Exclusive of certain (generally dated) monographs on the tintinnines, the literature on the oligotrichs *sensu lato* is not very extensive. The absence of modern major treatises was pointed out and regretted by Corliss (1961); and now, nearly a generation later, one is obliged to make essentially the identical comment. Reference is made at the end of the sections on the included suborders to the scattered pertinent papers which are available.

Suborder (1) Oligotrichina

It is among members of this suborder that one finds the prominently bipartite AZM and also frequent replacement of regular somatic ciliature either by a few short rows of widely spaced cirri-like bristles, used in a saltatorial kind of locomotion, or by an equatorially encircling band of very short "sensory" cilia. The more closely apposed inner membranelles of the AZM are used in feeding; the outer, often with longer cilia, fimbriate, and encircling (partially or entirely: "open" or "closed") the anterior end of the body, are most often employed in locomotion. Nematodesmata extend inward from the kinetosomes comprising AZM infraciliary bases. The body is usually rounded, although in some species it characteristically bears a long and curious tail (e.g., in *Tontonia*). One family possesses two structures lending considerable rigidity to the body: numerous polygonal cortical platelets of polysaccharide composition, typically covering the posterior hemisphere of the body, and an equatorial girdle of so-called "trichites." Loricae have rarely been described for any members of the group. Conjugation is of the temporary type.

Free-swimming forms are of a size varying from very small to quite large. Most of the members of the suborder are marine; but several important forms are found only in fresh-water habitats (e.g., species of *Halteria* and *Strombidinopsis*) and a few are common in moss or soil. A sizable species of *Strobilidium* is an inquiline in the gut of certain sea urchins; and a *Strombidium* has been found as an ectosymbiont on some of the same echinoid species. Although many species undoubtedly remain to be discovered and described, the present complement of only about 100 makes the group appear small in comparison with the 1,000-plus membership of the following suborder.

* * * * *

Much of the literature on the oligotrichs *sensu stricto* (i.e., the oligotrichines) has appeared in bygone years and thus may be found in such bibliographies as those offered by Corliss (1961), Kahl (1932b + 1935c), and Penard (1922). Papers on moss and soil forms often overlooked today include: Fantham & Porter (1945), Gellért (1956, 1957), Horváth (1956), Rao (1928), Sandon (1927), and Wenzel (1953). Deserving of special notice are the early but very careful observations of such men as Claparède & Lachmann (1858-1861), Dujardin (1841), Kent (1880–1882), and Lankester (1874), over a century ago. Until his passing, the leading specialist on members of all three included families was the late Fauré-Fremiet, and his major works on planktonic forms (1924, 1932b), on the tidal rhythm of an intertidal pool species (1948f), on binary fission (1953c), on their overall systematics (1950a, 1970a), and even on their fine structure (Fauré-Fremiet & Ganier, 1970b) remain indispensable accounts.

Tamar (1965, 1967, 1968, 1974) has published papers in a continuing series on the fresh-water genus *Halteria*, work reminiscent of earlier ones by such investigators as Szabó (1934, 1935). Grain (1972) has offered a thorough electronmicroscopic study of a species of the same genus, the only ultrastructural contribution to our knowledge of the whole suborder to date, other than Fauré-Fremiet & Ganier's (1970b) excellent paper on a marine *Strombidium*. Grim (1974) has studied the fibrillar system of *Halteria*, using protargol (silver) preparations. Recently, Deroux (1974) has presented a comprehensive analysis of morphogenesis (and other features) in the life cycle of a marine *Strobilidium*, pointing out, among other conclusions drawn, that Fauré-Fremiet's (1953c) concept of enantiotropism may not be entirely accurate in description of cell fission in oligotrichs. Deroux also emphasized the gulf between *Strobilidium* and other oligotrichines and the former's closeness to the tintinnines and even to the sporadotrichine hypotrichs. Jankowski (1974b) has described a *Strombidium* uniquely associated with an echinoid as an ectosymbiont. Salvano (1975a) has published a short paper comparing the reorganization bands of *Strombidium* and *Euplotes* employing UV microspectrographic analysis (see also Salvano, 1974a).

The single most important and most up-to-date review of the overall systematics of the oligotrichine group is included in the very helpful but rather short paper by Fauré-Fremiet (1970a), already cited above. Scattered new knowledge of a taxonomic-ecological nature, often including redescriptions of older species, may be found as minor parts of a number of recent larger works: Borror (1963b, 1965b, 1975), Dingfelder (1962), Dragesco (1963b, 1970), Fenchel (1968a), Tucolesco (1962a), and Vuxanovici (1962c, and earlier). As members of oceanic plankton communities, oligotrichine ciliates show an abundance and biomass worthy of attention (e.g., see Beers & Stewart, 1971, and references therein).

Suborder (2) Tintinnina

Closely related to the strobilidiid oligotrichines (see especially Fauré-Fremiet, 1970a), yet with a long evolutionary history of their own, the tintinnines are a widespread group of principally marine neritic or eupelagic forms whose total morphology and taxonomy have been dominated by differential properties of their loricae. The most prominent characteristic of the organism itself is its apically located ciliature; but this, of a typical oligotrichid nature, is of limited diagnostic value at infrasubordinal levels. Parts of the prominent AZM play a major role in locomotion (it is still not clear whether the posterior or anterior end normally moves foremost – perhaps either one? – as there are conflicting statements on this in the literature), and apparently in lorica-building, as well as in feeding.

There are additional characters setting these ciliates apart from others. These include the tentaculoids and the so-called accessory combs; the whole contractile system of the organism; the tapered posterior end of the organism's body, equipped with an adhesive tip used in attachment to the inner wall of the lorica; a lateral cytoplasmic lobe, which appears to be the site of secretion of a substance employed in construction of the lorica; fields or rows of short somatic ciliature, some presumably sensory in function; the absence of a contractile vacuolar system *per se*; and such ultrastructural discoveries as the "capsules torquées," "morulae," and "microbodies" (Laval, 1973), all of which warrant further study. The microtubular system associated with the kinetosomes of the AZM is also quite unique, though reminiscent of that known for the Hypotrichida. Some other features, shared with all or some of the members of the neighboring suborder of oligotrichines (and, interestingly enough, sometimes with certain of the hypotrichs: see Chapter 16), may be mentioned very briefly: for example, the unitary nature of the infraciliature of the paroral membrane ("stichomonad," according to de Puytorac et al., 1976); the replication bands in the predivision macronucleus (the macronuclei are small and several in number here); the alleged absence of a cytoproct and of kinetodesmata; a peculiar subtype of the apokinetal mode of stomatogenesis; and the presence of a perilemma external to the limiting cell membrane proper (apparently shared with representatives of only one family of the Oligotrichina, the Strombidiidae).

Sexuality has seldom been studied/encountered in any of the Oligotrichida: this is underscored by the complete absence of reference to it in Raikov's (1972a) encyclopedic review. There is some recent, though scanty, evidence that some tintinnines (specifically, *Tintinnopsis*) form micro- and macroconjugants, possibly with subsequent total fusion (Gold, 1971). Yet the same worker mentioned an earlier noticing of temporary conjugation between apparently morphologically undifferentiated conjugants of the same species; and these reported observations have all been based on cultured forms. The unknown effect(s) of the laboratory treatment plus the lack of data on all stages of the sexual process suggest that further information is needed before we can conclude much about the possible sexuality of these intriguing forms under natural conditions.

Fossil tintinnines were first discovered many decades ago and even figured some years before

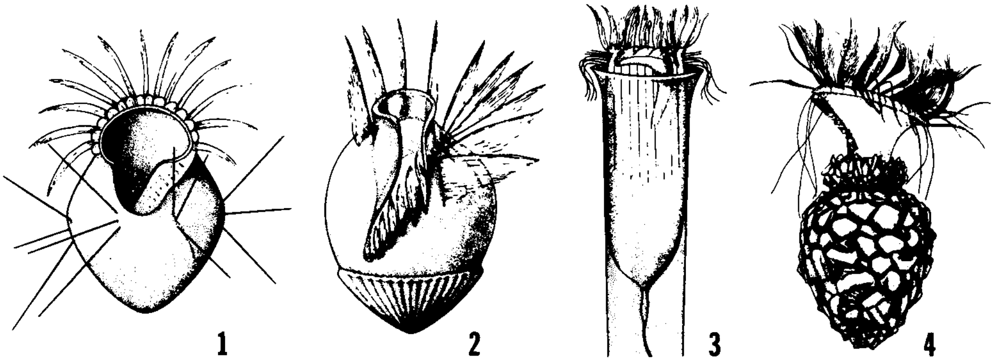

PLATE XVI. Representative oligotrichs (order Oligotrichida). Fig. 1. *Halteria*, suborder Oligotrichina. 2. *Strombidium*, suborder Oligotrichina. 3. *Eutintinnus*, suborder Tintinnina. 4. *Stenosemella* (misidentified in past as *Tintinnopsis*), suborder Tintinnina. [Additional figures appear in Chapter 20.]

the turn of the century. But most of the earlier forms were considered to be sarcodinid protozoa, and it has not been until near the middle of the present century that such fossilized loricae have been found in some abundance and properly identified. Species from more than 30 genera, in most cases genera with no known contemporary species, have now been described, either from free specimens or, more often, from sectioned substratum (principally limestone). Unfortunately, several "aberrant tintinnids," duly named, etc., may turn out, on closer study, to be only fragments of the palette of fossilized lamellibranch molluscs rather than genuine ciliate productions. I have included such genera in Chapter 20, but in an *incertae sedis* section. The geological time covered by bonafide tintinnine fossil findings now ranges from the Ordovician period (early in the Paleozoic era), some 400–450 million years ago, into the Pleistocene, one million years ago, with great abundance in the rocks of the Jurassic and Cretaceous periods of the Mesozoic era and of the still younger (*ca.* 50–60 million years old) Eocene of the Cenozoic.

The lorica demands further attention, if we are to continue to base the classification of tintinnine families, genera, and species on its shape, dimensions, composition, and substructure. Sizes (lengths) range from less than 50 µm to greater than 1,000 µm – possibly over 3,000 µm, if certain curious fossil discoveries (Radoičić, 1969a,b) are accepted – with usual range of 100–200 µm. The shape, while round in cross-section, varies from simple open-ended tubes of uniform diameter (a type limited mostly to a single family) to trumpet-, vase-, or cup-shaped forms of specifically varying dimensions, with or without collar, rim, or aboral horn and closed at the antapical end. The function(s) of the lorica is (are) quite unknown; one suggestion is that it contributes in some helpful way to the buoyancy of the encased organism. Some are constructed very solidly, often with agglutinated particles reinforcing the walls: such attached foreign matter may be composed of coccoliths, diatom frustules, or small particles of silica. Smooth or rough (even spined), some have spiraled modifications, others simply transverse or longitudinal markings of greater or lesser conspicuousness. A few are fenestrate. Still others are very delicate in construction and composition, gelatinous or membranous in consistency, and largely organic in nature. Some are hyaline and transparent, others opaque (or partially so). Tappan & Loeblich (1968) have erected two superfamilies based largely on differences in structure and composition of loricae: one group (roughly my first eight families, Chapter 20) with more solid, often agglutinated walls and sometimes with spiral structures; the second generally with thin, organic, nonagglutinated walls, without spirals (the remaining five families).

The wall(s) may consist of several layers, with or without addition of mineral components. The organic moiety has been said to consist of chitin, xanthoprotein, or pseudochitin; but, even with careful crystallographic examination and use of TEM and SEM, the exact chemical composition of the lorica seems to rest still uncertain at this time. Remane (1964, 1965, 1969), incidentally, favors wide taxonomic separation of the so-called calpionellidean fossil forms from all other tintinnines, fossil or recent, on the alleged basis that they are the only ciliates capable of producing originally (but really = agglutinated coccoliths?) calcareous loricae. But this proposal is not supported by Tappan & Loeblich (1968), who have reassigned such genera to families also containing modern forms with supposedly similar attributes.

As already mentioned above, most contemporary tintinnine species occur in marine ecosystems, as either eupelagic open-ocean forms or neritic coastal forms. Here they comprise a major component of the microscopic zooplankton, feeding on the smallest nannoplankters: thus they are important in the oceanic food chain. All oceans and seas contain them, often in great abundance. Species of half a dozen genera have been found in brackish water; and about a dozen species are known to live only in fresh water: *Codonella cratera* – possibly = *Tintinnopsis lacustris?* – and several (other) *Tintinnopsis* species are widely distributed in lakes, rivers, and even ponds. Fossil forms are best known from coccolith-bearing limestones (thus oceanic in origin); but some have also been found recently from near-shore facies (Eicher, 1965; Tappan & Loeblich, 1968).

I am now recognizing (see Chapter 20) a significant increase in the number of bonafide genera – from 83 to 108 – compared with that of the first edition of this work (Corliss, 1961); yet the number of families, 13, has long remained the same. There have been several new genera described since 1968, the date of the important taxonomic-nomenclatural treatises by Loeblich & Tappan (1968) and Tappan & Loeblich (1968). Laval's (1973) splendid cytological work on *Petalotricha* and members of several other genera, the first on tintinnine ultrastructure, has provided taxonomically valuable data and has set the stage for further research with electron microscopy on these fascinating pelagic forms. The total number of species to be accepted as bonafide represents a difficult question. At the moment – and many more surely remain to be discovered – I consider the number to be nearly 1,200, a figure greater than that comprising any other suborder or order in the phylum, although the sessiline peritrichs are close behind (see Chapter 13). But there is a possibility that many of those already described are not really distinct and have been inadequately studied (e.g., see Balech's, 1975, very recent critical review of the Undellidae). Natural variation in characters of the loricae, especially, may be greater than has been suspected within a single species (see observations of Bakker & Phaff, 1976; and Laval-Peuto, 1977).

Although the bulk of the better-known genera of tintinnines were first described in the great monographs of the first half of the present century, it may be interesting to note that about a dozen still-bonafide genera were reported well before 1900; eight have names which range between 90 and 175 years in age. In the past, fossil species have been associated with only one early-named genus, *Codonella*. Shortly after the turn of the century, the first "all-fossil" *Calpionella* was described. By contrast, practically all of the genera (with two exceptions) described as new within the past 15 years are comprised of totally extinct forms; but this is largely a reflection, of course, of the professional interest of their discoverers. I assign the acceptable fossil genera, perhaps conservatively, to one or the other of three families (Codonellidae, Codonellopsidae, Metacylididae), groups also well known for their extant (contemporary) genera and species. The all-fossil families Calpionellidae and Colomiellidae established by Bonet (1956), comprised essentially of the same genera, have not seemed to have met with wide acceptance and are not endorsed here (see Chapter 20).

* * * * *

The literature on this large suborder is extensive; it appears to fall under three broad areas. The bulk of the papers, old and new, are of an ecological or limnological nature, concerned primarily with distribution and/or the tintinnine composition of plankton. Paleontological contributions may be included here, also. Scattered papers are devoted to careful study of the biology, morphology, or morphogenesis of one or more selected species: in this group might appropriately be placed the few experimental investigations and the most modern cytological studies, including work on the chemical composition of loricae. Finally, a few works treat overall systematic, classificational, or nomenclatural problems. As might be expected, some workers have combined more than one approach in a single publication. A few publications of note from the first half of the present century should be mentioned before turning to more recent citations: Biernacka (1952), Brandt (1907), Campbell (1926, 1927, 1942), Colom (1934, 1948), Deflandre (1936), Entz (1909), Fauré-Fremiet (1908, 1924), Hada (1938), Hofker (1932), Jörgensen (1924), Kofoid (1930), Kofoid & Campbell (1929, 1939), Laackmann (1910), Osorio-Tafall (1941), and Schweyer (1910). Recall that Kahl (1932b) treated only fresh-water forms; but Jörgensen (1927) took care of the marine species at that time, and Campbell (1954) later included all forms, extinct and extant. A short while after that, Bonet (1956) monographed extinct material from Mexico, recognizing as new the two all-fossil families mentioned above. [Papers of several other early tintinnine specialists, serving as sources of figures in the appropriate plates of Chapter 20, are now (also) included in the bibliography, in a special addendum.]

Some sizable works, generally of an ecological-taxonomic nature and also including fossil studies, which have appeared within the past 10–15 years are the following: Bakker & Phaff (1976), Balech (1962, 1967, 1968, 1971a,b, 1975), Beers & Stewart (1971), Biernacka (1962), Borza (1971), Burkovsky (1973, 1974), Burkovsky et al. (1974), Calderón-Aragón & López-Ochoterena (1973), Colom (1965), Cosper (1972), Eicher (1965), Farinacci (1963), Göke (1963), Goulder (1976), Hada (1970), Hedin (1974, 1975b), Hilliard (1968), Keij (1974), Knauer & Nagy (1964), Marshall (1969), Murray & Taylor (1965), Nowak (1968), Radoičić (1969a,b, and others not cited), Rassoulzadegan & Gostan (1976), Remane (1964, 1965, 1969), Szczechura (1969), Tappan & Loeblich (1968), Trejo (1975), Turnšek (1965), Vitiello (1964), Wood (1967), and Zeitzschel (1966, 1967, 1969).

Recent refined studies on the cytology or physiology of tintinnines, sometimes employing SEM and TEM, including papers on the composition of lorica walls, are these: Biernacka (1965), Gold (1971, 1973), Gold & Morales (1975a,b, 1976, 1977), Gold & Pollingher (1971), Hedin (1975a, 1976a,b), Laval (1971, 1973; Laval-Peuto, 1975, 1977), Lecal (1967), Remane (1963, 1969), and Tappan & Loeblich (1968).

Finally, post-1960 overall treatments of the systematics, classification, and nomenclature of the whole suborder may be found in Corliss (1961), Loeblich & Tappan (1968), Schwarz (1964), and Tappan & Loeblich (1968). And factors in their evolution, as part of the oceanic plankton, have been mentioned by Tappan & Loeblich (1973), the first such discussion since Kofoid's (1930) often cited essay of nearly half a century ago.

Chapter 16

Class Polyhymenophora: (3) The Hypotrichs, a Ubiquitous and Highly Evolved Group

Possibly representing the pinnacle of development – or, at least, of ciliary differentiation – in the evolution of the ciliated protozoa, the hypotrichs are well known to many biologists because of their ubiquitousness, their conspicuousness, and the striking nature of some of their morphological features. Today, some of them are also becoming very popular as the experimental organism in sophisticated research in various aspects of cell biology. In fact, it is a little surprising that we do not (as yet) have a "Biology of *Euplotes*" to match the volumes which have appeared on other similarly important and widely known ciliate genera, such as *Blepharisma, Paramecium, Stentor,* and *Tetrahymena.* Nearly 500 species of hypotrichs have been described to date, and the group is thus one of the largest among the 23 orders recognized by the writer. Its free-living members are often found with high frequency in a wide range of habitats: freshwater, brackish, marine, sand, soil, edaphic, sewage effluent, etc. Only a few species are symbiotic on or in other organisms.

As already noted for various other polyhymenophoran groups, the hypertelic development or "polymerization" of the adoral zone of membranelles (or "paramembranelles," according to de Puytorac & Grain, 1976) also represents one of the most outstanding features of the hypotrichs. The AZM is all the more striking when combined, as here, with absence of simple somatic cilia and a dorsoventrally flattened body. The only genus with a reduced AZM is *Aspidisca.* Possibly an even more prominent character are the cirri, located at specific but scattered sites or in more or less uninterrupted longitudinal rows on the ventral or lateral surfaces and representing an "oligomerization" of an allegedly ancestral uniform, holotrichous, "simple" ciliation. Often relatively huge in size (their infraciliary bases may contain as many as 120 kinetosomes!) and functioning in both feeding and locomotion, these organelles are routinely declared to be unique in the Hypotrichida: this is not completely accurate, for there are cases of the appearance of cirri in several other orders, as I have pointed out in preceding chapters. Yet their universality, their abundance, and the significance of the roles which they play in the present order cannot be matched elsewhere. The patterns exhibited by cirri are also unique here and are of considerable diagnostic value at lower taxonomic levels. When they occur in isolated groups, rather than in continuous rows (although "longitudinal streaks" are still recognizable), they are standardly named by their location, as follows: frontal cirri (= frontals), frontoventrals, midventrals, left and right marginals, transverse (or anals), and caudals. There is still other ciliature associated with these organisms. In the oral area may be found from none to several paroral membranes ("diplostichomonads" or occasionally "polystichomonads," according to the very recent view of de Puytorac et al., 1976). And occurring in sparse pairs on the dorsal surface of the body are short nonmotile cilia ("bristles"), arranged in widely separated longitudinal rows, said to be "sensory" in function. Incidentally, the "silverline system," both ventral and dorsal and studied from both dynamic and static points of view, has been most useful in the systematics and classification of hypotrichs. At the infrageneric level, however, there is danger in too heavy reliance on apparent differences in details unless the range of natural variation has been carefully taken into account (Gates, 1977).

Not particularly large in body size, these ciliates are perhaps as conspicuous by virtue of their modes of movement as by the presence of their prominent compound ciliature. Elongate or oval in form and dorsoventrally flattened, they are cursorial and creeping organisms and show great mobility and dexterity in their movements. Rapidly darting a short distance forward, then as quickly withdrawing, changing direction unexpectedly, using both oral and somatic ciliature to effect such changes, the creatures are fascinating to watch and can hardly be ignored! They are the only true "walkers" in the phylum. Their massive, complex fibrillar systems, both somatic and buccal, are today under intensive study ultrastructurally (e.g., see the very recent work by de Puytorac et al., 1976). But the reader – for sheer joy – must see such exemplary detailed light-microscopic work as that by Tuffrau (1965); nor should one forget the pioneering microsurgical investigation of hypotrich fibers carried out by Taylor (1920) nearly 60 years ago. Electron microscopy, by the way, has sounded the final death knell for a neuromotorium or "cytobrain" in these (as well as other) ciliates.

Hypotrichs have been long and widely studied from a morphogenetic approach, and the results of such research have been of value in a number of areas of cell biology as well as in ciliate systematics. Modes of stomatogenesis appear to be parakinetal in the primitive hypotrichs (e.g., *Hypotrichidium* and *Kahliella* and apokinetal (formerly, "*de novo*") in all the others. Binary fission is homothetogenic, as is considered basically true for all ciliates; but rather than isotomic (or anisotomic) in the case of hypotrichs, Fauré-Fremiet (1961b) preferred the term "isoblastic" to describe the mode they generally exhibit. A startling "rediscovery" by Curds (1966) was the occurrence (e.g., in *Histriculus*) of a very curious kind of endogenous budding, mentioned by Kent (1880–1882) long ago. A cytoproct is present, in both fresh-water and marine forms, as is also a contractile vacuole plus its pore. Mucocysts are plentiful. Encystment is common, and the phenomenon has been studied extensively in several species. Conjugation has also been frequently observed; generally it is of the temporary type, though total (Raikov, 1972a) in some species. Several hypotrichs produce loricae; a few others live temporarily within a loosely fitting tube – and some of these tubicolous species form colonies. A number of hypotrichs contain symbiotic zoochlorellae; and a few, notably in the genus *Uroleptus*, possess a naturally pigmented cytoplasm, rose- or violet-colored. As is true of many algivorous ciliates, members of the present order may show a coloration via their ingested food materials (such as green or brown from eating diatoms). Amicronucleate races have been reported (Beers, 1946). Another characteristic feature, though known in other groups as well, are the reorganization bands appearing in the macronucleus preceding cell division. Macronuclei are commonly two, sometimes four (and occasionally dozens), in number and ovoid in shape. But in the euplotids – the forms in which macronuclear reorganization has most often and most profitably been studied – the organelle is C- or E-shaped, lending itself beautifully to detailed cytological, cytochemical, and molecular examination of the phenomenon. All hypotrich macronuclei are homomerous.

I have already mentioned the widespread occurrence of hypotrichs, both geographically and by types of habitats (and see below). I suspect that *Euplotes* may be the most cosmopolitan (fresh-water, marine, and "terrestrial") genus of free-living forms in the entire phylum. Growth of many hypotrichs outside their natural habitat is also easily maintained, even to the extent of monoxenic or, occasionally, axenic cultures; thus their nutritional proclivities have been under investigation in several laboratories for some time. In nature, they are typically bottom-dwellers, with the major exception of the fresh-water planktonic species, and feed mostly on bacteria and algae. But a few are carnivorous, devouring other ciliates to satisfy their nutritional demands; and members of *Stylonychia* have even been known to become cannibalistic (Giese & Alden, 1938). Overall, it is perhaps best to consider hypotrichs as omnivores. A good start has been made in studies on hypotrich genetics, mating types now having been identified in over half a dozen species of *Euplotes, Oxytricha, Stylonychia,* and *Uronychia*. In fact, *Euplotes* is next in line behind *Paramecium* and *Tetrahymena* as ciliates which lend themselves to quite sophistocated research from the point of view of sexual phenomena, genetics, and cytogenetics. The total fusion of conjugants noted in two species of *Urostyla* and one of *Pseudourostyla* is of considerable interest (Heckmann, 1965; Moldenhauer, 1965; Takahashi, 1973, 1974). Unique to hypotrichs is the fascinating prenuptial dance or "mating play" of preconjugants (Grell, 1951), now thought to be caused by the chemoattractant action of some kind of gamone.

Taxonomically, the order has always been recognized as a closely knit assemblage, with the combination of universal presence of cirri, extensive AZM, elongate or oval dorsoventrally flattened body form, and cursorial mode of movement clearly bringing them together, on the one hand, and separating them as a group from the rest of the ciliates, on the other. For a very long time the total number of families widely accepted remained at the low number of three, one of which was very small and one very large. Kahl's (1932b, 1935b) monograph of all species then known contained some 34 genera. Corliss (1961) suggested recognition of more than half a dozen families, though he offered diagnoses of only five, assigning 71 genera (including several subgenera) to them and observing that the family Oxytrichidae was the largest in the (sub)phylum with respect to numbers of genera. Later that same year, Fauré-Fremiet (1961b), in a brief but very important taxonomic work (though one unfortunately riddled with nomenclatural errors), erected two suborders (see below), each containing four families (several new). More recently, Borror (1972a), in a significant but somewhat conservative revision of the order, characterized six families and 50 genera, listing 310 acceptable species; he did not endorse Fauré-Fremiet's two suborders. In a still more recent (though woefully out-of-date) monograph by Stiller (1974b), restricted to consideration of only fresh-water and "terrestrial" hypotrichs, some 45 genera (in seven families), containing about 240 species, were accepted; suborders were not mentioned.

In the present work (see also Corliss, 1975b, 1977a; de Puytorac et al., 1974), I have re-adopted Fauré-Fremiet's two suborders, although – influenced by Borror (1972a) – I had omitted them from my earlier classification (Corliss, 1974a). Together, these contain 11 families, 85 genera, and 475 species. (Are *three* suborders possibly needed? See Addendum, page 174). Representative forms are depicted in the set of figures on page 171 (Plate XVII). The literature on all hypotrichs is considered together, following the subordinal diagnoses.

Suborder (1) Stichotrichina

Theoretically, the species assigned here are supposed to possess relatively delicate cirri which are also numerous and are "basically" arranged on the ventral surface of the body in 3–12 continuous longitudinal (sometimes spiraled) rows or series. Such "primitive" hypotrichs are reminiscent of certain heterotrichs, since the small cirri are hardly more noticeable than simple cilia in some cases. Indeed, in a number of spirofilid species the base of a cirrus may contain as few as four kinetosomes. Yet members of certain other (bonafide?) stichotrichine genera possess the more typical hypotrich cirri, with quite large infraciliary bases: taxonomically, such facts are disturbing! (Also, see Addendum, page 174).

The mode of stomatogenesis may be considered parakinetal in at least some stichotrichines; division has yet to be studied with care in many of the species. Cirral morphogenesis varies in its patterns, seeming to overlap with some of those manifest in members of the second suborder. In some genera the body is very elongate, stretching out posteriorly in a tail-like process (e.g., *Psammomitra*). Still another variation in the usual shape is represented by species with a spiraled body form (e.g., *Atractos, Urostrongylum*). In *Pseudourostyla* and *Urostyla* total conjugation has been observed, a phenomenon unusual outside peritrichs, chonotrichs, and (some) suctorians. In *Paraholosticha*, Tuffrau & Fryd-Versavel (1977) have just described a unique cystic division.

Essentially all members of the Stichotrichina are free-living forms; they are found practically everywhere – including the sands of intertidal zones, where they are facultative residents. A few live in temporary tubes; several in genuine loricae. The long known case of close association between a hypotrich and another organism is that of *Kerona polyporum* on *Hydra*; this is a classical instance of ectocommensalism and one frequently observed in teaching laboratories of invertebrate zoology or even of beginning biology.

Tuffrau's (1970a,b) phylogenetic studies nicely link the stichotrichines to the heterotrichs, on the one hand, and to the sporadotrichines, on the other. Albaret's (1974, 1975) observations on certain hypotrich-like characters of his heterotrich suborder Plagiotomina (see Chapter 14) are relevant in this regard. As a group, the Stichotrichina has fewer and less well-known species, though a greater number of genera and families, than are to be found in the following suborder.

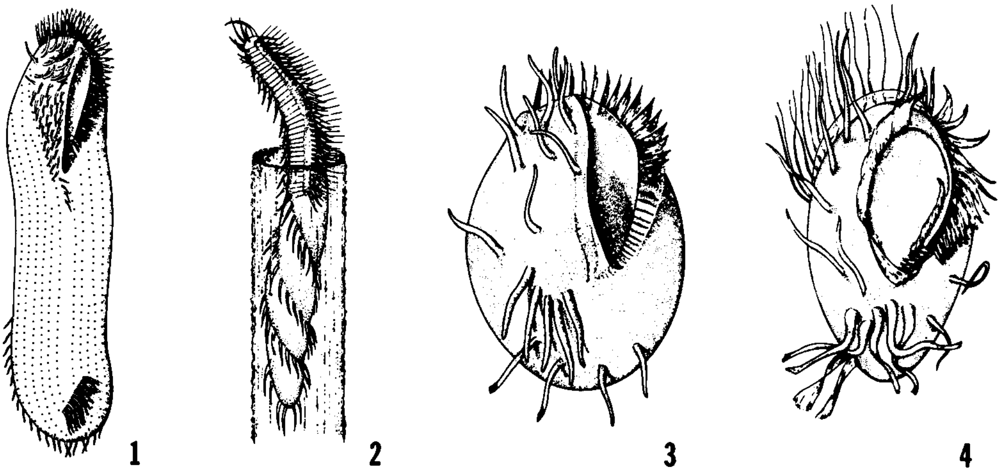

PLATE XVII. Representative hypotrichs (order Hypotrichida). Fig. 1. *Urostyla*, suborder Stichotrichina. 2. *Stichotricha*, suborder Stichotrichina. 3. *Euplotes*, suborder Sporadotrichina. 4. *Diophrys*, suborder Sporadotrichina. [Additional figures appear in Chapter 20.]

Suborder (2) Sporadotrichina

Basically, five (occasionally more) "longitudinal streaks" or series of cirri, exemplified or determinable by the frontoventrals, are recognizable here; but the cirri are localized in specific regions of the ventral surface rather than in the noninterrupted lines typical of the stichotrichines. Also, they are often heavier and more prominent, some becoming extremely conspicuous organelles dominating the entire body morphology (e.g., in *Aspidisca, Diophrys*, and *Uronychia*). [If not such, should the genera bearing them comprise a separate suborder? See page 174.] Probably phylogenetically traceable to a kind of parakinetal mode, stomatogenesis in many sporadotrichines seems better classified as being apokinetal. The anlage for the new buccal organelles appears in an isolated region of the ventral surface (though often near the base of a transverse cirrus), sometimes in a minute subpellicular pouch which is present only at the beginning of the process. Microtubular tracts interconnect cirral bases; and kinetodesmata have been seen.

The body shape is usually ovoid or only slightly elongate with rounded ends; but some species are quite lengthy, a few even conspicuously tailed (e.g., *Ancystropodium*). Others (e.g., *Gastrocirrhus*) appear as if they possessed a truncated anterior end. Species of *Discocephalus* show a rather strikingly distinct head or "cephalic" region, sometimes even with a narrower "neck" (see the excellent figures in Dragesco, 1960, 1965a, 1968a). Prominent though the AZM may be, the cirri, which may serve several functions, usually are clearly the more conspicuous feature, as mentioned above: in this way, sporadotrichine hypotrichs can be distinguished from other polyhymenophorans, many of which also possess a well-developed AZM, with ease. Hypotrich cysts have long been known. But Grimes' (1973a–d) recent studies on a species of *Oxytricha* have revealed a startling fact (and possibly a mortal blow to at least an aspect of the hypothesis of "continuity of infraciliature"); *viz.*, although all infraciliary cortical structures – including kinetosomes – are "lost" (checked carefully with TEM) in the encysted organism, they (re)appear *in exactly their proper sites* on excystment!

Sporadotrichines occur in as diverse habitats – sand, sea, soil, moss, acid ponds, marshes, bogs, fresh-water – as those of species of the first suborder; in addition, it is here that one finds all but one (*Kerona* on *Hydra*: see above) of the several examples of symbiotic forms in the order.

Two bonafide species of the ubiquitous *Euplotes* and one of *Aspidisca* are found as inquilines of certain sea urchins (Berger, 1965), although only one of the *Euplotes* seems to be known solely as such, the other having look-alike free-living strains as well. Another interesting but more esoteric situation is that of the unusual *Euplotaspis*, which was discovered by Chatton & Séguéla (1936) as a regular inhabitant of the branchial cavity of the ascidian *Ciona*. Finally, Fenchel (1965a) has reported finding a species of *Uronychia* in the mantle cavity of a marine lamellibranch mollusc. It is surprising that additional instances of adaptation of hypotrichs to some symbiotic mode of existence are not known (perhaps just not yet discovered?), since so many of their species are present in the vicinity of algae or are on coral or are in or on moribund sponges, etc., common locations of many potential hosts. Of perhaps more than passing interest is the claim by Renault & Roche (1898) that species of *Aspidisca*, *Euplotes* (called *Ploesconia* in their work), and a new genus *Cinetoconia* were present in fossil material from the Lower Eocene of Hérault, France. However, Deflandre & Deunff (1957), in a footnote on the matter, stated positively that the microfossils involved "ne sont sûrement pas des ciliés."

* * * * *

Because of their ubiquity and their distinctiveness, hypotrichs of both suborders have frequently been described and discussed in the literature, many of the papers bearing dates from the 19th and the early 20th centuries and even extending back to the monographs of O. F. Müller (e.g., 1786). Much of the older literature may be found in the bibliographies of several important reviews or compendia: Borror (1972a), Corliss (1961), Curds (1975a), Dragesco (1960), Fauré-Fremiet (1961b), Grell (1973), Kahl (1932b + 1935c), Stiller (1974b), Taylor (1941), and Tuffrau (1960). But I must make reference to the unsurpassable masterpiece of Stein (1859c), paralleling his magnificently illustrated treatise on the heterotrichs (mentioned in Chapter 14). From a more recent period of "historical ciliatology," the works of Fauré-Fremiet certainly deserve special citation: his active interest in hypotrichs spanned a period of more than 50 years (e.g., see Fauré-Fremiet, 1909, 1964). With respect to other pre-1960 papers and especially the contributions of the past 10–15 years, the references given below are arbitrarily divided into five broad fields or areas of research, with inevitable overlapping, very briefly listed-and-described as follows: (1) systematics, including general morphology, silverline system, distribution, ecology, and phylogeny; (2) ultrastructure (self-explanatory); (3) physiology, including growth and nutrition, en- and excystation, ciliary movement, fibrillar systems, regeneration, and morphogenesis; (4) nuclear studies, with emphasis on the phenomenon of macronuclear reorganization; and (5) genetics and sexual phenomena, including mating type of determination, etc.

(1) Systematics, morphology, silverline system, ecology, etc. The great bulk of this literature was published in pre-1960 times; recall, for example, such monographs or papers (although some are only partially devoted to hypotrichs *per se*) as: Bullington (1940), Chatton (1942), Chatton & Séguéla (1936, 1940), Cohn (1866), De Morgan (1926), Fantham & Porter (1945), Fauré-Fremiet (1954d, and others), Froud (1949), Gajewskaja (1926, 1933), Garnjobst (1934), J. von Gelei (1929, 1938, 1939b, 1944, 1954), Gellért (1956), Gruber (1884), Hegner (1926a,b), Horváth (1932, 1933, 1934, 1936), Ilowaisky (1926), Kahl (1928, 1932b, 1933), Kay (1945a), Kiesselbach (1936), Klee (1926), Klein (1928, 1932), Lepşi (1928, 1957), Lund (1935), Mansfeld (1923), Maupas (1883), Nozawa (1941), Ozaki & Yagiu (1942), Pierson (1943), Rühmekorf (1935), Sauerbrey (1928), Smith (1897, 1899, 1900), Stein (1859c), Sterki (1878), Stokes (1885, 1888) Tagliani (1922), Turner (1933), Wallengren (1900, 1901), Wang (1930a), Wenzel (1953), Weyer (1930), Wichterman (1942), Wrzesniowski (1870), Yocom (1918), and Young (1922).

The following relatively recent works have been selected as "representative": Agamaliev (1966, 1967, 1972), Agamaliev & Alekperov (1976), Berger (1965), Bick (1972), Borror (1963a,b, 1965a,b, 1969, 1972a,b, 1975), Buitkamp (1977), Buitkamp & Wilbert (1974), Burkovsky (1970a,b), Carter (1972), Cela (1972), Curds (1969, 1974, 1975a), Curds et al. (1974), Diller & Kounaris (1966), Dingfelder (1962), Dragesco (1960, 1963b, 1965a,b, 1966a,b, 1968a, 1970, 1972a,b), Dragesco & Njiné (1971), Fauré-Fremiet (1961b, 1964), Fenchel (1967, 1968a,b, 1969), Foissner (1976c), Génermont et al. (1976), Gittleson & Hoover (1969), Gliddon (1966), Grimes (1972), Grolière (1976), Hamm (1964), Hartwig (1973a,b, 1974), Hill & Reilly (1976), Jeffries & Mellott (1968), E. E. Jones (1974a), Magagnini & Nobili (1964), Pierson et al. (1968), Raikov (1962a, 1963e), Raikov & Kovaleva (1968), Ramírez-Montesinos & Pérez-Silva (1966), Sarmiento & Guerra (1960), Stiller (1974a,b, 1975), Tucolesco (1962a,b,), Tuffrau (1960, 1964a,c, 1965, 1972, 1975, 1977), Vuxanovici (1963b), Washburn & Borror (1972), Wichterman (1964), and Wilbert (1969).

(2) Ultrastructure. Papers cited here are largely of a general cytological nature; those more intimately related to morphogenetic, nuclear, or sexual events are, for the most part, included in subsequent sections (below), although often the subject matter really does not lend itself well to such arbitrary segregation. The pioneering work on overall hypotrich ultrastructure is that of Roth (1956, 1957). Results of more recent researches are to be found in: Fauré-Fremiet & André (1968a), Fischer (1974), Gliddon (1966), Grim (1966, 1967, 1968, 1970, 1972), Grimes (1972, 1973a,b), Heumann (1975), Hosoi (1973), Kloetzel (1974, 1975), Kluss (1962), Luporini & Magagnini (1970), Nobili (1967), Nobili & Rosati Raffaelli (1971), de Puytorac et al. (1976), Rosati Raffaelli (1970), Ruffolo (1974, 1976a,b), Ruthmann (1973), Shigenaka et al. (1973), Tuffrau et al. (1968), G. K. Walker (1975, 1976a,b), and Walker et al. (1975).

(3) Physiology of various kinds, including the vast area of morphogenesis. Older studies have dealt mainly with the fibrillar system, en- and excystment processes, locomotion, life cycles, and regeneration. Nutritional and enzymatic investigations have been limited by the inability to find suitable axenic culture media, although monoxenic cultures have been successfully used by a few physiologists working with *Euplotes* and *Stylonychia* (see reviews in Kidder, 1967a). Selected pre-1960 papers of lasting value include: Bishop (1943), Bonner (1954), von Brand (1923), Calkins (1911, 1921, 1925, 1929), Dawson (1919, 1920), Dembowska (1925, 1926, 1938), Fauré-Fremiet (1945b, 1948b, 1953a), Fauré-Fremiet et al. (1954), Garnjobst (1928, 1937), von Gelei (1934e), Giese & Alden (1938), Hammond (1937), Hammond & Kofoid (1937), Jacobson (1931), Kay (1945b), Lilly (1942, 1953), Lilly & Cevallos (1956), Lund (1935), Manwell (1928), Penn (1935), Reynolds (1932), Taylor (1920, 1928, 1941), Turner (1933), Wallengren (1900, 1901, 1902), Woodruff (1905), Yocom (1918), and Yow (1958).

In recent years the literature in this area, overall, has continued to swell; it is fair to say that the principal emphasis has been on morphogenetic phenomena in the life cycle of species belonging to such genera as *Euplotes* and *Urostyla* (or *Paraurostyla*). But *Aspidisca*, *Diophrys*, and *Stylonychia* (and still others) have also been studied; and ciliary movement, cysts, nutrition, effect of toxic substances, and growth have been investigated as well as stomatogenesis, cytokinesis, and regeneration (generally leaving consideration of nuclear phenomena and conjugation aside: see below). For example, note such works as: Alonso & Pérez-Silva (1963), Curds (1966), Deroux & Tuffrau (1965), Diller (1966, 1974, 1975), Fauré-Fremiet (1967c), Foissner & Schiffmann (1974), Frankel (1973a–c, 1974, 1975a), Frick (1968), Grim (1968), Grimes (1972, 1973a–d), Grolière (1969, 1970), Hashimoto (1961, 1962, 1963, 1964), Hunter (1959, 1963, 1964, 1969, 1974), Janisch (1961), Jerka-Dziadosz (1963, 1964a,b, 1965a,b, 1967, 1972a,b, 1974), Jerka-Dziadosz & Frankel (1969), Jerka-Dziadosz & Janus (1972), Johannes (1965), Kloetzel (1975), Lilly (1967), Luporini (1970), Machemer (1965, 1974), Okajima & Kinosita (1966), Persoone & Uyttersprot (1975), Pigoń (1962), Pigoń & Edstrom (1959), Prescott & Carrier (1964), Reuter (1963), Sapra & Dass (1970a,b), Tchang-Tso-Run & Pang (1974), Tuffrau (1964a,c, 1970a,b,), Tuffrau et al. (1976), Walker & Grim (1973), I. Walker (1975), and Wise (1965a,b).

(4) Nuclear studies. Principally because of the conspicuous changes in the macronucleus preceding binary fission of the whole organism, biologists have long been attracted to and interested in the "reorganization" or even "rejuvenation" – as it was thought to be – process in hypotrichs. The gross picture of the intriguing changes in macronuclear structure which last for several hours was detected many years ago by use of standard cytological staining methods; general descriptions were thus frequently published. But the breakthrough in understanding what was really happening at the macromolecular level came with such pioneering but elegant investigations on *Euplotes* as those by Fauré-Fremiet et al. (1957), employing electron microscopy, and Gall (1959), using

autoradiography. Studies of importance since that time – including investigations on other aspects of the nuclei in species of the same and different genera as well as further work on the chemical nature of the replication bands – are listed below. First, selected reference to additional outstanding nuclear-cytological papers of the pre-1960 decades may be given briefly as follows: Calkins (1919, 1930a,b), H. Raabe (1946, 1947), Summers (1935), Taylor & Farber (1924), Turner (1930, 1941), and some of the works cited elsewhere in these pages under other topics.

More recent works in the area of nuclear structure (including description of macronuclear "chromosomes"), chemistry, and function include: Alonso (1975), Alonso & Jareño (1974), Ammermann (1965, 1968, 1969, 1970, 1971, 1973), Ammermann et al. (1974), Curds (1966), Diller (1965), Jareño (1975), Jareño et al. (1972), Kimball & Prescott (1962), Kloetzel (1970), Kluss (1962), Lipps (1975), Lipps & Hantke (1975), Murti (1973), Pérez-Silva & Alonso (1966), Prescott (1962, 1966), Prescott & Kimball (1961), Prescott & Murti (1974), Prescott & Stone (1967), Rao & Ammermann (1970), Ringertz & Hoskins (1965), Ringertz et al. (1967), Ruthmann (1972, 1973), Salvano (1974b, 1975a,b), Spear & Lauth (1976), Suganuma (1969), Takahashi (1972), Wesley (1975), and Xinbai (1975). See also some of the papers cited in the following section.

(5) Genetics and sexual phenomena. Leaving aside the mere reporting of the occurrence of conjugation in various species of hypotrichs, the most helpful early reviews of Sonneborn (1947, (1957) cover – and discuss – much of the pre-1960 literature of pertinence. Still, a few of the older papers deserve mention here, including those classical monographic contributions by the giants of the 19th century: Balbiani (1861), Bütschli (1876), Hertwig (1889), and Maupas (1889). Omitting scattered papers of the early 1900's, the following works from the 1930–1950's with emphasis on demonstration of inheritance of specific characters and on pioneering research leading to consideration of mating-type systems in hypotrichs may be cited: Cohen (1934), Downs (1959), Katashima (1952, 1953, 1959a,b), Kay (1946a), Kimball (1939, 1941, 1942, 1943), Peshkovskaja (1948), Powers (1943), Rao (1958), and Siegel (1956).

In recent years, the emphasis has been on syngen and mating-type determinations; unfortunately, the door to "chemical genetics" is not yet very far open to the student of hypotrichs due to several factors ranging from peculiarities in the genetics itself of these organisms to difficulties in handling them under highly refined laboratory conditions. Examples of modern work in the overall area are the following: Alonso & Pérez-Silva (1966), Ammermann (1965), Diller (1965, 1966, 1975), Esposito et al. (1976), Grimes (1973d), Heckmann (1961, 1963, 1964, 1965, 1975: the last one on symbiotic bacteria in *Euplotes*), Heckmann & Frankel (1968), Heckmann & Siegel (1964), Heumann (1975), Hufnagel & Torch (1967), Ito (1963, 1971), Jareño et al. (1970), Katashima (1960, 1961, 1971), Kloetzel (1975), Kosaka (1970, 1972, 1973, 1974: last one on aging), Lipps (1974), Lueken (1973), Luporini & Dini (1975), Luporini & Nobili (1967), Miyake & Nobili (1974), Moldenhauer (1965), Nobili (1964a,b, 1965, 1966, 1967), Nobili & Luporini (1967), Pieri (1966), Prescott et al. (1973), Rao (1964, 1966, 1968b), Reiff (1968), Ricci et al. (1975), Siegel & Heckmann (1966), Takahashi (1973, 1974), and Wichterman (1967). See also some of the papers cited in the preceding section.

Addendum

As pointed out again in Chapter 20, many aggravating (challenging!?) taxonomic problems remain at all levels in hypotrich systematics. It is possible that recognition of a third – actually, a "middle" or "in-between" – suborder (to be mainly comprised of oxytrichid genera?) would offer some relief at *that* level. But, in my opinion, we ought to have more comparative data of direct relevance available to us before justifiably proposing "solutions" of such far-reaching significance as a way out of the predicaments in which we currently find ourselves with respect to the most suitable classification of these ubiquitous ciliates.

Chapter 17

Ciliate Evolution and Phylogeny

Evolution and phylogeny of the ciliates are subjects rather widely neglected by both protozoologists, many of whom are ciliate-watchers, and professional evolutionists or phylogeneticists, who might be expected to be interested in the application of general principles to such a circumscribed group of unicellular eukaryotic organisms. The reasons for this neglect are many (see Corliss, 1974c) and need not be reviewed here. The present chapter is devoted to brief consideration of the possible phylogenetic interrelationships among the higher (i.e., suprafamilial) taxa embraced by the phylum Ciliophora, based on my interpretation of the pertinent data available to date and on the ideas and hypotheses, some new and some old, related to such overall matters (see Chapter 3) – and keeping in mind the admonitions of Canella (1964a, 1971; and see Canella & Rocchi-Canella, 1976). Purposely omitted, for reasons of space, is treatment of the origin of the phylum from its inevitable nonciliate ancestry. A stimulating new idea on the subject has just appeared (Orias, 1976); the sparse older literature has been reviewed recently by the writer (Corliss, 1972e, 1975c, 1977b). In essentially all cases, some kind of flagellate has been implicated as progenitor or precursor. In general, however, with the notable exception of Orias' work, no discussion has been offered of exactly how such an evolutionary process might have occurred, fascinating though the topic is.

Of necessity, especially in restricting our attention to the suprafamilial taxa, data supporting the several "evolutionary series" which I recognize are derived almost exclusively from morphological-taxonomic studies, since they are practically the only relevant works available. But the accumulation of new morphological information of comparative value – derived primarily from the use of silver-impregnation techniques and electron microscopy – has been tremendous and, alone, would require a thorough overhauling of my own earlier views (Corliss, 1961). Molecular-genetic aspects (protozoological) are in somewhat of an underdeveloped state at this time; and physiological work is similarly seldom of pertinence for such taxonomically high-level synthetic considerations, although Hutner & Corliss (1976) have very recently made a preliminary attempt to arouse fresh interest in such approaches. Few essays on the overall evolution and phylogeny of the entire ciliate phylum exist. The important paper of Jankowski (1972a), though excluding reference to a number of groups, represents a valiant and invaluable effort; the very recent publications by de Puytorac & Grain (1976) and de Puytorac et al. (1976), with their concentration on the oral infraciliature, treat several pertinent aspects of the subject, as do the equally recent works (stressing other attributes) by Gerassimova & Seravin (1976), Hanson (1977), and Small (1976). Incidentally, the idea of a possible phylogenetic significance to the *shift in site* of the ciliate oral apparatus (briefly mentioned on page 81 of Chapter 6) is not particularly utilized in the considerations below, except in the case of the hypostomes.

Of some use in reading the following accounts may be the convenient "overview" of the relative positions of the currently endorsed orders and other taxa, the scientific names of which are used without diagnoses below, available in Table III, which is located at the end of Chapter 4. Relevant details about each major taxonomic group appear in appropriate earlier chapters (and Chapter 20), to which repeated citations are deliberately omitted throughout the present chapter. Definition of various terms used may be found in Chapter 2. Some appreciation of ciliate "taxonomic" interrelationships – as envisioned by others – may be gained from perusal of the several tables (IV–IX) in Chapter 18, schemes of classification published in recent years by workers from several major laboratories of ciliate research (and also including the "Honigberg Report" of the international Society of Protozoologists).

Eociliates and Early Descendants

The "eociliates" – or, at least, their present-day representatives or remnants – ought to be recognizable among those gymnostomes with "relict" nuclear characteristics, in my opinion (see Corliss, 1975c; Corliss & Hartwig, 1977). Members of the orders Primociliatida and Karyorelictida show not only the early stages in the appearance and evolution of the ciliate macronucleus (Raikov, 1963a, 1969, 1976b) but also relatively primitive characters of nonspecialized somatic ciliature (and infraciliature) and "simple" oral structures (cytostome-cytopharyngeal apparatus), the latter apically or laterally located and unaccompanied by what I would define as atrial, vestibular, or buccal ciliature. Stomatogenesis is apparently basically telokinetal. Furthermore, the organisms are mostly "endemic" interstitial forms (Dragesco, 1960, 1974; Hartwig, 1973a,b), occupying a habitat which may be considered a haven for primitive forms among many groups of small invertebrates (Corliss, 1974b; Corliss & Hartwig, 1977; and references therein). More complicated structures which are being discovered, especially with the help of electron microscopy (e.g., see Nouzarède, 1977; de Puytorac et al., 1973; Raikov et al.,1976), may be considered secondarily derived specializations, resembling the similar but nonhomologous features of certain "higher" forms by convergent evolution. In general, the rate of evolution may be postulated as having been rather slow among surviving eociliates for reasons that can only be guessed at today.

The Prostomatida, containing forms presumably showing increasing complexities within the group but all still at a relatively primitive evolutionary stage, may be thought of as representing the first ciliates "typical" of contemporary species. They exhibit a nuclear dualism which includes a polyploid macronucleus, yet they possess an uncomplicated infraciliature, apical (or near-apical) cytostome, perkinetal fission, and telokinetal stomatogenesis. Any specializations may be considered secondarily derived. Presumably from such species arose the main line(s) of ciliate evolution leading to the many orders considered below.

A special word might be said concerning the prostome suborder Archistomatina, which, in agreement with French workers (de Puytorac et al., 1974), I now place as the first group within the order Prostomatida (Corliss, 1975c, 1977a). It is true that its *extant* members are all endocommensals of vertebrate animals and show a number of unique features, such as concrement vacuoles, which might belie the appellation of "ancient" or "primitive." But it is not difficult to imagine that early (former) members of the archistomes were free-living forms, one of the first groups to leave some ancient biotope in exploration of new habitats. Aeons later, their surviving descendants could have come to reside in a different kind of stable habitat, the digestive tract of certain terrestrial vertebrates (currently limited mostly to horses and camels). But even today's archistomatine forms have retained the simplest type of circumoral infraciliature known (Grain et al., 1973). The second suborder, the Prostomatina, contains such living prototypes of (relative) simplicity as *Holophrya*. Members of the third, the Prorodontina, show only a few evolutionary advances, but characteristics so important that I believe they justify recognition of the group as a separate subordinal taxon.

The orders of haptorids and pleurostomatids seem to represent the height of evolutionary development within the subclass Gymnostomata. Their toxicysts have often become specialized, in kind or location, and the cytopharyngeal rhabdos more complex; and a number of new structures or organelles have appeared. The pleurostomatids have either remained in an interstitial (*sensu lato*) biotope or returned there, with appropriate adaptations to such surroundings. Should their macronuclei prove to have low ploidy numbers, this would support their origin "*in situ*" from a karyorelictid ancestry. Since, today, they have close relatives in other habitats, they are considered facultatively psammophilic. The diversity seen in the extant Haptorida suggests occurrence of a considerable degree of "explosive radiation" in this group, often apparently related to adoption of rapacious carnivorousness as a principal mode of food-getting. But stomatogenesis is still basically telokinetal and the cytostome apical (or near-apical), with no development of truly compound ciliature in the oral area.

Some evolutionary line out of the array of gymnostomes considered above appears to have led to the subclass Vestibulifera, as I envision the composition of the latter assemblage. With a relatively simple mouth apparatus, rarely toxicysts, bodies fundamentally with simple axes and holotrichous ciliation, the order of trichostomes, at least, does not seem to be far removed from a generalized prostomatid species. One group even possesses concrement vacuoles strongly reminiscent of those found in the archistomatine gymnostomes. Here, however, one may notice, for the first time in our progression up the ciliate evolutionary tree, the presence of a vestibulum, a depression leading from the outer body surface to a definitive cytostome (itself often still apical in position, as it were, though sunken) and typically lined with a somatically derived ciliature. Free-living species are found in widely ranging habitats; and endocommensalism is common in both vertebrate and invertebrate hosts (Grain, 1966a; Wolska, 1965b).

The great group of entodiniomorphids – removed from the old spirotrich fold by virtue of their exhibiting syncilíary tufts rather than true membranelles in their oral area (see details and review of earlier history in Canella, 1971; Corliss, 1974a,b; Jankowski, 1973c) – are placed as an order within the Vestibulifera along with the other more typical orders mainly because of the demonstrated presence of a vestibulum and a cytopharyngeal apparatus of the rhabdos-type. Furthermore, a neat connecting link is provided by the blepharocorythines, considered to be trichostomes but possessing a number of entodiniomorphid-like characteristics (see especially Wolska, 1971a–c, and references therein). On the other hand, the many specializations of the Entodiniomorphida, some surely brought about through adaptation to the restricted environment of the digestive tract of certain mammalian vertebrates, have influenced some workers (e.g., Jankowski, 1973c), to place them in an entirely separate, though neighboring, subclass. Obviously, a great deal of evolution has occurred within the entire group since its origin (Noirot-Timothée, 1960, 1969; Senaud & Grain, 1972; Wolska, 1971c). And its exhibition of what appears to be an apokinetal mode of stomatogenesis, usually found among the so-called "higher" ciliate groups (Corliss, 1973e), remains difficult to explain.

The relatively advanced vestibuliferan order Colpodida presumably arose from among the "lower" trichostomes, with some of the ciliature and infraciliature of its vestibulum becoming organized to quite a high degree (e.g., into two fields of "cirromembranelles"). Some workers (e.g., see the very recent papers of Lynn, 1976a–c) may insist that the oral ciliature here has thus become truly "buccal" in organization, ultrastructurally and otherwise. Yet *Colpoda* and its relatives show some quite primitive features as well, such as a single RNA-nucleolus in the macronucleus, common absence of conjugation, presence of reproductive and resting cysts, and lack of toxicysts or trichocysts. In division, many of the species appear to nicely recapitulate ancestral forms (Corliss, 1956; Fauré-Fremiet, 1963b; Stout, 1960a; Tuffrau, 1952).

Hypostomes and Their Diversification

Next on the scene, if we return to our hypothetical "main-line" of ciliate evolution, arrived the astonishingly diverse assemblage of forms best known today as the subclass of hypostomes, in considerable extension of the boundaries of the taxon originally visualized by Schewiakoff (1896) as containing the "ventral-mouthed gymnostomes." Such "ventralization," to adopt Deroux's excellent term (Deroux et al., 1974; but note origin of the concept in Fauré-Fremiet, 1961c), represented a significant advance, a major branching of the phylogenetic tree, one perhaps straining my characterization of the class Kinetofragminophora but serving as an evolutionary "proving ground" for the ciliate groups yet to arise. The hypostome body, though cylindrical in some groups, may become flattened dorsoventrally, with ciliature restricted to the ventral surface. More importantly, the cytopharyngeal apparatus has evolved into the more complex cyrtos (as compared with the preceding rhabdos); and the oral area sometimes has become sunken into what I call an atrium, provided with "atrial ciliature" or perhaps "pseudomembranelles." In a few groups, this ciliature – which, as a "hypostomial frange" (see Fauré-Fremiet, 1967a) composed of kinetofragments, primitively extended some distance beyond what subsequently became the atrium *sensu stricto* – has taken on characteristics reminiscent of the highly organized compound buccal ciliature of "higher" ciliate classes. In fact, some ultrastructural experts may claim that, in such cases, it *is* buccal ciliature (membranelles or polykineties): for example, see Grain et al. (1976) and Grolière (1974). Even the patterns of stomatogenesis in certain species have become complex and must be termed at least "advanced telokinetal"; some workers would describe them as parakinetal or buccokinetal in nature. But I like to think of such specializations as examples of the great diversity of "evolutionary experiments" tried out by the ancestors of our contemporary hypostomes. It seems to me that, in some instances, they may have led to "higher" groups; in others, they may signify dead-end specializations; in still others they may represent lines of convergence, without involvement of any basically homologous structures.

Many members of the huge order Cyrtophorida, whose origin among the more primitive synhymeniids and nassulids (latter group containing the once enigmatic *Pseudomicrothorax*: most recent reference, Peck, 1977b) is not evolutionarily difficult to imagine, can serve as "representative" hypostomes; and they show certain other major features in addition to those mentioned briefly above. A number of them have developed a complex adhesive organelle (the podite: see Deroux, 1977; Fauré-Fremiet, 1965a,c), with an "adhesive territory" as its homologous forerunner (Deroux, 1975), on the ventral surface near the posterior end of the body. Also their macronucleus is typically heteromerous, composed of two parts, the DNA-rich orthomere and the DNA-poor paramere. The relationship between the Cyrtophorida and the order Chonotrichida makes a most intriguing evolutionary story. Despite the unique appearance of the mature stage in the life cycle of chonotrichs, attention to their ontogeny and to such stable features as their macronucleus and secreted stalk some time ago produced evidence in favor of a close affinity with cyrtophorids (Dobrzańska-Kaczanowska, 1963; Fauré-Fremiet, 1950a, 1957b; Fauré-Fremiet et al., 1956a; Guilcher, 1951; Tuffrau, 1953). The infraciliary pattern of the chonotrich bud is certainly reminiscent of, if not homologous with, that of the ventral right-hand surface of adult cyrtophorids. More recently, comparative ultrastructural data (Grain & Batisse, 1974), ecological (host-symbiont) considerations (Fenchel, 1965b), and new ontogenetic information (Deroux, 1976a,b; and, now, 1977) has strengthened the closeness long supported on theoretical phylogenetic grounds (Corliss, 1956, 1961, 1968; Honigberg et al., 1964; Raabe, 1964a,c). Yet objections are still forthcoming from chonotrich specialists (e.g., see Jankowski, 1967a, 1973b,c; Mohr, 1966; Mohr et al., 1970) and some general protozoologists (e.g., see Cheissin & Poljansky, 1963; Poljansky & Cheissin, 1965). The undeniable explosive radiation so beautifully described by Jankowski (1973b) is influencing some workers – I believe unduly – to support a taxonomic status for the group at too high (independent class or subclass) a level of separateness.

The rhynchodids (as now redefined: see Corliss, 1975b) represent an aberrant group with uncertain affinities. But the ultrastructural data, particularly, which are now available (Khan, 1969; Lom & Kozloff, 1968, 1970; de Puytorac, 1969c) suggest an ancient phylogenetic affinity with other hypostomes; thus I no longer subscribe to the view (Chatton & Lwoff, 1949, 1950) that they may have arisen from a thigmotrichine (scuticociliate) group. The apostomes have long intrigued ciliatologists (Chatton & Lwoff, 1935a). Their specializations, the diversity within the order itself, and their complex polymorphic life cycles (uniquely involving alternation of hosts) speak to their separation at a reasonably high taxonomic level. Yet their thigmotactic field, their stomatogenesis (presumably derived from a telokinetal type), and their general ecological and infraciliary characteristics do not refute an origin among the "lower" hypostomes (Deroux et al., 1975; Jankowski, 1966a–c, 1972a).

The Unique Suctorians

The suctorians have traditionally been considered a most unique protozoan group, set apart by numerous workers from *all* other ciliates. The bases for this have resided in the unusual "key"

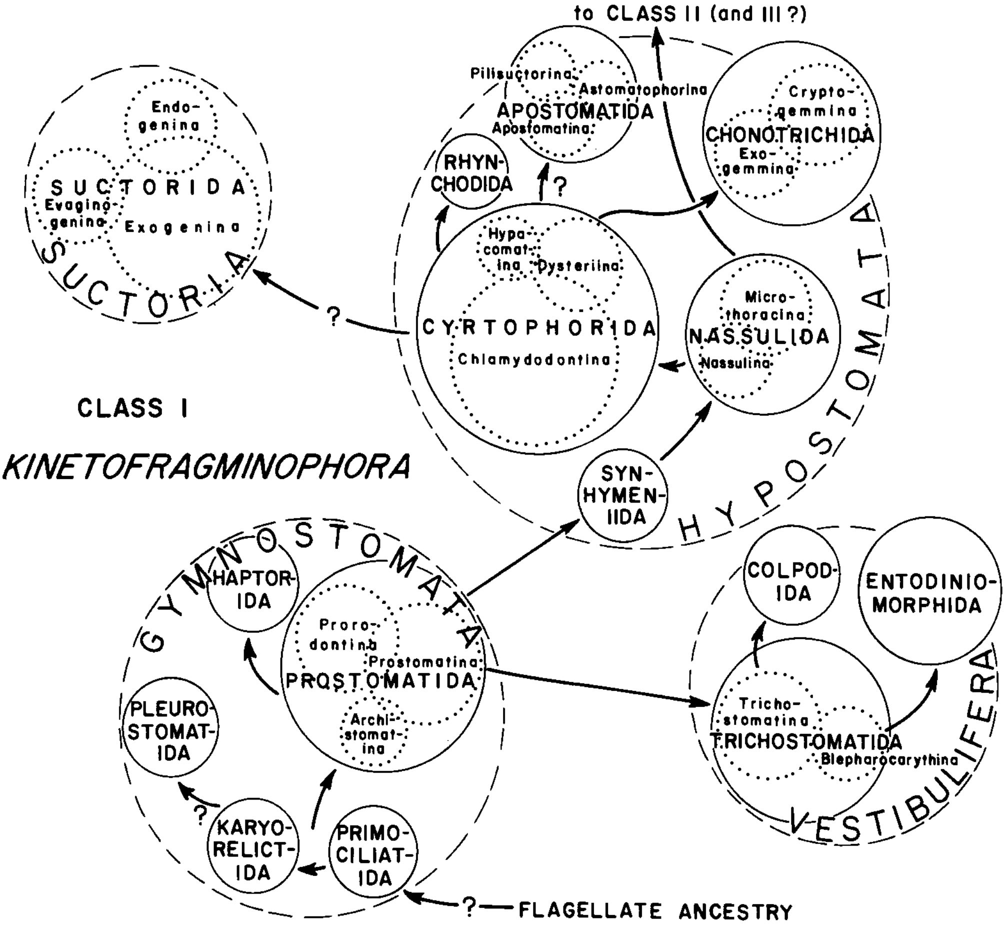

PLATE XVIII. Proposed phylogeny for the 15 orders comprising the four subclasses of the class Kinetofragminophora. Groups at the same level in the classificational hierarchy (i.e., at parallel taxonomic ranks in the Corlissian system) are depicted in a similar style. Phylogenetic relatedness is roughly indicated by inclusion, overlapping, or separation-distance of the various circles and/or by "interconnecting" arrows. Question marks appear sparingly, since the entire diagram is highly speculative. (See text for discussion.)

characters of presence of tentacles (with haptocysts) and stalks (from scopuloids), lack of cilia (in adult stage), exhibition of budding types of reproduction, and, often, production of micro- and macroconjugants which may fuse during conjugation. But the ideas and studies stemming from or stimulated by the early observations of Chatton et al. (1929), Fauré-Fremiet (1950a), Fauré-Fremiet & Guilcher (1947a), Guilcher (1948, 1950, 1951) – and even Collin (1912) and Kahl (1931a), who worked without benefit of techniques of silver impregnation – have made clear that the suctorians could easily have arisen from some "lower" kinetofragminophoran group. An example of recent direct support may be found in Millecchia & Rudzinska (1972); and indirect support is available in a number of other ultrastructural papers mainly concerned with different problems or groups (e.g., Holt et al., 1974; Lom & Corliss, 1971). Certainly the infraciliary pattern shown by a number of larval suctorians is reminiscent of, if not probably homologous with, that of the (right side of the) ventral surface of adult cyrtophorids and of chonotrich buds. The complexity of modes of budding in the Suctorida, involved in intraordinal phylogenetic problems, has been discussed by a number of experts on the subject – for example, Batisse (1975), Collin (1912), Guilcher (1951), Jankowski (1967a, 1972a, 1973c), and Kormos & Kormos (1957a, 1958a,b, 1961). I have recognized three suborders on the basis of gemmation patterns (Corliss, 1977a), whereas Batisse (1975) has liberally proposed seven.

Although I cannot accept the very large evolutionary gap between suctorians and other ciliate groups proposed or endorsed by Cheissin & Poljansky (1963), Jankowski (1967a, 1972a, 1973c, 1975), and Poljansky & Cheissin (1965), I do appreciate that for a very long period of time these organisms, as sessile and sedentary (adult) forms, must have existed apart from other ciliophorans, with development of many specializations often surely related to their attached mode of life. Thus I believe (in slight disagreement with de Puytorac et al., 1974) that a subclass (containing a single order) difference *is* fully justified, leaving unanswered the question of whether the progenitors of the group arose from within the earlier gymnostome subclass (e.g., from haptorids, on the basis of possible toxicyst and haptocyst similarity) or from some closer-by hypostome group. Personally, I favor the latter origin, which Batisse (1975) has recently supported and which Bütschli (1887–1889) essentially proposed nearly a full century ago!

Perhaps the principal difficulty in understanding suctorian phylogenetics lies in these ciliates' exhibition of polystomy via sucking tentacles. The mode of stomatogenesis is neither parakinetal nor buccokinetal; if it is considered apokinetal, it might have been derived from a kind of telokinetal type, in essence. But perhaps the earliest suctorians were monostomic. [In this regard, the generally overlooked paper by Matthes (1962) seemed to be an exciting one: he reported that species assignable to Stammer's genus *Spelaeophrya* might possess only "prehensile" tentacles, with the function of (the missing) suctorial tentacles perhaps being served by a single apical cytostome. If verifiable, the possible evolutionary implications would be worthy of considerable speculation! For example, might *Spelaeophrya*, then, be a very primitive suctorian, retaining possession of an ancestral cytostome? Or might it be a "missing link" organism? But I have just now learned from Matthes' laboratory – as this page was in the final proof-reading stage – that a new study in progress is revealing the presence, not absence, of bonafide suctorial tentacles in species of that genus. So any great excitement over the matter has become quite inappropriate.] There have been two (other truly) highly unusual (seemingly without *any* tentacles!) species of suctorians which have been studied ultrastructurally – otherwise, they would never have been so classified – but which are surely unrelated to one another, secondarily "simplified," and/or very highly evolved forms and thus should *not* be considered truly primitive. These are members of the genera *Cyathodinium* and *Phalacrocleptes* (see Paulin & Corliss, 1964, 1969, and Kozloff, 1966, plus Lom & Kozloff, 1967, respectively; and further comments appear in appropriate sections of Chapter 9).

A phylogenetic tree of sorts for members of the large class Kinetofragminophora is offered in Plate XVIII. Despite its obvious weaknesses (oversimplification, etc.), it may serve as a (very general) summary of the discussions presented briefly above. It is to be understood, of course, that it is the *ancestors* of members of certain present-day groups from which supposedly arose the ancestors of certain other groups which similarly contain some species still extant – in a *more or less* modified condition – today.

Oligohymenophorans, First of "Higher" Ciliates

Although many specializations are to be found among members of the preceding class, it is in the Oligohymenophora that one may recognize the first bonafide (consistent and persistent) appearance of a true buccal cavity with compound buccal ciliary organelles, membranes and membranelles (as defined in Chapter 2) arising from complex infraciliary kinetosomal bases. Phylogenetically earlier occurrences are perhaps explicable either as nonhomologous convergencies or as isolated independent origins being "tried out" evolutionarily in groups ancestral to the oligohymenophorans: not to completely deny the existence of still another alternative view, that certain of my kinetofragminophoran taxa simply rate a "promotion" to the present class. The more sophisticated oral apparatus may be very inconspicuous in some oligohymenophorans, while elaborate – or secondarily totally absent – in others. Stomatogenesis has evolved to the parakinetal or buccokinetal type, with the resulting definitive cytostome typically located at the bottom of a buccal or peristomial cavity or infundibulum. Differences are sufficient to allow recognition of two distinct subclasses and some four orders and eight suborders; but the amazing diversity noted for the preceding class is lacking in the present evolutionarily more conservative assemblage. And departed from the scene are both types (rhabdos and cyrtos) of the conspicuous kinetofragminophoran cytopharyngeal apparatus, never to reappear in the evolution of the so-called "higher" ciliates. Families and genera of the subclass Hymenostomata have been studied taxonomically (or morphogenetically) by many workers in recent years with emphasis on a phylogenetic approach, employing primarily silver-impregnation methods or electron microscopy or both (e.g., see, among scores of pertinent publications, the following few selected post-1970 papers: Antipa, 1972; Canella, 1971; Canella & Rocchi-Canella, 1976; Coats & Small, 1976; Corliss, 1971b, 1973b; Didier, 1971; Grolière, 1975a; Jankowski, 1973g; Lynn, 1975a; Lynn & Berger, 1973; McCoy, 1974c; Peck, 1975, 1977a; de Puytorac, 1972a; de Puytorac, Grolière, et al., 1974; Raabe, 1970a,b, 1971b, 1972; Rodrigues de Santa Rosa & de Puytorac, 1976; Roque, 1974).

The hymenostomes *sensu stricto* may be considered the first "advanced" ciliates to show a *tetrahymenal* organization in their buccal ciliature. This was a most exciting discovery when first noted because it laid the groundwork for postulating the origin of the entire spirotrich (polyhymenophoran) assemblage, with its conspicuous AZM (adoral zone of membranelles), from humbler beginnings (see Furgason, 1940). Today, however, the group so implicated in the 1940's and 1950's (see Corliss, 1961), the tetrahymenines, seems unlikely to have been directly involved in filling that particular role of evolutionary "gap-bridging." In fact, the main phylogenetic line in the class may have run directly through the scuticociliates, a more recently recognized order (Small, 1967). Although their mode of stomatogenesis is quite advanced, being buccokinetal in nature, they also show – as a group – a degree of simplicity and potential plasticity in cortical structures generally (including ultrastructural details), in absence of toxicysts, trichocysts, and nematodesmata, in presence of cysts, in wide ecological distribution (including interstitial habitats), in numerousness, and in their possibly relatively "uncomplicated" macronuclei. The Scuticociliatida may well have arisen from a nassulid-like ancestry, giving rise, in turn, to certain heterotrichs among the polyhymenophorans (see following section) and, at the same time, to members of such neighboring orders as the Astomatida and the Peritrichida, considered briefly below. Although their buccal apparatus in mature (interdivisional) forms is often superficially strikingly tetrahymenal in nature, the mode of stomatogenesis (involving a scutica, etc.) is basically so different from that of the hymenostomes that the groups are definitely distinct. Such a discovery underlines the great value of ontogenetic data in postulation of phylogenetic relationships, as is coming to be appreciated more and more today (Corliss, 1967a, 1968, 1969a, 1973e, 1974a,d, 1976; Evans & Corliss, 1964; Jankowski, 1972a; de Puytorac & Grain, 1976; Small, 1967, 1976; Tuffrau et al., 1974).

The order Astomatida, composed (very nearly) entirely of endosymbiotic forms, has long puzzled protozoan phylogeneticists, although progress has certainly been made in recognizing that the loss of a mouth here is a secondary and thus "regressive" character, not a primitive one (as thought earlier), and that features of the infraciliature *sensu lato* may be used to advantage in trying to determine the most likely origin of the group. Astomatous forms are known from a number of other ciliate orders, of course, and an early step in understanding the "true" astomatids involved elimination of such species from the order. Some more of this kind of action may be necessary. That the bulk of the true astomes arose from within the subclass Hymenostomata – via the scuticociliate suborder Thigmotrichina or as a branch of an early line which led (also) to that suborder – has now long been believed (since its early postulation by de Puytorac, 1954) and seldom disputed. Yet the haunting possibility remains of a close trichostome-astome relationship, at least for certain groups (Kaczanowski, 1965; de Puytorac, 1959a). And Foissner's (1976b)

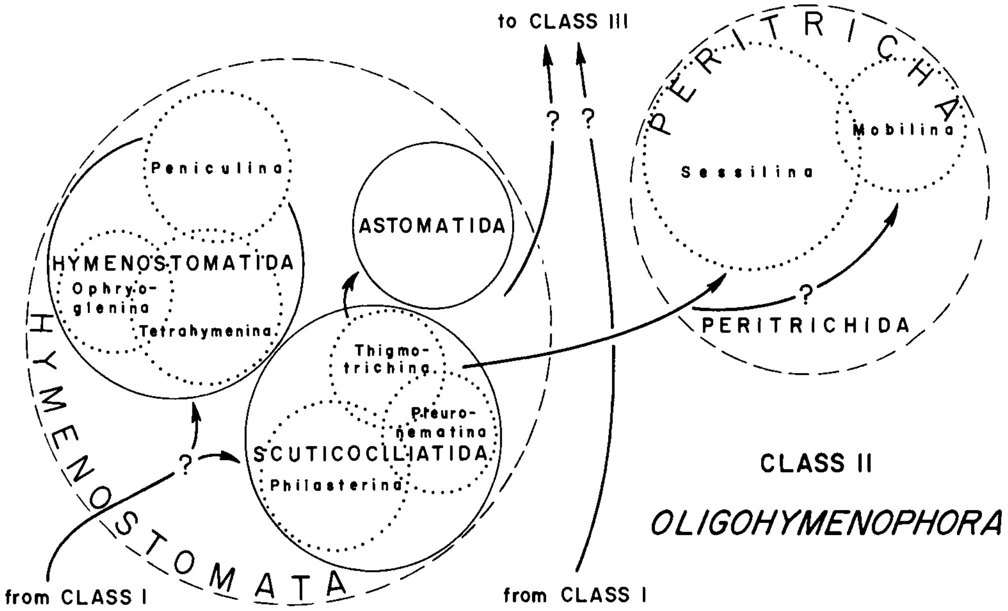

PLATE XIX. Proposed phylogeny for the four orders comprising the two subclasses of the class Oligohymenophora. (See general comments under preceding Plate XVIII.)

very recent discovery of an alleged free-living species does not particularly help matters. Despite modern-day efforts (e.g., see Grain & de Puytorac, 1974; de Puytorac, 1972a), is it possible that the Astomatida "may still be a polyphyletic group" (Corliss, 1975b)?

The subclass Peritricha represents still another perennial phylogenetic puzzle for protistologists, because its apparent uniquenesses (many! see Chapter 13) make difficult the conception of its origin from ancestors resembling members of any other contemporary ciliate group (Corliss, 1956; Raabe, 1964b). But homologies (with hymenostomes, especially) first suggested on the basis of comparative studies carried out principally with the use of techniques of silver impregnation (Chatton & Villeneuve, 1937; Fauré-Fremiet, 1950a, 1965b; Lom, 1964) and subsequently buttressed by observations via TEM (Fauré-Fremiet et al., 1962; Lom et al.,1968; Noirot-Timothée in Grain, 1969; Noirot-Timothée & Lom, 1965) appear to be valid, despite the objections voiced by workers such as Finley (1974, and see references therein), Raabe (1964b), and, in a milder vein, Cheissin & Poljansky (1963) and Jankowski (1973c). The peritrichs clearly seem to have close phylogenetic affinities with certain of the pleuronematine-thigmotrichine scuticociliates, with "evidence" ranging from intuitive hypothetical deductions to ultrastructural similarities in (allegedly) homologous infraciliary structures.

With respect to the two peritrich suborders, Lom (1975) has recently suggested that their evolution has very likely occurred in parallel from a common ancestral stock. This is in contrast to the widely accepted idea that the Mobilina arose from the Sessilina. Numerous taxonomic studies have been made of families and genera within the two groups; not many, however, have really treated the problems involved from an overall phylogenetic or evolutionary point of view. A few recent investigations in which such an approach was employed, at least partially, would include: for the more diverse sessiline taxa, Foissner (1976a), Foissner & Schiffmann (1975, 1976), Jankowski (1967a, 1973c), Lom (1963b, 1964), and Raabe (1964b); for the mobilines, essentially only Lom (1963c, 1975), and Raabe (1963a, 1964b).

In Plate XIX, I have suggested an evolutionary arrangement of taxa to indicate possible interconnections in the phylogeny of the major groups comprising the class Oligohymenophora.

Polyhymenophorans, Most Recent of Ciliates

Widespread agreement still exists that the spirotrichs, members of the conspicuous class Polyhymenophora, probably represent the most highly evolved (i.e., most recently arisen) major group within the phylum and, as well, the most compact and taxonomically least controversial assemblage of species. On the other hand, dozens of specialized characteristics have appeared among its subgroups and scores of unsolved phylogenetic problems do await the interested student. The fact that, with rare exception, all polyhymenophorans are united by their common possession of a well-developed set of compound buccal organelles, the AZM, and by the frequent absence of simple somatic ciliature (replaced by compound somatic organelles, the cirri, in at least one major group) does not eliminate the difficulties of tracing intraclass relationships. However, with the indispensable aid of silver-impregnation techniques, ontogenetical studies, and, now, electron microscopy, reasonable progress is being made in solution of a number of the long-recognized problems in spirotrich evolution.

By virtue of their ubiquity, plasticity, and frequently holotrichous somatic ciliation, the heterotrichs are probably justifiably considered to be the stem group. The parakinetal mode of stomatogenesis exhibited by many heterotrichs (Corliss, 1973e; Villeneuve-Brachon, 1940) is reminiscent of the condition in tetrahymenine hymenostomes. Exact origin of the multipartite AZM, however, remains a mystery: it now seems to me altogether too simplistic to imagine that it arose merely by direct multiplication of the tripartite set in such a form as *Tetrahymena*, stimulating though that notion was when first proposed by Furgason (1940) and popularized by Fauré-Fremiet (1950a) and Corliss (1956, 1961). Among the scuticociliates, perhaps more likely forerunners of heterotrichs, one may find genera whose species do indeed show more than three membranelles comprising the AZM (e.g., *Porpostoma* and *Protocruzia*, the latter even classified as a heterotrich by many workers); but the situation is complicated by differences in stomatogenesis in the two groups. And homologies are not clear with respect to either the paroral membrane or the "membranelles." It is also possible that the Polyhymenophora, via certain known or unknown heterotrich genera, evolved directly from some hypostome, or even karyorelictid gymnostome – there are interesting similarities in nuclear characteristics, the possession of postciliodesmata, contractility, etc. (see especially the very recent works by Gerassimova & Seravin, 1976, and Raikov et al., 1976) – ancestry, bypassing (or paralleling) the entire class Oligohymenophora: such is the deplorable state of our present knowledge!

Within the Heterotrichida are now recognized six suborders (Corliss, 1977a), groups showing distinct differences yet also overall uniting similarities. Although it makes sense to consider (along with Jankowski, 1964b) some subset of the Heterotrichina as representing the most primitive (of extant) members of the order, the curious Plagiotomina may be a better candidate. As we are now learning from Albaret's careful work (Albaret, 1973b, 1974, 1975; Albaret & Grain, 1973), *Plagiotoma* possesses a number of interesting nonspecialized characters; but some are probably related to its totally endosymbiotic existence in lumbricid oligochaetes. Exhibiting a laterally flattened body, uniform ciliation, a subequatorial cytostome, and parakinetal stomatogenesis, it also – frustratingly enough – bears an infraciliature, fibrillar system, and cirri-like groups of cilia which are very similar to structures found in one of the groups (see Stichotrichina) of the supposedly highly evolved order Hypotrichida (Tuffrau, 1972). The great bulk of polyhymenophorans are free-living, but there is a major group (the symbiotic clevelandelline heterotrichs) with very specialized structures, often including a macronuclear karyophore and, in some, a functional sucker and a buccal apparatus located at the posterior (antapical) pole of the organism. Presumably it represents an evolutionary offshoot from a free-living ancestry (Albaret, 1975; Jankowski, 1968e).

The other heterotrichid suborders are not particularly troublesome from a phylogenetic point of view. The small suborder Armophorina, with amazing morphological modifications apparently closely correlatable with their polysaprobic mode of life, presumably arose from a

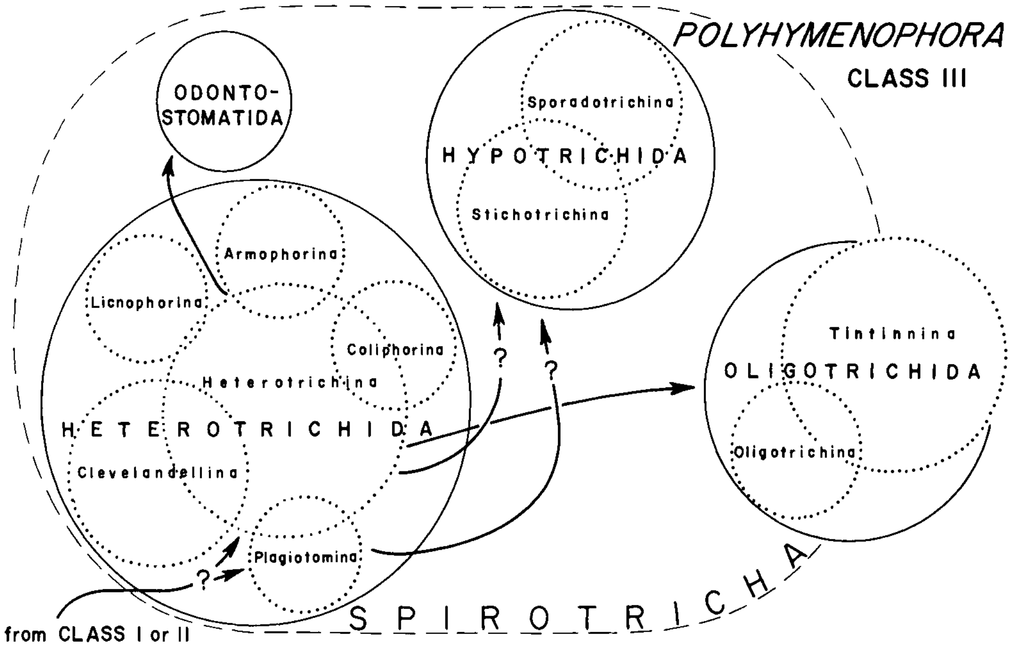

PLATE XX. Proposed phylogeny for the four orders comprising the subclass Spirotricha of the class Polyhymenophora. (See general comments under preceding Plate XVIII.)

Brachonella-like form within the heterotrichine family Metopidae (Jankowski, 1964b). The Coliphorina, distinguished principally by its universal production of loricae, seems clearly to have an affinity with the stem heterotrich group. Members of another suborder, the Licnophorina, though with striking differences in their overall morphology, also are surely "good" heterotrichs. But both of these last-mentioned suborders, especially, may be considered to represent evolutionarily dead-end groups. A spirotrich order also closely related to the heterotrichines, presumably having arisen from *Metopus* (Jankowski, 1964b), is the Odontostomatida.

The Oligotrichida represent a special case. Based primarily on the findings and ideas of Deroux (1974), Fauré-Fremiet (1970a), Fauré-Fremiet & Ganier (1970b), Grain (1972), Laval (1973), and Tappan & Loeblich (1968, 1973), two conclusions of high-level phylogenetic import may be drawn: first, that the oligotrichs *sensu stricto* and the tintinnids ought to be reunited into a single order (reversing their separation by Corliss, 1956, 1961; Hall, 1953; Honigberg et al., 1964; and others); secondly, that distinctions between oligotrichs *sensu lato* and other member orders of the polyhymenophoran assemblage may be strong enough to warrant consideration of classificational separation at the level of subclass (no one has yet done this, although Jankowski, 1967a, came close to it; and the suggestion is included in Corliss, 1975b). In such a case, heterotrichs, odontostomes, and debatably the hypotrichs would comprise the spirotrichs *sensu stricto* and the oligotrichs would stand alone in a second polyhymenophoran subclass. Recall that the oligotrichs *sensu lato* have already been purged of the odontostomes and, especially, of the entodiniomorphids. Despite present-day differences, it is a plausible supposition that the group evolved from some basic heterotrich line. The alternative, to have had its ancestry separately back among the oligohymenophorans, has few data in its support. It seems to share some significant characteristics with the hypotrichs, such as apokinetal stomatogenesis and manifestation of reorganization bands preceding macronuclear division — and the latter group has long been assumed to have arisen from some heterotrich predecessor. But the oligotrichs, as recognized today, more likely split off from the heterotrich stem at a separate early date.

Although *all* present-day ciliates may be thought of as representing the "evolutionary peak of development" within their own particular taxa and although certain groups do stand out by the nature of their specializations, the order Hypotrichida may be thought of as being the most highly evolved ciliophoran assemblage by virtue of the kind of structures its members possess and the relative complexity of such organelles. Top among such characteristics are the cirri, compound somatic ciliature rarely found in other orders and certainly representative of an evolutionary advance over the simple, single cilia so commonly found in other groups. The hypertelic development ("polymerization") of the AZM is another such character. To these may be added the dorsally located "sensory bristles," the macronuclear reorganization bands, the dorsoventrally flattened body, a highly complex fibrillar system, and the (typically) apokinetal mode of stomatogenesis, specializations which also seem to support the proposal that the Hypotrichida are at the pinnacle of evolution among the Ciliophora. The path of origin of the hypotrichs cannot be exactly known; but their ancestors must have sprung either from a generalized heterotrichine "main-line" source or possibly from among the predecessors of the (limited extant) membership of the suborder of plagiotomines, whose hypotrich-like attributes have been very briefly mentioned above. Within the order, various phylogenetic lines are recognized on the basis, in particular, of numbers and arrangements of the ventrally placed cirri. Patterns of cirral morphogenesis also provide helpful clues with respect to possible intraordinal affinities. Stomatogenesis is very important as well, and the recent data and ideas of Tuffrau (1970a,b, 1972; and Tuffrau et al., 1974) are especially relevant. He has determined that in certain primitive hypotrichs, such as *Kahliella* and *Hypotrichidium*, the mode exhibited appears to be parakinetal. In these cases, a particular line of modestly developed cirri on the ventral surface may be considered as the stomatogenic kinety, a homologue, in effect, of the similarly named kinety (or kineties) in various heterotrichs (including *Plagiotoma*) or even in oligohymenophorans such as *Tetrahymena*. The recognition of two suborders, first proposed by Fauré-Fremiet (1961b) on the major basis of differences in patterns and numbers of cirri, is supported by Tuffrau and French workers in general (see de Puytorac et al., 1974); it has been opposed, on morphogenetic grounds, by Borror (1972a), who claimed substantial overlapping of ontogenetic traits in the genera allegedly assignable to one or other of the suborders on static pattern alone. The matter must remain controversial, at least until many more comparative data are available. Maybe additional (see p. 176) suborders will need to be recognized to properly indicate intraordinal evolutionary divergencies.

Possible phylogenetic affinities among the suprafamilial groups comprising the class Polyhymenophora are revealed in Plate XX. The Oligotrichida are purposely shown as bulging out of the (single) subclass Spirotricha (see remarks on preceding page). Finally, in Plate XXI, in a different style, a "tree" for the entire phylum is offered, subject to the usual shortcomings of oversimplification, lack of tridimensionality, use of solely contemporary forms, etc., not to mention the perennial overriding factor of our woeful lack of desirable data on all of the groups involved.

It may be historically worth recording the major past attempts at production of (original figures of) ciliate "phylogenetic trees." Arranged chronologically, they are: Schewiakoff (1896); Lepşi (1926; and see text of 1929); Fauré-Fremiet (1950a); Corliss (1956, 1960a, 1961, 1962a, 1968 – the later papers introducing only slight revisions); Jankowski (1967a, 1973b,c; and see text of 1972a); Corliss (1974a), a drastic revision over earlier "trees" but differing little from the arrangement shown on the following page; and – just out – Hanson (1977), using "representative" plesiomorphs for the various ordinal groups and their (highly selective) "semic" traits.

Note of explanation with respect to Plate XXI. Figures are of "representative genera" larger drawings of which appear in plates of Chapters 6–16. Included taxonomic names are limited to ordinal (capital letters) and subordinal (italics) groups; but Table II or III, the immediately preceding plates, or Chapter 20 may be consulted for further information. Dashed lines separate the three classes. Phylogenetic interrelationships are broadly indicated by arrows more or less "connecting" various of the groups. Because of the acknowledged and inevitably speculative nature of the whole "tree," question marks are used sparingly.

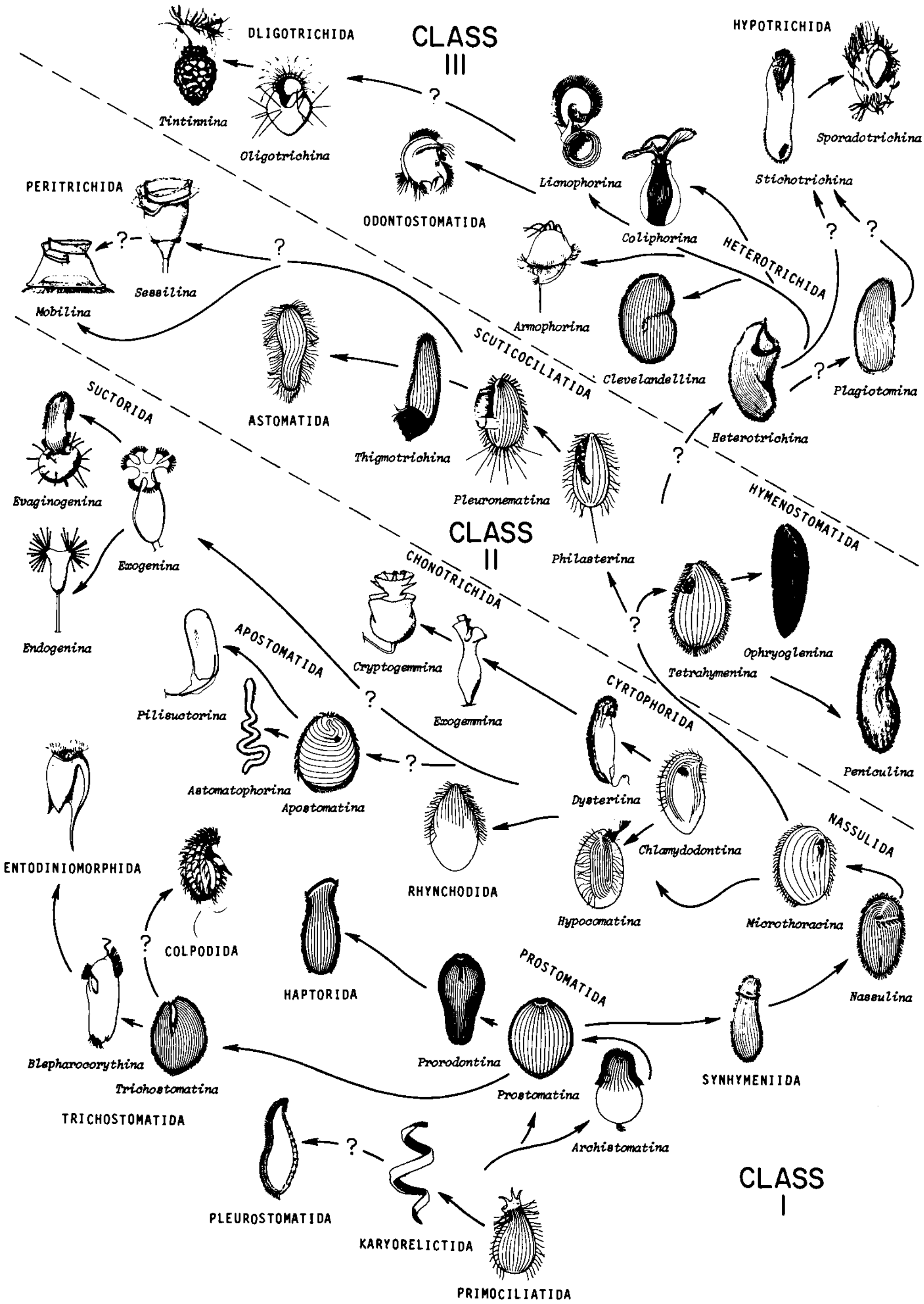

PLATE XXI. Phylogenetic "tree" for the subgroups comprising the entire phylum Ciliophora. (See note of explanation, bottom of page 185.)

Chapter 18

Comparison of Present Classification with Other Recent Major Proposals

Ever since Stein's (1859c, 1867) incomparable publications of more than a century ago, protozoologists have been placing groups of ciliates into one hierarchical arrangement or another based on knowledge of their characteristics available at the time and on interpretation of the relative taxonomic value of such data. In Chapter 1, I have traced the history of the older attempts (see also Corliss, 1974a; Jankowski, 1967a); here I wish to focus attention, albeit briefly, on the modern systems of classification used or proposed anew since the first edition of this book (Corliss, 1961). Such schemes, in general, either have followed the ideas of the older German schools of protozoology (i.e., are founded on the Bütschlian and/or the Kahlian schemes, themselves largely dating back to Stein and Schewiakoff); or, sometimes with slight alteration or addition, have been based essentially on the Faurean scheme (as presented by Corliss, 1961, or, with little change, by Honigberg et al., 1964); or have been refreshingly original in conception, as seen most notably in the works of Jankowski (1967a, 1973c). But still another kind, most recent of all and the first to utilize ultrastructural data to advantage (while salvaging the presumably better parts of preceding systems), may be seen in the works published by the modern French school of protistology (de Puytorac et al., 1974; de Puytorac & Grain, 1976; de Puytorac et al., 1976) and by the writer (Corliss, 1974a,b, 1975b, 1977a; and see Chapter 20). Finally, in this last category might also be placed the ideas, presented very recently in preliminary form, by Gerassimova & Seravin (1976), Seravin & Gerassimova (1977), and Small (1976). [All of these post-1973 plans have yet to be broadly tested, although the Corlissian scheme has already been adopted in works by Margulis (1974b) and Noble & Noble (1976).]

In Table I of Chapter 1, I have offered outlines of the classifications which dominated the periods 1880–1930 and 1930–1950, the Bütschlian and Kahlian eras in the history of ciliate systematics (Corliss, 1974a). And Tables II and III (in Chapters 1 and 4, respectively) reveal the widely accepted Faurean scheme (which originated in the heuristic paper by Fauré-Fremiet, 1950a) and my own post-Faurean (= Corlissian) system, neither of which thus requires repeated discusssion here. But those earlier tables may be useful in comparing such schemes with the several others treated briefly below.

First, it may be helpful to review, succinctly, the dozen or so major taxonomic controversies continually confronting the ciliatologist who attempts to draw up an arrangement of the various groups, whether for so-called "research" *or* "teaching" purposes. A number of these have been mentioned, in different contexts, in preceding chapters. The last three are particularly the ones involved in on-going discussion and debate among those of us currently embroiled in searching for the best ways to utilize ultrastructural information taxonomically at suprafamilial levels. An overall problem, by the way, is the matter of "lumpers" versus "splitters" in ciliate systematics, a topic recently covered elsewhere (Corliss, 1976).

1. Inclusion or exclusion of the opalinids (Metcalf's "Protociliata"). These forms are still called ciliates by some modern writers (see below), although widely treated today as either flagellates or protozoa entirely separate from both assemblages (latest note on the controversial subject: Corliss, 1977b).

2. Position or rank of the suctorians. There are three schools of thought, still: that they should be totally separate from ciliates *sensu stricto*; that they are an equivalent subdivision (i.e., one of three to five high-level groups) among ciliates *sensu lato*; or that they are (merely) an order or superorder, alongside others, within some one class or subclass. The number of suctorian sub-

groups to be recognized is also a very controversial matter.

3. Position of the peritrichs. The problem here is similar to that mentioned for the suctorians (above), except that the involved levels in the hierarchy are usually lower by one.

4. Position of the chonotrichs. This evokes a situation again reminiscent of the two described above. While there is general agreement that these forms have had their ancestry among certain cyrtophorid hypostomes, the extent of the impact of this phylogenetic assumption on the classificational assignment of the group remains quite debatable.

5. Position of the entodiniomorphids. Even if there is eventually widespread acceptance of the idea that they are no longer "good" spirotrichs, the degree of their relationship to – or independence from – the (other) vestibuliferan ciliates rests a discussable subject.

6. Position of the scuticociliates. How independent are they from the hymenostomes is the question some workers are asking; and how much subdivision do they warrant within the group.

7. Integrity of the "thigmotrichs." One view is that they may be past their usefulness as an independent taxon, even at the relatively low level of suborder; a similar view is that they ought to be amalgamated with the pleuronematine group; another is, let them stand.

8. Fate of various "small and difficult" groups: rhynchodids, synhymeniids, apostomes, pilisuctorines, etc. Additional knowledge may bring such groups closer together (or closer to other taxa already members of larger, relatively better-known groups) or, on the other hand, may accentuate their distinctness.

9. Position of the tintinnines. Their closeness to oligotrichs *sensu stricto* is considered problematical, as well as the proper level within the hierarchy for the next-higher-level group containing them (both).

10. Relative importance of morphogenetic data. In classification, ontogenetic or life cycle information can be quite helpful; exactly how valuable it should be considered in high-level taxonomy is the question. Modes of stomatogenesis stand as a specific example.

11. Position of forms presumably possessing "primitive" macronuclei. There is sharp disagreement over how much taxonomic weight to give to such a characteristic.

12. Number of subdivisions of "gymnostomes" to recognize. Again, essentially a problem of judgment with respect to relative weighting of characters available from different sources of phenetic information. Lumpers and splitters seem equally adamant here.

13. Relative importance of different infraciliary ultrastructures. Some workers claim that "oral area" characteristics are more useful than somatic; some say that a certain level of kinetidal (somatic) structure is more conservative (thus taxonomically more valuable) than others; etc. Classificationally affected are several major groups: pleurostomatids, colpodids, certain nassulids, various heterotrichs, hypotrichs, etc.

Older schemes, understandably, have as a rule been more conservative in handling the kinds of taxonomic problems listed above. Curiously enough, however, the diversity represented by the total assemblage of ciliates is often reflected inconsistently or even contradictorily by such an "easy way out." For example, the "unique" chonotrichs may be given an independent status at a very high level, while the "unique" karyorelictids, prorodontines, archistomatines, blepharocorythines, rhynchodids, pilisuctorines, philasterines, armophorines, or plagiotomines may be given no recognition at all above the level of family.

Users of Bütschli-Kahlian or Neo-Kahlian Schemes

A number of leaders in protozoology may be assigned to this broad category with respect to the classifications of the Ciliophora which they have adopted in their books or monographs. It is perhaps worthy of note that, with the exception of their treatment by Matthes & Wenzel (1966), the ciliates have not been the exclusive concern in the cases mentioned below but are dealt with as only one group within the "phylum" Protozoa.

Variations exist. Authors such as Grell (1968, 1973), Lundin & West (1963), Matthes & Wenzel (1966), and Westphal (1974, 1976) follow classifications which – except for slight

Table IV. Post-1960 Russian and Polish classifications systems*

Cheissin & Poljansky Scheme (1963)	Raabe Scheme (1964a)	Raabe Scheme (1964c)
Subphylum CILIOPHORA (= Heterocaryota)	Phylum CILIOPHORA	Phylum CILIATA
	Subphylum CILIATA	
Ciliata (= Infusoria)	Holotricha	Holotricha
Holotricha	Gymnostomata	*Holotricha*
Gymnostomatida	Apostomea	Gymnostomata
Trichostomatida	Suctoria	Trichostomata
Hymenostomatida	Trichostomata	Apostomea
Astomatida	Hymenostomata	*Hymenotricha*
Apostomatida	Thigmotricha	Hymenostomata
Thigmotrichida	Astomata	Thigmotricha
Spirotricha	Spirotricha	Astomata
Heterotrichida	Heterotricha	Spirotricha
Oligotrichida	Oligotricha	Heterotricha
Tintinnoida	Tintinnoidea	Hypotricha
Entodiniomorphida	Odontostomata	Oligotricha
Odontostomatida (= Ctenostomatida)	Hypotricha	Odontostomata
Hypotrichida	Entodiniomorpha	Entodiniomorpha
Peritricha	Peritricha	Peritricha
Sessiliida	Sessilia	Sessilia
Mobiliida	Mobilia	Mobilia
Chonotricha		Suctoria
Suctoria		Dendrocometida
		Acinetida
		Ephelotida

*Classes are indicated in boldface; subclasses, in italics; and orders in Roman type; suborders, not stressed by the authors, have been omitted from the table.

changes – are strongly reminiscent of the Bütschlian scheme, more or less in its original form plus the subsequent addition of Metcalf's (1923) "protociliates" via Doflein & Reichenow (1927–1929), Kudo (1931), and Wenyon (1926). Grell, however, excludes the opalinids and reduces the separateness of the suctorians by granting them only ordinal status; and Matthes & Wenzel also leave out the "protociliates." Cheissin & Poljansky (1963) and Poljansky & Cheissin (1962, 1965) present a system quite neo-Kahlian in nature: the opalinids are dropped and the suctorians are given a level (subclass) equivalent to the peritrichs, chonotrichs, holotrichs, and spirotrichs; and there are other minor improvements over Bütschli's and Kahl's schemes (see Table IV, left-hand column). Raabe's (1964a,c) classifications differ between themselves (outstandingly in the case of the Suctoria), though published in the same year, and are rather unique, particularly the second one (see Table IV, center and right-hand columns). Still, they are more conservative than the Faurean arrangement and show major similarities to Poljansky's and other modernized Kahlian schemes. A noteworthy difference between the Russian and Polish classifications is in the rank given to the chonotrichs: Raabe absorbs them among his gymnostomes, convinced of their affinities there by the work of French and Polish investigators, whereas his colleagues from Leningrad consider them to be a separate group at a high taxonomic level.

Some workers have offered compromises. For example, Chorik (1968) appears to follow the Faurean scheme, but has kept the peritrichs at a neo-Kahlian rank. And Kudo (1966), in the fifth and last edition of his well-known textbook, professes to follow the "new systematics" of Fauré-Fremiet and Corliss but grants the peritrichs a slightly higher standing and (re)elevates the Suctoria to an independent class rank. Manwell (1961, 1968) fully adopts the Faurean scheme except for retaining (albeit with reservations) the opalinids as "primitive ciliates."

Users of the Faurean Scheme or of the Honigberg Report

The original classification of ciliates by Fauré-Fremiet (1950a), along with its adoption and very minor revision by Corliss (1956, 1961), represented a major change over the classical German schemes, as has already been discussed in various parts of this book (see above, and especially Chapter 1 with its Table II). Based mainly on data from silver-impregnated material, including structural changes noted in the morphogenetics of fission and stomatogenesis, with new phylogenetic interpretations of the taxonomic significance of such information, the classification quite rapidly found wide acceptance among ciliatologists, ecologists, parasitologists, physiologists, writers of textbooks on protozoology and invertebrate zoology, and others.

In 1964, the Honigberg Report appeared. It offered a revised classification of all groups of the protozoa, following years of work by an international committee of specialists (Honigberg et al., 1964). The Faurean scheme was essentially adopted for the Ciliophora, although modifications or "compromises" were presented with respect to several of the major areas of controversy listed on a previous page of this chapter. The opalinids were excluded and the chonotrichs were reduced in rank; but the peritrichs and suctorians were given the rank of subclass, yet placed near the holotrichs rather than following the spirotrichs – a subtle move not without significance (see Table V). Therefore, the "Honigberg system" showed some affinity for the classical treatment of the ciliates and some deference to the views voiced by men like Poljansky and Raabe; yet, in large measure, it followed the Faurean scheme. Within the past dozen years, it has been very widely followed, with many of the adherents of the Faurean classification swinging over to it, including Corliss (e.g., see 1967b, 1968) himself. Of course, pre-1964 or 1965 writers who have not published again on the subject have not had an opportunity to make the "switchover"; but it is interesting to note that some workers have chosen not to do so (see below).

Some influential authors who have followed the Faurean system (generally via Corliss, 1961) include: Barnes (1963), Borror (1973a), Curtis (1968), Dragesco (1970), Fenchel (1967, 1968a), Hall (1964), Lepşi (1965), Levine (1961), Mackinnon & Hawes (1961), Manwell (1961, 1968: though essentially retaining the opalinids as ciliates), Meglitsch (1967), Pitelka (1963), Rothschild (1961, 1965: in a skeleton classification of all living animals), Sandon (1963), and J. C. Thompson

Table V. Classification of ciliates in the Honigberg Report (after Honigberg et al., 1964)*

Subphylum CILIOPHORA

Ciliatea

- *Holotrichia*
  - **Gymnostomatida**
    - Rhabdophorina
    - Cyrtophorina
  - **Trichostomatida**
  - **Chonotrichida**
  - **Apostomatida**
  - **Astomatida**
  - **Hymenostomatida**
    - Tetrahymenina
    - Peniculina
    - Pleuronematina
  - **Thigmotrichida**
    - Arhynchodina
    - Rhynchodina
- *Peritrichia*
  - **Peritrichida**
    - Sessilina
    - Mobilina
- *Suctoria*
  - **Suctorida**
- *Spirotrichia*
  - **Heterotrichida**
    - Heterotrichina
    - Licnophorina
  - **Oligotrichida**
  - **Tintinnida**
  - **Entodiniomorphida**
  - **Odontostomatida**
  - **Hypotrichida**
    - Stichotrichina
    - Sporadotrichina

***The single class is indicated in large boldface; subclasses, in italics; orders, in small boldface; and suborders, in Roman type.**

(1972). Writers who have adopted or transferred to the scheme presented in the Honigberg Report (Honigberg et al., 1964) are, in a partial listing, the following: Adam et al. (1971), Baker (1969), Barnes (1974), Bick (1972), Curds (1969, 1975b), Fernández-Galiano (1964), Gittleson & Hoover (1969), Hutner (1973), A. R. Jones (1974), E. E. Jones (1974a), Kudo (1966: but retaining a high-level independent status for the Suctoria), Levine (1973), López-Ochoterena (1966), Meglitsch (1972), Nobili (1969), and Sleigh (1973).

Canella (1964a, 1971; and see Canella & Rocchi-Canella, 1976), who has roundly criticized all classifications, has not yet, interestingly enough, proposed one of his own.

Contributions of Jankowski

Jankowski has written scores of important papers, many of which are cited in appropriate places throughout this book. This is not the place to review all of his diverse works but to pay due tribute (once again: see Corliss, 1974a) to his monographs concerned with overall problems of classification and phylogeny of the ciliates, works often neglected – perhaps, in part, because of their recency and, in part, because of their relative inaccessibility (published only in the Russian language, etc.). The publications relevant here (Jankowski, 1967a, 1972a, 1973b,c; and, now, 1975) are concerned with three different, though interrelated, Jankowskian systems of classification.

In his first effort in this area (Jankowski, 1967a), a paper delayed several years in its appearance in print, Jankowski brilliantly developed a "neo-Bütschlian" approach to the relationship of the major ciliate groups, recognizing three classes, the Gymnostomea, the Ciliostomea (containing three large subclasses, the Fragmophora, Tetrahymenophora, and Polyhymenophora), and

Table VI. First Jankowskian scheme of classification (after Jankowski, 1967a)*

Subphylum CILIOPHORA

- **Gymnostomea**
  - **Prostomatida**
    - Paramastigina
    - Cyclotrichina
    - Epitrichina
  - **Sciadophorida**
    - Acrostomatina
    - Amphileptina
- **Ciliostomea**
  - *Fragmophora*
    - Leiotrichidea
      - **Trichostomatida**
      - **Hypostomatida**
      - **Apostomatida**
        - Incitophorina
        - Astomophorina
      - **Pilisuctorida**
    - Chonotrichidea
      - **Chonotrichida**
  - *Tetrahymenophora*
    - Axotrichidea
      - **Ambihymenida**
        - Nassulina
        - Microthoracina
      - **Hymenostomatida**
        - Tetrahymenina
        - Peniculina
        - Ophryoglenina
        - Pleuronematina
      - **Thigmotrichida**
        - Diplohymenina
        - Deuterostomatina
      - **Rhynchodida**
      - **Astomatida**
    - Peritrichidea
      - **Sessilida**
        - Thigmodiscina
        - Stylophorina
        - Loricina
        - Natantina
      - **Mobilida**
  - *Polyhymenophora*
    - Polytrichidea
      - **Heterotrichida**
        - Heterotrichina
        - Coliphorina
        - Cyathomorphina
      - **Armophorida**
      - **Odontostomatida**
      - **Hypotrichida**
        - Stichotrichina
        - Sporadotrichina
    - Oligotrichidea
      - **Licnophorida**
      - **Oligotrichida**
        - Oligotrichina
        - Tintinnina
      - **Entodiniomorphida**
- **Tentaculifera**
  - **Acinetida**
  - **Astrosomatida**
  - **Dendrocometida**
    - Dendrocometina
    - Dendrosomatina
  - **Oligostomatida**

*Classes are indicated in large boldface; subclasses, in italics; superorders, in large Roman (ending in -idea); orders, in small boldface; and suborders, in Roman type (ending in -ina).

Table VII. Second Jankowskian scheme of classification (after Jankowski, 1973c)*

Subphylum CILIOPHORA

Ciliata

- *Holotricha*
  - Gymnostomata
    - **Gymnostomatida**
      - Prostomatina
      - Sciadophorina
  - Fragmophora
    - **Hypostomatida**
    - **Apostomatida****
      - Incitophorina
      - Astomophorina
      - Pilisuctorina
    - **Trichostomatida**
  - Hymenotricha
    - **Ambihymenida**
      - Nassulina
      - Microthoracina
    - **Hymenostomatida**
      - Tetrahymenina
      - Ophryoglenina
      - Peniculina
      - Pleuronematina
    - **Thigmotrichida**
      - Diplohymenina
      - Deuterostomatina
      - Hysterocinetina
    - **Astomatida**
    - **Rhynchodida**
- *Chonotricha*
  - **Chonotrichida**
    - Exogemmina
    - Endogemmina
- *Entodiniomorpha*
  - **Entodiniomorphida**
- *Peritricha*
  - **Sessilida**
    - Thigmodiscina
    - Stylophorina
    - Loricina
    - Natantina
  - **Mobilida**
- *Spirotricha*
  - **Heterotrichida**
    - Heterotrichina
    - Coliphorina
    - Licnophorina
  - **Armophorida**
  - **Odontostomatida**
  - **Hypotrichida**
    - Stichotrichina
    - Sporadotrichina
  - **Oligotrichida**
    - Oligotrichina
    - Tintinnina

Suctoria

- Exogenea
  - **Podophryida**
  - **Ephelotida**
  - **Vermigemmida**
- Endogenea
  - **Acinetida**
  - **Dendrocometida**

*Classes are indicated in large boldface; subclasses, in italics; superorders, in large Roman; orders, in small boldface; and suborders (ending in -ina), in Roman type.

**Subordinal names for divisions of this group are adapted from Jankowski (1967a), since they did not actually appear in Jankowski (1973c); the pilisuctorines are considered an order in Jankowski (1967a and 1973b) but again a suborder in Jankowski (1975).

the Tentaculifera (see Table VI). In his text, though not in his own table, he mentioned separation at a superclass level of "Ciliata" for his first two classes and "Suctoria" for the Tentaculifera. The major areas or sources of characters used in his comparative diagnoses were life patterns and modes of reproduction, zones of ciliature (somatic and "preoral"), manner of feeding, types of oral apparatus and modes of stomatogenesis, nuclear characteristics, and presence or absence of loricae. In his thought-provoking work on ciliate phylogeny (Jankowski, 1972a), the same scheme, in effect, was used. The influence of his classification on that used in this book is evident (compare Table III, Chapter 4, with Table VI), although vast differences are also apparent.

Nearly 10 years later, Jankowski (1973c) produced a major revision, one also referred to in his great monograph on the chonotrichs (Jankowski, 1973b). Most of his basic original ideas were dropped or modified, although many of the same data were used, and the five more or less traditional (see Cheissin & Poljansky, 1963) major subdivisions were endorsed, plus the addition of one of his own (to take care of the entodiniomorphids, which he was the first to remove from the spirotrichs). Thus he recognized a (separate) class Suctoria and the following five subclasses of Ciliata: the Holotricha, Chonotricha, Entodiniomorpha, Peritricha, and Spirotricha (see Table VII, and note its similarities to parts of Table IV). He was influenced considerably by some of Raabe's (1964c) ideas concerning nomenclature and interrelationships of members of the "higher" holotrichs.

As this chapter was being prepared in final form, a copy of Jankowski's (1975) very compact abstract entitled (English translation) "A Conspectus of the New System of Subphylum Ciliophora Doflein, 1901" became available to me. Presumably it represents an advance notice of a large monographic work yet to appear in print. Its 1½ pages are comprised almost entirely of names of taxa in a skeletal outline of classification; unfortunately, the many new names proposed must be considered as *nomina nuda* until full descriptions of the associated taxa themselves are available (see Chapters 19, 20). Nevertheless, I am using them in Table VIII as a possible "prediction of things to come." The principal "advance" over his earlier works (Jankowski, 1973b,c) appears to be a multiplication (greater than a doubling!) of taxa at the ordinal and subordinal levels, as may be noted by comparing Tables VII and VIII, including a great expansion within his class Suctoria. And over 90 new families are proposed (i.e., that many novel familial names are included in small print in the abstract)! It is worthy of note, however, that he has revived some of his better (in my opinion) ideas of 1967, recognizing again a (now expanded) subclass Fragmophora and a subclass Tetrahymenophora, along with the usual subclasses for the Chonotricha, Entodiniomorpha, Peritricha (or Cyclohymenophora), and Spirotricha (or Polyhymenophora). I must remark – while awaiting his future publications – that I cannot see the advantage of so much splitting of former groups, including the suctorian assemblage. Further, I believe that loricae are given too much taxonomic weight in his system. Certain orders (or suborders) seem to be very much in wrong locations: for example, the cyathomorphids (which are really suctorians), the nassulids and microthoracids, and the rhynchodids. Also, I am disappointed that the primitive macronuclear condition of certain of his "fragmophorans" was not taken into greater taxonomic account. Nevertheless, it is most refreshing to study the results of the cogitation of a ciliatologist with the lively imagination and bold and novel approaches so characteristic of Jankowski.

System of de Puytorac and Colleagues

The recent proposal of de Puytorac et al. (1974; and see some very recent refinements in de Puytorac & Grain, 1976) is being widely studied around the world (and, as one of its authors myself, I am hardly a disinterested spectator!). As pointed out elsewhere, the first version of my own new scheme (Corliss, 1974a,b) – which, as a *non*"group-think" production, could be more uninhibited, less of a compromise, and more easily amenable to subsequent instant repair – was published concomitantly. More recently (Corliss, 1975b, 1977a), I attempted to formulate a "new new" classification – the one adopted in this book – which might bring the French and Corlissian schemes closer together. As may be noted by comparative study of Table IX and Table III

Table VIII. Third Jankowskian scheme of classification (after Jankowski, 1975)*

Subphylum CILIOPHORA

Ciliata

- **Ciliostomata**
  - *Fragmophora*
    - Prostomatida
      - Paramastigina
      - Inferotrichina
      - Prionostomatina
      - Trachelocercina
      - Rhynchophorina
      - Cyclotrichina
      - Didesmina
    - Orthostomatida
    - Plagiopylida
    - Pleurostomatida
      - Amphileptina
      - Loxodina
      - Scaphotrichina
      - Thysanophorina
    - Rhynchostomatida
    - Rimostomatida
    - Colpodida
    - Isotrichida
    - Paraisotrichida
    - Blepharocorythida
      - Pharyngotrichina
      - Apotrichina
    - Pycnotrichida
    - Cyathomorphida
    - Synhymenida
      - Synhymenina
      - Scaphidiodontina
    - Hypostomatida
      - Chilodonellina
      - Dysteriina
      - Cyrtohymenina
    - Apostomatida
      - Cyrtostomatina
      - Gemmotomina
      - Sanguicolina
      - Nephrocolina
      - Pilisuctorina
    - Hypocomida
      - Macrostomatina
      - Hypocomina
  - *Chonotricha*
    - Exogemmida
    - Cryptogemmida
      - Dorsofragmina
      - Ventrofragmina
  - *Entodiniomorpha*
    - Entodiniomorpha
- **Membranellophora**
  - *Tetrahymenophora*
    - Nassulida
      - Paranassulina
      - Nassulina
    - Microthoracida
      - Cyrtopharyngina
      - Microthoracina
    - Peniculida
      - Frontoniina
      - Quadrulina
    - Hymenostomatida
      - Tetrahymenina
      - Philasterina
      - Ophryoglenina
    - Thigmotrichida
      - Pleuronematina
      - Diplohymenina
      - Deuterostomatina
      - Hysterocinetina
      - Parastomatina
    - Rhynchodida
    - Astomatida
      - Hoplitophryina
      - Anoplophryina
      - Haptophryina
  - *Peritricha (= Cyclohymenophora)*
    - Sessilida
      - Scyphidiina
      - Stylophorina
      - Natantina
      - Loricina
    - Mobilida
  - *Spirotricha (= Polyhymenophora)*
    - Heterotrichida
      - Blepharismina
      - Plagiotomina
      - Condylostomatina
      - Bursarina
      - Stentorina
      - Coliphorina
    - Licnophorida
    - Armophorida
    - Odontostomatida
    - Hypotrichida
      - Stichotrichina
      - Sporadotrichina
    - Oligotrichida
      - Strombidiina
      - Tintinnina
- **Suctoria**
  - Tomogenea
    - Podophryida
  - Endogenea
    - Acinetida
      - Acinetina
      - Dendrosomatina
      - Endosphaeriina
  - Inversogenea (= Evaginogenea)
    - Discophryida
    - Dendrocometida
  - Exogenea
    - Paracinetida
      - Paracinetina
      - Ephelophagina
    - Ephelotida
  - Vermigenea
    - Vermigemmida
      - Spelaeophryina
      - Ophryodendrina

*Classes (and the two "infraclasses") are indicated in large boldface; subclasses, in italics; superorders (all occurring under the Suctoria only), in large Roman; orders, in small boldface; and suborders (all ending in -ina), in Roman type. Several, but not all, of Jankowski's suggested "equivalent" names are given, in parentheses.

(in Chapter 4), however, I have only partially succeeded in that self-assigned task. Nevertheless, overall the points of similarity are many; those of conflict, few. The latter are mostly related to my unilateral recognition of macronuclearly primitive taxa among the gymnostomes; my general distaste for usage of superorders, until we know more about the groups being so combined or excluded; and my firm insistence on accepting a greater breakdown (i.e., more suborders) within such orders as the prostomatids, cyrtophorids, apostomatids, suctorids, and scuticociliatids, as a reflection of the formerly unappreciated but great diversity existing within those groups. Still other differences exist, but they are not particularly revealed at suprafamilial levels: certain important families are shifted to entirely different subclasses in the French system – for example, from the vestibuliferans to the hypostomes and from the hypostomes to the hymenostomes (see Chapter 20). On the positive side, a number of what I consider to be improvements in my own present classification over the one originally proposed three years ago may be credited to continuous suggestions from French colleagues (e.g., as published in de Puytorac & Grain, 1976); and, at the same time, some of my ideas have been influential in bringing about modifications in the 1974 French system.

The classification produced by the modern French school of ciliatology is, much like my own, founded in considerable measure on comparative ultrastructural cytology: "background" sources of many of their data are to be seen in Didier (1971), Grain (1969), and Grain et al. (1973). But its heavy emphasis on the oral area and, seemingly, its relative neglect of other attributes (including macronuclear features, some specialized cytoplasmic or somatic organelles, some aspects of morphogenesis, and certain physiological or ecological factors) comprising what I call the "constellation of characters" necessary for recognizing phylogenetic interrelationships (see Chapter 3) have been the major cause for the development of significant differences between our two arrangements of what are basically the same taxa. As alluded to above (and see below), there have very recently appeared some new papers indicating some further modifications in the original "de Puytorac et al." scheme; unfortunately, it is too late to include or reflect these directly in Table IX, already in an "in press" state when such works have become available. However, the French workers still have not, to my knowledge, published a revised outline themselves, although surely one will be forthcoming. Their own post-1974 contributions which are bound to have an impact on their original system include: Albaret (1975), Batisse (1975), Deroux (1975, 1976a,b, 1977), Deroux et al. (1974), Deroux et al. (1975), Detcheva (1976), Didier et al. (1977), Grain et al. (1976), Grolière (1974, 1975a,b), Laval-Peuto (1975), Nouzarède (1977), de Puytorac & Grain (1976), de Puytorac et al. (1976), Rodrigues de Santa Rosa & Didier (1976), and Rodrigues de Santa Rosa & de Puytorac (1976).

Some Additional Very Recent Ideas

Available too late for treatment in any detail here – but, furthermore, presented by their authors, to date, in only preliminary form – are the very recent suggestions of several additional ciliatologists. Calling attention to the fact that such new ideas affecting ciliate classification are "brewing," however, is alone well worth the insertion of a few lines on the final pages of this chapter.

Gerassimova & Seravin (1976) – and now (just out!) see Seravin & Gerassimova (1977) – have proposed a new "macrosystem" of ciliates, dividing the phylum into two new classes – the Kinetodesmatophora and the Postciliodesmatophora – based on the alleged presence of (only, primarily, or in well-developed form) kinetodesmata in members of the first group, and similarly, only postciliodesmata (= conspicuous stacks of postciliary microtubular ribbons associated with somatic kinetosomes) in the second. Assigned to their first new class would be the hymenostomes *sensu lato*, the peritrichs, and, interestingly enough, the apostomes; to the second, the gymnostomes, vestibuliferans, hypostomes (except for apostomes), suctorians, and spirotrichs. An awareness of the postciliodesma (first named in the works cited above) was realized in karyorelictids in slightly earlier work (see review in Raikov et al., 1976), and in considerably earlier

Table IX. French scheme of classification (after de Puytorac et al., 1974)*

Phylum CILIOPHORA

- **Kinetofragmophora**
  - *Gymnostomata*
    - **Prostomatida**
      - Archistomatina
      - Prostomatina
    - **Pleurostomatida**
  - *Vestibulifera*
    - **Trichostomatida**
    - **Colpodida**
    - **Entodiniomorphida**
  - *Hypostomata*
    - Nassulidea
      - **Synhymenida**
        - Nassulopsina
        - Synhymenina
      - **Nassulida**
        - Nassulina
        - Microthoracina
    - Phyllopharyngidea
      - **Cyrtophorida**
      - **Chonotrichida**
        - Exogemmina
        - Endogemmina
    - Suctoridea
      - **Suctorida**
    - Rhynchodea
      - **Rhynchodida**
    - Apostomatidea
      - **Apostomatida**
- **Oligohymenophora**
  - *Hymenostomata*
    - **Hymenostomatida**
      - Tetrahymenina
      - Ophryoglenina
      - Peniculina
    - **Scuticociliatida**
      - Philasterina
      - Pleuronematina
    - **Astomatida**
  - *Peritricha*
    - **Peritrichida**
      - Sessilina
      - Mobilina
- **Polyhymenophora**
  - *Spirotricha*
    - **Heterotrichida**
      - Heterotrichina
      - Armophorina
      - Coliphorina
      - Licnophorina
      - Plagiotomina
    - **Odontostomatida**
    - **Hypotrichida**
      - Stichotrichina
      - Sporadotrichina
    - **Oligotrichida**
      - Oligotrichina
      - Tintinnina

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*Classes are indicated in large boldface; subclasses, in italics; superorders (all ending in -idea), in large Roman; orders, in small boldface; and suborders (ending in -ina), in small Roman type.

research (as the Km fiber) in heterotrichs (e.g., they were seen, though not fully appreciated, 20 years ago in *Stentor*: see review in Huang & Pitelka, 1973; and see appropriate references in Chapter 14).

Small (1976), independently, has proposed a different division of the phylum into two major parts; but, similarly, he has based his idea largely on ultrastructural information. In the cytostome-cytopharyngeal area of all mouth-bearing ciliates there are "perioral" kinetosomes of one sort or another. According to Small's scheme, groups with transverse microtubules arising in association with such kinetosomes and lining the cytopharynx are to be placed in a subphylum Rhabdophora; whereas groups with postciliary microtubules of similar origin and similarly involved (in the cytopharynx or in the buccal cavity in the case of "higher" forms) are to be allocated to a subphylum Cyrtophora. The subphyla are additionally separated by a morphogenetic difference: during fission, the parental mouthparts are not resorbed in members of the first group, but generally are in the second. Small's "rhabdophorans" would embrace all gymnostomes and most of my vestibuliferans; his "cyrtophorans" would include all other major taxa (except suctorians: see below) – notably, the hypostomes, the colpodids (a major taxonomic shift), and all oligo- and polyhymenophorans. The suctorians, for the moment, are placed by Small to one side, as an "enigmatic" group. So we have here still another novel approach deserving continued study.

Also worthy of at least brief mention is the work of a young "newcomer" to the field of ciliate systematics. Lynn (1976a–c, 1977) has applied a numerical taxonomic analysis – primarily, to date, to members of solely the vestibuliferan colpodid group – combining it with his "structural conservatism" hypothesis (in which he favors somatic kinetidal organelles over oral ultrastructures) and obtaining some provocative results concerning interrelationships of the forms involved. In these very recent publications, he has predicted extension of his novel methods to study of ciliates representing many more groups. Thus Lynn is bound to conclude, eventually, that the information which he will (is) obtain(ing) either supports or refutes other systems of classification, whether "old" or very recent. Such additional investigations are awaited with interest.

Addendum

When this chapter was finally "in press," I obtained copies of two further abstracts by Jankowski (1976a,b). One is concerned with cyrtophorid hypostomes and the other with sessiline peritrichs. Each contains numerous new generic names, generally for species already known in the literature under different, established names; that is, he is suggesting new genera by splitting up older ones (a perfectly legitimate taxonomic procedure). Data supporting these nomenclatural actions, however, are very limited in these brief abstracts. Presumably – as in the case of the Jankowski (1975) abstract (see above) – his latest proposals will be expanded and discussed in a forthcoming monograph or series of monographs. But the names referred to here have reached me altogether too late for necessary critical consideration and/or possible inclusion (fully or partially) in my present classification system (Chapter 20).

Chapter 19

Taxonomic-Nomenclatural Principles and Procedures

The basic taxonomic principles involved in presenting a full scheme of classification are not unique to ciliatology, so they hardly require extensive discussion here. Nor are the attendant difficulties unique, either! General zoological principles and rules are treated in such standard works as Blackwelder (1967), Hennig (1966), Mayr (1969), Remane (1956), and Simpson (1945, 1961); and the ICZN (International Code of Zoological Nomenclature, 1961, 1964) may be consulted for handling of nomenclatural problems affecting taxa at infraordinal levels. See also such diverse but pertinent works as Clifford & Stephenson (1975), Hull (1970), Jeffrey (1973), and Sneath & Sokal (1973). Since 1961, I have published several papers dealing with taxonomic-nomenclatural practices in protozoology *per se* (e.g., Corliss, 1962a,b, 1963b, 1972b, 1976, 1977a), including even the application of "common sense and courtesy" whenever possible (Corliss, 1972a); and, over the years, I have had considerable experience in treating ciliate cases of varying complexity.

Many biologists are especially perplexed as to what names to use for taxa above the family-level (since the various Codes of Nomenclature do not govern names at the higher levels), how to spell them, to whom to credit them, how to date them, how to "emend" them, etc. Yet handling the taxonomic names for which official rules do exist is also a chore for numerous workers: but even innocent confusion can lead to eventual chaos! Thus, it may be advisable to consider, however briefly, the nomenclatural procedures followed in this book (particularly in Chapter 20), including occasional examples, when appropriate, and mention of the rationale behind decisions made. In many instances, taxonomic judgment cannot be divorced from a "mere" problem of nomenclature, since it is a system of classification which gives rise to nomenclatural predicaments. So procedures of both kinds may be involved in some of the discussions below.

Treatment of Names in General

With respect to orthography, I have, when so obliged by the Code, automatically corrected names which were incorrectly spelled or written (this includes use of diacritical marks, hyphens, etc.); and I have repaired names of higher taxa which were poorly formed etymologically. But it is worth noting that incorrectly formed *generic* names cannot be changed, Dobell (1939) and other such purists notwithstanding. Detected errors in authorships and dates have automatically been emended in Chapter 20, without comment. Also I have arbitrarily ended all ordinal names with the suffix "-ida" and subordinal names with "-ina." Misspellings or variants in the form of a valid name, at any level, are considered as (junior) synonyms; they are cited by me in the following chapter only in appropriate cases (which, however, are quite numerous). Regarding authorships of names, I have always believed that credit should be given to the original proposer (assuming — or preferably knowing — that he or she offered more than merely the new "word" in a non-annotated list), with retention of the original date, no matter how the name may have been spelled, if the taxon concerned has not been shifted to an entirely different level in the hierarchy. Many taxonomists, however, take personal credit for a name even if all that they have done is to modify the suffix a bit (e.g., in cases of suprageneric or suprafamilial names). Such an action, in my opinion, is both discourteous and quite unnecessary — it certainly is not required by any rules. But moving the group whose name is under consideration a significant distance up or down the scale — that is, greatly elevating (or reducing) the position of the taxon (thus appreciably changing its concept as well as its diagnosis or composition) – does ordinarily represent a good reason for changing the authorship. In other words, mere use of the same stem of the names involved does *not* oblige subsequent workers to give blanket "credit" to the first originator of the "base" word.

Often one sees credit for a name given to two persons, the original promulgator of it and a later reviser; but this solution to handling the problem of older names must be approached with caution, because at least two matters are involved. On the one hand, there is the simple nomenclatural matter of emendation of a name: thus the "Parameciens" of Dujardin (1840), repaired to "Paramaeciidae" by Kent (1880–1882), could conceivably be written, today, as Parameciidae Dujardin, 1840 *emend.* Kent, 1881 (although note that the spelling in this case has been slightly further corrected with passage of time). Personally, I am opposed to this, as mentioned above: it is sufficient and reasonable enough to record the complete name simply as Parameciidae Dujardin, 1840. On the other hand – and I believe that this is much more important – when the *concept* of the taxon has been changed (radically different or expanded diagnosis, etc.), there might be a good reason to recognize the name of the reviser. Since this would then become a *taxonomic* not a *nomenclatural* matter, it is not and cannot be covered by the Code or any direct extension of it. In such cases, the word "*sensu*" might be more appropriate to use than the word "*emend.*" to connect the two author's names; *viz.*, X-idae Browne, 1899 *sensu* Smythe, 1967. Yet I should advise that even such a legitimate "double-authorship" be used *exceedingly sparingly*! Literally hundreds of named ciliate taxa have been so revised, and *repeatedly* so revised. Therefore, the taxonomic-nomenclatural literature would become fantastically cluttered up with all sorts of combinations of authors-and-dates, if they were all shown accompanying a given taxonomic name. In any major revisory work, the fact(s) can always be made clear in the text with respect to the most valuable taxonomic contribution(s) toward our understanding of a given group, with appropriate literature citations, etc., regardless of who is credited with its name.

Treatment of Ordinal and Higher Names

Since no suprafamilial name comes under jurisdiction of the Code, any maker of a system of classification involving the higher taxonomic categories is free to choose any names he or she desires: old names, more recent names, or new names of one's own invention – no holds are barred! But it seems to me both logical and courteous to employ labels which already exist, with proper credit to their promulgators, unless there are sound reasons for not doing so. A major complication lies in the fact that often the diagnoses or boundaries of groups are being changed in a newly proposed arrangement of taxa, and one has to decide whether or not this constitutes adequate justification for abandoning reasonably accurate names already available in the literature. But since, as I have implied above, our concepts of the definition and composition of the majority of higher-level ciliate groups are constantly changing, a uniformly consistent practice of name-changing (even for "good" reasons) would wreak havoc with stability, make the learning of such names a nearly impossible feat, and weaken further what limited respect biologists in general already may hold for taxonomists.

What to do with the multitude of names which *do* already exist for given higher categories? In Chapter 20, I have attempted to list as synonyms any well-established or seriously proposed names which I have rejected – presumably for a defensible reason – as my "first choice" for the name of an included taxon. And I have worked sincerely to reduce the number of novel names. Many of Jankowski's numerous new names appear as synonyms: a frustrating difficulty here, however, is that often we have not (yet) been supplied with sufficient data on the exact boundaries of his "new" groups. Sparingly, I have used the expression "*pro parte*" (*p.p.*) to advantage, in citing names which are only partial synonyms of the name chosen as most appropriate. [Space does not permit direct inclusion of authors and dates of names (at any level) which I treat as "invalid" for the taxa concerned. I am aware of the possible value of such information to some readers: the excluded data, therefore, are available from my files on request.]

Treatment of Familial Names

Subfamilies (and subgenera), along with superfamilies (and superorders), have not been adopted in the present classification scheme. Such action does not invalidate them, of course; but the categories are relatively rare in the case of ciliates, anyway, and I do not feel that they are of much value until they are better defined or understood. In some few cases, I have elevated a subfamily (or subgenus) of the literature to familial (or generic) rank; "credit" is still given to the original author and date of the name involved, as required by the rules. Acceptable familial names, on occasion, may be based on names of type-genera which have fallen as junior synonyms. In fact, in accordance with an express provision of the Code (Article 40), a familial name, after the year 1960, is not to be changed if the name of the type-genus on which it is based falls as a junior synonym. The sole case of this among the 204 bonafide families of Chapter 20 is Spirofilidae von Gelei, 1929, a name based on *Spirofilum* which, itself, is now considered as a junior synonym of *Hypotrichidium*.

When the name of the type-genus of a family has been discovered to be a junior homonym, the name of the family formed from it has to be rejected. The proper familial name must be changed to one based on the valid replacement generic name, with its new authorship; but the *date* of the original name – for purposes of possible future nomenclatural disputes, etc. – is retained, along with an indication of the date of the replacement name. For example, the ciliate name *Polydinium* is a junior homonym of the flagellate *Polydinium*, so a replacement name of *Polydiniella* was proposed by Corliss (1960b). A ciliate subfamily Polydiniinae Kofoid, 1935 – corrected by Corliss and then permissibly raised to family rank by Noirot-Timothée (1960), who, however, mistakenly considered it as a "fam. nov." – can now, incorporating all changes properly, be recorded as "Polydiniellidae Corliss, 1960 (1935)." For future possible nomenclatural purposes, as mentioned above, the date given in parentheses is the "legal" date of origin of the familial name, much repaired though it has become, including "loss" of the name of the original proposer of the taxon, etc. In Chapter 20, however, I have purposely *not* included the second (earlier) dates in such cases, for reasons of simplicity and clarity. Rarely will they be of interest or of use to anyone but a nomenclatural specialist, and the details required for a thorough investigation of a particular problem of this sort should not be sought in a book of the present kind – the original literature must be consulted.

When a "new" family is formed by the amalgamation of two or more former familial groups, certain nomenclatural procedures are to be followed. The type-genera and the older or oldest familial names cannot be ignored: Kahl (1930–1935), unfortunately, was guilty of breaking this rule in a number of cases. Priority can be set aside by successful petition to the International Commission on Zoological Nomenclature, but the reasons presented must be persuasive. When a large family is fragmented – which is more often the case than amalgamation – two rules should be kept in mind. The new, smaller groups are to be given the oldest valid familial names available to them; and the "fragment" containing the type-genus of the original single family must retain the original familial name. In an otherwise most important work, Fauré-Fremiet (1961b) ignored these particular precepts most flagrantly, causing considerable confusion in the subsequent hypotrich literature.

Treatment of Generic Names

The rules for formation, preservation, emendation, etc. of generic names which are presented in the zoological Code are followed as conscientiously as possible. In Chapter 20, junior synonyms are supplied in parentheses after the author and date of the accepted (senior synonym) name, if they are post-1900 names or have provided the stem of one of the family-name synonyms. Older, long-unused synonyms are deliberately grouped together in a single place (Table X in the introductory section of that chapter). Pre-Linnaean authorships, invalid, of course, are abandoned for that reason: one still frequently sees "Hill, 1752" after such important generic names as *Cyclidium, Enchelys,* and especially *Paramecium.* Sir John did, indeed, name those groups, but the official starting point for zoological nomenclature dates from 1758, year of the 10th edition of Linnaeus' *Systema Naturae,* and any actions taken earlier cannot be recognized. The next (i.e., first post-1758) user gets the credit: for example, O. F. Müller (1773) for *Paramecium* (even though he spelled it "*Paramaecium*").

Generic names which are replacements for homonyms, as explained above under families, take the authorship of the person proposing the new name. They may show both dates; but, as explained above for familial names, I have not included such a detail here. For example, *Epalxis* Roux, 1899, can now, strictly speaking, be written "*Epalxella* Corliss, 1960 (1899)" but I have dropped the "(1899)" in the interests of brevity and simplicity. A replacement name is to be identified as *nomen novum* when it is first proposed; later, it is written with the new author and date, as explained above. The type- and all other contained species should be listed, as *new combinations* ("n. comb.") in the paper first using the replacement name. A *nomen nudum* is a name proposed without any description of the taxon involved – thus a "naked" and legally unrecognizable name (until the taxonomic description "catches up" with it). A number of the latter are deliberately presented in Chapter 20: see explanation there. Other kinds of names (*nomen dubium, nomen oblitum,* etc.) are treated briefly in the glossary of Chapter 2, where a number of nomenclatural terms of quite widespread usage are defined.

The very common practice of placing the name of a *former* genus of some species which has been transferred to a different genus between the latter generic name and the specific epithet, enclosing it in parentheses, is a most harmful error! For an example of commission of this "crime" on a wholesale scale, see Kahl's (1930–1935, etc.) otherwise excellent taxonomic works. *That* spot and *that* use of parentheses is, by the Code, to be reserved *solely* for a *sub*generic name, if one exists and if one wishes to show it. Thus, for example, *Loxocephalus (Uronema) simplex should* mean or indicate that *Uronema* is one (there must be at least two, the first of which would be the nominate subgenus, using the same name as that of the genus) of the taxonomic subdivisions of the genus *Loxocephalus.* But Kahl (1931c) was using that combination to inform the reader that the species *L. simplex* had formerly been a member of *Uronema,* still a perfectly good and separate genus. This malpractice is particularly confusing in those many cases in which genera well established in their own right are seemingly being designated as subgenera of still other recognized genera and vice versa, purely because of the (in itself quite legitimate) shifting about of a few individual species.

More than a hundred genera of the Ciliophora have inadvertently been given names preoccupied by the generic names of other (animal) organisms, and these ciliate junior homonyms – under the zoological Code – cannot be used as valid names of "good" ciliates. Some 50% of these cases, however, turn out today to be – or to be available as – junior synonyms of perfectly good names, and thus need no longer be of practical concern (i.e., they are "harmless" as long as they remain as junior synonyms). Hopefully, no modern-day Poche (1913) or Strand (e.g., 1928, 1942, with respect to protozoan names) – leading "armchair nomenclaturists" of their day – will rise up and, having virtuously perused some multi-volume *nomenclator* and noted all possibly interpretable homonyms, produce a lot of unnecessary new names (followed, of course, by *their* names as the authors!). In the other half of the cases just mentioned, however, there has been no way to escape the necessity for replacement names. A number of ciliatologists have been involved in such legitimate and necessary activity over the years; in preparation of the first edition of this book, I was obliged to suggest some 30 such names myself (Corliss, 1960b, 1961). A few more are proposed, in place, in the present edition: by me or by others, as indicated.

Before any taxonomist commences to publish a new name, a check should be made, via various sources of information, which will help avoid the possible choice of a name already preoccupied, which would then have to be replaced when or if the embarrassing error is discovered at a later date. Three compilations may be highly recommended as sources: Neave (1939–1975) and Schulze et al. (1926–1954), for direct lists of names, plus dates, etc.; and, useful in a slightly different way, the *Zoological Record*, established in 1864 and still going strong (though inevitably running a few years behind). For hints on naming new taxa in general, at any level, the reader is referred to a number of the taxonomic texts (and the Code with its helpful though often overlooked appendices on formation of names, etc.) cited at the beginning of this chapter and to the several papers of the author bearing on the subject (particularly Corliss, 1962b), also referred to earlier. Books such as Brown (1956) are indispensable as sources of Latin and Greek roots and stems suitable for forming a new scientific name with any particular meaning desired.

Taxonomic Innovations

Vast changes over the classification system of the first edition (Corliss, 1961) are apparent throughout the present volume. A number of them have been introduced in recent papers of mine (e.g., Corliss, 1974a,b, 1975b, 1977a). Also, many such "improvements" over older schemes have appeared in publications of colleagues in the field, notably Jankowski (e.g., 1967a, 1973c) and de Puytorac (e.g., de Puytorac et al., 1974; de Puytorac & Grain, 1976), but also other workers have been significantly involved (see Chapter 18). Alterations at the class and ordinal levels have been the most noticeable. But numerous reassignments of older familial and generic groups – not to mention incorporation and placement (or rejection) of the newer taxa proposed in recent years – have been made as well, usually without (space for) extended explanation or discussion in this book. Comparison of the ciliate section of such a standard textbook as Kudo (1966) with the contents of the following chapter will, for example, make abundantly – if frustratingly – clear the tremendous changes (and, I believe, advancement) in our knowledge of the systematics and classification of these protozoa during the past 10–15 years.

The taxonomic innovations of this volume which generally have *not* been specifically mentioned in earlier chapters are the groups newly erected or newly described formally for the first time (exclusive of their peculiar *nomina nuda* treatment in Corliss, 1977a) in the pages of Chapter 20. Although, as in the first edition, I have deliberately tried to keep such cases to a minimum (preferring their publication elsewhere prior to appearance of the book), I have been obliged by circumstances to propose or endorse proposal of several of them here.

Ordinal Level. The only taxon described as new at this level is the suctorian suborder Evaginogenina. The name and the idea are ascribed and credited to Jankowski, but since the first characterization of the group appears here, the date is properly declared to be that of this book: thus, in my judgment, authorship and date of this taxon should now read "Jankowski, n. subord."; and, in the future, "Jankowski in Corliss, 1978." [Year to read "1979" if book publication delayed.]

Familial Level. Some 16 families are established as new (technically, only the name is new in one case). Ten are credited to authors other than myself (and one is shared by de Puytorac and me), but all will bear the date of the book. The taxa involved are the Buetschliellidae, Clausilocolidae, Cryptochilidae, Cyrtocaryidae, Endosphaeridae, Furgasoniidae, Heliophryidae, Histiobalantiidae, Lembadionidae, Nassulopsidae, Operculariidae, Phacodiniidae, Protocaviellidae, Scaphidiodontidae, Termitophryidae, and Troglodytellidae. Type-genera may be considered to be designated automatically – trusting that the rules of nomenclature will permit such a liberty – by use of specified generic names in formation of the familial names proposed as new. Incidentally, if any of these familial groups are independently described elsewhere – by the same or different workers – before appearance here, the earlier dates (and authorships) must, naturally, prevail in the future.

Generic Level. Six homonymous generic names are formally replaced by new names for the first time: four by me, one by Jankowski, one by Lom (*Eilymophrys, Eminothigma, Oxychonina, Patronella, Propyxidium,* and *Tucolesca*). Their locations (as well as those of any other taxa) in the classification scheme may be found by use of the Systematic Index. Type-species are named in their new combinations in each case. One (additional) genus is named as new: *Pusilloburius* n. g. Its type- and only species is a ciliate originally described as a member of another genus. [The two dozen or so *nomina nuda* in Chapter 20 are counted as bonafide genera; but, strictly, they have absolutely *no* validity until published (again) with proper descriptions, type-species, etc.]

Chapter 20

The Ciliate Taxa, including Families and their Genera

The present chapter, in large measure, is independent of the others and quite self-contained. Here, in one place, an attempt is made to diagnose or characterize, of necessity in a succinct manner, all suprageneric taxa assignable to the phylum Ciliophora: this task has never been carried out in such detail since Bütschli (1887–1889) – recalling that Kahl's (1930–1935) great series, while invaluably including species descriptions, omitted entirely certain major higher groups – and there is no comparison between the size of the total assemblage then and now. All genera, though not described, are listed, supplying author, date, and synonyms. Also an indication of the number of accepted species is given for each genus; and drawings of many of the more important forms are included in the accompanying plates of figures. Details, discussions of controversial matters, revelation of the rationale behind the new classification, evolutionary interrelationships, definition of terminology employed, general taxonomic-nomenclatural principles, rich citation of pertinent literature sources, etc. are still to be found only in the preceding chapters. Two recent papers (Corliss, 1975b, 1977a) contain condensations of some of the main features of the classification presented here; but the information on the following pages appears in a greatly expanded form and also, in any instances of differences or discrepancies (and there are a few), may be considered as the more "correct" or "final" version.

Style and Format

The suprageneric taxa are arranged, to the best of my ability and based on the available data (often extremely scanty), in supposed phylogenetic order. This, despite its problems, seemed preferable to using chronological considerations, commonness *vs.* rarity, or a purely alphabetical arrangement. But the included genera are presented alphabetically, each name followed by its author and date of first valid description. If the generic name is a replacement for one obliged to fall as a homonym, it is followed by the homonymous name, in parentheses and preceded by the word "for," with additional synonyms following. Sometimes junior synonyms are themselves (unreplaced) homonyms, as explained in Chapter 19. Remarks and comments are kept to a minimum but are considered indispensable here and there for clarity.

The category "*incertae sedis*" is also used sparingly, particularly in view of the fact that we are honestly in the dark concerning exact relationships of the various ciliate taxa, at all levels, in the great majority of cases. But I have reserved its use for the families and, especially, the genera which most blatantly seem to demand restudy in order to arrive at even a reasonable guess as to their appropriate assignment in the overall scheme. I prefer making an "intuitive try," however, to helplessly and hopelessly appending *all* "enigmatic" groups at the end of the classification (which would result, one might say, in a case of the appendage wagging the book). Incidentally, I must be held responsible for the assignment of families to orders, genera to families, etc., as presented in this book, whether such allocations are in agreement or not with those made by others, including recent specialists working on the taxonomic groups concerned.

Other stylistic matters, including treatment of *nomina nuda* and of data on species per genus, etc., are covered in the following sections or require no special explanation. Throughout this lengthy chapter, an attempt has been made to offer taxonomic and nomenclatural information as clearly and palatably as possible, without sacrifice of accuracy, and yet not burden the non-specialist reader/user with space-consuming data of very minor general significance.

Synonyms and *Nomina Oblita*

With respect to synonyms (including variants in spelling) in general, authors and dates – with exceedingly rare exception (such as in some very recent cases) – are not given. Primarily this is to save space (there are hundreds of them!) and to avoid confusion; furthermore, determining such little- or seldom-needed data with accuracy would often have required an incredible amount of additional research beyond the scope of the present volume. Many important synonymous names of the higher taxa do occur elsewhere in this book, with direct or indirect indication of authorship and date in such places (e.g., see citation of many of Jankowski's names in tables of Chapter 18). The suprafamilial names which I have chosen to use are considered the most appropriate for the taxa concerned, whether they were first proposed long ago or very recently: my penchant for favoring the contributions of "old-timers," however, is clearly evident.

At the generic level, I have arbitrarily decided to retire a large group of essentially junior synonyms which have never been resurrected (i.e., raised to the independent level of senior synonym) for periods ranging from 75–200 years. These "senior-citizen" names have either been truly "*nomina oblita*" – forgotten names – or *nomina dubia* (associated practically from the first with doubtful genera); many have been buried unnoticed in older monographs of the early 19th century, while others – rather sadly, in retrospect – have been perpetuated in the literature through their being copied mechanically and purposelessly from one book to another, always as junior synonyms, through scores of years. In my opinion, no good is served by including these in the regular pages of my classification, so I have decided to relegate them to a single place, Table X. Though not including authorships or dates, there are two reasons for not leaving them out of this book entirely: some subsequent investigator may actually find a legitimate reason to resurrect one or two of them; and making them "visible" here may prevent the accidental proposal of an identical name as "new" by an otherwise uninformed future worker.

One or two of the names in Table X are less than 75 years old – these are scattered cases since the turn of the century of unnecessarily proposed replacement names for homonymous names already recognized as junior synonyms (thus requiring no new names). They deserve to be forgotten. On the other hand, all synonymous names older than 75 years are *not* included in the table; a few do appear, instead, in the classification section of this chapter, especially if they have been involved as type-genera of old *familial* names included there as synonyms. Finally, two of the names in the table (*viz.*, *Cercaria* and *Opalina*), still quite usable today with reference to *other* groups or organisms, are included because they were so often employed during the early decades of taxonomic ciliatology in accounts concerned with certain species of bonafide ciliates, now, fortunately, safely ensconced under legitimate *ciliate* generic names.

Treatment of *Nomina Nuda*

Elsewhere (Corliss, 1977a), I have very recently attempted to justify inclusion in my classification of some six dozen names (two-thirds of them at the generic level) made *nomina nuda* by my very action, pointing out the value of knowing where these yet- (but presumably soon-) to-be-described taxa fit in the overall system and predicting that, by time of appearance of this book, many of the necessary characterizations of the new groups would have been published (validating the names as of such times). All of the suborders and 18 or so families involved are indeed described now (in this book or earlier elsewhere by other workers). Of the approximately four dozen genera in the *nomina nuda* state a few months ago (Corliss, 1977a), exactly half have now been validated (my own, in this book; others, elsewhere), thus perhaps vindicating my "rashness" in deliberately publishing such "naked" names in advance. Many of the remaining ones, designated in following pages as "[unpublished] " following generic and author names (see below), may still be expected in the literature of the next year or so (as I am generally assured by personal communication from the workers involved). Some of Jankowski's "new" names require special

Table X. *Nomina oblita*: ciliate generic names invalid for at least 75 years*

Acarella
Acidophorus
Acinetoides
Acomia
Aglenophrya
Alastor
Alderia
Alyscum
Apgaria
Arachnella
Arachnidium
Arachnidiumia
Archimedea
Asellicola
Aulax
Aulaxella

Baeonidium
Benedenia

Caenomorphina
Calcaria
Campylopus
Caudalina
Cephalorhynchus
Ceratidium
Cercaria
Chromatophagus
Chytridium
Claparedia
Clypeolum
Clypoleum
Coccudina
Cordylosoma
Craspedarium
Craspedonotana
Craspedonotus
Cricocoleps
Cypridium
Cyrtostomum

Dendrella
Dicella
Dictyocoleps
Digitophrya
Diplagiotricha
Dipleurostyla
Diplomastax
Diplomestoma
Diplopsyla
Diplostyla
Disoma
Districha
Drepanena
Drepanidium
Drepanina
Drepanoceras
Dysteropsis

Ecclissa
Ehrenbergius
Euodon
Euploea

Fungella

Gasterochaeta
Gastrochaeta
Gervasius
Glenopanophrys
Glenotrochilia
Glossa
Gymnopharynx

Habrodon
Halsis
Harmodirus
Himantophorus
Himantopus
Huxleya
Hymenostoma

Iduna

Lagynus
Leptodesmus
Leucophra

Megatricha
Meniscostomum
Mitophora
Monomastix
Monostylus

Nematopoda
Nothopleurotricha
Numullella

Opalina
Ophionella
Ophryocerca
Opisthiotricha
Opisthodon
Orcula
Otostoma

Pamplota
Panophrys
Pantotricha
Peitiadia
Pelamphora
Pelecida
Pelekydion
Peltierius
Pericometes
Peridinopsis
Periocometes
Peripheres
Phialina
Phragelliorhynchus
Pinacocoleps
Plagiotricha
Planicola
Planiplota
Planiplotes
Platytrichotus
Polypenlaus
Proboscella
Prosopsenus
Ptyxidium

Rinella

Salpistes
Schizopus
Schizosiphon
Siagonophorus
Sisyridion
Sisyriodon
Sparotricha
Spastostyla
Spirostomina
Spirotricha
Stappersia
Stylocola
Styloplotes
Styloptotes

Tetrastyla
Thuricolopsis
Thurophora
Torquatina
Tribulina
Trichoda
Tricholeptus
Trichomecium
Trichorhynchus
Trypanococcus
Turbinella
Turpinius

Urceolopsis

Valvularia
Vasia

Wagneria
Woodania

Ypsistoma

Zoocladium

*See further explanation in the text concerning these "best forgotten" names, junior synonyms or *nomina dubia* for a very long time (> 200 years in several cases!). Note that, *purposely*, none is included in the full classification system presented on subsequent pages of this chapter.

explanation (see below). The proper dates and authorships to be used for these *nomina nuda* (or, more often, former *nomina nuda*) require a further comment or two.

(1) In the cases *above* the generic level, the *name* is credited to the original author – whether another worker or myself – but it is to be considered as *new* in *this book* and thus will bear the date of this book. But, in those instances in which ciliatologists other than myself are the name-proposers, the authorship-of-the-book must also accompany the date, preceded by the word "in," in any future citation of the complete name. An example will illustrate this: "Cryptochilidae Berger, n. fam." appears among the scuticociliates on a subsequent page of this chapter. The name is validated by the inclusion of a proper description following it (which, incidentally, was *not* done in Corliss, 1977a). In the future, this is properly referred to as: "Cryptochilidae Berger in Corliss, 1978" (assuming "1978" is indeed the year of appearance of the present volume). In another example, on the other hand, *viz.*, "Phacodiniidae n. fam.," there is no need to show the authorship, since it is my own creation; and, in the future, it should be written simply as: "Phacodiniidae Corliss, 1978," since this book is the first work in which the taxon is being described.

(2) In the cases *at* the generic level – *unless* they represent *nomina nova* (*n. n.*) presented as replacement names for homonyms (in which instances they bear my name and the book-date, if mine, or the name of someone else, if being proposed by others) – the names must *remain as nomina nuda* if their associated descriptions have (still) not appeared somewhere in the published literature. Since *descriptions* of new *genera*, unlike the situation for families and suborders, are not (with one exception), included in this book, such names cannot be validated here. Rather than specifically label them as "*nomina nuda*" or mark them with an asterisk (as was done in Corliss, 1977a), they are printed as in this example: "*Mugardia* Small [unpublished]." Until proper diagnoses *are* published, the names must remain as "naked" names. Recall, also, that type-species need to be designated, etc., and – in accordance with provisions of the Code – no genus can be described, after 1931, without inclusion of at least one species.

(3) A final possible complication! Unknown to me, the names (and their descriptions) from both categories discussed above (particularly the suprageneric one) may well be "in press" somewhere (else) *at this very time*. In such cases, the earlier date (and outlet) of actual publication would prevail. And if the names proposed happened to be different (here and in the other place) for the same taxa, then the later one would fall as a junior synonym of the other one in conformity with regular provisions of the Code of Nomenclature.

Problem of Jankowskian Names

In a number of places throughout this book, the prolific works of Jankowski, arch-splitter at all taxonomic levels, have been mentioned. He appears to have in press or nearly ready for press (e.g., see Chapter 18) a number of papers containing taxonomic names many of which have already been published, *though without descriptions*, either in abstracts or "in passing" in other major papers. I have tried to handle these diverse cases as judiciously and generously as possible, keeping in mind that taxonomic as well as nomenclatural judgments are often involved and that – unknown at this moment – his "full" works may appear while the present book is in press. Familial names are especially involved – nearly 100 are "illegally" published as "new" in his recent abstract (Jankowski, 1975) alone. In several cases, I have presented his names as new in this book, as explained above. Many of his proposed families seem to represent too great a splitting, although we can hardly tell until the formal descriptions are available; so numerous names of this sort I list as synonyms without comment (though, strictly speaking, they should perhaps be identified some way as the *nomina nuda* which they really are). Such actions of mine do not at all prevent the subsequent resurrection of these names (and their taxa). In a few cases, other workers or I have coincidentally seen the need for erecting a new taxon, complete with new name, etc. I have been obliged – probably to Jankowski's understandable dismay – to accept the proposals more familiar or more completely described in preference to his (naked) names, which then fall as synonyms (at best). In instances *above* the familial level, future workers will have the privilege of choosing the name they prefer, regardless of date of appearance of the taxonomic descriptions involved; but at the rank of family, priority must be recognized.

At the generic level, in cases of his *nomina nuda* (but recall that Jankowski has also published many fine accounts which include new names *not* falling into such a category), I have either accepted his names (though rarely and only for some special reason), considered them (the usual case) as junior synonyms, or – especially with respect to those appearing in Jankowski's (1976a,b) latest abstracts (see end of Chapter 18) – disregarded them altogether at this time. His published *nomina nova*, as replacement names, *are* quite acceptable, since they require no description of the taxon they're associated with (though one should name the type-species in its new combination).

Data on Species

The present book is not the appropriate place to include much information concerning the lowest taxonomic level, *viz.*, the species. (Even the included illustrations are commonly labeled only to genus.) Following publication of the first edition (Corliss, 1961), which contained far less material at the infraordinal levels in general, a number of colleagues had urged me to consider giving the identification of the type-species of each genus in this second edition. The idea had to be dropped, not only for reasons of space but also because so many of the more than 1,100 included genera will require in-depth taxonomic revisory attention before anyone can be exactly certain of the identity of the type-species (admittedly, a sorry state of affairs!). But I have carried out a review sufficient to determine information on the *number* of species per genus, giving the reader a rough notion of the distribution of the 7,200 (or so) total species known to date for the phylum. Because of the impossibility of "absolute precision" without the in-depth research mentioned above, I am employing descriptive terms to cover ranges of numbers above the level of "single" species: "few" indicates *ca.* 2–4; "several" = 5–12; "many" = 13–35; and "very many" means >36. A further indication is given of the probable approximate number when it is 50 or greater, because such a situation is so unusual among genera of any protozoan group.

It may be interesting to note that nearly 50% of all ciliate genera are monotypic, containing but a single species (too many splitters among taxonomic ciliatologists? see Corliss, 1976). Another 40% or so have fewer than 13 species. Only 25 genera (slightly >2%) contain *ca.* 50 or more species (Corliss, 1977a, 1978a). The "big eight" among these – with allegedly > 75 described species each – are *Acineta, Cothurnia, Epistylis, Opercularia, Spathidium, Tintinnopsis, Trichodina* (possibly with 200, a *huge* number by ciliate standards!), and *Vorticella*, genera not too well distributed among the several classes and subclasses in that five of them belong to the single order Peritrichida. But more sophisticated approaches (including multivariate morphometrics, etc. and renewed attention to environmental effects via laboratory culturing, etc.) may drastically reduce the number of "real" species in some of these bulging genera, as I have remarked earlier.

Nomenclatural Notes, Abbreviations, Figure References

On the following pages, names of all authors of a taxonomic name are written out in full, even when the authorship is multiple, with a single (but important) exception. Whenever "de Puytorac et al., 1974" appears after a name, it is to be understood to stand for the following complete (far too lengthy to print repeatedly!) list of co-authors: de Puytorac, Batisse, Bohatier, Corliss, Deroux, Didier, Dragesco, Fryd-Versavel, Grain, Grolière, Hovasse, Iftode, Laval, Roque, Savoie & Tuffrau! The entire citation of the implicated paper may be seen in the bibliography (Chapter 22).

Abbreviations (*not* italicized if directly following a *generic* name) include: *ca.* = approximately; hom. = homonym; *n. n.* = *nomen novum*; *non* = not; *p.p.* = *pro parte*; *s.l.* = *sensu lato*; *s.s.* = *sensu stricto*; syn(s). = synonym(s). Brackets are usually used around any remark or comment. Figure references, placed at the end of generic entries for which illustrations have been included, are to drawings or micrographs anywhere in the book, though predominantly to the numerous figures comprising Plates XXII–XXXII of the present chapter.

Phylum CILIOPHORA Doflein, 1901

(syns. Ciliae, Ciliozoa, Cytoidea, Eozoa, Heterocaryota, Heterokaryota, Infusoria; also Ciliata [Cilatea, Ciliasida, Euciliata] + Suctoria [Suctorea], Gymnostomea + Ciliostomea + Tentaculifera, Kinetodesmatophora + Postciliodesmatophora, and Rhabdophora + Cyrtophora)

Eukaryotic, unicellular, heterotrophic protists (size, 10–4,500 μm), free-swimming or sessile, with cilia (simple or compound) in at least one stage of life cycle; complex cortical infraciliature, somatic plus often oral; pellicular alveoli; microtubular or microfibrillar structures, often kinetosome-associated, and extrusomes common; fission homothetogenic and often perkinetal, isotomic or anisotomic, and occasionally multiple; nuclear dualism (rare exceptions), one or more diploid micro- and one to several polyploid (rarely diploid or oligoploid) macronuclei, with acentric mitosis and "gametic" meiosis; conjugation, temporary or total, widespread; generally monostomic, but some groups mouthless or polystomic; contractile vacuole typically present, often also a cytoproct; feeding modes, osmotrophy to phagotrophy; broad distribution, diverse aquatic and edaphic habitats, with ecto- or endosymbiosis exhibited by a number of species.

Class I. KINETOFRAGMINOPHORA de Puytorac et al., 1974

(for Kinetofragmophora or Kinetophragmophora; syns. Aspirigera *p.p.*, Aspirotricha *p.p.*, Ciliostomata, Holotricha (Holotrichia, Holotricharina) *p.p.*, Postciliodesmatophora *p.p.*; Stomatea *p.p.*; and Gymnostomea + Fragmophora + Entodiniomorpha + Chonotricha + Suctoria)

Oral ciliature, of kinetofragments, basically circumoral, atrial, or vestibular in position and nature (when present at all); cytostome frequently apical or near-apical, directly on surface of body (polar or ventral) or preceded by a vestibulum; one group polystomic (suctorial tentacles); cytopharyngeal apparatus, as found in most major groups, is either a rhabdos or a cyrtos (each with prominent nematodesmata), typically conspicuous; stomatogenesis fundamentally telokinetal, though apokinetal in one major group; many species with toxicysts, some with kinetodesmata, a few with trichocysts, and one whole group with postciliodesmata; generally typical nuclear dualism, but one group homokaryotic and a second with dependent, diploid macronuclei; modes of fission include budding or other bizarre types in a number of species; conjugation is usually temporary, but total in many members of two groups; widespread in diverse habitats, free-living to endoparasitic; often carnivorous in feeding habit.

Subclass (1) Gymnostomata Bütschli, 1889

(syns. Gymnostomatida-Rhabdophorina *s.l.*, Gymnostomorida *p.p.*, Homotricha *p.p.*)

Cytostome, at or near body surface, located apically, subapically, or laterally; limited oral ciliation, but often uniform holotrichous somatic ciliation; cytopharyngeal apparatus of rhabdos type; toxicysts common; single nucleus (one very small group), micro- and macronucleus both diploid (one major group of psammophilic forms), and macronucleus oligoploid (rarely) or highly polyploid (rest of the groups); body size often large, and many species carnivorous.

Order 1. PRIMOCILIATIDA Corliss, 1974

(syns. Paramastigina *p.p.*, Primociliatida-Homokaryotina; *non* Homokaryotica [= Protociliata-Opalinata])

Homokaryotic forms (two or more nuclei, but all allegedly diploid with RNA-rich nucleolus); small body size; cytostome apical, slit-like, partially encircled by cytoplasmic protuberances; body convex dorsally; cilia principally on ventral surface; marine benthic organisms, mainly algivorous.

Family STEPHANOPOGONIDAE Corliss, 1961

(for Belaridae)

With characteristics of order (above).

Stephanopogon Entz, Sr., 1884. Few species. Pl. III, Fig. 3; VI 1; XXII 1.

Order 2. KARYORELICTIDA Corliss, 1974

(syns. Epitrichina, Inferotrichina, Karyorelictina, Loxodina, Primociliatida-Karyorelictina, Protoheterotrichida, Rhynchophorina, Trachelocercina)

Dual nuclear apparatus, but macronuclei diploid, nondividing; fragile, highly thigmotactic, often elongate; oral area apical or ventral; contractile vacuolar system often, apparently, absent; obligate interstitial forms, all marine, except one genus.

Family TRACHELOCERCIDAE Kent, 1881

With characteristics of order *s.s.* (above). Cytostome apical; body fragile, often extremely elongate, with thigmotactic cilia primarily on ventral surface; all marine.

Trachelocerca Ehrenberg, 1833. Many species. Pl. XXII, Fig. 10.

Trachelonema Dragesco, 1958. Several species. Pl. XXII, Fig. 4.

Tracheloraphis Dragesco, 1958. Very many species. Pl. III, Fig. 4; V 4, 18; XXII 5, 6.

Incertae sedis: *Gruvelina* Delphy, 1939; *Nephrocerca* Delphy, 1939; *Protrichophora* Delphy, 1939: each with single species.

Family LOXODIDAE Bütschli, 1889

(syns. Ciliofaureidae, Cryptopharyngidae, Drepanostom[at]idae, Kentrophoridae)

Cytostome, when present, slit-like, on concave body surface; body laterally compressed, with ciliation on right side only; primarily psammophilic forms, all marine except for *Loxodes*.

Kentrophoros Sauerbrey, 1928 (syns. *Centrophorella*, *Centrophorus* [hom.]). Many species. Pl. VI, Fig. 2; XXII 2, 3.

Loxodes Ehr., 1830 (syn. *Drepanostoma* [hom.]. Several spp. Pl. III, Fig. 10; V 12a; XXII 9.

Remanella Kahl, 1933. Many species. Pl. III, Fig. 28; XXII 11.

Family GELEIIDAE Kahl, 1933

Cytostome ventral, near anterior end of body; large, elongate, highly contractile forms, with uniform somatic ciliature and possibly complex oral ciliature and infraciliature; macronucleus perhaps polyploid (oligoploid) in some species; marine psammophilic forms.

Avelia Nouzarède, 1977 (for *Avela* Nouzarède, 1975 [hom.]; syn. *Avella*). Few species.

Geleia Kahl, 1933. Many species. Pl. XXII, Fig. 7.

Incertae sedis in order Karyorelictida:

Ciliofaurea Dragesco, 1960 (for *Faurea*), several species (Pl. XXII, Fig. 13); *Corlissia*

1960 (for *Corlisia*), single species (Pl. XXII, Fig. 12) [placed in a family Corlissiidae by Jankowski (1966b), a decision which I do not endorse]; *Cryptopharynx* Kahl, 1928, few species (Pl. XXII, Fig. 8) [placed in a cyrtophorid family Cryptopharyngidae (subclass Hypostomata) by Jankowski (1967a), a decision which I do not accept].

Order 3. PROSTOMATIDA Schewiakoff, 1896

(syns. Paramastigina *p.p.*, Prostomata *p.p.*, Prostomina *p.p.*)

With characteristics of subclass *s.s.* (above). Cytostome apical or subapical; circumoral infraciliature unspecialized; macronucleus polyploid; species widely distributed.

Suborder (1) Archistomatina de Puytorac et al., 1974

(syns. Cyclotrichina *p.p.*, Didesmina)

Cytostome apical; circumoral kinetosomes nonpaired but closely packed; somatic ciliation uniform or limited to tufts or bands; no toxicysts; concrement vacuole present; body ovoid to pyriform; endocommensals, principally in horses and camels but also in rodents, hippopotami, etc.

Family BUETSCHLIIDAE Poche, 1913

(for Prorotrichidae; syns. Paraisotrichopsidae, Sulcoarcidae)

With characteristics of suborder (above). Body often of small size.
Alloiozona Hsiung, 1930. Single species. Pl. II, Fig. 9; XXII 21.
Ampullacula Hsiung, 1930. Single species.
Amylophorus Pereira & Almeida, 1942. Single species.
Blepharocodon Bundle, 1895. Single species.
Blepharoconus Gassovsky, 1919. Few species. Pl. XXII, Fig. 22.
Blepharomonas Kopperi, 1937. Single species.
Blepharoplanum Kopperi, 1937. Single species.
Blepharoprosthium Bundle, 1895. Single species. Pl. VI, Fig. 3; XXII 17.
Blepharosphaera Bundle, 1895. Few species. Pl. XXII, Fig. 19.
Blepharozoum Gassovsky, 1919. Single species.
Buetschlia Schuberg, 1888. Single species. Pl. XXII, Fig. 20.
Buissonella da Cunha & Muniz, 1925. Single species.
Bundleia da Cunha & Muniz, 1928. Single species.
Cucurbella Thurston & Grain, 1971. Single species. Pl. XXII, Fig. 18.
Didesmis Fiorentini, 1890. Few species. Pl. XXII, Fig. 23.
Hemiprorodon Strelkow, 1939. Single species.
Holophryoides Gassovsky, 1919. Single species. Pl. XXII, Fig. 14.
Holophryozoon Jírovec, 1933. Single species.
Kopperia Corliss, 1960 (for *Malacosoma*). Single species.
Levanderella Kopperi, 1937. Single species.
Meiostoma Sandon, 1941. Single species.
Paraisotrichopsis Gassovsky, 1919. Single species.
Pingius Hsiung, 1932. Single species.
Polymorphella Corliss, 1960 (for *Polymorpha*). Few species. Pl. XXII, Fig. 15.
Prorodonopsis Gassovsky, 1919. Single species.
Protolutzia da Cunha & Muniz, 1925. Single species.
Pseudobuetschlia Jírovec, 1933 (for *Buetschliella* Jírovec [*non* Awerinzew]). Single species.

Sciurula Corliss, 1960 (for *Sciurella*). Single species.

Sulcoarcus Hsiung, 1935. Single species. Pl. XXII, Fig. 16.

Suborder (2) Prostomatina Schewiakoff, 1896

Generally unspecialized in all characteristics, as in order *s.s.* and subclass *s.s.* (above). Microphagous; no toxicysts; loricae produced by several species.

Family HOLOPHRYIDAE Perty, 1852

(syn. Enchelyidae *p.p.*)

Cytostome apical, round; body radially symmetrical; ciliation uniform; cytopharyngeal apparatus of simple rhabdos type.

Acaryophrya André, 1915 (syn. *Balanophrya* Kahl, 1930 [long erroneously considered the senior syn.]). Few species.

Holophrya Ehrenberg, 1833. Few to many species? Pl. II, Fig. 1; VI 4; VII 1; XXII 24.

Incertae sedis: Balanion Wulff, 1922. Single species.

Family METACYSTIDAE Kahl, 1926

Generally unspecialized, but distinguished by production of pseudochitinous loricae of several shapes; one or more caudal cilia.

Metacystis Cohn, 1866. Many species.

Pelatractus Kahl, 1930. Few species.

Vasicola Tatem, 1869. Several species. Pl. XXII, Fig. 26.

Suborder (3) Prorodontina Corliss, 1974

Cytostome apical or subapical, round or oval, sometimes in shallow atrium; unique brosse on dorsal surface near anterior pole; somatic toxicysts common; skeletal plates in one genus; most species carnivores or scavengers, a few algivorous.

Family PRORODONTIDAE Kent, 1881

(syns. Amphibot[h]rellidae [for Amphibothridae], Bursellopsidae, Helicoprorodontidae, Urotrichidae)

With characteristics of suborder *s.s.* (above).

Bursellopsis Corliss, 1960 (for *Bursella*). Few species.

Helicoprorodon Fauré-Fremiet, 1950. Few species. Pl. XXII, Fig. 34.

Placus Cohn, 1866. Few species. Pl. XXII, Fig. 33.

Plagiocampa Schewiakoff, 1892. Many species. Pl. XXII, Fig. 36.

Prorodon Ehr., 1833. Very many (> 50?) species. Pl. IV, Fig. 9a; VI 5; VII 5; XXII 27, 28.

Pseudoprorodon Blochmann, 1886. Several to many species.

Rhagadostoma Kahl, 1926 (syn. *Rhagdostoma*). Few species.

Spathidiopsis Fabre-Domergue, 1889 [*non* Kahl, 1926] (syns. *Placus* p.p., *Thoracophrya*). Several species.

Spiroprorodon Fenchel & Lee, 1972. Single species. Pl. XXII, Fig. 35.

Urotricha Claparède & Lachmann, 1859 (syn. *Balanitozoon*). Many species [deserve family of their own?]. Pl. III, Fig. 13; V 14; XXII 25.

Incertae sedis: Amphibothrella R. & L. Grandori, 1934 (syn. *Amphibotrella*); *Peridion* Vuxanovici, 1962; *Peridionella* Vuxanovici, 1963: each with single species.

Family COLEPIDAE Ehrenberg, 1838

With general features of suborder (above). Body characteristically barrel-shaped, bearing uniquely calcified cuirass (armored plates in longitudinal rows, with small lateral teeth); prominent anterior and caudal thorns often present; long caudal cilium common; active scavengers.

Coleps Nitzsch, 1827. Many species. Pl. V, Fig. 34; XXII 29–31.
Tiarina Bergh, 1881. Few species. Pl. XXII, Fig. 32.

Order 4. HAPTORIDA Corliss, 1974

(syns. Acrostomatina, Cyclotrichina *p.p.*, Dileptida, Paramastigina *p.p.*, Prionostomatina, Raptorida, Rhynchostomatida, Sciadophorida [-ina] *p.p.*, Toxistomia *p.p.*)

Cytostome apical or subapical, oval or slit-like, sometimes not permanently open; cytopharynx eversible in some species; coronal ciliature and field of clavate "sensory" cilia often present; toxicysts localized, typically in or near oral area; rhabdos complex; kinetodesmata reported; rapacious carnivores, some equipped with proboscis and a few with (nonsuctorial) tentacles.

Family ENCHELYIDAE Ehrenberg, 1838

(syns. Enchelidae, Enchelynidae, Lacrymariidae, Trachelophyllidae)

With characteristics of order *s.s.* (above); cytostome in number of species located at distal end of long flexible neck.

Chaenea Quennerstedt, 1867 (syns. *Chaenia*, *Choenia*). Many species. Pl. XXII, Fig. 37.
Chilophrya Kahl, 1930. Few species.
Crobylura André, 1914. Single species.
Echelyodon Claparède & Lachmann, 1859. Many species. Pl. XXII, Fig. 42.
Enchelys O. F. Müller, 1773 (syns. *Balantidion*, *Enchelis*). Many spp. Pl. VII, Fig. 2; XXII 41.
Gymnozoum Meunier, 1910. Single species.
Haematophagus Woodcock & Lodge, 1921. Single species.
Ileonema Stokes, 1884. Few species.
Lacrymaria Bory de St. Vincent, 1826 (syns. *Lacrimaria*, *Lacrimatoria*). Very many (nearly 50?) species. Pl. XXII, Figs. 44–49.
Lagynophrya Kahl, 1927. Many species.
Lagynurus Mansfeld, 1923. Single species.
Longitricha Gajewskaja, 1933. Single species.
Microregma Kahl, 1930. Few species.
Nannophrya Kahl, 1933. Few species.
Pithothorax Kahl, 1926 (syns. *Gymnopithus*, *Micropithus*). Few species.
Plagiopogon Stein, 1859. Few species.
Quasillagilis Busch, 1920. Single species.
Rhopalophrya Kahl, 1926. Several to many species. Pl. XXII, Fig. 38.
Schewiakoffia Corliss, 1960 (for *Maupasia*). Single species.
Spasmostoma Kahl, 1927. Single species.
Sphaerobactrum Schmidt, 1920. Single species.
Thalassiomastix Busch, 1923. Single species.
Trachelophyllum Claparède & Lachmann, 1859. Several species. Pl. XXII, Fig. 43.
Urochaenia Savi, 1913. Single (+ another?) species.

Incertae sedis: Microcardiosoma and *Microchoanostoma* Vuxanovici, 1963: single species each.

Family SPATHIDIIDAE Kahl in Doflein & Reichenow, 1929

(syns. Bryophyllidae, Homalozo[on] idae, Legendreidae, Perispiridae)

Cytostome slit-like, generally located apically on nonciliated ridge of body, facilitating ingestion of large prey; body often flask- or sack-shaped, flattened, with truncate anterior end.

Bryophyllum Kahl, 1931. Several to many species. Pl. XXII, Fig. 53.
Cranotheridium Schewiakoff, 1893. Few species. Pl. XXII, Fig. 54.
Diceratula Corliss, 1960 (for *Diceras*). Few species.
Enchelydium Kahl, 1930. Several species.
Homalozoon Stokes, 1890. Several species. Pl. XXII, Fig. 55.
Lacerus Jankowski, 1967 (syn. *Legendrea* p.p.). Single species. Pl. XXII, Fig. 52.
Legendrea Fauré-Fremiet, 1908. Few species. Pl. XXII, Fig. 51.
Micromidas Delphy, 1938. Single species.
Penardiella Kahl, 1930. Few species.
Perispira Stein, 1859. Few species. Pl. XXII, Fig. 61.
Spathidiodes Kahl, 1926 (syn. *Spathidiella*). Few species.
Spathidioides Brodsky, 1925. Few species.
Spathidiosus Gajewskaja, 1933. Single species.
Spathidium Dujardin, 1841 (syn. *Spathidiopsis* Kahl [*non* Fabre-Domergue]). Very many (well over 100) species. Pl. III, Fig. 11; VI 7; VII 3; XXII 39, 40.
Thysanomorpha Jankowski, 1967 (syn. *Legendrea* p.p.). Single species. Pl. XXII, Fig. 50.

Incertae sedis: Proboscidium Meunier, 1910. Single species.

Family TRACHELIIDAE Ehrenberg, 1838

(syns. Branchioecetidae, Dileptidae, Myriokaryonidae, Teuthophryidae)

Cytostome circular, distant from extreme anterior end of body at base of proboscis; lengthy, prominent nematodesmata in cytopharynx; abundant toxicysts; multiple proboscides in a few species; body size often large.

Branchioecetes Kahl, 1931. Few species.
Dileptus Dujardin, 1840. Many to very many spp. Pl. III, Fig. 5; V 35; VII 7; XXII 65–67.
Micruncus Delphy, 1938. Single species.
Myriokaryon Jankowski, 1973 (syn. *Pseudoprorodon* p.p.). Single sp. Pl. XXII, Figs. 82, 83.
Paradileptus Wenrich, 1929 (syn. *Tentaculifera*). Several species. Pl. XXII, Figs. 68, 69.
Teuthophrys Chatton & de Beauchamp, 1923 (syns. *Teutophrys, Triloba* [hom.]). Single (+ perhaps another) species. Pl. XXII, Figs. 70, 71.
Trachelius Schrank, 1803. Several species. Pl. XXII, Fig. 58.

Incertae sedis: Ctenoctophrys Weill, 1946. Single species.

Family DIDINIIDAE Poche, 1913

(for Cyclodinidae; syns. Cyclotrichiidae, Liliimorphidae, Mesodiniidae)

Cytostome apical (antapical in *Mesodinium*); cytopharynx, eversible in some species, equipped with multiple kinds of toxicysts; ciliation reduced to one or more circumferential bands on rotund body; "sensory bristles" usually clearly detectable.

Acropisthium Perty, 1852. Single species.
Askenasia Blochmann, 1895. Few species. Pl. XXII, Fig. 74.

Astrostoma Alekperov [unpublished; author informed, name junior homonym]. Single species.
Choanostoma Wang, 1931. Single species. Pl. XXII, Fig. 77.
Cyclotrichium Meunier, 1910. Several species. Pl. XXII, Figs. 56, 57.
Didinium Stein, 1859. Several spp. Pl. I, Figs. 9, 14; III 16; V 3, 10a, 11a, 31–33; XXII 59, 60.
Dinophrya Bütschli, 1889 (syn. of *Acropisthium*?). Two(?) species. Pl. XXII, Figs. 72, 73.
Liliimorpha Gajewskaja, 1928 (syn. *Liliomorpha*). Single species.
Mesodinium Stein, 1863. Several species. Pl. XXII, Figs. 63, 64.
Monodinium Fabre-Domergue, 1888. Several species. Pl. IV, Fig. 27; XXII 62.
Zonotrichium Meunier, 1910. Single species.

Family ACTINOBOLINIDAE Kahl, 1930

(for Actinobolidae)

Cytostome apical; uniform holotrichous somatic ciliation; retractable nonsuctorial tentacles, with associated toxicysts, widely distributed over body.
Actinobolina Strand, 1928 (for *Actinobolus*). Few species. Pl. V, Fig. 7h; VI 6; XXII 75, 76.
Belonophrya André, 1914. Single species.
Dactylochlamys Lauterborn, 1901. Single species.
Enchelyomorpha Kahl, 1930. Single species.

Incertae sedis in order Prostomatida or Haptorida:

Baznosanuia Tucolesco, 1962; *Celeritia* Tucolesco, 1962; *Pseudoenchelys* Tucolesco, 1962; *Racovitzaia* Tucolesco, 1962 (a junior homonym): each with single, small, cavernicolous species. Also "uncertain" is the following family:

Family PROTOHALLIIDAE da Cunha & Muniz, 1927

(for Halliidae [for Rhipidostom(at)idae])

Body small, ovoid, with apical disc and posterior anal papilla; oral ciliature short, inconspicuous; somatic ciliation uniform; prominent cytopharyngeal apparatus, very near anterior end of body; omnivorous; endocommensal in capybaras.
Protohallia da Cunha & Muniz, 1927 (for *Hallia* [for *Rhipidostoma*]). Single species.

Order 5. PLEUROSTOMATIDA Schewiakoff, 1896

(syns. Amphileptina *p.p.*, Pleurostomata, Pleurostom[at]ina, Scaphotrichina, Thysanophorina)

Cytostome vent- or slit-like, along edge (ventral surface?) of laterally compressed body, with nearby ciliature showing left-right differentiation; macronuclei possibly of low ploidy number; often large (sometimes with lengthy, attenuated anterior end), voracious carnivores, widely distributed and facultatively interstitial.

Family AMPHILEPTIDAE Bütschli, 1889

(syns. Litonotidae, Loxophyllidae)

With characteristics of order (above).
Acineria Dujardin, 1841. Few species.

Amphileptus Ehrenberg, 1830. Several species. Pl. XXII, Fig. 78.
Heminotus Kahl, 1933. Single species.
Hemiophrys Wrzesniowski, 1870 (syn. of *Amphileptus*?). Many species. Pl. XXII, Fig. 84.
Litonotus Wrzesniowski, 1870 (for *Leionota*; syn. *Lionotus* [hom.]). Many to very many species. Pl. XXII, Figs. 79–81.
Loxophyllum Dujardin, 1841. Many to very many species. Pl. VI, Fig. 8; XXII 85–89.

Subclass (2) **Vestibulifera** de Puytorac et al., 1974

(syn. Synciliophora *s.l.*)

Cytostome characteristically preceded by a vestibular cavity, latter lined with more or less distinctive ciliature (but ontogenetically of somatic origin); toxicysts rare; syncilia common in one group, and vestibular cilia organized into "cirromembranelles" in another; stomatogenesis basically telokinetal, though apokinetal in the specialized group with synciliary tufts; edaphic and fresh- and salt-water forms, inquilines in echinoids, and endocommensals in herbivorous mammals.

Order 1. TRICHOSTOMATIDA Bütschli, 1889

Prostomatine gymnostome-like; vestibular ciliature noncomplex, derived during fission from terminal portions of somatic kineties; cytostome (and vestibulum) sometimes antapical; concrement vacuole present in a few forms; majority of species endocommensals in vertebrate hosts.

Suborder (1) Trichostomatina Bütschli, 1889

(syns. Balantidiida, Isotrichida, Orthostomatida, Paraisotrichida, Plagiopylida, Pycnotrichida, Rimostomatida, Trichostomata, Trichostom[at]-orida, Trichostomina)

With characteristics of order *s.s.* (above), and often with dense somatic ciliation. [Warrants splitting into several separate suborders?]

Family PLAGIOPYLIDAE Schewiakoff, 1896

(syns. Paraplagiopylidae, Parasonderiidae, Schizocary[um]idae)

Anteriorly located cytostome (and vestibulum); dorsoventrally flattened body, with uniform ciliation; free-living in fresh-water, marine, salt-marsh, and interstitial biotopes and endocommensals in digestive tracts of echinoids and hippopotami.
Lechriopyla Lynch, 1930. Single species. Pl. XXIII, Fig. 3.
Paraplagiopyla Thurston & Grain, 1971. Single species.
Parasonderia Fauré-Fremiet, 1973. Few species. Pl. XXIII, Fig. 6.
Plagiopyla Stein, 1860. Several species. Pl. VII, Fig. 6; XXIII 1, 2.
Sonderia Kahl, 1928. Several species. Pl. VIII, Fig. 1; XXIII 4.
Sonderiella Kahl, 1928. Single species.
Incertae sedis: Schizocaryum Poljansky & Golikova, 1957. Single species [rather unique in number of ways; deserves family of its own?]. Pl. III, Fig. 14; XXIII 13.

Family COELOSOMIDIDAE Corliss, 1961

(for Coelosom[at]idae; syns. Conchostomatidae, Paraspathidiidae)

Elongate, marine forms, little differentiated; body not flattened; vestibulum apical.
Coelosomides Strand, 1928 (for *Coelosoma*). Pl. II, Fig. 2; XXIII 5.
Conchostoma Fauré-Fremiet, 1963. Single species. Pl. XXIII, Fig. 7.
Incertae sedis: Epimecophrya Kahl, 1933, single species; *Paraspathidium* Noland, 1937, few species [perhaps gymnostomes?].

Family TRICHOSPIRIDAE Kahl, 1926

(syn. Spirozonidae)

Anteroventrally located vestibulum; special band of cilia spiraling posteriorly, otherwise uniform ciliation; with or without caudal tuft.
Spirozona Kahl, 1926. Single species.
Trichospira Roux, 1899. Single species. Pl. XXIII, Fig. 8.

Family TRIMYEMIDAE Kahl, 1933

(syn. Sciadostom[at]idae)

Body small, tapered at both ends; cytostome (and vestibulum) near apical end; somatic ciliature restricted to several anteriorly located spirals; prominent caudal bristle; polysaprobic forms, fresh-water and marine.
Trimyema Lackey, 1925 (syn. *Sciadostoma*). Several species. Pl. IV, Fig. 25; XXIII 9, 10.

Family MARYNIDAE Poche, 1913

Vestibulum apical; attached (often colonial) forms, producing gelatinous loricae; aboral end foremost in free-swimming stage.
Maryna Gruber, 1879. Several species. Pl. I, Fig. 36; XXIII 12.
Mycterothrix Lauterborn, 1898 (syn. of *Maryna*?). Few species. Pl. XXIII, Fig. 11.

Family BALANTIDIIDAE Reichenow in Doflein & Reichenow, 1929

(syn. Paranyctotheridae)

Cytostome at base of anteriorly located vestibulum; uniform somatic ciliation; parasitic in diverse hosts: insects, frogs, snakes, guinea pig, pig, monkey, chimpanzee, orang-utang, man.
Balantidium Claparède & Lachmann, 1858 (syns. *Balantidiopsis* Bütschli [*non* Penard], *Balantioides, Parabursaria, Paranyctotherus*). Many to very many (perhaps 50?) species [but all bonafide?]. Pl. V, Fig. 12b; VIII 2; XXIII 14–16.

Family PYCNOTRICHIDAE Poche, 1913

(syns. Infundibuloriidae, Muniziellidae, Nicollellidae, Pycnothricidae)

Cytostome (and vestibulum) apical, subequatorial, or even antapical in position; holotrichous somatic ciliation; endocommensals in various herbivorous mammals, including gundis, hyraxes, capybaras, camels, cattle, water buffaloes, and the red spider monkey.
Buxtonella Jameson, 1926. Single species. Pl. XXIII, Fig. 20.
Collinina Chatton & Pérard, 1921 (for *Collinella*). Single species. Pl. XXIII, Fig. 19.
Infundibulorium Bozhenko, 1925. Single species.
Muniziella da Fonseca, 1939. Single species [very large body and other differences; deserves

family of its own?].
Nicollella Chatton & Pérard, 1919. Single species. Pl. XXIII, Fig. 18.
Pycnothrix Schubotz, 1908. Single species. Pl. XXIII, Fig. 17.
Taliaferria Hegner & Rees, 1933. Single species.

Family ISOTRICHIDAE Bütschli, 1889

Cytostome at or near antapical pole; body of medium size, ovoid; uniform, dense somatic ciliation; several contractile vacuoles; widely found in ungulate ruminants, but *Protoisotricha* is from rodents and an *Isotricha* was once reported from the cockroach.
Dasytricha Schuberg, 1888. Few species. Pl. XXIII, Fig. 22.
Isotricha Stein, 1859. Few to several species. Pl. VIII, Fig. 3; XXIII 21.
Protoisotricha Kopperi, 1937. Single species.

Family PARAISOTRICHIDAE da Cunha, 1917

(syn. Enterophryidae *p.p.*)

Cytostome at or near apical pole; body ovoid to pyriform; uniform somatic ciliation, often plus anterior tuft of longer cilia; concrement vacuole present; common endocommensals in horses, but also in capybaras, guinea pigs, and elephants.
Enterophrya Hasselmann, 1918 [resurrected genus]. Few species.
Paraisotricha Fiorentini, 1890. Few species. Pl. XXIII, Fig. 23.
Rhizotricha Wolska, 1964. Single species.
Incertae sedis: Helicozoster Latteur, 1967. Single species.

Family PROTOCAVIELLIDAE Grain, n. fam.

In general, similar to preceding family; but cytostome located medially on ventral surface of body, no concrement vacuole, shorter vestibular ciliature, and species are endocommensals in rodents only. [I understand that Grain is planning to erect such a family; so it is only proper to credit him with the name. But, since the first characterization (composed by me) is appearing here, I believe that the family should bear the date of the present work, unless Grain's description should appear elsewhere first.]
Hydrochoerella da Cunha & Muniz, 1925. Single (+ another?) species.
Protocaviella Kopperi, 1937. Single species.

Suborder (2) Blepharocorythina Wolska, 1971

(syns. Apotrichina, Blepharocorythida, Pharyngotrichina)

Oral area apical, retractable; prominent frontal lobe and distinctive corkscrew-like process also apical; vestibulum deep; body of small size, with somatic ciliation markedly reduced; remnant of concrement vacuole present; principally in horses, with a few species in elephants and cattle.

Family BLEPHAROCORYTHIDAE Hsiung, 1929

(syns. Blepharocoridae, Blepharocorydae, Circodiniidae, Raabenidae, Spirocorythidae)

With characteristics of the suborder (above).
Blepharocorys Bundle, 1895. Several species. Pl. VIII, Fig. 4; XXIII 24.
Charonina Strand, 1928 (for *Charon*; syn. *Charonella*). Single (bonafide) species.

Charonnautes Strelkow, 1939. Single species. Pl. XXIII, Fig. 25.
Circodinium Wolska, 1971. Single species. Pl. XXIII, Fig. 28.
Ochoterenaia Chavarria, 1933. Single species. Pl. XXIII, Fig. 26.
Pararaabena Wolska, 1968. Single species.
Raabena Wolska, 1967. Single species. Pl. XXIII, Fig. 27.
Spirocorys Wolska, 1969. Single species.

Order 2. ENTODINIOMORPHIDA Reichenow in Doflein & Reichenow, 1929

(syns. Entodiniomorpha, Entodiniomorphina, Entodiniorida, Syntricha *p.p.*)

Vestibular and somatic ciliature greatly reduced, appearing only in tufts (though these may be arranged in spiraled bands) and functioning as syncilia; oral area retractable in a number of species; pellicle firm and thickened, often drawn out posteriorly into spines, and body laterally flattened; prominent skeletal plates characteristic of many species; cytoproct distinct; stomatogenesis seemingly apokinetal; widely found as commensals in mammalian (mainly artiodactylan and perissodactylan) hosts, with species of one family in anthropoid apes.

Family OPHRYOSCOLECIDAE Stein, 1859

(syn. Cunhaiidae)

Synciliary tufts limited principally to oral (or adoral) area (retractable) plus a single anterodorsal group; number of contractile vacuoles variable (1–5); skeletal plates commonly present; in such artiodactylan ruminants as cattle, sheep, goats, deer *s.l.*, the antelope, caribou, bison, buffalo, ox, and close relatives, and camels (plus one species in a rodent, the guinea pig).
Caloscolex Dogiel, 1926. Single species.
Campylodinium Jankowski, 1975 (for *Amphacanthus* Dogiel, 1926 [hom.]). Single species.
Cunhaia Hasselmann, 1918. Single species [in guinea pig]. Pl. XXIII, Fig. 33.
Diplodinium Schuberg, 1888 (syn. *Anoplodinium* p.p.). Many species. Pl. XXIII, Figs. 31, 32.
Diploplastron Kofoid & MacLennan, 1932. Single species.
Elytroplastron Kofoid & MacLennan, 1932. Single species. Pl. XXIII, Fig. 34.
Enoploplastron Kofoid & MacLennan, 1932. Several species.
Entodinium Stein, 1859. Very many (*ca.* 50?) species. Pl. II, Fig. 15; VIII 5; XXIII 29, 30.
Eodinium Kofoid & MacLennan, 1932 (syn. *Anoplodinium* p.p.). Several species.
Epidinium Crawley, 1923. Several species. Pl. I, Fig. 13; III 30; VIII 6; XXIII 35, 36.
Epiplastron Kofoid & MacLennan, 1933. Few species.
Eremoplastron Kofoid & MacLennan, 1932. Many species. Pl. XXIII, Fig. 40.
Eudiplodinium Dogiel, 1927. Many species.
Metadinium Awerinzew & Mutafowa, 1914. Several species.
Ophryoscolex Stein, 1859. Few species. Pl. V, Fig. 37; XXIII 37–39.
Opisthotrichum Buisson, 1923. Single species.
Ostracodinium Dogiel, 1927. Many species.
Polyplastron Dogiel, 1927. Several species.

Family CYCLOPOSTHIIDAE Poche, 1913

Ciliature in adoral zone retractable; synciliary tufts in dorsal and caudal areas variable in number (0–4) and nonretractable; one to several contractile vacuoles; skeletal plates in some species; in horses, zebras, rhinoceroses, and tapirs and occasionally in elephants, capybaras, and hippopotami.
Bertolinella Carpano, 1941. Single species.

Bozasella Buisson, 1923. Single species.
Cycloposthium Bundle, 1895. Several species. Pl. XXIII, Figs. 41, 42.
Diplolophus Hollande & Batisse, 1959 [raised from subgenus]. Few species. Pl. XXIII, Fig. 43.
Lavierella Buisson, 1923. Single species.
Prototapirella da Cunha, 1919 (syn. *Protoapirella*). Few species. Pl. XXIII, Fig. 46.
Rhabdothorax Latteur & Bousez, 1970. Single species. Pl. XXIII, Fig. 44.
Toxodinium da Cunha, 1938. Single species.
Tricaudalia Buisson, 1923. Single species.
Trifascicularia Strelkow, 1931. Single species.
Tripalmaria Gassovsky, 1919. Single species. Pl. XXIII, Fig. 47.
Triplumaria Hoare, 1937. Few species. Pl. XXIII, Fig. 45.

Incertae sedis: Monoposthium Thurston & Noirot-Timothée, 1973, single species; *Parentodinium* Thurston & Noirot-Timothée, 1973, few species [hippopotamus forms: deserve own family?].

Family POLYDINIELLIDAE Corliss, 1960

(for Polydiniidae)

Synciliary tufts of adoral zone nonretractable; 4–12 "accessory ciliary ribbons" partially encircling body, also nonretractable; contractile vacuoles small, numerous; skeletal plates present, variable in number and size; in elephants only.
Elephantophilus Kofoid, 1935. Single species. Pl. XXIII, Fig. 56.
Polydiniella Corliss, 1960 (for *Polydinium*). Few species. Pl. XXIII, Fig. 55.
Pterodinium Latteur & Dartevelle, 1971. Single species.
Thoracodinium Latteur, 1958. Single species. Pl. XXIII, Fig. 54.

Family SPIRODINIIDAE Strelkow, 1939

Adoral zone of ciliature retractable; syncilia in "ribbons" or bands, nonretractable; one or two contractile vacuoles; no skeletal plates; in horses.
Cochliatoxum Gassovsky, 1919 (syn. *Cochliotoxon*). Single species. Pl. XXIII, Fig. 49.
Spirodinium Fiorentini, 1890. Single species. Pl. XXIII, Fig. 50.

Family DITOXIDAE Strelkow, 1939

(syn. Triadiniidae)

Four somatic synciliary "ribbons" in addition to adoral zone ciliature, all nonretractable; one or two contractile vacuoles; no skeletal plates; predominantly in horses.
Ditoxum Gassovsky, 1919. Few species. Pl. XXIII, Fig. 51.
Tetratoxum Gassovsky, 1919. Few species. Pl. XXIII, Fig. 48.
Triadinium Fiorentini, 1890. Few species.

Family TELAMODINIIDAE Latteur & Dufey, 1967

(for Telamodidae)

Adoral ciliature retractable; five "accessory ciliary ribbons" partially encircling body, nonretractable; two or three skeletal plates present; elongate macronucleus; in the wart-hog. [Erected as a subfamily, should this group be absorbed by the Spirodiniidae (above)?]
Megadinium Latteur & Dufey, 1967. Single species. Pl. XXIII, Fig. 53.
Telamodinium Latteur & Dufey, 1967. Single species. Pl. XXIII, Fig. 52.

Teratodinium Latteur & Dufey, 1967. Single species.

Family TROGLODYTELLIDAE n. fam.

Adoral ciliature retractable; four "accessory ciliary ribbons" partially encircling body, nonretractable; body fusiform, often tailed; eight contractile vacuoles, in two rows on left side of body; large skeletal plates, dorsal and ventral, coming together to envelope anterior half of organism; L-shaped macronucleus, in anthropoid apes only. [Stimulated by a comment in Noirot-Timothée (1960) – and by the descriptions in Brumpt & Joyeux (1912), Latteur & Dufey (1967), and Swezey (1934) – I decided several years ago to erect a separate family for this organism; Jankowski (1975), independently and by coincidence, has very recently suggested the same familial name in an abstract but without giving a characterization of the group.]

Troglodytella Brumpt & Joyeux, 1912. Few species (in chimpanzee, gorilla). Pl. VIII, Fig. 7; XXIII 57.

Order 3. COLPODIDA de Puytorac et al., 1974

(syns. Cyrtolophos[id]ida, Platyophryida)

Some vestibular ciliature organized into two fields of "cirromembranelles"; stomatogenesis, sometimes with discrete primordium, basically telokinetal; body of many species highly asymmetrical, but detorsion before binary or palintomic fission; somatic kinetids typically with kinetosomes in pairs, both ciliferous; macronucleus possibly of low ploidy; cysts common; in freshwater or edaphic (including "terrestrial" and coprophilic) habitats; occasional symbiont in molluscs.

Family COLPODIDAE Ehrenberg, 1838

(syns. Bursostom[at]idae, Kalometopiidae)

Cytostome at base of often well-developed, well-ciliated vestibulum; body typically kidney-shaped, with distorted ciliary rows; fission commonly multiple, within reproductive cysts; no (or poorly visible, impermanent?) cytoproct; one *Colpoda* species noted in a skink (lizard).

Bresslaua Kahl, 1931. Few species. Pl. XXIII, Figs. 71, 72.

Bursostoma Vörösváry, 1950. Single species. Pl. XXIII, Fig. 68.

Colpoda O. F. Müller, 1773 (syns. *Kolpoda, Repoma*). Many species. Pl. I, Fig. 17; II 3, 10; V 36; VIII 8, XXIII 58–64.

Kalometopia Bramy, 1962. Single species. Pl. XXIII, Fig. 83.

Tillina Gruber, 1879 (syn. *Pseudocolpoda*). Several species. Pl. IV, Fig. 7; XXIII 65–67.

Family WOODRUFFIIDAE von Gelei, 1954

(syns. Bryophryidae, Platyophryidae, Woodruffidae)

More or less distinctive "adoral row" of oral organelles, otherwise reminiscent of colpodids (above) in general features (but of nassulid hypostomes or even spirotrichs in some others). [I have expanded this taxonomically controversial family to include the additional genera listed below; and I provisionally consider it to represent an "advanced" vestibuliferan group probably related to the following equally controversial family Cyrtolophosididae (which some workers treat as a philasterine scuticociliate group and others as a unique hypostome order near the Nassulida).]

Cirrophrya Gellért, 1950. Single species. Pl. XXIII, Fig. 69.

Platyophrya Kahl, 1926. (syn. *Telostoma* [hom.]). Several species. Pl. XXIII, Figs. 76, 77.

Woodruffia Kahl, 1931. Several species. Pl. XXIII, Figs. 73–75.

Incertae sedis: *Bryophrya* Kahl, 1931, few to several species (Pl. XXIII, Fig. 70); *Rhyposophrya*

Kahl, 1933, single (+ another?) species.

Family CYRTOLOPHOSIDIDAE Stokes, 1888

(syns. Cyrtolophosidae, Cyrtolophosiidae)

Body small, narrow-ovoid; somatic ciliation uniform but sparse, with conspicuous anterior tuft; oral ciliature apparently atypical, with stomatogenesis possibly unique; cysts common; transparent gelatinous lorica or tube typical; in fresh-water habitats. [See comments under preceding family.]

Cyrtolophosis Stokes, 1885 (syn. *Balantiophorus*). Few to several spp. Pl. XXIII, Figs. 78–82.

Incertae sedis in order Trichostomatida or Colpodida:

> *Grandoria* Corliss, 1960 (for *Lagenella*), enigmatic and sole genus, with single species, in unacceptable family Grandoriidae Corliss, 1960 (for Lagenellidae [for Centrostom(at)idae]); *Opisthostomatella* Corliss, 1960 (for *Opisthostomum*), single species [perhaps bona-fide genus in trichostomatid family Marynidae (above)?]; *Orcavia* Tucolesco, 1962, single (cavernicolous) species; *Rigchostoma* Vuxanovici, 1963, single species; *Sigalasia* Delphy, 1938, single species; *Sulcigera* Gajewskaja, 1933, sole genus, with single species, in perhaps acceptable but unplaceable family SULCIGERIDAE Gajewskaja, 1933 (syn. Sulcigeriidae).

Subclass (3) **Hypostomata** Schewiakoff, 1896

(syns. Gymnostomatida-Cyrtophorina, Gymnostomorida *p.p.*, Homotricha *p.p.*, Hypostomatida, and Hypostomina [but *all* greatly expanded])

Cytostome ventral (and fundamentally so: no migration ontogenetically from apical position); cytopharyngeal apparatus typically of the cyrtos type; oral area may be sunk into an atrium, with more or less organized atrial ciliature; body flattened dorsoventrally or cylindrical, often with reduced somatic ciliation; morphogenesis of fission may be complex, with stomatogenesis of an advanced telokinetal type or even parakinetal- or buccokinetal-like; fibrous trichocysts in one group; many free-living species, microphagous or algivorous, but ecto- and endocommensals (usually with invertebrate hosts) also common.

Order 1. SYNHYMENIIDA de Puytorac et al., 1974

(for Synhymenida; syns. Nassulopsina, Scaphidiodontina, Synhymen[i]ina)

Hypostomial frange extensive, winding around anterior part of body; bipolar kineties; body cylindrical, with holotrichous ciliation; no atrium; stomatogenesis parakinetal-like; free-living, predominantly fresh-water forms, though some marine and a number interstitial.

Family NASSULOPSIDAE Deroux, n. fam.

Body generally large but elongate and radially symmetrical; multiple parts to hypostomial frange, encircling much of anterior fifth of body just below level of the cytostome-cytopharyngeal apparatus and separate from preoral suture line; row of 4–5 medially located contractile vacuole pores down ventral surface; macronucleus elongate; quite widely found in fresh-water, occasionally edaphic, habitats, with one or two species marine. [Deroux has for some time been planning to establish this group as a family, so I am crediting him with the name (but as of now); Jankowski (1975), working independently, suggested the same name but with no characterization.]

Nassulopsis Fauré-Fremiet, 1959. Several species. Pl. I, Fig. 11; IX 1; XXIV 1.
Phasmatopsis Deroux [unpublished]. Single species.

Family ORTHODONELLIDAE Jankowski, 1968

(syn. Synhymen[i]idae)

Body roughly ovoid, with asymmetrical lobe or beak to the left; one uncertain species very elongate with narrow, pointed tail; single lengthy "membrane," coursing across ventral surface just below oral area and turning anteriad out into the beak, along the preoral suture line; predominantly in fresh-water habitats. [Jankowski's (1967g) *Synhymenia* was erected for von Gelei's (1939c) *Nassula heterovesiculata*.]

Orthodonella Bhatia, 1936 (for *Orthodon*; syn. *Rhabdodon* [hom.]). Few spp. Pl. XXIV, Fig. 2.
Synhymenia Jankowski, 1967 (syn. *Nassula* p.p.). Single species. Pl. XXIV, Fig. 3.
Zosterodasys Deroux [unpublished]. Single species.
Incertae sedis: Eucamptocerca da Cunha, 1914. Single species. Pl. XXIV, Fig. 4.

Family SCAPHIDIODONTIDAE Deroux, n. fam.

Broad anterior end, with body gently tapered posteriorly; hypostomial frange similar to that of the Orthodonellidae (above), but simpler and less conspicuous; mostly marine forms. [As in the case of the Nassulopsidae (above), this family is credited to Deroux; Jankowski (1975), once again, also proposed the familial name here, but without characterization.]

Chilodontopsis Blochmann, 1895 (syn. *Chlamydodontopsis*). Single (recognizable?) to several (in the literature) species. Pl. XXIV, Figs. 6, 7.
Scaphidiodon Stein, 1859. Few species. Pl. XXIV, Fig. 5.

Order 2. NASSULIDA Jankowski, 1967

(syns. Ambihymenida, Cyrtohymenostomatida, Parahymenostomatida)

Hypostomial frange often not extensive, limited to left side of ventral surface, and sometimes reduced to 3–4 "pseudomembranelles" ("pavés" of French workers) in an oral atrium; distinct preoral suture; stomatogenesis complex, parakinetal- or buccokinetal-like in many species; trichocysts especially characteristic of one suborder. [In a number of characteristics, some members of this order appear to be more closely allied to certain groups within the following class Oligohymenophora than to their "fellow" (neighboring) hypostome order Cyrtophorida (below).]

Suborder (1) Nassulina Jankowski, 1967

(syns. Cyrtohymenina, Paranassulina)

With characteristics of order *s.s.* (above); body typically large and cylindrical, with holotrichous ciliation; fresh-water and marine forms, with filamentous algae common as food; pellicle highly distensible.

Family NASSULIDAE de Fromentel, 1874

(for Odontoholotrichidae; syns. Cyrtohymenostomatidae, Enigmostomatidae, Liosiphonidae)

Body roughly ellipsoidal, uniformly ciliated; hypostomial frange short but multiple, often extending along preoral suture; prominent cytopharyngeal apparatus; contractile vacuole pore single, midventral; algivorous forms, widespread in fresh-water and occasionally brackish and marine habitats. [Jankowski's (1975) *Enigmostoma* was erected for Dragesco's (1972a) *Nassula ougandae.*]

Enigmostoma Jankowski, 1975 (syn. *Nassula* p.p.). Single species. Pl. XXIV, Fig. 13.

Nassula Ehrenberg, 1833 (syn. *Liosiphon*). Many spp. Pl. IV, Figs. 9b, 31; IX 2; XXIV 8–12.

Incertae sedis: *Archinassula* Kahl, 1935; *Chilodina* Šrámek-Hušek, 1957; *Cyrtohymenostoma* Das et al., 1969; *Stomatophrya* Kahl, 1933: each with single species.

Family PARANASSULIDAE Fauré-Fremiet, 1962

(syn. Enneameronidae)

Body ovoid to elongate-ovoid, uniformly ciliated; hypostomial frange restricted to 3–4 "pseudomembranelles" in oral atrium surrounding cytostome-cytopharyngeal complex *s.s.*; preoral suture entirely separate; contractile vacuole pore on dorsal surface; found solely in marine habitats.

Enneameron Jankowski, 1964 (syn. *Paranassula* p.p.). Single species. Pl. XXIV, Figs. 14, 15.

Paranassula Kahl, 1931. Few species. Pl. XXIV, Fig. 16.

Family FURGASONIIDAE n. nom.

(for Cyclogrammidae)

Body ovoid to ellipsoidal, uniformly ciliated; hypostomial frange appearing as four definitive organelles in atrial area, reminiscent of buccal ciliature in oligohymenophorans; prominent cytopharyngeal apparatus; contractile vacuole pore midventral in location; fusiform trichocysts reported; typically in fresh-water habitats. [On the basis of ultrastructure of the oral infraciliature, Grain et al. (1976) have recently erected a new oligohymenophoran order, Parahymenostomatida, for this family; but the cytopharyngeal apparatus is quite nassulid-like. Deroux had been planning to establish the group (as hypostomes) at the family-level; Jankowski (1975) and de Puytorac & Grain (1976) each independently published the name "Cyclogrammidae," but without characterization of the group. My belated discovery that the name *Cyclogramma* Perty, 1852 (*possibly* 1849, though not verifiable) is preoccupied by *Cyclogramma* Doubleday, 1847 (a lepidopteran genus legitimately named in a figure, with full text appearing early in 1849) necessitates its replacement for the ciliated protozoa involved. I propose, rather than an altogether new name, use of the little-known junior synonym *Furgasonia*, the name given by Jankowski (1964b, p. 272) – rather incidentally suggested in his monograph on polysaprobic heterotrichs – to *Nassula tricirrata* von Gelei, 1932, an organism with obvious "*Cyclogramma*" characteristics. The replacement familial name thus becomes Furgasoniidae, formally authored by me as of this date.]

Furgasonia Jankowski, 1964 (for *Cyclogramma*; syn. *Nassula* p.p.). Possibly several species. Pl. II, Fig. 4; XXIV 17, 18.

Suborder (2) Microthoracina Jankowski, 1967

(syns. Cyrtopharyngina, Microthoracida)

Hypostomial frange reduced drastically to (or replaced by?) a few short kinetal segments bearing "pseudomembranelles" and sometimes set in a shallow atrium; body, frequently broadly ellipsoidal (with right side more rounded), occasionally crescentic, and often laterally flattened, with firm pellicle and sparsely ciliated; fibrous trichocysts (fibrocysts) present; species typically fresh-water or edaphic, often cyst-forming; but the enigmatic *Discotricha* is marine.

Family LEPTOPHARYNGIDAE Kahl, 1926

(syns. Pseudomicrothoracidae, Trichoderidae [for Trichopelm(at)idae])

With general characteristics of suborder (above). Three "pseudomembranelles" on left side of oral area and stomatogenesis parakinetal- or even buccokinetal-like.

Leptopharynx Mermod, 1914 (syn. *Trichoderum* [for *Trichopelma*]). Several species. Pl. XXIV, Figs. 19, 20.

Pseudomicrothorax Mermod, 1914 (syns. *Chilodonopsis, Craspedothorax*). Few species. Pl. V, Figs. 10c, 11c; IX 3; XXIV 21.

Stammeridium Wenzel, 1969 (for *Stammeriella*). Single species. Pl. XXIV, Fig. 22.

Family MICROTHORACIDAE Wrzesniowski, 1870

(syns. Conchophryidae, Discotrichidae, Drepanomonadidae, Trochiliopsidae)

With characteristics of suborder *s.s.* (above); but *Discotricha* dorsoventrally flattened, etc.

Drepanomonas Fresenius, 1858 (syn. *Pseudocristigera*). Several spp. Pl. XXIV, Figs. 23, 24.

Hemicyclium Eberhard, 1862. Single species. Pl. XXIV, Fig. 26.

Microthorax Engelmann, 1862. Many species. Pl. XXIV, Fig. 25.

Trochiliopsis Penard, 1922. Single species.

Incertae sedis: *Conchophrys* Chatton, 1911, single species; *Discotricha* Tuffrau, 1954, single named species (probably two) [quite likely deserves family of its own?], Pl. XXIV, Figs. 27, 28; *Hexotricha* Conn in Conn & Edmondson, 1918 (syn. *Hexotrichia*), few species; *Kreyella* Kahl, 1931, single species; *Microdiaphanosoma* Wenzel, 1953 (for *Diaphanosoma*), single species.

Order 3. CYRTOPHORIDA Fauré-Fremiet in Corliss, 1956

(syns. Cyrtophorina *p.p.*, Phyllopharyngidea *p.p.*)

Hypostomial frange not identifiable as such; oral area occupied by several short double-rows of kinetosomes (outer ciliferous) located anteriad to complex cyrtos (circlet of a few large nematodesmata enclosing numerous microtubular sheets radially oriented); preoral suture skewed far to left; body frequently dorsoventrally flattened, with somatic ciliature restricted to ventral surface and often an adhesive organelle at posterior end; macronucleus (except one suborder) heteromerous, stomatogenesis telokinetal (parakinetal, according to some workers), but involving extensive morphogenetic movements; a widespread group, mostly marine, with scores of species yet to be properly described; numerous free-living forms, but also many ectocommensals and a few species parasitic on fish gills. [Deroux (1976a) has very recently named and characterized the three suborders needing recognition here (Corliss, 1975b); Jankowski (1975), working in parallel, proposed names, without description, which I am treating as synonyms, below: his "Dysteriina," however, is identical to Deroux's name for that group.]

Suborder (1) Chlamydodontina Deroux, 1976

(syn. Chilodonellina)

With characteristics of order *s.s.* (above). Ventral ciliature thigmotactic, with no prominent specialized adhesive organelle; body broad in shape and flattened dorsoventrally.

Family CHILODONELLIDAE Deroux, 1970

(syn. Chilodontidae [for Odontohypotrichidae])

Broad thigmotactic zone; body width < 2/3 length, with pronounced anterior "beak" to left; some *Chilodonella* harmful on gills of fresh-water fishes. [We have here revival of Bütschli's long abandoned Chilodontidae, the name of which has to be replaced, however, because Ehrenberg's original name for the type-genus, *Chilodon*, has fallen as a junior homonym.]

Chilodonella Strand, 1928 (for *Chilodon*). Many spp. Pl. III, Fig. 29; IV 9c; IX 4; XXIV 29.
Phascolodon Stein, 1859. Few species. Pl. XXIV, Fig. 31.
Pseudochilodonopsis Foissner [unpublished]. Few species.
Thigmogaster Deroux, 1976. Single species. Pl. XXIV, Fig. 32.
Trithigmostoma Jankowski, 1967 (syn. *Chilodonella* p.p.). Single species. Pl. XXIV, Fig. 30.

Incertae sedis: *Chilodonatella* Dragesco, 1966; *Odontochlamys* Certes, 1891; *Phyllotrichum* Engelmann, 1875: each with single species.

Family CHLAMYDODONTIDAE Stein, 1859

(syn. Chlamidodontidae)

Thigmotactic zone localized; body shape nearly ellipsoidal, with width > 2/3 length.

Chlamydodon Ehrenberg, 1835 (syn. *Chlamidodon*). Several species. Pl. XXIV, Figs. 33, 34.
Cyrtophoron Deroux, 1975. Single species. Pl. XXIV, Fig. 35.

Family LYNCHELLIDAE Jankowski, 1968

Thigmotactic zone broad, with curious structureless protrusions in several species; preoral arcs of ciliature isolated.

Atopochilodon Kahl, 1933. Single species. Pl. XXIV, Fig. 39.
Chlamydonella Deroux, 1970. Few species. Pl. XXIV, Fig. 38.
Coeloperix Deroux, 1976. Few species.
Gastronauta Engelmann, 1875 (syn. *Gastronanta*). Few species. Pl. XXIV, Fig. 36.
Lynchella Kahl, 1933. Several species. Pl. XXIV, Fig. 37.

Incertae sedis: *Lophophorina* Penard, 1922. Single species.

Suborder (2) Dysteriina Deroux, 1976

Less conservative in body form (narrower than in first suborder) and in specializations in oral area; definitive adhesive organelle (podite); species widespread and numerous, mainly marine.

Family PLESIOTRICHOPIDAE Deroux, 1976

Infraciliature *Chilodonella*-like; adhesive apparatus located centrally in ventral depression.

Atelepithites Deroux, 1976. Single species.
Pithites Deroux & Dragesco, 1968. Single species.
Plesiotrichopus Fauré-Fremiet, 1965. Few species. Pl. XXIV, Fig. 40.
Trochochilodon Deroux, 1976. Single species. Pl. XXIV, Fig. 41.

Family HARTMANNULIDAE Poche, 1913

(for Onychodactylidae; syns. Allosphaeriidae, Trichopodiellidae)

Adhesive organelle posterior, free from ciliary field on left; some uniquenesses in infraciliary patterns; *Brooklynella* harmful as gill symbiont of marine fishes.

Aegyriana Deroux, 1975. Few species. Pl. IV, Fig. 18a; XXIV 42.
Brooklynella Lom & Nigrelli, 1970. Single species. Pl. IV, Figs. 18b, 49; V 12c.
Chlamydonyx Deroux, 1977. Single species.
Hartmannula Poche, 1913 (for *Onychodactylus*). Few species.
Microxysma Deroux, 1977. Single species.
Orthotrochilia Deroux, 1977. Few species.
Parachilodonella Dragesco, 1966. Few species. Pl. XXIV, Fig. 43.
Paratrochilia Kahl, 1933. Single species.
Sigmocineta Jankowski, 1967. Single species. Pl. XXIV, Fig. 47.
Trichopodiella Corliss, 1960 (for *Trichopus*). Few species. Pl. XXIV, Fig. 44.
Trochilioides Kahl, 1931. Several species. Pl. IV, Fig. 18c; XXIV 45, 46.

Incertae sedis: Allosphaerium Kidder & Summers, 1935, several species [on carapace and gills of littoral amphipods – deserve family of their own?]; *Horocontus* Deroux, 1977, single species.

Family DYSTERIIDAE Claparède & Lachmann, 1858

(syn. Erviliidae)

Many species of small body size; general reduction in somatic ciliature; left ciliary field always in two parts; cytopharyngeal capitula often prominent; posteroventral podite may protrude conspicuously; widely distributed organisms, mainly marine, frequently symphorionts.

Agnathodysteria Deroux, 1977. Single species.
Dysteria Huxley, 1857 (syns. *Aegyria, Ervilia* [hom.]). Many to very many species. Pl. IV, Fig. 17; XXIV 48–51.
Hartmannulopsis Deroux & Dragesco, 1968. Single species. Pl. XXIV, Fig. 52.
Mirodysteria Kahl, 1933 (syn. *Microdysteria*). Few species.
Schedotrochilia Deroux, 1977. Single species.
Trochilia Dujardin, 1841. Several species. Pl. IX, Fig. 5; XXIV 53.

Suborder (3) Hypocomatina Deroux, 1976

(syns. Hypocomida, Hypocomina + Macrostomatina, Rhynchodina)

Somatic ciliature restricted to ventral surface and oral ciliature reduced; cytopharyngeal tube protrudes from body (in first family); macronucleus, band-like, not heteromerous; adhesive organelle inconspicuous in right-ventral pit or fosette; dorsal surface of body clearly convex (humped); practically all species ecto- or endocommensals, on wide range of marine hosts.

Family HYPOCOMIDAE Bütschli, 1889

With characteristics of suborder *s.s.* (above); hosts: peritrichs, brittle stars, tunicates.
Hypocoma Gruber, 1884. Few species. Pl. IX, Fig. 6; XXIV 54.
Parahypocoma Chatton & Lwoff, 1939. Few species. Pl. III, Fig. 19; XXIV 55.
Rhynchocoma Jankowski, 1975 (for *Heterocoma* Chatton & Lwoff, 1939 [hom.]). Single species.

Family CRATERISTOMATIDAE Jankowski, 1967

Rotund, but not large, ovoid body, with relatively numerous rows of cilia on ventral surface; cytostome wide and, like cytopharynx, constantly open (no feeding by suction); continuously mobile forms, carnivorously feeding on other ciliates in same mantle cavity of host (the common barnacle).

Crateristoma Jankowski, 1967. Single species. Pl. XXIV, Fig. 56.

Order 4. CHONOTRICHIDA Wallengren, 1895

(syns. Phyllopharyngidea *p.p.*, Scaiotricha *p.p.*)

Ciliature in adult forms limited to atrial area (sometimes = entire ventral surface of body), which may be funnel-shaped with a simple cytopharyngeal apparatus (no surrounding circlet of nematodesmata) at the bottom; adhesive organelle produces stalk or pedicel, always noncontractile; macronucleus heteromerous; reproduction solely by budding; migratory tomites bear two fields of cilia on concave ventral surface and an adhesive gland posteriorly; conjugants, of unequal size, invariably undergo total fusion; no cytoproct or contractile vacuoles; body often vase-shaped, with pellicle quite rigid and frequently adorned with collar, lobes, and/or spines; widely found as symphorionts on gills, mouthparts, and/or other appendages of marine, brackish, and fresh-water crustaceans, principally amphipods, isopods, and copepods (but also decapods, nebaliids, and others); one species attaches to a marine alga.

Suborder (1) Exogemmina Jankowski, 1972

External budding, commonly only one bud at a time; body long and cylindrical, relatively large, and typically with well-developed collar; spines absent or poorly developed; usual attachment by undistinguished pedicel (rather than "true" stalk); macronuclear orthomere directed apically; species occur on marine, brackish, and fresh-water crustaceans (amphipods, isopods, mysids, decapods) and one marine alga.

Family LOBOCHONIDAE Jankowski, 1967

Body elongate, bottle-shaped, not flattened; apical end simple, conical, slightly flared, often with two dorsal lobes; collar distinct; no spines; pedicel typical of suborder; macronucleus ovoid; presumably primitive forms, found only in marine or brackish habitats – but with very wide distribution – on isopods and amphipods, with one unique species on an alga.

Eleutherochona Jankowski, 1971 (syn. *Stylochona* p.p.). Single species (on algae).

Lobochona Dons, 1940. Few species. Pl. XXIV, Fig. 57.

Oenophorachona Matsudo & Mohr, 1968. Few species. Pl. XXIV, Fig. 65.

Toxochona Jankowski, 1972. Single species.

Family FILICHONIDAE Jankowski, 1973

Body cylindrical or bottle-shaped, large, not flattened; apical end simple, conical and unadorned; collar distinct and markedly elongate, with several heavy spines nearby; pedicel low and broad; macronucleus ovoid; marine, on isopods.

Aurichona Jankowski, 1973. Single species.

Filichona Jankowski, 1973. Single species. Pl. XXIV, Fig. 61.

Family PHYLLOCHONIDAE Jankowski, 1972

Body leaf-shaped, not elongate, flattened dorsoventrally; apical end drawn out uniquely into huge, broad, flat plate; collar absent; some short lateral spines; pedicel in form of wide disc; macronucleus massive; marine, on isopods.

Phyllochona Jankowski, 1972. Single species.

Family HELIOCHONIDAE Jankowski, 1972

Body bottle-shaped, elongate to sac-like, not flattened; apical end large, flat, fanned out, bearing rows of conspicuous spines giving whole structure a fimbriated appearance; collar distinct, usually short; pedicel typical of suborder; macronucleus ovoid; marine or brackish habitats, on amphipods.

Heliochona Plate, 1888. Few species. Pl. XXIV, Figs. 58, 59.
Heterochona Jankowski, 1972. Several species. Pl. XXIV, Fig. 62.

Family CHILODOCHONIDAE Wallengren, 1895

Body ovoid or pyriform, massive, not flattened; apical end large, cylindrical, flaring slightly; collar indistinct or absent; no spines; body walls markedly thickened; long, wide, solid stalk (rather than pedicel typical of suborder); macronucleus elongate; widely distributed on marine decapods in littoral and sublittoral habitats.

Chilodochona Wallengren, 1895. Few species. Pl. XXIV, Fig. 60.
Cryptochona Jankowski, 1973. Single species.
Mystichona Jankowski [unpublished]. Single species.
Vasichona Jankowski, 1972. Single species.

Family SPIROCHONIDAE Stein, 1854

Body vase-shaped, elongate, not flattened; apical end flared, with dorsal wall multiply-spiraled in characteristic helical coils (as many as half a dozen full turns); collar short; no spines; pedicel low and broad; macronucleus ovoid; on gammarid amphipods (generally the gills) in fresh-water, brackish, and marine habitats.

Cavichona Jankowski, 1973. Many species. Pl. XXIV, Fig. 66.
Serpentichona Jankowski, 1973. Single species.
Spirochona Stein, 1852. Several species. Pl. III, Fig. 21; IX 7; XXIV 63, 64.

Suborder (2) Cryptogemmina Jankowski, 1975

(syns. Endogemmina, Dorsofragmina + Ventrofragmina)

Internal budding, with up to eight tomites in brood pouch or crypt; body small, often flattened and angular, with reduced collar; spines common and of several types; stalk, of varying length, typically present; macronuclear orthomere directed antapically; species occur solely on marine crustaceans, littoral and open ocean (amphipods, copepods, cyamids, nebaliids), including epibionts of whales. [Although I used "Endogemmina Jankowski, 1972" in earlier papers (Corliss, 1975b, 1977a), I am endorsing Jankowski's (1975) own substituted name "Cryptogemmina" here because of its peculiar appropriateness.]

Family ISOCHONIDAE Jankowski, 1973

Body cylindrical, elongate; apical end conical, rather small and undistinguished; collar short; no spines; stalk sometimes long; crypt of moderate size; macronucleus ovoid; very wide distribution on appendages or shell of amphipods, nebaliids, cyamids, etc., including the "whale-lice" found on species of several genera of whales from various oceans. [Although I was unaware of it at the time (Corliss, 1977a), the "*nomina nuda*" names of three provisional genera which I included in the family Stylochonidae (below) had, in effect, already been replaced by Jankowski (1971); and the three groups of organisms involved are, now, more properly assigned here.]

Cyamichona Jankowski, 1971. Few species.
Inermichona Jankowski, 1971. Few species.
Isochona Jankowski, 1973. Several species. Pl. XXIV, Fig. 75.
Thalassochona Jankowski, 1971. Few species.
Trichochona Mohr, 1948. Few species.

Family ACTINICHONIDAE Jankowski, 1973

Body small, usually flattened; apical end conical, not flattened, sometimes with a fold, and with conspicuous spines in some species; collar may be elongate; body wall often thickened; pedicel present, rather than stalk; crypt of varying size; macronucleus ovoid; marine, on nebaliids, with very wide distribution.

Actinichona Jankowski, 1973. Few species. Pl. XXIV, Fig. 70.
Carinichona Jankowski, 1973. Single species.
Crassichona Jankowski, 1973. Single species.
Cristichona Jankowski, 1973. Few species. Pl. I, Fig. 24.
Kentrochonopsis Doflein, 1897. Single species. Pl. XXIV, Fig. 71.
Rhizochona Jankowski, 1973. Single species.

Family STYLOCHONIDAE Mohr, 1948

Body leaf-like, markedly flattened dorsoventrally; apical end flattened, extending out laterally, with distinct folds and sometimes heavy spines; collar very short; body may have large, elongate spines or rows of papillae; crypt often very deep; macronucleus ovoid; stalk of varying length, sometimes unusually long (for chonotrichs); marine, on nebaliids. [Three genera described by Jankowski (1971) which were included in this family by Corliss (1977a) more appropriately belong in the Isochonidae (above); see further explanation there.]

Armichona Jankowski, 1973. Few species. Pl. IX, Fig. 8.
Ctenochona Jankowski, 1973. Single species. Pl. XXIV, Fig. 69.
Dentichona Jankowski, 1973. Single species.
Eriochona Jankowski, 1973. Few species.
Flectichona Jankowski, 1973. Few species.
Oxychonina n. n. [published here, with explicit permission of the original describer, for *Oxychona* Jankowski, 1973, name preoccupied by *Oxychona* Moench, 1852 (mollusc)]. Few species [type-species: *O. multifida* (Jankowski, 1973) n. comb.]. Pl. XXIV, Fig. 74.
Paraoxychona Jankowski, 1973. Single species.
Pterochona Jankowski, 1973. Single species.
Spinichona Jankowski, 1973. Single species. Pl. XXIV, Fig. 76.
Stylochona Kent, 1881. Several species. Pl. XXIV, Figs. 67, 68.

Family ECHINICHONIDAE Jankowski, 1973

Body rhombic or spindle-shaped, markedly flattened dorsoventrally; apical end flattened, flared widely, sometimes with fold or two; collar distinct, narrow, low; spines and papillae generally absent or indistinct; stalk quite long in some species; crypt very deep and broad; macronucleus somewhat elongate; marine, on nebaliids.

Coronochona Jankowski, 1973. Single species.
Echinichona Jankowski, 1973. Few species.
Eurychona Jankowski, 1973. Single species.

Family INVERSOCHONIDAE Jankowski, 1973

(syn. Pleochonidae)

Body sometimes elongate, small, flattened dorsoventrally; apical end very broad, flattened, usually simple but occasionally with a few spines; collar distinct; very heavy, well-developed body spines in some species; exceedingly short pedicel present; crypt relatively shallow; macronucleus elongate; marine, on nebaliids, with wide distribution.

Ceratochona Jankowski, 1973. Few species.
Chonosaurus Jankowski, 1973. Few species. Pl. XXIV, Fig. 73.
Inversochona Jankowski, 1973. Single species.
Kentrochona Rompel, 1894. Few species. Pl. XXIV, Fig. 72.
Pleochona Jankowski, 1973. Single species.

Order 5. RHYNCHODIDA Chatton & Lwoff, 1939

(syns. Ancistrocomina, Rhynchodea *p.p.*, Toxistomia *p.p.*)

Single, knobbed, anteriorly located tentacle, equipped with toxicysts and serving as an ingestatory tube; adult forms small, either devoid of ciliature or with it mostly restricted to an anteroventral thigmotactic field; reproduction often by budding, with ciliated (in two fields) larval forms; symbiotic (parasitic) on gills or mouthparts of diverse invertebrates, fresh- and salt-water, but most often on gills of marine bivalve molluscs.

Family ANCISTROCOMIDAE Chatton & Lwoff, 1939

(syn. Cepedellidae)

Somatic ciliature present, but concentrated over anterior half of organism; body shape ovoid to pyriform, with sucking tube sometimes clearly protruding from anterior end; parasitic in both fresh-water and marine invertebrates – polychaetes, a phoronid, and others – but found principally in the mantle cavity of molluscs (many kinds, including a chiton).

Ancistrocoma Chatton & Lwoff, 1926 (syn. *Parachaenia*). Few species. Pl. XXIV, Fig. 79.
Anisocomides Chatton & Lwoff, 1950. Single species.
Colligocineta Kozloff, 1965. Few species.
Crebricoma Kozloff, 1946. Single species. Pl. XXIV, Fig. 78.
Enerthecoma Jarocki, 1935. Few species.
Goniocoma Chatton & Lwoff, 1950. Single species.
Heterocinetopsis Jarocki, 1935. Few species.
Holocoma Chatton & Lwoff, 1950 (syn. of *Ancistrocoma*?). Single species.
Hypocomagalma Jarocki & Raabe, 1932. Few species.
Hypocomatidium Jarocki & Raabe, 1932. Few species.
Hypocomella Chatton & Lwoff, 1924 (syns. *Heterocineta, Hypocomatophora*). Many species. Pl. XXIV, Fig. 81.
Hypocomides Chatton & Lwoff, 1922. Several species.
Hypocomidium Raabe, 1938. Few species.
Hypocomina Chatton & Lwoff, 1924. Single species.
Ignotocoma Kozloff, 1961. Single species. Pl. V, Figs. 7f, 12d.
Insignicoma Kozloff, 1946. Single species. Pl. III, Fig. 27; XXIV 80.
Isocomides Chatton & Lwoff, 1950. Single species.
Kozloffiella Raabe, 1970. Single species. Pl. XXIV, Fig. 77.
Nordicoma Jankowski [unpublished]. Single species.
Raabella Chatton & Lwoff, 1950. Few species. Pl. IX, Fig. 9.
Syringopharynx Collin, 1914 (syn. of *Ancistrocoma*?). Single species.

Incertae sedis: Cepedella Poyarkoff, 1909. Single species.

Family SPHENOPHRYIDAE Chatton & Lwoff, 1921

(syns. Gargariidae, Lwoffidae, Pelecyophyridae)

Adult form without cilia (except one species), body of various shapes; tentacle short; commonly on gills of marine and fresh-water bivalve molluscs.

Gargarius Chatton & Lwoff, 1934 (syn. *Rhynchophrya* Raabe *non* Collin [hom.]). Single species. Pl. XXIV, Fig. 82.
Lwoffia Kozloff, 1955. Single species [adults ciliated].
Pelecyophrya Chatton & Lwoff, 1922. Single species.
Sphenophrya Chatton & Lwoff, 1921. Several species. Pl. XXIV, Fig. 83.

Order 6. APOSTOMATIDA Chatton & Lwoff, 1928

(syns. Apostomea, Apostomina)

Cytostome inconspicuous or absent in certain stages, typically with a unique rosette (secretory function?) nearby in the oral area; stomatogenesis considered telokinetal, often with involvement of three or four specialized kinetofragments; mature forms show holotrichous somatic ciliation, generally arranged in fewer than 22 dextrally spiraled rows, with fields of strongly thigmotactic cilia; reproduction may involve palintomy; well-developed true kinetodesmata present; typically a contractile vacuole plus pore, but no cytoproct; macronucleus homomerous in trophonts, heteromerous in tomites of many species; complex, polymorphic life cycles; symbiotic (parasitic) in or on predominantly marine hosts (rarely fresh-water, and only one possible terrestrial host – edaphic acari – reported), with a number of invertebrate groups involved; apostomes *s.s.* most commonly found in hermit crabs, shrimps, and copepods (with sea anemones as alternating host, for species with such an obligate cycle).

Suborder (1) Apostomatina Chatton & Lwoff, 1928

(syns. Cyrtostomatina, Gemmotomina, Incitophorina)

With characteristics of order *s.s.* (above); commonly in marine, occasionally fresh-water, crustacean hosts (members of one genus are symbionts of other apostomatines; and an atypical family is found in polychaete annelids).

Family FOETTINGERIIDAE Chatton, 1911

(syns. Gymnodinioidae, Gymnodinioididae, Phtorophryidae, Polyspiridae; and possibly Kofoidellidae and Perezellidae)

With characteristics of the suborder *s.s.* (above); exceptional genera are *Ophiuraespira* in ophiuroid echinoderms, *Pericaryon* in ctenophores, and *Phtorophrya* on other apostomatines.

Calospira Chatton & Lwoff, 1935. Single species. Pl. XXIV, Fig. 85.
Foettingeria Caullery & Mesnil, 1903. Single species. Pl. IX, Fig. 10; XXIV 86.
Gymnodinioides Minkiewicz, 1912 (syns. *Larvulina* p.p., *Oospira* [hom.], *Physophaga*). Several species. Pl. XXIV, Fig. 87.
Hyalophysa Bradbury, 1966. Single species.
Hyalospira Miyashita, 1933. Single species.
Metaphrya Ikeda, 1917. Single species.
Ophiuraespira Chatton & Lwoff, 1930. Single species. Pl. XXIV, Fig. 84.

Pericaryon Chatton, 1911. Single species.
Phoretophrya Chatton, A. & M. Lwoff, 1930 (syn. *Phtoretophrya*). Single species.
Phtorophrya Chatton, A. & M. Lwoff, 1930. Several species.
Polyspira Minkiewicz, 1912. Single species.
Rosea de Puytorac [unpublished]. Single species.
Spirophrya Chatton & Lwoff, 1924. Single species. Pl. I, Fig. 23.
Synophrya Chatton & Lwoff, 1926. Single species.
Terebrospira Debaisieux, 1960 (for *Chattonia*). Few species.
Traumatiophtora Chatton & Lwoff, 1930 (syn. *Traumatiophora*). Single species.
Vampyrophrya Chatton & Lwoff, 1930. Few species.
Incertae sedis: Jeppsia Corliss, 1960 (for *Chattonella*); *Kofoidella* Cépède, 1910; *Perezella* Cépède, 1910: each with single species.

Family CYRTOCARYIDAE n. fam.

(syn. Cyrtocaryumidae)

Body of trophont pear-shaped, ciliation holotrichous; no cytostome, no rosette; tomite very small, with area of strongly thigmotactic cilia; single caudal cilium; large, partially coiled macronucleus; found in lateral caeca of digestive tube in polychaete annelids. [Jankowski (1975) independently suggested a new family, "Cyrtocaryumidae," but without characterization. Hovasse's (1950) curious *Spirobuetschliella* (elongate, with spiraled ciliature) may also belong here. Are these poorly known polychaete symbionts better placed in the following suborder?]

Cyrtocaryum Fauré-Fremiet & Mugard, 1949. Single species. Pl. XXIV, Fig. 90.
Incertae sedis: Spirobuetschliella Hovasse, 1950. Single species.

Suborder (2) Astomatophorina Jankowski, 1966

(syns. Astomophorina, Nephrocolina, Sanguicolina)

No cytostome (in stages of life cycles known to date), but remnants of oral ciliature; body often elongate, vermiform; somatic ciliature markedly thigmotactic; reproduction by monotomy, palintomy, or strobilation – in last case, catenoid colonies may result; hosts include cephalopods, amphipods, and isopods.

Family OPALINOPSIDAE Hartog, 1906

(syn. Chromidinidae)

Very elongate, vermiform trophonts, attached by their anterior end to host tissue; fission by catenulation (in first genus listed below), producing long chain of loosely connected individuals; ciliation holotrichous, in highly spiraled pattern; found in liver, kidney, and gonads of squid and octopus.

Chromidina Gonder, 1905. Few (perhaps only one) species. Pl. IX, Fig. 11; XXIV 89.
Opalinopsis Foettinger, 1881. Few (perhaps only one) species.

Family COLLINIIDAE Cépède, 1910

Body of trophont small, roughly inverted-ovoid in shape; holotrichous ciliation except for broad bare band medially coursing down dorsal surface; known life cycle much like that of apostomatines, with rosette, specialized kinetal segments in "oral" area, etc.; found in coelomic fluid of amphipods and isopods. [The sanguicolous "*Anoplophrya*" species of the literature belong here. But is the family better placed in the first suborder (above)?]

Collinia Cépède, 1910 (syn. *Anoplophrya* p.p.). Several species. Pl. XXIV, Fig. 88.

Suborder (3) Pilisuctorina Jankowski, 1966

Mature forms (*Conidophrys*) nonciliated, immobile, characteristically impaled on setae of host, with migrating tomite – produced by strobilation – ciliated but without cytostome; species of other genera permanently in so-called "neotenic" tomite stage, body with ventral adhesive organelle, sometimes mouthless, and showing distinctive pattern of infraciliature; hosts include marine amphipods, isopods, decapods, and cirripeds, plus possibly (needing reconfirmation) a terrestrial mite.

Family CONIDOPHRYIDAE Kirby, 1941

(for Pilisuctoridae; syns. Ascophryidae, Askoellidae, Conidiophryidae)

With characteristics of suborder (above). [Should *Ascophrys* and *Askoella* be separated out into at least a second family, as Jankowski (1967c, 1972a) has suggested?]

Ascophrys Campillo & Deroux, 1974. Single species. Pl. XXIV, Fig. 91.

Askoella Fenchel, 1965. Few species. Pl. XXIV, Fig. 93.

Conidophrys Chatton & Lwoff, 1934 (syns. *Conidiophrys*, *Conidophrya*). Few species [one reported from mites, by Dindal (1973)]. Pl. IX, Fig. 12; XXIV 92.

Subclass (4) Suctoria Claparède & Lachmann, 1858

(syns. Acineta[e], Acinetaria, Acinetina, Acinet[o]idea, Actinifera, Actinosuctorifera, Atricha, Dystricha, Suctorasina, Suctorea, Suctoriae, Suctorifera, Suctoriorida, Tentaculifer[id]a, Tentaculiferiae, Toxistomia *p.p.*)

Multiple (few to many, rarely none) ingestatory suctorial tentacles, containing numerous microtubules – arranged peripherally – and haptocysts distally (at tips); mature form customarily sedentary, without cilia (though with an infraciliature), and often with a scopuloid-produced noncontractile stalk of varying length; migratory motile larval form, produced by some mode of budding, generally bearing cilia (often considered as predominantly comprising a "right-ventral" field) but no tentacles or stalk; contractile vacuole and pore present, but no cytoproct; conjugation of different kinds, but frequently total with unequal conjugants; body often (though not universally) of conspicuous size and attached to variety of substrata; species many and widespread, predominantly as symphorionts on diverse marine or fresh-water organisms (largely invertebrates), but some as endocommensals in hosts ranging from other ciliates to vertebrates.

Order SUCTORIDA Claparède & Lachmann, 1858

(syns.: see those of subclass, above)

With characteristics of subclass (above); great diversity of "hosts" as substrata (see page 107).

Suborder (1) Exogenina Collin, 1912

(syns. Ephelophagina, Ephelotida, Ephelotina, Exogenea, Oligostomatida *p.p.*, Ophryodendrina, Paracinetida, Paracinetina, Podophryida, Podophryina, Spelaeophryina, Thecacinetina, Tomogenea, Vermigemmida, Vermigenea)

Exogenous budding, most often monogemmic (but polygemmic in some species), with no appreciable invagination of parental cortex; small permanent field of nonciliferous kinetosomes in vicinity of contractile vacuole; migratory larval form typically large *or* lengthy, the former with complex ventral ciliature (derived from parental kinetosomal field) but some of the latter practically devoid of cilia, vermiform, and incapable of swimming; number of species with actinophores, some with prehensile as well as suctorial tentacles, and bodies of many of diverse size (often large) and shape; majority marine, typically solitary forms, and free-living or ectocommensal.

Family PODOPHRYIDAE Haeckel, 1866

(syns. Lecanophryidae, Ophryocephalidae, Sphaerophryidae)

Adults small, pyriform or spherical, with tentacles apical or evenly distributed; usually with stalk or lorica; larvae, commonly produced one at a time and sometimes as large as adult, frequently cylindrical, with broad equatorial band of cilia; generally fresh-water forms, often attached to other ciliates.

Kystopus Jankowski, 1967 (syn. *Podophrya* p.p.). Single species. Pl. XXV, Fig. 6.
Mucophrya Gajewskaja, 1928. Single species.
Ophryocephalus Wailes, 1925. Single species.
Podophrya Ehrenberg, 1838. Very many (perhaps 50) species. Pl. I, Fig. 15; X 1; XXV 1, 2.
Sphaerophrya Claparède & Lachmann, 1859 (syn. of *Podophrya*?). Several species. Pl. V, Fig. 7a; XXV 3.
Incertae sedis: Lecanophrya Kahl, 1934 (syn. *Collinophrya*). Few species. Pl. XXV, Fig. 12.

Family PARAPODOPHRYIDAE Jankowski, 1973

Like the Podophryidae (above), but adults never loricate; budding solely monogemmic; entirely free-living, fresh-water forms.

Parapodophrya Kahl, 1931. Several species. Pl. XXV, Fig. 4.

Family URNULIDAE Fraipont, 1878

(syns. Metacinetidae, Paracinetidae)

Adults spherical, in complex lorica with openings for tentacles; larvae ovoid, with somewhat spiraled ciliary band; marine and fresh-water forms.

Metacineta Bütschli, 1889. Few species. Pl. XXV, Fig. 17.
Paracineta Collin, 1911 (syn. *Hallezia* [hom.] p.p.). Many species. Pl. XXV, Fig. 5.
Urnula Claparède & Lachmann, 1859. Few species. Pl. XXV, Fig. 16.

Family EPHELOTIDAE Kent, 1882

(syn. Hemiophryidae)

Adults large, truncate-spherical, with peripheral prehensile tentacles surrounding regular suctorial tentacles at apical end of body; some species loricate; multiple larvae produced synchronously, ellipsoidal and flattened, with ciliary field horseshoe-shaped; marine forms.

Actinocyathula Corliss, 1960 (for *Actinocyathus*). Single species.
Ephelota Wright, 1858 (syn. *Hemiophrya*). Many species. Pl. I, Fig. 6; III 18; V 7g; X 3; XXV 7, 8.
Metephelota Willis, 1945. Single species.
Podocyathus Kent, 1882. Few species.
Tunicophrya Jankowski, 1973 (syn. *Ephelota* p.p.). Single species.

Family SPELAEOPHRYIDAE Jankowski in Batisse, 1975

Adults cylindrical or conical, with corona of apical tentacles (prehensile as well as suctorial types?); larvae vermiform, cylindrical; all fresh-water forms. [Jankowski (1967a) suggested the familial name, but without characterization; Batisse (1975), generously crediting the group to Jankowski, was actually the first to describe it.]

Spelaeophrya Stammer, 1935 (syns. *Hydranthosoma, Hydrophrya, Spathocyathus*). Few to several species (symphorionts on shrimp antennae). Pl. XXV, Figs. 13, 14.

Family RHABDOPHRYIDAE Jankowski, 1970

Adult body cylindrical (and occasionally branched), appearing segmented, with tentacles grouped in fascicles at the different levels (sometimes involving actinophores); larvae cylindrical, vermiform; marine forms, on shrimp. [Jankowski (1967a) proposed the familial name but offered no characterization until later (Jankowski, 1970). Batisse (1975) accepted the group as Jankowski's, revising it somewhat. I am crediting the family (revising it still further) to Jankowski, but as of the date of his second paper.]

Dendrosomides Collin, 1906. Few species. Pl. XXV, Figs. 9, 10.

Rhabdophrya Chatton & Collin, 1910. Several species.

Trophogemma Jankowski, 1970. Single species. Pl. XXV, Fig. 18.

Family STYLOSTOMATIDAE Batisse, 1975

(syns. Asteriferidae, Stylostomidae)

Adults somewhat vase-shaped, with apical arms bearing fascicles of tentacles; tomite body drawn out distally; marine forms. [Jankowski (1975), independently, actually proposed the familial name shortly before Batisse (1975), but included no characterization of the group.]

Asterifer Jankowski, 1967 (syn. *Ophryodendron* p.p.). Single species. Pl. X, Fig. 2.

Stylostoma Milne, 1886. Single species.

Family OPHRYODENDRIDAE Stein, 1867

Adults of somewhat baggy or irregular shape, broadly attached to substratum (with or without definitive stalk); tentacles in fascicles on one or more extensible branches; tomites long and fusiform; marine forms.

Loricodendron Jankowski, 1973 (syn. *Ophryodendron* p.p. — Batisse's recent species, *O. hollandei*). Single species. Pl. V, Fig. 7b.

Ophryodendron Claparède & Lachmann, 1859. Many species [probably some of them not congeneric]. Pl. XXV, Fig. 11.

Schizactinia Jankowski, 1967 (syn. *Ophryodendron* p.p.). Single species.

Family TACHYBLASTONIDAE Grell, 1950

Two (alternating) generations: one, loricate and often attached to stalk of *Ephelota*, produces *ca.* 16 small unitentaculate forms which pierce the pellicle of the *Ephelota* body; these become the other generation, which lives parasitically within the host's cytoplasm and produces large ciliated larvae which, in turn, attach to host stalk, become loricate, and repeat the cycle.

Tachyblaston Martin, 1909. Single species. Pl. XXV, Fig. 15.

Family THECACINETIDAE Matthes, 1956

Adult stalked, loricate, with tentacles grouped apically; larvae ellipsoidal, flattened, or vermiform, with ventral ciliated band; predominantly marine forms (some on nematodes, etc.).

Canellana Jankowski, 1967 (syn. *Thecacineta* p.p.). Single species.
Corynophrya Kahl, 1934. Several species.
Praethecacineta Matthes, 1956. Few species. Pl. XXV, Fig. 20.
Thecacineta Collin, 1909. Many species. Pl. I, Fig. 33; XXV 19.

Family PHALACROCLEPTIDAE Kozloff, 1966

Body small, of flattened hemispherical shape, with neither cilia nor infraciliature at any stage of life cycle; very short tentacles; parasitic on polychaete annelids. [Highly aberrant organisms, with exact affinities totally unknown. Provisionally placed here.]

Phalacrocleptes Kozloff, 1966. Single species. Pl. XXV, Fig. 21.

Suborder (2) Endogenina Collin, 1912

(syns. Acinetida, Acinetina, Astrosomatida, Dendrosomatida, Dendrosomatina, Endogenea, Endosphaeriina, Oligostomatida *p.p.*)

Endogenous budding, with one or more monogemmic or polygemmic larvae produced completely internally and becoming free-swimming in brood pouch *before* emergence through birth pore; small permanent field of nonciliferous kinetosomes near contractile vacuole responsible for larval ciliature; migratory larval form small, with encircling band(s) of cilia; adults usually small (but ramified and of enormous size in some groups), often loricate, sometimes colonial, with tentacles frequently in fascicles but without actinophores; in fresh-water and marine habitats, with ectosymbiotic forms common (plus some endocommensals) in wide range of hosts.

Family ACINETIDAE Stein, 1859

(syns. Acinetopsidae, Allantosomatidae, Pseudogemmidae, Solenophryidae)

Adults nearly always loricate and stalked, with stalk persisting in some but not all endosymbiotic forms; tentacles in few fascicles, or even reduced to a single organelle; larvae small, ovoid; widely distributed species, in variety of habitats (and on/in many of the hosts listed on page 107).

Acineta Ehrenberg, 1833. Very many (> 75) species described [but many probably should be removed]. Pl. V, Figs. 6, 7c; X 4; XXV 22–26; XXIX 38.
Acinetides Swarczewsky, 1928. Single species.
Acinetopsis Robin, 1879. Several species. Pl. XXV, Fig. 27.
Arcosoma Jankowski, 1967 (syn. *Allantosoma* p.p.). Single species.
Cryptophrya Jankowski, 1973. Single species.
Dactylophrya Collin, 1909. Single species. Pl. XXV, Fig. 36.
Dactylostoma Jankowski, 1967 (syn. *Dactylophrya* p.p.). Single species.
Lecanodiscus Jankowski, 1973 (syn. *Discophrya* p.p.). Few species.
Loricophrya Matthes, 1956 (syn. *Loricaphrya*). Several to many species.
Multifasciculatum Goodrich & Jahn, 1943. Few species. Pl. XXV, Fig. 28.
Plicophrya Jankowski, 1975 (for *Donsia* Jankowski, 1967 [*non* Hadži, 1951). Single species.
Pottsiocles Corliss, 1960 (for *Pottsia*; syn. *Pottsiodes*). Few species. Pl. XXV, Fig. 34.
Pseudogemma Collin, 1909. Few species. Pl. XXV, Fig. 25.
Pseudogemmides Kormos, 1935. Single species.

Solenophrya Claparède & Lachmann, 1859. Many species. Pl. XXV, Fig. 31.
Squalorophrya Goodrich & Jahn, 1943 (syn. *Squalophrya*). Few species. Pl. XXV, Fig. 30.
Suctorella Frenzel, 1891. Single species.
Tokophryella Jankowski, 1973 (syn. *Podophrya* p.p.). Single species.
Trematosoma Batisse, 1972 (syn. *Acineta* p.p.). Single species. Pl. V, Fig. 12e; XXV 29.

Incertae sedis: Allantosoma Gassovsky, 1919, several species, in horses, Pl. XXV, Fig. 50; *Cucumophrya* Kunz, 1936, single species.

Family DENDROSOMATIDAE Fraipont, 1878

(syns. Dendrosomidae, Rhynchetidae, Tokophryidae)

Adult stalkless (with rare exception), aloricate, occasionally planktonic, with body shape pyriform to truncate to branching; tentacles sometimes highly specialized or greatly reduced in number; often multiple budding; larvae small, with transverse band of cilia; widespread, especially in fresh-water (even on turtles); several endosymbiotic species and crustacean gill parasites.

Anarma Goodrich & Jahn, 1943. Few species. Pl. XXV, Fig. 38.
Baikalodendron Swarczewsky, 1928. Single species. Pl. XXV, Fig. 41.
Baikalophrya Swarczewsky, 1928. Few species.
Brachyosoma Batisse, 1975 (syn. *Hallezia* [hom.] p.p.). Few species.
Choanophrya Hartog, 1902. Several species. Pl. XXV, Fig. 32.
Dendrosoma Ehrenberg, 1838. Few species. Pl. I, Fig. 41; XXV 40.
Erastophrya Fauré-Fremiet, 1944. Single species. Pl. XXV, Fig. 37; XXIX 44.
Gorgonosoma Swarczewsky, 1928. Single species.
Hypophrya López-Ochoterena, 1964. Single species. Pl. XXV, Fig. 33.
Lernaeophrya Pérez, 1903 (syn. *Lernaerophrya*). Single species. Pl. XXV, Fig. 39.
Rhyncheta Zenker, 1866. Few species. Pl. XXV, Fig. 35.
Staurophrya Zacharias, 1893. Single species.
Thaumatophrya Collin, 1912. Single species.
Tokophrya Bütschli, 1889 (syn. *Tocophrya*). Very many (*ca.* 50) species [all bonafide?]. Pl. I, Fig. 5; X 5; XXV 46–48.
Tokophryopsis Swarczewsky, 1928. Single species.

Family TRICHOPHRYIDAE Fraipont, 1878

(syns. Actinobranchiidae, Caprinianidae [for Capriniidae], Marinectidae)

Body flattened, stalkless, but with fascicles of tentacles from slight protuberances; larvae small, ciliated; widely distributed species, with some found on gills of fresh-water fishes. [Restudy of the budding process here may oblige transfer of the family to suborder Evaginogenina (below), near the Heliophryidae. All *Trichophrya* valid? Should *Phagobranchium* be syn. of *Capriniana*?]

Actinobranchium Jankowski, 1967 (syn. *Trichophrya* p.p.). Single species. Pl. XXV, Fig. 45.
Astrophrya Awerinzew, 1904. Single species. Pl. XXV, Fig. 42.
Capriniana Strand, 1928 (for *Caprinia*). Single species.
Marinecta Jankowski, 1973 (syn. *Trichophrya* p.p.). Few species.
Phagobranchium Jankowski, 1967 (syn. *Trichophrya* p.p.). Single species. Pl. XXV, Fig. 43.
Tetraedrophrya Zykoff, 1902. Single species.
Trichophrya Claparède & Lachmann, 1859. Many species. Pl. V, Fig. 12f; XXV 44.

Family ENDOSPHAERIDAE Jankowski, n. fam.

(syn. Endosphaeriidae)

Small, ovoid forms, with neither stalk nor tentacles; budding monogemmic; occur solely as endoparasites of peritrich ciliates. [Jankowski (1967a) proposed only the familial name, without characterization; I am happy to credit the group to him, but as of the date of this book.]
Endosphaera Engelmann, 1876. Few species.
Physaliella Penard, 1920. Single species.

Suborder (3) Evaginogenina Jankowski, n. subord.

(syns. Cyathomorphida, Cyathomorphina, Dendrocometida, Dendrocometina, Discophryida, Discophryina, Evaginogenea, Inversogenea)

Evaginative budding, with development of a single (monogemmic) larva, in a typical brood pouch but with occurrence of cytokinesis only *after* full emergence of the "everted" bud; no field of kinetosomes in vicinity of contractile vacuole; larvae often ellipsoidal, flattened, bearing distinctive patterns of cilia on ventral surface; adults sessile (with or without stalk), occasionally in lorica, often hemispherical and bearing tentacles either scattered singly or in fascicles at the ends of sometimes massive arms or trunks; of widespread occurrence, especially as fresh-water or marine symphorionts, with species of one endosymbiotic genus showing a strikingly aberrant life cycle. [Named by Jankowski (1975), though totally without description, and partially characterized in an abstract by Curry & Butler (1974), the group is here credited to Jankowski, but as of the date of this book.]

Family DISCOPHRYIDAE Collin, 1912 [*non* Cépède, 1910]

(syn. Rhynchophryidae)

With simpler characteristics of suborder *s.s.* (above); no arms or trunks bearing tentacles; seldom with loricae; larva, bud, or swarmer typically large; all free-living (or symphoriontic).
Caracatharina Kormos, 1961 (for *Catharina*). Single species.
Discophrya Lachmann, 1859 [*non* Stein, 1860]. Several spp. Pl. I, Fig. 7; X 7; XXV 51–53.
Echinophrya Swarczewsky, 1928. Single species.
Periacineta Collin, 1909. Several species. Pl. XXV, Fig. 54.
Peridiscophrya Nozawa, 1938. Single species.
Prodiscophrya Kormos, 1935. Single species.
Rhynchophrya Collin, 1909 [*non* Raabe, 1935]. Single species.

Family HELIOPHRYIDAE n. fam.

Body discoidal and often small, flattened against substratum; thickened pellicle, with specialized "fringed" border around attached base of body; stalkless, aloricate; tentacles (large, conspicuously knobbed, and extensible to many times body diameter) arranged in several fascicles arising from slight protuberances of body; dendritic macronucleus; numerous contractile vacuoles; avidly carnivorous, with nonspecific prey (other ciliates); migratory form large, cylindrical, with many rows of cilia; widely found in fresh-water habitats. [Influenced by findings of such workers as Dragesco et al. (1955), Lanners (1973a,b), Matthes (1954a), and Spoon et al. (1976), I am erecting this family here as new, with *Heliophrya* as type-genus. Further studies may reveal a closer kinship between it and the endogenine Trichophryidae than indicated by their present taxonomic separation; also problematical is the possible relationship between certain species now assigned to *Discophrya* and those allocated to *Heliophrya*.]
Cyclophrya Gönnert, 1935. Few species.
Heliophrya Saedeleer & Tellier, 1930 (syn. *Craspedophrya*). Few to several species. Pl. V, Fig. 6; XXV 59–61.

Platophrya Gönnert, 1935. Single species. Pl. XXV, Fig. 58.

Family DENDROCOMETIDAE Haeckel, 1866

(syn. Discosomatellidae, Stylophryidae)

With the more specialized or more bizarre characteristics of suborder *s.l.* (above), though no species endosymbiotic. Arms or trunks bearing tentacles at their ends represent most conspicuous feature; larvae lenticular; wide distribution, with many species ectocommensals on crustaceans (e.g., on gammarids of fresh-water Lake Baikal).

Cometodendron Swarczewsky, 1928. Many species.
Dendrocometes Stein, 1852. Several species. Pl. V, Fig. 7d; X 6; XXV 55–57.
Dendrocometides Swarczewsky, 1928. Single species.
Discosomatella Corliss, 1960 (for *Discosoma*). Single species.
Stylocometes Stein, 1867. Single species.
Stylophrya Swarczewsky, 1928. Few species. Pl. XXV, Fig. 49.

Family CYATHODINIIDAE da Cunha, 1914

(syn. Enterophryidae *p.p.*)

Ovoid, stalkless adult stage fleeting, but typically produces two ciliated buds simultaneously; these budded larvae, pyriform in shape, retain extensive ciliature, have a row of very short tentacles ("endosprits"), and persist as the dominant stage in the life cycle; endocommensals in digestive tract of domestic and wild guinea pigs.

Cyathodinium da Cunha, 1914 (syns. *Cyathodinioides, Enterophrya* p.p.). Several species. Pl. V, Fig. 7e; X 8; XXV 62.

Incertae sedis in class Kinetofragminophora:

Arachnidiopsis Penard, 1918 [amazing organism, seen on several occasions (see Penard, 1922); but possibly not a ciliate at all!]; *Dysterioides* Matthes, 1950 [still another enigmatic — and incompletely described — ciliate (found on the gills of certain land snails), which Matthes (1950a) tentatively assigned to the hypostome family Dysteriidae]; *Euploia* Lohmann, 1920 [more data needed on this interesting pelagic ciliate which seems to be more gymnostome- *(sensu lato)* than hypotrich-like]; *Silenella* Fenchel, 1965 [a hypostome or a larval stage of a chonotrich or suctorian?]: each with single species.

GENERAL NOTE ON FIGURES OF PLATES XXII–XXXII

Some 600 ciliate genera are illustrated in the 1,100 or so retouched or redrawn figures selected from the widely scattered research literature (dating from Leeuwenhoek to the present) to comprise the 38 "plate-pages" of this chapter. The generic names employed are considered to be the proper ones for the species portrayed: very often the producer of the original figure used quite a different name, but space restrictions prohibit supplying such historical details in the explanations. Names of the actual species involved, citation of particular papers, and notes on the organism itself as well as on the staining techniques, etc. are seldom given, for the same reason of lack of room for such information (some of which would require rather lengthy explanation to be truly useful, and some cases are so controversial that they must await the attention of specialists). The labeled figures of earlier Plates I–V, however, hopefully fulfill some of this need. [Concluded on page 312.]

EXPLANATION OF FIGURES

PLATE XXII (pages 244–246)

Page 244. Fig. 1. *Stephanopogon* [only homokaryotic ciliate genus described to date] (Dragesco). 2, 3. *Kentrophoros* (Noland). 4. *Trachelonema* (Dragesco). 5, 6. *Trachelorapbis* (Raikov, Dragesco). 7. *Geleia* (Calkins). 8. *Cryptopharynx* (Kirby). 9. *Loxodes* (Dragesco). 10. *Trachelocerca* (Dragesco). 11. *Remanella* (Dragesco). 12. *Corlissia* (Dragesco). 13. *Ciliofaurea* (Dragesco). 14. *Holophryoides* (Gassovsky). 15. *Polymorphella* (Hsiung). 16. *Sulcoarcus* (Hsiung). 17. *Blepharoprosthium* (Hsiung). 18. *Cucurbella* (Thurston & Grain). 19. *Blepharosphaera* (Hsiung). 20. *Buetschlia* (Schuberg). 21. *Alloiozona* (Hsiung). 22. *Blepharoconus* (Hsiung). 23. *Didesmis* (Grain). 24. *Holophrya* (Dragesco). 25. *Urotricha* (Dingfelder). 26. *Vasicola* [with lorica added] (Dragesco et al.). 27, 28. *Prorodon* (Dragesco). 29–31. *Coleps* (Leeuwenhoek, Noland, Noland). 32. *Tiarina* (Fauré-Fremiet).

Page 245. Fig. 33. *Placus* (Dragesco). 34. *Helicoprorodon* (Fauré-Fremiet). 35. *Spiroprorodon* (Fenchel & Lee). 36. *Plagiocampa* (Fauré-Fremiet & André). 37. *Chaenea* (Dragesco). 38. *Rhopalophrya* (Kirby). 39, 40. *Spathidium* (Wenzel, Wang & Nie). 41. *Enchelys* (Dragesco). 42. *Enchelyodon* (Dragesco). 43. *Trachelophyllum* (Dragesco). 44–49. *Lacrymaria*, contracted and extended (Fauré-Fremiet, Dragesco, O. F. Müller, O. F. Müller, Calkins, Noland–unpub.). 50. *Thysanomorpha* (Kahl). 51. *Legendrea* (Penard). 52. *Lacerus* (Penard). 53. *Bryophyllum* (Fryd-Versavel et al.). 54. *Cranotheridium* (Jankowski). 55. *Homalozoon* (Dragesco). 56, 57. *Cyclotrichium* (Bary & Stuckey, Fauré-Fremiet). 58. *Trachelius* (Roux). 59, 60. *Didinium*, and didinia attacking and devouring *Paramecium* (Dragesco, Mast).

Page 246. Fig. 61. *Perispira* (Dewey & Kidder). 62. *Monodinium* (Fauré-Fremiet). 63, 64. *Mesodinium* (Noland, Dragesco). 65–67. *Dileptus* (Dragesco, Calkins, Dingfelder). 68, 69. *Paradileptus* (Dragesco, Wenrich). 70, 71. *Teuthophrys*, trophont and dividing form (Wenrich, Chatton & de Beauchamp). 72, 73. *Dinophrya* (Fauré-Fremiet, Ernst for Small–unpub.). 74. *Askenasia* (Fauré-Fremiet). 75, 76. *Actinobolina*, tentacles retracted and extended (Fauré-Fremiet, Wang & Nie). 77. *Choanostoma* (Wang & Nie). 78. *Amphileptus* (Dragesco). 79–81. *Litonotus* (Dragesco, Dragesco, Schewiakoff). 82, 83. *Myriokaryon* (Jankowski, Dragesco). 84. *Hemiophrys* (Dragesco). 85–89. *Loxophyllum* (O. F. Müller, O. F. Müller, Schewiakoff, Dragesco, Sauerbrey).

PLATE XXIII (pages 247–249)

Page 247. Figs. 1, 2. *Plagiopyla* (Kahl, Jankowski). 3. *Lechriopyla* (Lynch). 4. *Sonderia* (Dragesco). 5a,b. *Coelosomides* (Fauré-Fremiet). 6a,b. *Parasonderia* (Fauré-Fremiet). 7. *Conchostoma* (Fauré-Fremiet). 8. *Trichospira* (Jankowski). 9, 10. *Trimyema* (Jankowski, Fauré-Fremiet). 11. *Mycterothrix* (Lepşi). 12. *Maryna* (Stammer). 13. *Schizocaryum* (Berger). 14–16. *Balantidium* (Kudo, Wenyon, Wenyon). 17. *Pycnothrix* (Chatton & Pérard). 18. *Nicolella* (Chatton & Pérard). 19. *Collinina* (Chatton & Pérard). 20. *Buxtonella* (Jameson). 21. *Isotricha* (Bělař in Hartmann). 22. *Dasytricha* (Grain). 23. *Paraisotricha* (Grain). 24. *Blepharocorys* (Grain). 25. *Charonnautes* (Wolska). 26. *Ochoterenaia* (Wolska). 27. *Raabena* (Wolska). 28. *Circodinium* (Wolska).

Page 248. Figs. 29, 30. *Entodinium* (Kofoid & MacLennan). 31, 32. *Diplodinium* (Kofoid & Christenson). 33. *Cunhaia* (Hasselmann). 34. *Elytroplastron* (Kofoid & MacLennan). 35, 36. *Epidinium* (Kofoid & Christenson, Sharp). 37–39. *Ophryoscolex* (Kofoid & MacLennan, Noirot-Timothée, Stein). 40. *Eremoplastron* (Kofoid & MacLennan). 41, 42. *Cycloposthium* (Bundle, Hollande & Batisse). 43. *Diplolophus* (Hollande & Batisse). 44. *Rhabdothorax* (Latteur & Bousez). 45. *Triplumaria* (Latteur et al.). 46. *Prototapirella* (da Cunha). 47. *Tripalmaria* (Gassovsky). 48. *Tetratoxum* (Gassovsky). 49. *Cochliatoxum* (Gassovsky). 50. *Spirodinium* (Davis). 51. *Ditoxum* (Gassovsky). 52. *Telamodinium* (Latteur & Dufey). 53. *Megadinium* (Latteur & Dufey). 54. *Thoracodinium* (Latteur & Dufey). 55. *Polydiniella* (Kofoid). 56. *Elephantophilus* (Kofoid). 57. *Troglodytella* (Swezey).

Page 249. Figs. 58–64. *Colpoda* (Burt, Dragesco, Dragesco, Dragesco, Bradbury & Outka, Novotny et al., Gellért). 65–67. *Tillina* (Fauré-Fremiet & André, Dingfelder, Dragesco). 68a,b. *Bursostoma* (Vörösváry). 69. *Cirrophrya* (Gellért). 70. *Bryophrya* (Kahl). 71, 72. *Bresslaua* [with captured *Cyclidium*(?) in food vacuole in first figure] (Kahl, Claff et al.). 73–75. *Woodruffia* (Johnson & Larson, Prelle, Dingfelder). 76, 77. *Platyophrya* (Gellért, Grolière). 78–82. *Cyrtolophosis* (Stokes, Kahl, Kahl, Kahl, von Gelei). 83. *Kalometopia* (Bramy).

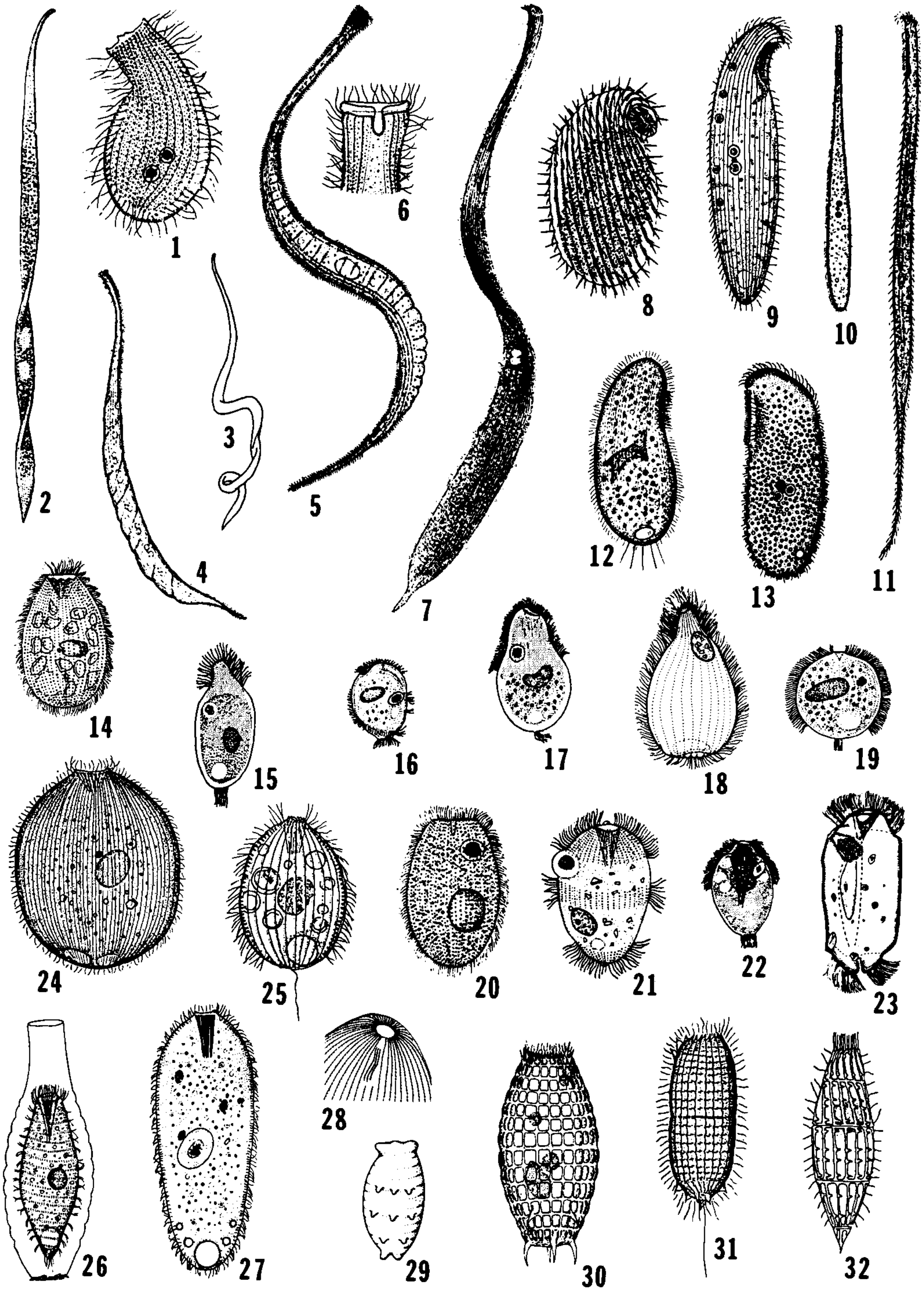

PLATE XXII. Class Kinetofragminophora, subclass Gymnostomata: selected genera. [See page 243 for figure explanations.]

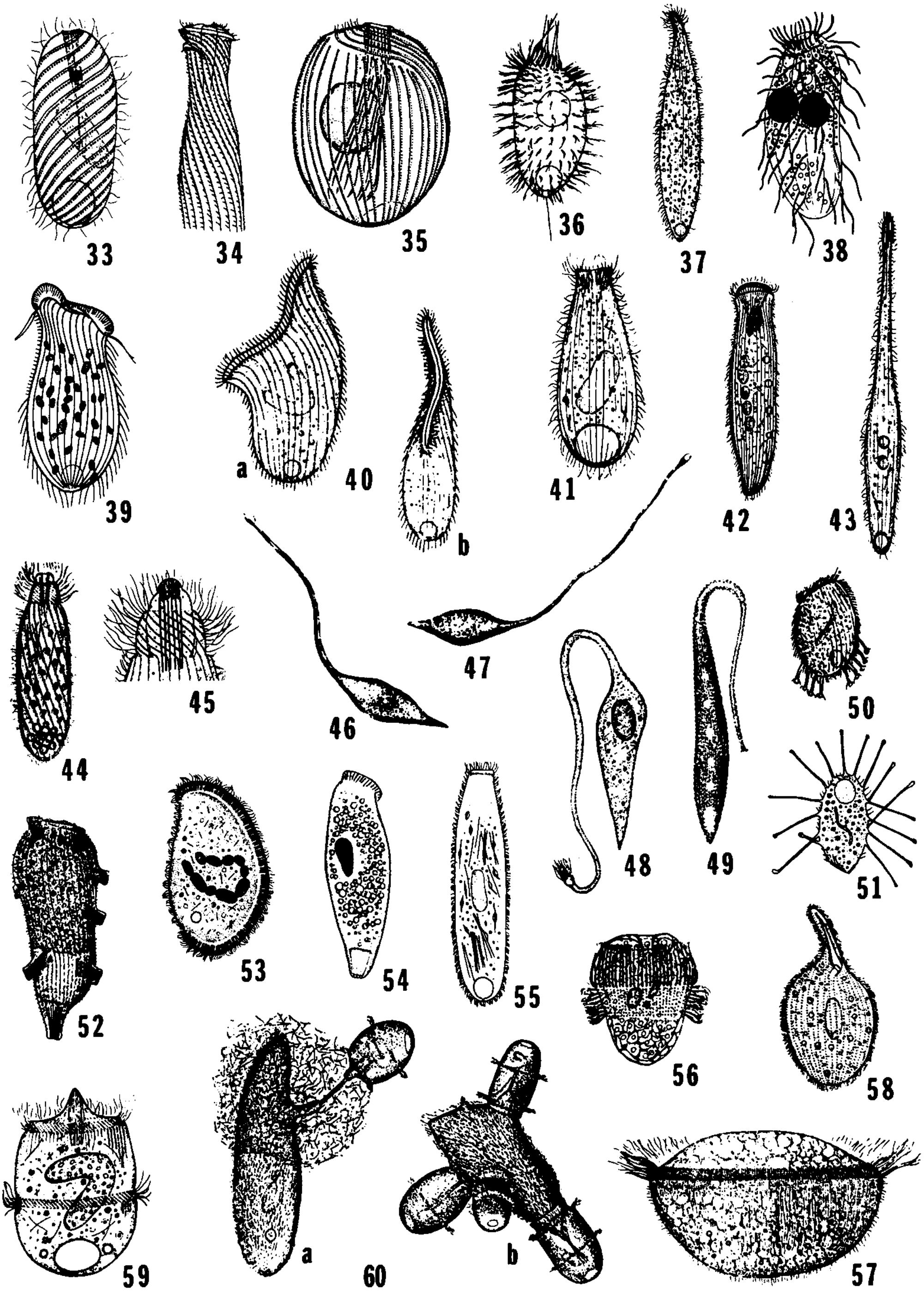

PLATE XXII, continued. [See page 243 for figure explanations.]

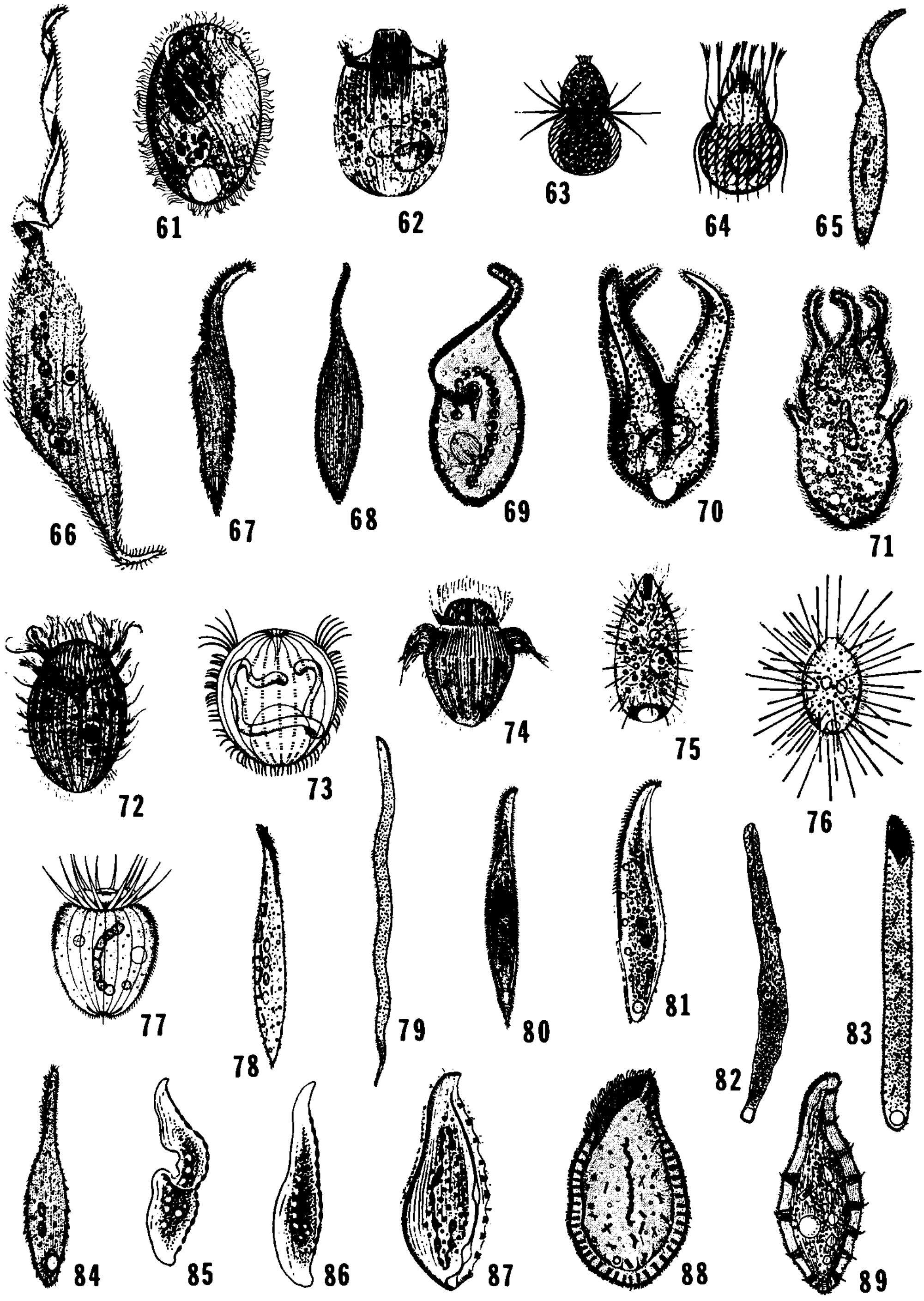

PLATE XXII, concluded. [See page 243 for figure explanations.]

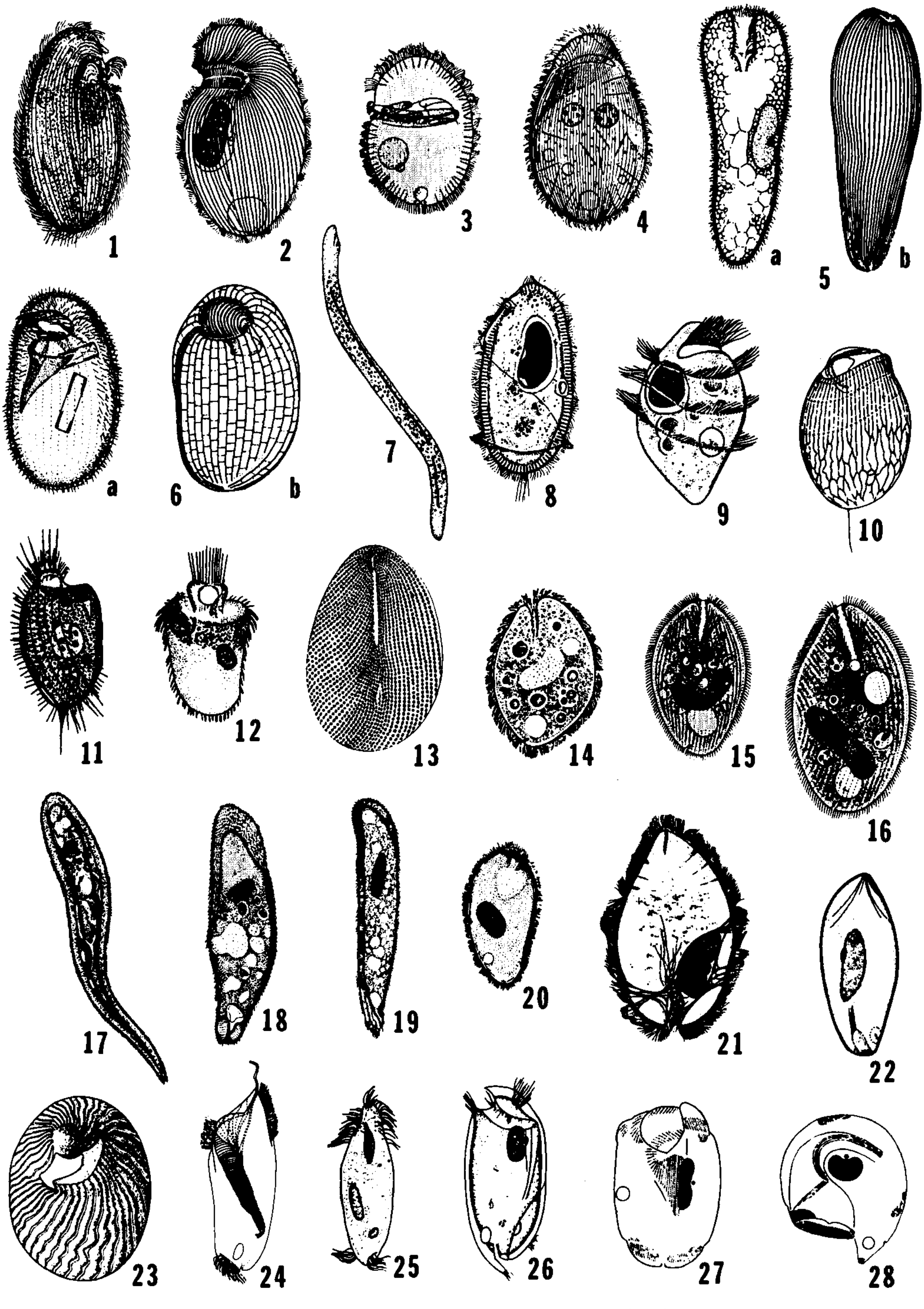

PLATE XXIII. Class Kinetofragminophora, subclass Vestibulifera: selected genera. [See page 243 for figure explanations.]

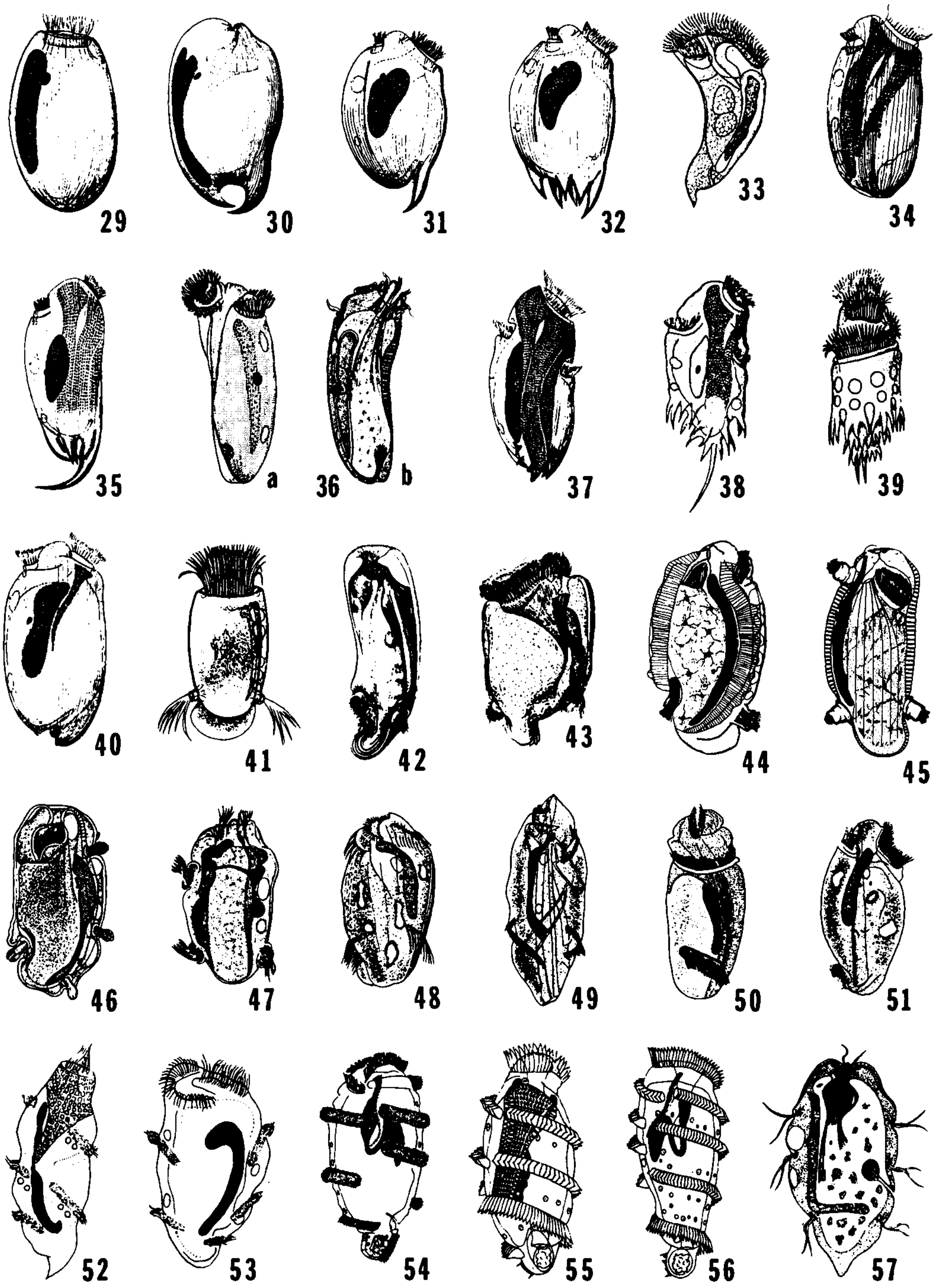

PLATE XXIII, continued. [See page 243 for figure explanations.]

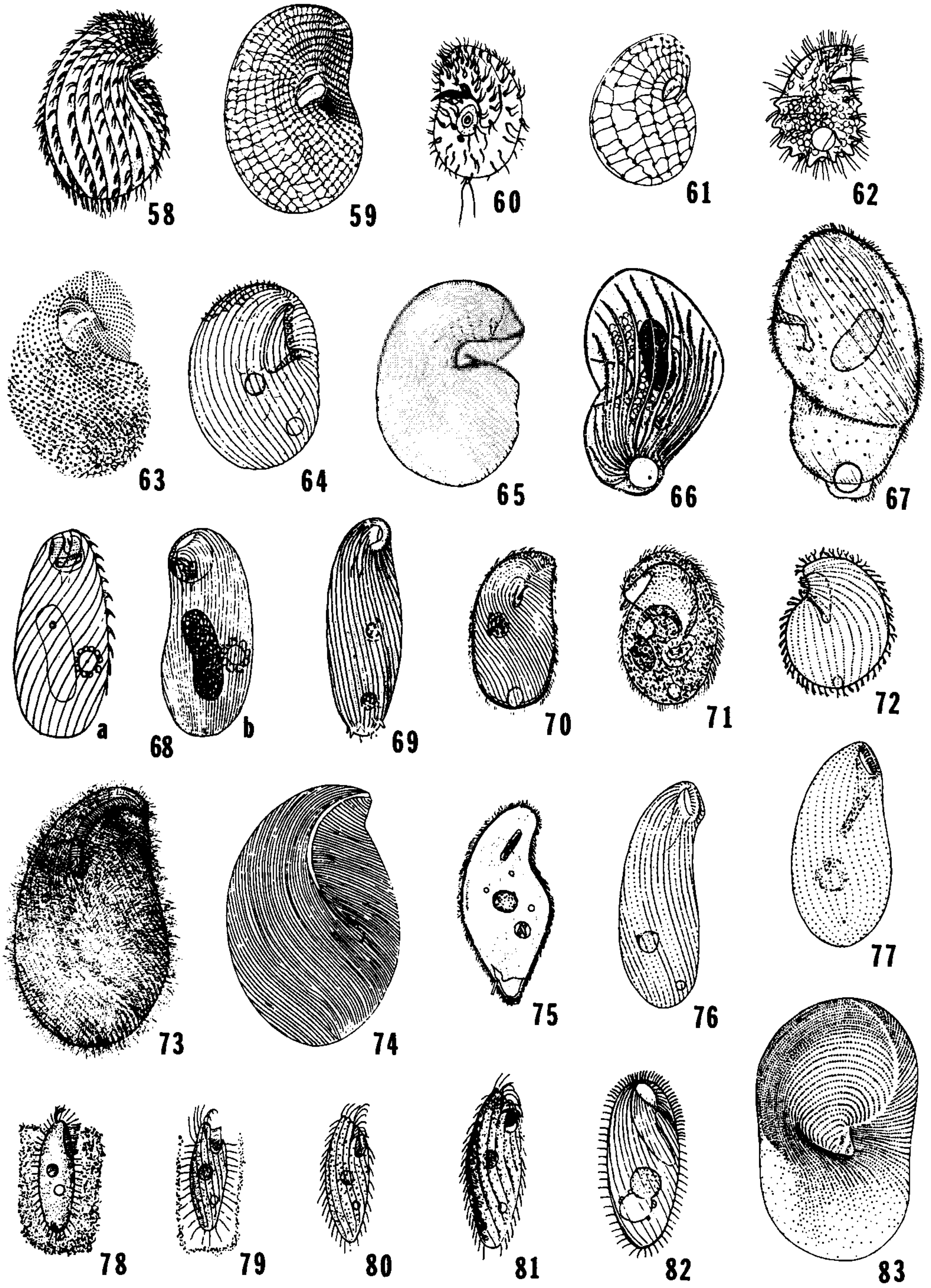

PLATE XXIII, concluded. [See page 243 for figure explanations.]

EXPLANATION OF FIGURES

PLATE XXIV (pages 251–254)

Page 251. Fig. 1. *Nassulopsis* (Jankowski). 2. *Orthodonella* (Jankowski). 3. *Synhymenium* (Jankowski). 4. *Eucamptocerca* (da Cunha). 5. *Scaphidiodon* (Dragesco). 6, 7. *Chilodontopsis* (Ozaki & Yagiu, Agamaliev). 8–12. *Nassula* (Schewiakoff, Fauré-Fremiet, Dingfelder, Jankowski, Dingfelder). 13a,b. *Enigmostoma* (Dragesco). 14, 15. *Enneameron* (Fauré-Fremiet, Ozaki & Yagiu). 16. *Paranassula* (Noland). 17, 18. *Furgasonia* (Dragesco, Fauré-Fremiet). 19, 20. *Leptopharynx* (Savoie, Prelle). 21a,b. *Pseudomicrothorax* (Dragesco). 22. *Stammeridium* (Wenzel). 23, 24. *Drepanomonas* (Wenzel, Penard). 25. *Microthorax* (Kahl). 26. *Hemicyclium* (Kahl). 27, 28. *Discotricha* (Dragesco, Tuffrau).

Page 252. Fig. 29. *Chilodonella* (Mackinnon & Hawes). 30. *Trithigmostoma* (Mackinnon & Hawes). 31. *Phascolodon* (Dingfelder). 32. *Thigmogaster* (Deroux). 33, 34. *Chlamydodon* (Ozaki & Yagiu, Fauré-Fremiet). 35a,b. *Cyrtophoron* (Deroux). 36. *Gastronauta* (Deroux). 37. *Lynchella* (Deroux). 38. *Chlamydonella* (Deroux). 39. *Atopochilodon* (Deroux). 40. *Plesiotrichopus* (Fauré-Fremiet). 41. *Trochochilodon* (Deroux). 42. *Aegyriana* (Deroux). 43. *Parachilodonella* (Dragesco). 44. *Trichopodiella* (Fauré-Fremiet). 45, 46. *Trochilioides* (Dragesco, Jankowski). 47. *Sigmocineta* (Jankowski). 48–51. *Dysteria* (Stein, Dragesco, Kahl, Jankowski). 52. *Hartmannulopsis* (Deroux & Dragesco). 53. *Trochilia* (Dragesco). 54. *Hypocoma* (Deroux). 55. *Parahypocoma* (Burreson). 56a,b. *Crateristoma* (Jankowski).

Page 253. Figs. 57–76. Chonotrichs. 57. *Lobochona* (Jankowski). 58, 59. *Heliochona*, adult with bud, and enlarged view of apical end (Guilcher, Jankowski). 60a,b. *Chilodochona*, adult and bud (Guilcher). 61a,b. *Filichona*, with enlarged view of apical end (Jankowski). 62. *Heterochona* (Matsudo & Mohr). 63, 64. *Spirochona*, adult with bud, and enlarged view of apical end (Stein, Guilcher). 65. *Oenophorachona*, with bud (Jankowski). 66. *Cavichona* (Jankowski). 67, 68. *Stylochona*, adult with bud, and pair of mature forms (Jankowski, Kent). 69. *Ctenochona*, with bud (Jankowski). 70. *Actinichona*, with two buds (Jankowski). 71. *Kentrochonopsis*, with multiple buds (Doflein). 72. *Kentrochona* (Rompel). 73. *Chonosaurus* (Jankowski). 74. *Oxychonina*, with bud (Jankowski). 75. *Isochona*, with bud (Jankowski). 76. *Spinichona* [redrawn to highlight spines] (Jankowski). 77–83. Rhynchodids. 77. *Kozloffia* (Kozloff). 78. *Crebricoma* (Raabe). 79. *Ancistrocoma* (Kozloff). 80. *Insignicoma* (Kozloff). 81. *Hypocomella* (Kozloff). 82. *Gargarius* (Chatton & Lwoff). 83. *Sphenophrya*, with bud (Chatton & Lwoff).

Page 254 (top two rows). Figs. 84–93. Apostomes. 84. *Ophiuraespira* (Chatton & Lwoff). 85. *Calospira* (Chatton & Lwoff). 86. *Foettingeria* [production of tomites in cyst by palintomy] (Chatton & Lwoff). 87a,b. *Gymnodinioides*, trophont and tomite (Chatton & Lwoff). 88. *Collinia*, protomite (de Puytorac & Lom). 89a,b. *Chromidina*, trophont and tomite (Chatton & Lwoff). 90a,b. *Cyrtocaryum*, trophont and tomite (Fauré-Fremiet & Mugard). 91. *Ascophrys*, tomite (Campillo & Deroux). 92. *Conidophrys*, tomite (Jankowski). 93. *Askoella*, tomite (Jankowski).

PLATE XXV (pages 254–256)

Page 254 (bottom two-thirds). Figs. 1–18. Suctorians [beginning of]. 1, 2. *Podophrya*, adult and bud (Dingfelder, Guilcher). 3. *Sphaerophrya* (Lauterborn). 4. *Parapodophrya*, capturing *Colpidium* (Kahl). 5. *Paracineta* (Maupas). 6a,b. *Kystopus*, adult inside *Paramecium* and mature bud settling on fresh host (Jankowski). 7, 8. *Ephelota*, adult and bud (Hertwig, Guilcher). 9, 10. *Dendrosomides*, with large bud and group of attaching buds (Collin, Guilcher). 11. *Ophryodendron*, with large bud (Collin). 12. *Lecanophrya* (Kahl). 13, 14. *Spelaeophrya*, adult and bud (Stammer, Nie & Lu). 15. *Tachyblaston*, with buds (Martin). 16. *Urnula* (Kormos & Kormos). 17. *Metacineta* (Collin). 18. *Trophogemma* (Jankowski).

Page 255. Fig. 19a,b. *Thecacineta*, adult with bud, and separate bud (Matthes). 20. *Praethecacineta* (Batisse). 21. *Phalacrocleptes* (Kozloff). 22–26. *Acineta* [showing buds in first and last figure and attached parasitic *Pseudogemma*, another suctorian, in next-to-last figure] (Maupas, Kellicott, Wang & Nie, Batisse, Guilcher). 27. *Acinetopsis* (Robin). 28. *Multifasciculatum* (Goodrich & Jahn). 29a,b. *Trematosoma*, adult [capturing a flagellate] and bud (Guilcher). 30. *Squalorophrya* (Goodrich & Jahn). 31. *Solenophrya* (Hull). 32. *Choanophrya*, with bud (Collin). 33. *Hypophrya* (López-Ochoterena). 34. *Pottsiocles*, bud (Chatton & Lwoff). 35. *Rhyncheta* (Hitchen & Butler). 36. *Dactylophrya* (Collin). 37. *Erastophrya* [anchored to peritrich *Apiosoma*] (Fauré-Fremiet). 38. *Anarma* (Goodrich & Jahn). 39. *Lernaeophrya* (Gönnert). 40. *Dendrosoma*, portion of colony (Kent). 41. *Baikalodendron* (Swarczewsky). 42. *Astrophrya* (Awerinzew). 43. *Phagobranchium* (Davis). 44. *Trichophrya* (Bütschli). 45. *Actinobranchium* (Calkins).

Page 256. Figs. 46–48. *Tokophrya*, adults and buds (Matthes & Stiebler, Collin, Fauré-Fremiet & Guilcher). 49. *Stylophrya* (Swarczewsky). 50. *Allantosoma* (Hsiung). 51–53. *Discophrya*, adult with developing bud, a mature bud, another adult (Collin, Fauré-Fremiet & Guilcher, Matthes). 54. *Periacineta*, bud (Guilcher). 55–57. *Dendrocometes*, adult, bud, another adult with developing bud (Bütschli, Fauré-Fremiet & Guilcher, Small–unpub.). 58. *Platophrya* (Gönnert). 59–61. *Heliophrya*, bud and adults and view of a feast on captured *Paramecium* (Dragesco et al., Bick, Spoon et al.). 62. *Cyathodinium* (Lucas). [Mature or separated suctorian buds also known as swarmers.]

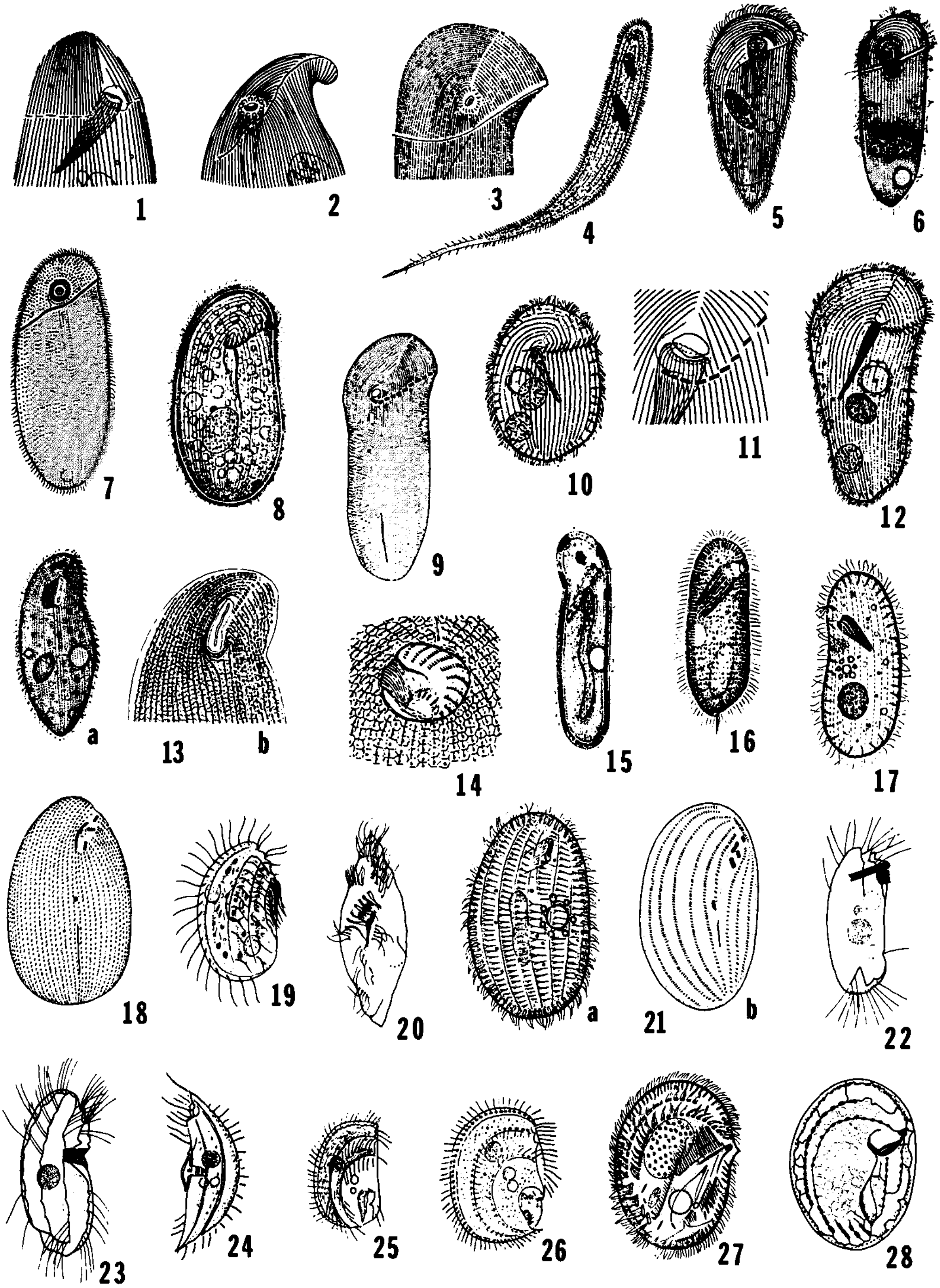

PLATE XXIV. Class Kinetofragminophora, subclass Hypostomata: selected genera. [See page 250 for figure explanations.]

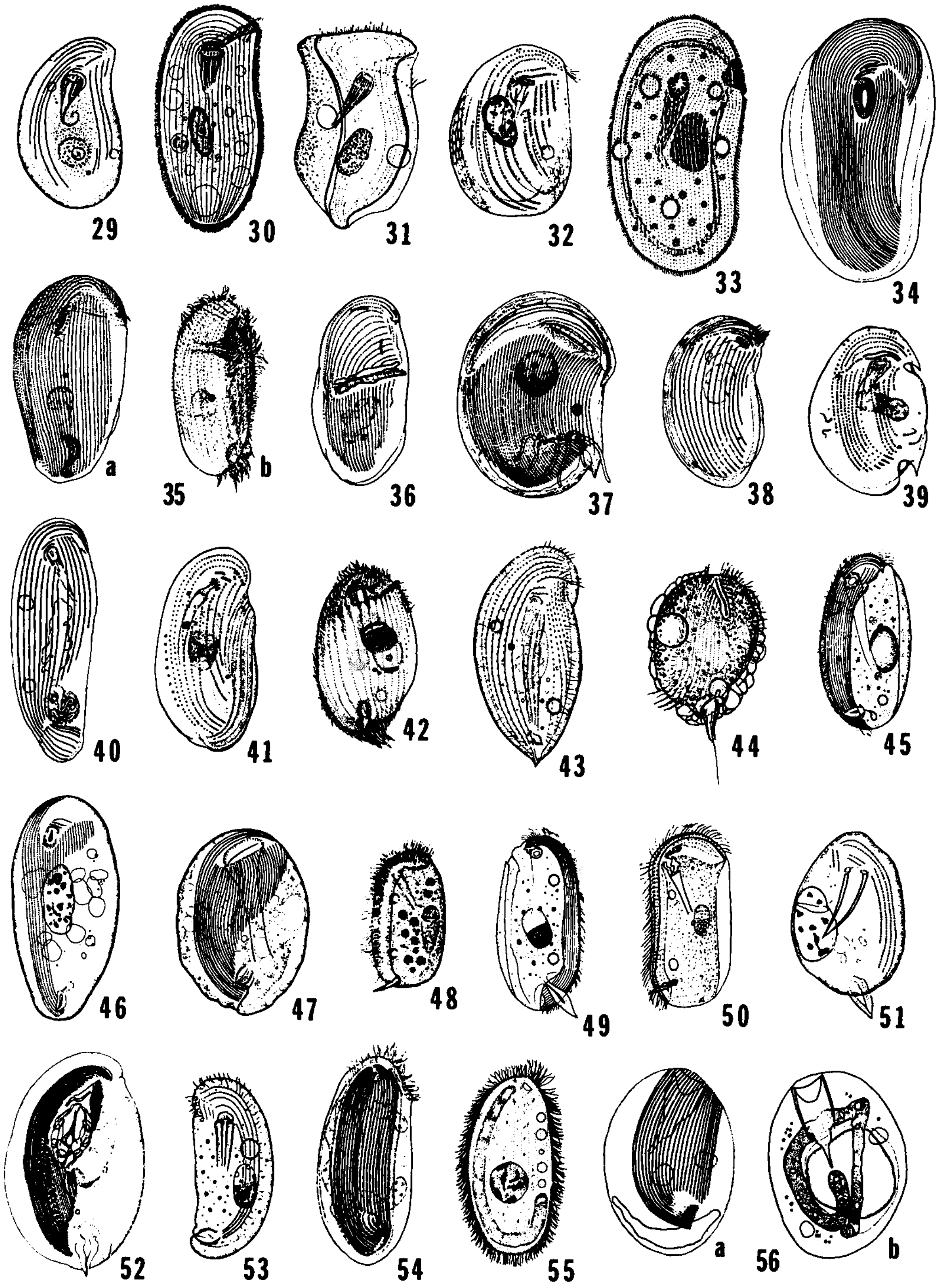

PLATE XXIV, continued. [See page 250 for figure explanations.]

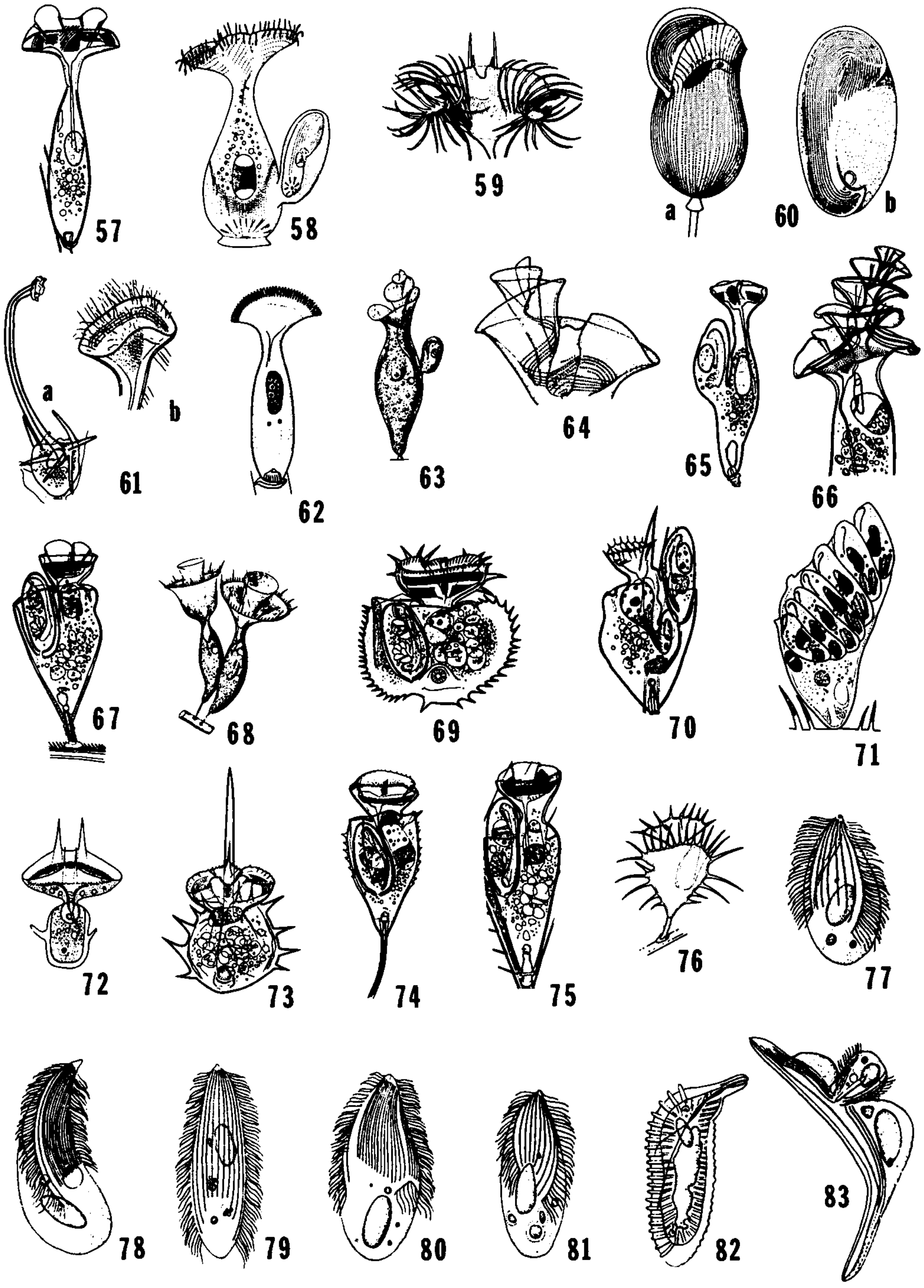

PLATE XXIV, continued. [See page 250 for figure explanations.]

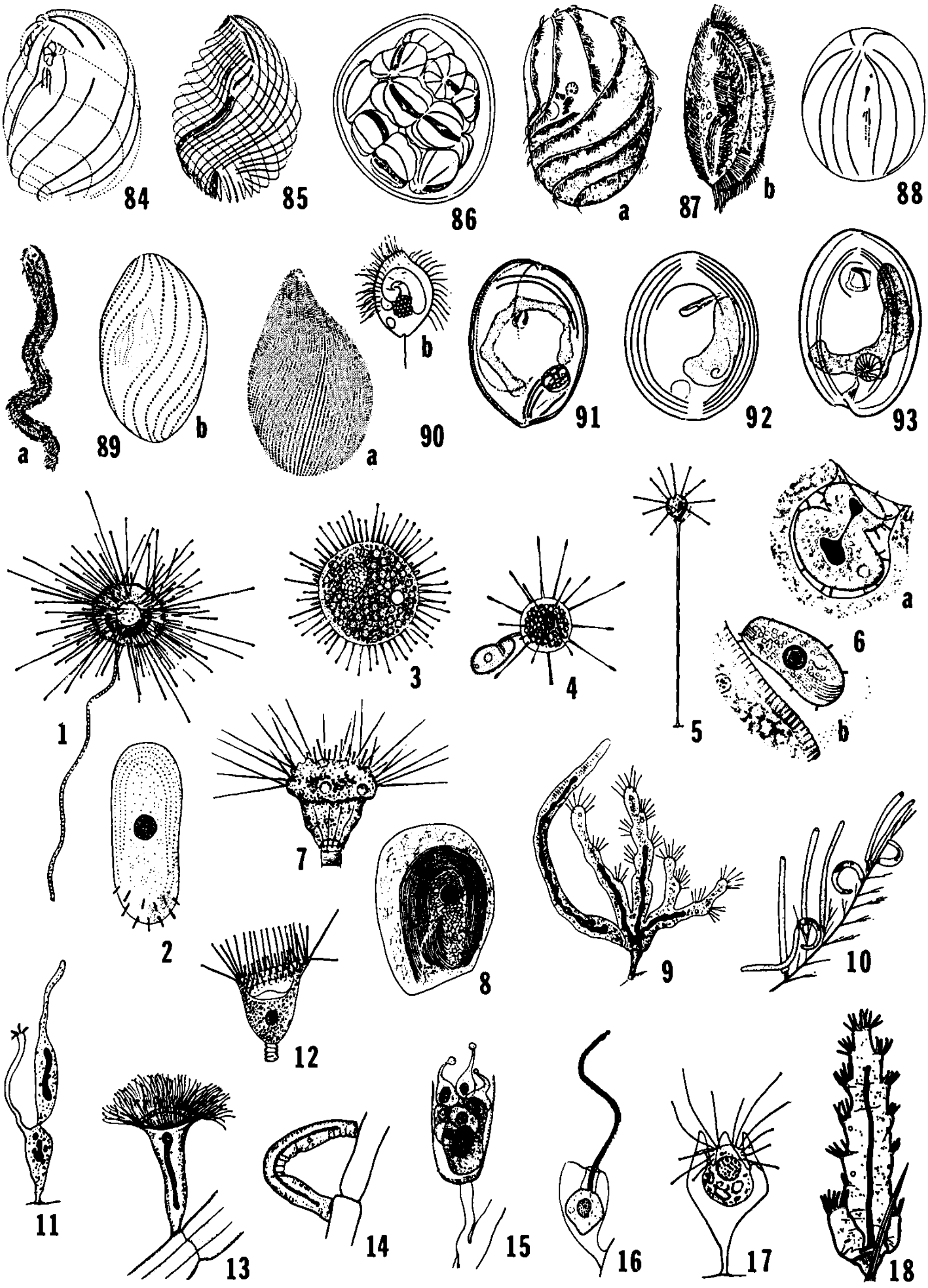

PLATE XXIV, concluded [top two rows]. PLATE XXV. Class Kinetofragminophora, subclass Suctoria: selected genera. [See page 250 for figure explanations.]

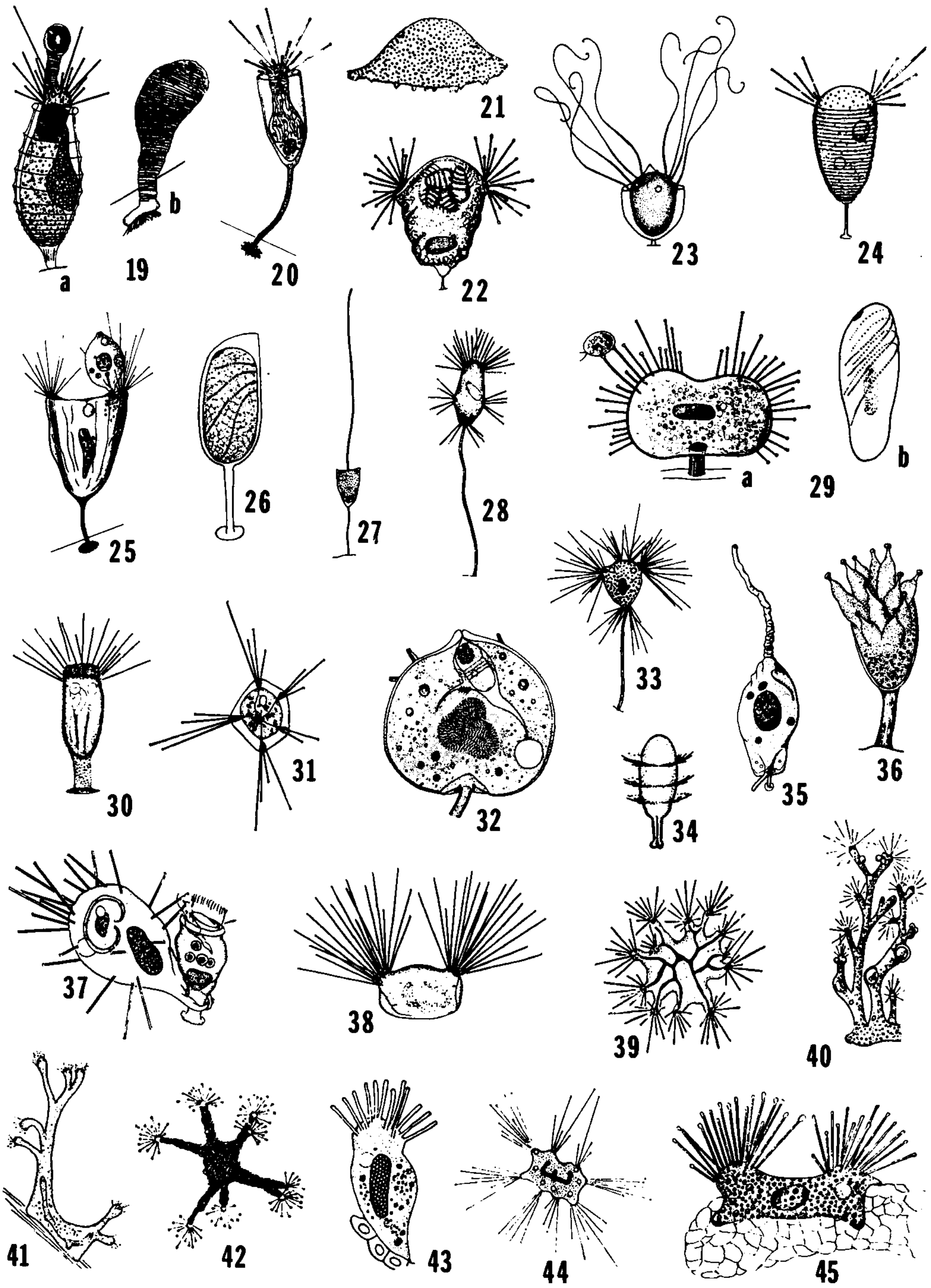

PLATE XXV, continued. [See page 250 for figure explanations.]

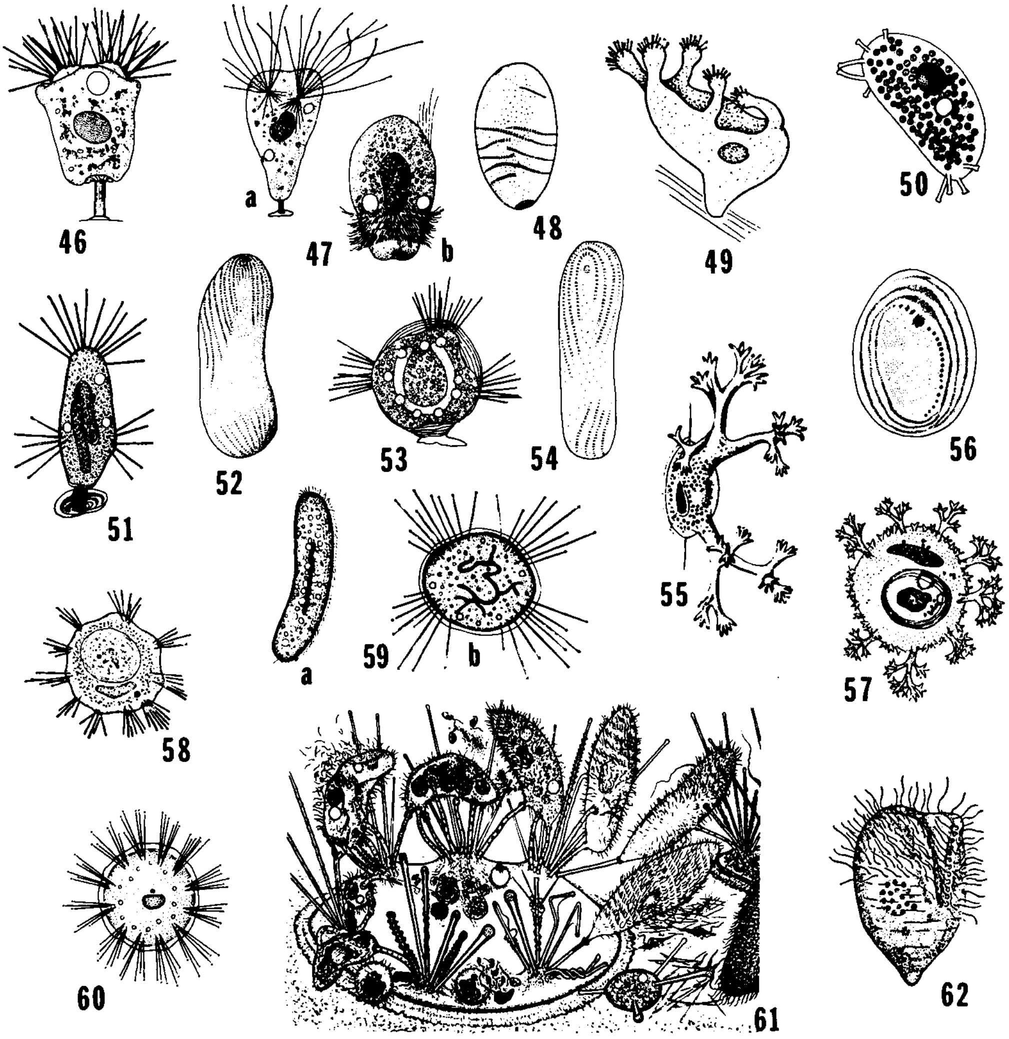

PLATE XXV, concluded. [See page 250 for figure explanations.]

Class II. OLIGOHYMENOPHORA de Puytorac et al., 1974

(syns. Aspirigera *p.p.*, Aspirotricha *p.p.*, Holotricha [Holotrichasina, Holotrichia] *p.p.*, Kinetodesmatophora *p.p.*, Membranellophora [Membranellata] *p.p.*, Stomatea *p.p.*; Axotrichidea + Peritrichidea; Hymenotricha (*sensu* Raabe) + Peritricha; Tetrahymenophora + Cyclohymenophora)

Oral apparatus, distinct from the somatic ciliature, comprised of a well-defined paroral membrane plus several membranelles or peniculi typically located in a buccal cavity or infundibulum on the ventral surface of the body, with a cytostome at the base of the cavity (though neither ciliature nor cytostome present in one order); cytopharynx generally inconspicuous; stomatogenesis parakinetal or buccokinetal; kinetodesmata regularly and generally conspicuously present; trichocysts and nematodesmata common in a principal subgroup in which mucocysts are rare; in modes of fission, some (but limited) variation shown; conjugation usually temporary, but solely total in one major group; widely distributed as free-living or symbiotic forms, with many as symphorionts and one entire order endocommensalistic; often microphagous in feeding habits, but the endocommensalistic order entirely osmotrophic.

Subclass (1) **Hymenostomata** Delage & Hérouard, 1896

(syns. Homoiotricha *p.p.*, Tetrahymenophora *s.s.*)

Buccal structures, when not absent altogether, usually inconspicuous; typically uniform, often heavy, somatic ciliation; body generally of medium size; found in diverse habitats, with nonsymbiotic forms predominantly from fresh-water biotopes. [Grain et al. (1976) have very recently erected a new order, the Parahymenostomatida, which they assign to this subclass. The (few) organisms involved have been allocated in this book to the order Nassulida (class Kinetofragminophora); but the matter certainly deserves further serious consideration.]

Order 1. HYMENOSTOMATIDA Delage & Hérouard, 1896

(syns. Hymenostom[at]orida, Hymenostomida, Hymenostomina)

With characteristics of subclass *s.s.* (above). Well-defined buccal cavity (with rare exception), typically with paroral membrane plus tripartite AZM (or peniculi ± quadrulus); fusiform, explosive trichocysts in one suborder; mostly free-living, fresh-water forms. [Third suborder distinctly different from first two, possibly deserving independent ordinal status.]

Suborder (1) Tetrahymenina Fauré-Fremiet in Corliss, 1956

(syn. Tetrahymenorina)

With the more conservative characteristics of the order (above). Relatively inconspicuous "UM + AZM" mouthparts, generally, and one family secondarily mouthless; stomatogenesis parakinetal; preoral but no postoral suture; mucocysts common, but no trichocysts or oral nematodesmata; widespread fresh-water microphagous forms (a few edaphic and/or histophagous, and several polymorphic with carnivorous macrostome stage) plus some symbiotic species, latter (whether facultative or obligate forms) associated mainly with invertebrate hosts.

Family TETRAHYMENIDAE Corliss, 1952

(syns. Deltopylidae, Frontoniidae *p.p.*, Leucophry[i]dae)

With general characteristics of suborder *s.s.* (above); body pyriform to elongate-ovoid to cylindrical in shape; membranellar bases of uniform width; one to three (up to nine in *Lambornella*) postoral kineties, rightmost one typically stomatogenic; some species with caudal cilium; members of one genus (*Tetrahymena*) unique in exhibiting polymorphism (microstome-macrostome stages, cysts, etc.) and (endo)symbiosis in variety of hosts (slugs, snails, clams, enchytraeid worms, midges, mosquitoes, tadpoles, fishes, etc.); fresh-water or edaphic habitats.

Colpidium Stein, 1860 (syn. *Dexiostoma*). Several species. Pl. IV, Figs. 23, 43; VII 8, 9; XXV 4; XXVI 5, 8, 11–15.

Deltopylum Fauré-Fremiet & Mugard, 1946. Single species. Pl. III, Fig. 24; XXVI 23, 24.

Lambornella Keilin, 1921 (resurrected genus). Few species. Pl. XXVI, Figs. 16–18.

Stegochilum Schewiakoff, 1893. Few species. Pl. XXVI, Fig. 20.

Tetrahymena Furgason, 1940 [*a nomen conservandum;* principal syns. *Leptoglena, Leucophrydium, Leucophrys, Paraglaucoma* (of Kahl *and* of Warren [hom.]), *Protobalan-*

tidium, Roquea, Tetrahymen, Tetrahymenia, Turchiniella]. Many species. Pl. I, Figs. 1, 2; II 5, 11; III 7; IV 4, 5, 35, 36, 38–40; V 5, 15, 20, 16–28; XI 1; XXVI 1–10.

Incertae sedis: Blepharostoma Schewiakoff, 1893, single species; *Malacophrys* Kahl, 1926, few spp.

Family GLAUCOMIDAE Corliss, 1971

(syns. Frontoniidae *p.p.*, Tetrahymenidae *p.p.*)

Body ovoid to ellipsoidal; buccal cavity large; infraciliary base of second or third membranelle much wider (in rows of kinetosomes) than others; 5–10 postoral kineties, rightmost one stomatogenic; no caudal cilia; all species free-living, generally microphagous; fresh-water, occasionally edaphic, habitats.

Chasmatostoma Engelmann, 1862. Single species.
Dichilum Schewiakoff, 1889. Few species.
Epenardia Corliss, 1971. Single species. Pl. XXVI, Figs. 37–39.
Espejoia Bürger, 1908. Single species. Pl. V, Fig. 12g; XXVI 40–42.
Glaucoma Ehrenberg, 1830 (syn. *Dallasia*). Several species. Pl. IV, Figs. 28, 41, 42; VII 4; XXVI 25–35.
Glaucomella Grolière, 1977 (syn. *Glaucoma* p.p.). Single species. Pl. XXVI, Fig. 36.
Monochilum Schewiakoff, 1893. Few species. Pl. XXVI, Fig. 19.
Physalophrya Kahl, 1931. Few species.
Pseudoglaucoma Kahl, 1931. Single (perhaps two?) *moss* species. [Kahl's lone *marine* species, given a new generic name in this book, is placed in an *incertae sedis* position within the order Scuticociliatida, suborder Philasterina. But the *moss* form, *P. muscorum*, is here designated the type-species and thus retains the original generic name.]

Incertae sedis: Dexiotrichides Kahl, 1951; *Discozoon* Vuxanovici, 1960; *Pinchatia* Shibuya, 1931; *Pleurochilidium* Stein, 1860: each with single species.

Family TURANIELLIDAE Didier, 1971

Large body, elongate-ovoid (tapering posteriorly) in shape, with conspicuous oral structures in anterior half; buccal ciliature comprised of membranelles resembling peniculi and quadrulus, yet stomatogenesis parakinetal, as in the Glaucomidae; somatic ciliature, including several postoral kineties, typically tetrahymenine; no nematodesmata nor trichocysts, but also no mucocysts; dimorphic life cycle, with macrostome form carnivorous on other ciliates; fresh-water habitats. [Taxonomically controversial group, placed by some in the suborder Peniculina.]

Turaniella Corliss, 1960 (for *Turania*). Single species. Pl. XXVI, Fig. 43.

Family CURIMOSTOMATIDAE Jankowski, 1968

(syn. Curinostomatidae)

Mouthless forms; body small, pyriform to ovoid in shape; silverline system much like that of *Tetrahymena* (family Tetrahymenidae, above); obligate endosymbiont in tissues or cavities of fresh-water snails, limpets, clams, and turbellarians.

Curimostoma Kozloff, 1954 (syn. *Curinostoma*). Single species. Pl. IV, Fig. 3; XXVI 21, 22.
Dogielella Poljansky, 1925. Few species.

Incertae sedis in suborder Tetrahymenina:

Family SAGITTARIIDAE R. & L. Grandori, 1935

(for Proshymenidae)

Conspicuous buccal ciliature of unknown composition, apically located; small body size, with sparse somatic ciliation plus caudal cilium; found in soil.

Sagittaria R. & L. Grandori, 1934. Single species.

Suborder (2) Ophryoglenina Canella, 1964

Oral ciliature deep in buccal cavity, complex in conformation and comportment, with "watchglass organelle" (often accompanied by pigment mass) characteristically in vicinity; stomatogenesis parakinetal, regularly with oral replacement of parental mouthparts; preoral suture present, postoral less distinct; body size large, conspicuous in trophont-tomont stage; polymorphic life cycle, including cysts and palintomic reproduction; histophagous forms, generally feeding on moribund or wounded fresh-water invertebrates, though several species attack healthy fishes (marine as well as fresh-water) to host's eventual detriment.

Family OPHRYOGLENIDAE Kent, 1881

With characteristics of suborder *s.s.* (above). Fresh-water, histophagous (occasionally parasitic) forms, with slender, inconspicuous theronts; number of tomites (produced within cyst) varies, 4–128.

Ophryoglena Ehrenberg, 1831. Many species. Pl. I, Fig. 19; XI 2; XXVI 44–47.

Protophryoglena Mugard, 1949 (syn. of *Ophryoglena*?). Single species.

Family ICHTHYOPHTHIRIIDAE Kent, 1881

(syns. Cryptocaryonidae, Ichthyophthiridae)

Oral ciliature possibly less complex than in ophryoglenids, but similar in many other characteristics; encysted tomont (away from host) can be of great size, producing hundreds (up to 2,000) tomites by palintomic fission; trophonts invade epithelial tissues of marine or fresh-water fishes, causing white spot disease; few species, but widespread distribution.

Cryptocaryon Brown, 1951. Single (marine) species. Pl. XXVI, Fig. 51.

Ichthyophthirioides Roque & de Puytorac, 1966 (syn. of *Ichthyophthirius*?). Single species.

Ichthyophthirius Fouquet, 1876. Single (possibly more?) species. Pl. XXVI, Figs. 48–50.

Suborder (3) Peniculina Fauré-Fremiet in Corliss, 1956

(syns. Trichohymenostomata and Vestibulata *sensu* von Gelei; Frontoniina + Quadrulina; Peniculida)

Peniculi of oral ciliature deep in buccal cavity (itself sometimes preceded by oral-area depression or groove, the prebuccal cavity); stomatogenesis buccokinetal; distinct pre- and postoral sutures; spindle trichocysts and nematodesmata, but not mucocysts, of common occurrence; many species with endosymbiotic algae or bacteria; sizable but monomorphic, generally microphagous, forms, often without cysts; widely distributed, predominantly in fresh-water habitats. [This suborder possibly warrants elevation to separate ordinal status.]

Family PARAMECIIDAE Dujardin, 1840

With characteristics of suborder *s.s.* (above). Conspicuous prebuccal cavity (formerly called a "vestibulum") leading to equatorially located buccal cavity; oral ciliature comprised of distinctive paroral membrane, two peniculi, and single quadrulus; two contractile vacuoles. [The "slipper-shaped animalcules," so long and (relatively) well known: see drawings in Plate XXVI, especially.]

Paramecium O. F. Müller, 1773 (syns. *Cypreostoma, Helianter, Param[a]ecidium, Paramaecium, Paramoecium*). Many species, now [see Sonneborn (1975a), Vivier (1974)]. Pl. II, Fig. 6; III 6; IV 45; V 1, 9, 10b, 11b, 12h, 17, 21, 23–25, 29, 30, 32; VII 10; XI 3; XXII 60; XXV 6, 61; XXVI 52–63.

Incertae sedis: Physanter Jankowski, 1975 (for *Faurella* Roque, 1966 [hom.]). Single species.

Family FRONTONIIDAE Kahl, 1926

(for Chiliferidae)

Prebuccal area shallow or absent; several ophryokineties to right of oral area; three peniculi in buccal cavity, in anterior third of body; cytostome expansible, and area rich in nematodesmata and specialized phagoplasm; single contractile vacuole; body usually large; cysts common in some species; mostly herbivorous in feeding preference and free-living, but one species commensal on gills of *Amphioxus.*

Disematostoma Lauterborn, 1894. Several species. Pl. IV, Fig. 30; XXVI 68, 69.

Frontonia Ehrenberg, 1838. Many species. Pl. IV, Fig. 7; V 16; XXVI 64–67.

Frontoniella Wetzel, 1927. Few species.

Wenrichia Jankowski, 1967 (syn. *Disematostoma* p.p.). Single species. Pl. XXVI, Fig. 70.

Incertae sedis: Schistophrya Kahl, 1933; *Sigmostomum* Gulati, 1925: each with single species.

Family CLATHROSTOMATIDAE Kahl, 1926

(syn. Clathrostomidae)

Quite similar to the Frontoniidae (above); cytopharyngeal "basket" of nematodesmata particularly striking.

Clathrostoma Penard, 1922. Several species. Pl. XXVI, Fig. 71.

Family UROCENTRIDAE Claparède & Lachmann, 1858

(syn. Calceolidae)

Body short, cylindrical, with two broad encircling bands of closely set cilia plus an eccentric posterior tuft; no depressed prebuccal area, and buccal cavity subequatorial in location; contractile vacuole single, with multiple collecting canals; common planktonic or polysaprobic organisms in fresh-water habitats.

Urocentrum Nitzsch, 1827 (syn. *Calceolus*). Single species. Pl. II, Fig. 14; IV 37; XXVI 76, 77; and in *Frontispiece.*

Family STOKESIIDAE Roque, 1961

(syn. Maritujidae)

Distinctively cone- (with rounded angles) or heart-shaped body, with relatively large buccal area covering much of the apical (base of cone) and ventral surfaces of the organism; otherwise, much like other peniculines.

Marituja Gajewskaja, 1928. Single species. Pl. XXVI, Fig. 75.

Parastokesia Jankowski, 1967 (syn. *Disematostoma* p.p.). Single species. Pl. XXVI, Fig. 74.

Stokesia Wenrich, 1929. Single species. Pl. XXVI, Fig. 78.

Family NEOBURSARIDIIDAE Dragesco & Tuffrau, 1967

Large (up to 710 μm in length), "heterotrich-looking" (an extensive false AZM, etc.), pan-tropical peniculine, perhaps most like *Stokesia* (preceding family) in general characteristics though more like *Paramecium* in shape; prominent trichocysts; two contractile vacuoles; carnivorous on other ciliates.

Neobursaridium Balech, 1941. Single species. Pl. XXVI, Fig. 72.

Family LEMBADIONIDAE Jankowski, n. fam.

Unique in extensiveness of buccal cavity, occupying nearly entire ventral surface; buccal ciliature, however, reduced to large "membrane" on left and modest one on right, though infraciliature (and its fibrillar system) rather complex; body fully ciliated, often with tuft of longer cilia caudally; single contractile vacuole. [Jankowski (1967a) proposed the familial name, but with no description or characterization; I am crediting him with the group, but as of the date of the present work.]

Lembadion Perty, 1849. Several species. Pl. V, Fig. 38; XI 4; XXVI 73.

Order 2. SCUTICOCILIATIDA Small, 1967

Body typically small to medium in size; ciliation uniform, though sometimes sparse, often including specific thigmotactic area(s) and one or more caudal cilia; a director-median common to many species; paroral membrane sometimes the dominating feature of the oral ciliature, which may lie in an extended but shallow buccal cavity; stomatogenesis buccokinetal with complex morphogenetic movements and unique involvement of a scutica (which may persist in the trophont as a scutico-vestige); mucocysts prominent; large, elongate, cortically located, often-fused mitochondria conspicuously present; cysts widespread; particularly abundant in marine habitats, free-living or in symbiotic association with primarily invertebrates (especially molluscs, echinoids, and annelids), but also some edaphic and fresh-water forms.

Suborder (1) Philasterina Small, 1967

(syns. Deuterostomatina *p.p.*, Pseudocohnilembina)

Infraciliature of paroral membrane may show reduced "a" and no "c" segment, while "b" is always clearly present; scutico-vestige separate and posterior to paroral, often in anterior part of distinct director-meridian; mucocysts and mitochondria very prominent; body size generally small; most commonly in brackish or marine habitats, including sand; numerous species free-living, but number of others occur as inquilines in sea urchins or as commensals in molluscs, coelenterates, annelids, sipunculids, and even the sea horse.

Family PHILASTERIDAE Kahl, 1931

(syns. Frontoniidae *p.p.*, Paralembidae, Paranophryidae, Porpostomatidae, possibly Protocruziidae)

Body elongate to finger-shaped, though small and ovoid in some genera, with anterior end bluntly tapered; life cycle typically monomorphic (but *Potomacus* exhibits microstome-macrostome transformation); uniform ciliation, generally with single caudal cilium; lengthy, usually shallow, buccal cavity or depression, typically with three (many in *Porpostoma*) adoral ciliary organelles (sometimes anarchic fields of ciliferous kinetosomes rather than membranelles) arranged more or less in an anteroposterior line in center or left of center of oral area; predominantly free-living marine forms, though several histophagous on or in sponges, tubularian coelenterates, sea horses, polychaete annelids, crabs (in blood), etc. [Family too heterogeneous?]

Glauconema Thompson, 1966. Single species.

Glauconema Thompson, 1966. Single species.
Helicostoma Cohn, 1866. Single species.
Madsenia Kahl, 1934. Single species. Pl. XXVII, Fig. 7.
Miamiensis Thompson & Moewus, 1964. Single species. Pl. XXVII, Fig. 16.
Mugardia Small [unpublished]. Single species.
Paralembus Kahl, 1933 (for *Lemboides*). Few to several species. Pl. XXVII, Fig. 8.
Paranophrys Thompson & Berger, 1965 (syn. *Anophrys* p.p.). Several species. Pl. IV, Fig. 8; XXVII 11, 12.
Parauronema Thompson, 1967. Single species. Pl. XXVII, Fig. 9.
Philaster Fabre-Domergue, 1885. Few species. Pl. IV, Fig. 51; XXVII 1–3.
Philasterella Evans [unpublished]. Single species.
Philasterides Kahl, 1931. Single species.
Potomacus Thompson, 1966 (syn. *Potamacus*). Single species. Pl. XXVII, Fig. 10.
Incertae sedis: Metanophrys de Puytorac, Grolière, Roque & Detcheva, 1974, Pl. XXVII, Fig. 6; *Porpostoma* Möbius, 1888 (syn. *Porpostomum*), Pl. V, Fig. 12i; XXVII 4, 5: each with single species.

Family URONEMATIDAE Thompson, 1964

Body small, elongate-ovoid, sparsely ciliated, with anterior pole conspicuously naked and caudal cilium or cilia at posterior pole; buccal ciliature relatively inconspicuous in long and shallow depression, and "membranelle" number 1 entirely nonciliferous; scutico-vestige bears cilia; in marine or fresh-water habitats, occasionally edaphic.

Homalogastra Kahl, 1926. Few species.
Pseuduronema Hoare, 1927. Single species.
Urocyclon Small [unpublished]. Single species.
Uronema Dujardin, 1841. Many to very many species. Pl. XXVII, Figs. 13–15; *Frontispiece.*
Uronemopsis Kahl, 1931. Single species. Pl. XXVII, Fig. 18.
Uropedalium Kahl, 1928. Few species. Pl. XXVII, Fig. 17.

Family COHNILEMBIDAE Kahl, 1933

(for Lembidae)

Body slender, finger-shaped, tapering to point anteriorly; long caudal cilium; most conspicuous in narrow oral depression is a false "double-membrane" – one membranelle plus adjacent (left side) row of somatic ciliature (n^th^ kinety); in marine (including Great Salt Lake) habitats.

Cohnilembus Kahl, 1933 (for *Lembus*). Several to many species. Pl. XXVII, Figs. 20–23.

Family ENTORHIPIDIIDAE Madsen, 1931

Body large, flattened laterally, posterior end tapered to tail; dense, uniform somatic ciliation, with single caudal cilium; oral area, with two well-developed membranelles, overhung by frontal lobe of body; inquilinic in widely distributed species of sea urchins, algivorous within host intestine.

Entorhipidium Lynch, 1929. Several species. Pl. XXVII, Fig. 28.

Family ENTODISCIDAE Jankowski, 1973

(possible syn. Gullmarellidae)

Body of medium size, ovoid, dorsoventrally compressed, with small caudal projection bearing single bristle; buccal ciliature inconspicuous, located anteriorly on ventral surface; inquilines of sea urchins (*Entodiscus*), commensals in bivalve molluscs (*Pectenita*), or in esophagus of sipunculids (*Cryptochilidium*).

Cryptochilidium Schouteden, 1906 (syn. *Symbionecta*). Single species [not to be confused with *Cryptochilum*!]. Pl. XXVII, Figs. 24, 25.
Entodiscus Madsen, 1931. Few species. Pl. XXVII, Fig. 27.
Pectenita Jankowski, 1973. Single species. Pl. XXVII, Fig. 26.

Family CRYPTOCHILIDAE Berger, n. fam.

Body moderate to large in size, heavily ciliated, commonly with caudal projection bearing one or more longer cilia; buccal organelles shifted posteriorly in some genera, but retain similarity in general morphology and morphogenesis; inquilinic in sea urchins, plus a few species in wood-boring molluscs. [Family is erected here with credit to Berger, who has been planning to describe it, but as of the date of the present publication in which the first characterization appears.]

Biggaria Kahl, 1934. Single species [echinoid host]. Pl. V, Fig. 41; XXVII 29, 30.
Biggariella Profant [unpublished]. Single species.
Cryptochilum Maupas, 1883. Few to several species [not to be confused with *Cryptochilidium*!]. Pl. XXVII, Figs. 31, 32.
Metaxystomium Berger [unpublished]. Few species.
Metoikos Berger & Thompson [unpublished]. Single species.
Tanystomium Berger [unpublished]. Single species.
Thigmozoon Santhakumari & Nair, 1973 (syn. *Biggaria* p.p.). Few species [molluscan host].
Yagiua Profant [unpublished]. Single species.

Family THYROPHYLACIDAE Berger in Corliss, 1961

(syn. Thyrophylaxidae)

Large, ovoid, laterally compressed body, heavily ciliated, with minute caudal projection and prominent anterodorsal suture; large, deep buccal cavity, with somatic(?) kineties on right wall and somewhat reduced buccal ciliature (though membranelle number 2 large); numerous micronuclei, and even more contractile vacuole pores; carnivorous endocommensals of echinoids.

Plagiopyliella Poljansky, 1951. Single species.
Thyrophylax Berger in Corliss, 1961. Single species. Pl. XXVII, Fig. 33.

Family LOXOCEPHALIDAE Jankowski, 1964

(syn. Cardiostomatellidae)

Body elongate-ovoid, generally uniformly ciliated, with caudal cilium or cilia and (in some genera) naked apical end; pronounced parateny near anterior end; clearcut postoral suture replacing director-meridian in some species; buccal cavity small, anteroventral, with ciliature reminiscent of *Tetrahymena*; common polysaprobic forms in fresh-water (occasionally brackish) habitats.

Dexiotricha Stokes, 1885. Several species. Pl. IV, Figs. 26, 44; XXVII 37–39.
Loxocephalus Eberhard, 1862. Several species. Pl. XXVII, Figs. 34–36.
Paradexiotricha Grolière, 1975. Single species.
Paratetrahymena Thompson, 1963. Single species.
Incertae sedis: *Cardiostomatella* Corliss, 1960 (for *Cardiostoma*). Few spp. Pl. XXVII, Figs. 42, 43.

Family CINETOCHILIDAE Perty, 1852

Small to very small, flattened body, ovoid to ellipsoidal (sometimes looking very much like a baseball catcher's mitt!) in shape, with sparse ciliature limited to ventral surface plus one or more long caudal cilia; oral area, sometimes disproportionately large, midventral and much like *Tetrahymena* (or *Dexiotricha*, above) in its buccal ciliature; cytoproct occupies all of director-meridian area on foreshortened ventral surface of some species; widespread fresh-water polysaprobic and edaphic forms, with fewer species from brackish or marine habitats.

Cinetochilum Perty, 1849. Several species. Pl. XXVII, Figs. 46, 47.
Platynematum Kahl, 1935 (for *Platynema*). Several species.
Pseudoplatynematum Bock, 1952. Few species.
Sathrophilus Corliss, 1960 (for *Saprophilus*). Several species. Pl. XXVII, Figs. 40, 41.
Incertae sedis: Colpodopsis Gourret & Roeser, 1888. Few species. Pl. XXVII, Fig. 44.

Family UROZONIDAE Grolière, 1975

(syn. Urozonatidae)

Very small ovoid body, with single equatorial belt of somatic ciliature plus a single long caudal cilium; deep buccal cavity, but oral organelles greatly reduced in number, size, and complexity; common in polysaprobic fresh-water biotopes. [Jankowski (1975), independently, proposed the familial name (without diagnosis) earlier in the year 1975 than did Grolière (1975a); but the latter worker provided a characterization and recognized the proper taxonomic location of the organism, so I am crediting the family to him.]

Urozona Schewiakoff, 1889. Single species. Pl. XXVII, Fig. 45.

Family PSEUDOCOHNILEMBIDAE Evans & Thompson, 1964

(syn. Anophryidae)

Body small, elongate-pyriform, with sparse somatic ciliature and single caudal cilium; buccal area long and shallow, provided with two distinctive "membranes" on right (two membranelles in tandem plus the paroral); practically all marine (including brackish and halophilic habitats), free-living forms or scavengers, with occasional species inquilinic in echinoids; but fresh-water and coprozoic strains known in one species.

Pseudocohnilembus Evans & Thompson, 1964. Several spp. Pl. II 13; XII 1; XXVII 50–53.
Incertae sedis: Anophrys Cohn, 1866. Single bonafide species (*A. sarcophaga*, a marine scavenger), in my opinion; the crab-blood form described is a *Paranophrys*? Pl. XXVII, Fig. 48.

Family THIGMOPHRYIDAE Chatton & Lwoff, 1926

(syns. Cochliodomidae, Conchophyllidae, Myxophyllidae)

Body laterally flattened, uniformly and heavily ciliated; thigmotactic ciliature, on anterior left surface of body, very dense; buccal cavity at or near posterior pole, with reduced and inconspicuous buccal ciliature; symbionts in mantle cavity (or occasionally the slime) of terrestrial (pulmonate) and especially marine (generally bivalve) molluscs, with one species endocommensal in nemertine worm living in bivalve mantle cavity. [Some workers would place this family in the following suborder.]

Cochliodomus Raabe, 1971. Single species.
Cochliophilus Kozloff, 1945. Few species. Pl. XXVII, Fig. 57.
Conchophyllum Raabe, 1936. Single species. Pl. XXVII, Fig. 58.
Myxophyllum Raabe, 1934. Single species. Pl. XXVII, Fig. 56.
Thigmophrya Chatton & Lwoff, 1923. Several species. Pl. XXVII, Figs. 54, 55.

Incertae sedis in suborder Philasterina (all monotypic genera except second and third):

Andreula Kahl, 1934; *Aristerostoma* Kahl, 1926; *Balanonema* Kahl, 1931, Pl. XXVII, Fig. 19; *Bizonula* Corliss, 1960 (for *Bizone*); *Cryptostomina* Fedele, 1938 (for *Cryptostoma*); *Eurychilum* André, 1910; *Gullmarella* Fenchel, 1964 [in family Entodiscidae?], Pl. XXVII, Fig. 59; *Lembadionella* Kahl, 1933; *Protocruzia* de Faria, da Cunha & Pinto, 1922 (syn. *Protocrucia*) [see remarks under family Spirostomidae of class Polyhymenophora]; *Ptyssostoma* Hentschel, 1927; *Pusilloburius* n. g. (syn. *Pseudoglaucoma* p.p.), type-species *P. labiatus* (Kahl, 1931) n. comb. [the genus is defined, in effect, in Kahl's (1931c, pp. 335, 348) description (to save space, not repeated here) of his *Pseudoglaucoma labiata*; however, Kahl's *P. muscorum* species, type by (my) subsequent designation (here), remains in his original genus (see family Glaucomidae, order Hymenostomatida)]; *Rhinodisculus* Mansfeld, 1923; *Sertumia* Tucolesco, 1962, Pl. XXVII, Fig. 49.

Suborder (2) Pleuronematina Fauré-Fremiet in Corliss, 1956

(syns. Deuterostomatina *p.p.*, Pleuronematorina)

Paroral membrane often prominent, its infraciliary base tripartite, with a short "a" and an elongate "b" segment and with "c" as a permanent scutico-vestige; cytostome equatorial or subequatorial in location; caudal cilia conspicuous in many species; rarely (room for) a directormeridian; two types of mucocysts *sensu lato*; body size typically small to very small (with occasional striking exception); widely distributed as free-living (including psammophilic) marine species, but some commensalistic in molluscs and others in fresh-water and edaphic habitats, with a few coprozoic forms.

Family PLEURONEMATIDAE Kent, 1881

(for Aphthoniidae)

With characters of suborder *s.s.* (above); dominating feature is the paroral membrane, sometimes present as a stiff velum and distinctly curling around the subequatorial cystome; multifragmented paroral (segment "b") in one species; long, stiff caudal cilia; some species possibly have trichocysts?; in fresh-water and (especially) marine habitats, occasionally associated with some invertebrate as an ectocommensal (e.g., *Pleurocoptes* on hydractinian coelenterates).

Pleurocoptes Wallengren, 1896. Single species. Pl. IV, Fig. 29; V 40; XXVII 64.

Pleuronema Dujardin, 1836. Many species. Pl. IV, Fig. 50; XXII 2; XXVII 60–63, 73.

Schizocalyptra Dragesco, 1968. Single species. Pl. XXVII, Fig. 71.

Incertae sedis: Hippocomos Czapik & Jordan, 1977. Single species. Pl. XXVII, Fig. 70.

Family CYCLIDIIDAE Ehrenberg, 1838

Body ovoid to elongate-ovoid, generally small to very small, with sparse ciliation and distinctive caudal cilium; cytostome variable in position and buccal ciliature less prominent than in the Pleuronematidae; macronucleus and large micronucleus often located in anterior third of body; widely distributed forms, from fresh-water, brackish, marine, interstitial, edaphic, and even coprozoic habitats.

Abathostoma Berger [unpublished]. Single species.

Calyptotricha Phillips, 1882. Single species.

Cyclidium O. F. Müller, 1786. Many species. Pl. I, Fig. 8; III 8; V 39; XXIII 71; XXVII 65–69. [*Note*: Fig. 39, Pl. V, is probably *not* a *Cyclidium*.]

Mesogymnus Berger [unpublished]. Single species.

Incertae sedis: Cristigera Roux, 1899, many species, Pl. XXVII, Figs. 74–76; *Ctedoctema* Stokes, 1884, few species, Pl. XXVII, Figs. 77, 78.

Family HISTIOBALANTIIDAE de Puytorac & Corliss, n. fam.

Body elliptical in outline, with right side slightly concave and anterior end a little narrower than posterior; generally of large size; dense somatic ciliation, interspersed with longer bristles; prominent buccal cavity, medially located on ventral surface, containing distinctive tetrahymenal organization of buccal ciliary organelles plus scutico-vestige, though paroral membrane not prominent; two sizable macronuclei, with several micronuclei; commonly facultatively psammophilic forms, both fresh-water and marine habitats. [Establishment of this family has been planned for some years by de Puytorac and me; Jankowski (1975), coincidentally, recently suggested the same familial name, but without characterization of the group.]

Histiobalantium Stokes, 1886 (syns. *Histerobalantidium, Histiobalantidium, Histiobalantum*). Few species. Pl. XXVII, Figs. 72, 73.

Family PENICULISTOMATIDAE Fenchel, 1965

Body kidney-shaped, large, strongly flattened laterally, densely ciliated; oral area subequatorial on ventral margin, with buccal ciliature clearly detectable; huge macronucleus; commensal in mantle cavity of marine bivalve mollusc (*Mytilus edulis*) but also in fresh-water clams and certain sea urchins.

Echinosociella Berger [unpublished]. Single species.

Mytilophilus Antipa & Small [unpublished]. Single species.

Peniculistoma Jankowski, 1964 (syns. *Conchophthirus* p.p., *Ciliomorgania, Demorgania, Kidderia* [hom.], *Morgania* [hom.]). Single species [originally described by Kidder (1933a) as a conchophthirid; transferred to new genus by Jankowski (1964b, p. 272)]. Pl. XXVII, Figs. 79, 80.

Family THIGMOCOMIDAE Kazubski, 1958

Body flattened laterally, bluntly tapered posteriorly, with clearly delineated area of thigmotactic ciliature on concave surface; posterior half of body sparsely ciliated; cytostome at an equatorial level, with buccal ciliature not highly developed; endoparasitic in renal organ of terrestrial snails.

Thigmocoma Kazubski, 1958. Single species. Pl. XXVII, Fig. 81.

Family CONCHOPHTHIRIDAE Kahl in Doflein & Reichenow, 1929

(syn. Conchophthiriidae)

Body laterally compressed, generally ellipsoidal to broadly reniform in shape, with dense and uniform ciliation; buccal cavity relatively small, located nearly equatorially on ventral surface; commensals in mantle cavity (on gills) of fresh-water bivalve molluscs. [Some workers would place this family in the following suborder.]

Conchophthirus Stein, 1861 (syn. *Conchophthirius*). Several spp. Pl. V 12j,22; XXVII 82–84.

Conchoscutum Raabe, 1947. Single species.

Incertae sedis in suborder Pleuronematina:

Larvulina Penard, 1922. Single bonafide species.

Suborder (3) Thigmotrichina Chatton & Lwoff, 1922

(syns. Arhynchodina, Diplohymenina, Hysterocinetina, Parastomatina, Stomatina, Stomodea, Thigmotricha, Thigmotrichida)

Buccal ciliature mostly subequatorial in location, often spiraled around posterior pole of the body or there in reduced form; segment "c" of paroral membrane (the scutico-vestige) usually indistinct; strongly developed thigmotactic ciliature and/or pronounced sucker or adhesive disc characteristically present at apical pole; director-meridian and cytoproct apparently often absent; somatic ciliation uniform, frequently heavy, and body laterally compressed in many species; all symbionts: one major group widely occurring in lamellibranch molluscs, fresh-water or marine, and another mainly in oligochaete annelids, although other hosts occasionally involved.

Family ANCISTRIDAE Issel, 1903

(syns. Ancistrumidae, Boveriidae, Dragescoidae, Protophryidae)

Body of small to medium size, occasionally elongate, with anterior thigmotactic ciliature not set apart from other somatic kineties; ventral oral area courses nearly length of body, with cytostome moving progressively posterior-poleward; buccal ciliature conspicuous, winding in arc of > 360° around antapical pole in some species; widely found in mantle cavity and, less often, intestine of marine and fresh-water molluscs (prosobranch limpets, pulmonates, lamellibranchs) and respiratory organ of holothurian echinoderms.

Ancistrella Cheissin, 1930. Single species.

Ancistrum Maupas, 1883 (syns. *Ancistruma*, *Ancystrum*). Probably only a few bonafide species, though many described. Pl. IV, Fig. 24; XXVII 85.

Ancistrumina Raabe, 1959 (for *Ancistrina*). Many species [Raabe]. Pl. XXVII, Fig. 86.

Boveria Stevens, 1901. Few species [well known in shipworms]. Pl. XII, Fig. 4; XXVII 91, 92.

Dragescoa Jankowski, 1974. Few species [deserve family of their own?]. Pl. XXVII, Fig. 87.

Eupoterion MacLennan & Connell, 1931 (syn. of *Ancistrum*?). Single species.

Fenchelia Raabe, 1970. Single species.

Proboveria Chatton & Lwoff, 1936. Few species. Pl. IV, Fig. 1.

Protophrya Kofoid, 1903. Single species. Pl. XXVII, Fig. 88.

Protophryopsis Raabe, 1959. Single species.

Semiboveria Raabe, 1970. Single species.

Nomen inquirendum: Isselina Cépède, 1910. Single species. [If this questionable name is judged valid, the now well-established *Ancistrumina* (above) might be obliged to fall as a junior synonym of *Isselina*, an unfortunate event which Raabe (1970a) apparently did not foresee in his consideration of the genera involved.]

Family HEMISPEIRIDAE König, 1894

Body often small, with somatic ciliature in reduced number of spiraled rows in many species (becoming oblique and even almost horizontal in some); distinct thigmotactic area of reduced dorsal kineties enclosed in a système sécant, very pronounced in certain genera; arrangements of buccal ciliature parallel those seen in the Ancistridae, but the ciliature is often reduced when at the posterior pole and forms an arc of < 180°; in mantle cavity of marine and fresh-water molluscs or on integument of certain echinoderms. [Does *Nucleocorbula* (see separate family, below) more appropriately belong here?]

Ancistrospira Chatton & Lwoff, 1926. Single species. Pl. IV, Fig. 2.

Cheissinia Chatton & Lwoff, 1949 (for *Tiarella*). Single species. Pl. XXVII, Fig. 94.

Hemispeira Fabre-Domergue, 1888 (syn. *Hemispeiropsis*). Few spp. Pl. XII 3; XXVII 89, 90.
Plagiospira Issel, 1903. Single species. Pl. XXVII, Fig. 93.
Protospira Raabe, 1968. Single species.

Family HYSTEROCINETIDAE Diesing, 1866

(syns. Ladidae, Ptychostom[at]idae)

Body of medium to large size, somewhat flattened laterally, densely ciliated; prominent thigmotactic sucker, essentially at apical end of body, comprised of segments of left-anterior kineties surrounded by nonciliated strip or field (often giving it a horseshoe shape) and generally strengthened by fibers or other skeletal structures; buccal apparatus, reduced or even rudimentary, at antapical pole; reproductive methods include posterior budding or catenulation in some species; widespread as commensals in intestine of oligochaete annelids, aquatic or terrestrial, with a few species of two genera (*Hysterocineta, Ptychostomum*) in gut of certain fresh-water snails.
Coelothigma de Puytorac, 1968. Single species.
Cotylothigma Raabe, 1949. Few species.
Craticuloscuta Kozloff, 1965. Few species.
Drilocineta Raabe, 1972. Few species. Pl. XXVII, Fig. 97.
Elliptothigma Meier, 1954. Few species.
Eminothigma Jankowski, n. n. (for *Puytoracia* Raabe, 1972 [discovered by Jankowski to be homonym of *Puytoracia* Bonnet, 1970 (testaceous rhizopod)]). Three species; type-species, *E. kozloffi* (de Puytorac, 1968) n. comb. Pl. XXVII, Fig. 107.
Epicharocotyle Kozloff, 1965. Single species. Pl. XXVII, Fig. 106.
Hysterocineta Diesing, 1866 (syn. *Ladopsis*). Several species. Pl. XXVII, Figs. 95, 96.
Kozloffia de Puytorac, 1968. Single species. Pl. XXVII, Fig. 110.
Kysthothigma Raabe, 1949 (syn. *Kystothigma*). Few species. Pl. XXVII, Fig. 111.
Preptychostomum de Puytorac, 1968. Few species. Pl. XXVII, Fig. 102.
Protoptychostomum Raabe, 1949. Few species. Pl. IV, Fig. 14; XXVII 100, 101.
Ptychostomum Stein, 1860 (syn. *Lada* [hom.]). Many species. Pl. XXVII, Figs. 98, 99.
Taeniocineta Raabe, 1972. Single species. Pl. XXVII, Fig. 105.
Thurstonia de Puytorac, 1968. Single species. Pl. XXVII, Fig. 109.

Family PROTANOPLOPHRYIDAE Miyashita, 1929

(syn. Protoanoplophryidae)

Body laterally compressed and highly Astomatida-like in appearance: often elongate (up to 1,500 μm), with lengthy macronucleus, thickened pellicle, two rows of numerous contractile vacuoles, dense and uniform ciliation, and budding possible; buccal apparatus, reduced and inconspicuous, located short distance from apical pole; commensal in intestine of prosobranch snails.
Protanoplophrya Miyashita, 1929 (syn. *Protoanoplophrya*). Few species. Pl. III, Fig. 32; XXVII 103, 104.

Family NUCLEOCORBULIDAE Santhakumari & Nair, 1970

Large, cylindrical, with spiraled rows of somatic ciliature running nearly at right angles to long axis of body; prominent aboral sucker or adhesive disc; buccal ciliature appears to be at posterior pole; huge, branching macronucleus; in mantle cavity of shipworm (eulamellibranch mollusc). [The organism was possibly figured upsidedown; it seems to possess several important hemispeirid characteristics and may not deserve separate familial standing.]
Nucleocorbula Santhakumari & Nair, 1970. Single species. Pl. XXVII, Fig. 108.

Incertae sedis in suborder Thigmotrichina:

Syndaetor Berger [unpublished]. Single (or more?) species, in echinoids [deserves family of its own?].

Incertae sedis in order Scuticociliatida:

Agigea Lepşi, 1965. Single species [small organism, figured (Lepşi, 1965, p. 836) but not described verbally].

Order 3. ASTOMATIDA Schewiakoff, 1896

(syns. Anoplophryida, Anoplophryin[e]a, Anoplophrymorphida, Astomat[e]a, Astom[at]ina, Haptophryina, Hoplitophryina)

Body relatively large, especially often lengthy, cylindrical or flattened-ovoid, uniformly ciliated, mouthless; an infraciliary endoskeleton of considerable complexity may be present, frequently with elaborate holdfast organelle at anterior end of body; typically anisotomic fission, sometimes involving budding with chain-formation; contractile vacuoles present, in one or two rows, but cytoproct absent; universally endosymbiotic (possibly one exception: see first family, below), with majority found in digestive tract of oligochaete annelids from soil, fresh-water, brackish, or marine habitats; but some species in polychaetes, leeches, turbellarians, or molluscs, and one major group exclusively in tailed amphibians.

Family ARCHIASTOMATIDAE Foissner, 1976

Mouthless, medium large, ovoid, with holotrichous ciliation, mucocysts, lengthy macronucleus, multiple micronuclei, and scattered contractile vacuoles; but no endoskeleton, no thigmotactic cilia, and found entirely *free-living*; special feature: prominent, centrally located, regularly pulsating ("contractile"?) central vacuole; taken from a eutrophic pool in the Austrian Alps. [See Foissner (1976b); the family is provisionally accepted and placed here, but the organism remains a most puzzling one in need of further and more intensive study.]

Archiastomata Foissner, 1976. Single species. Pl. XXVIII, Fig. 1.

Family ANOPLOPHRYIDAE Cépède, 1910

(syns. Herpetophryidae, Metastom[at]idae, Orchitophryidae)

No endoskeleton, apical hooks, or suckers, but area of thigmotactic cilia often present; reproduction without chain formation; body relatively small, ovoid to elongate-ovoid; primarily in terrestrial oligochaetes, though some species presumably from other hosts (e.g., the dubious *Orchitophrya* was found in sea-star gonads and an *Anoplophrya* reported from lobster gut).

Almophrya de Puytorac & Dragesco, 1969. Few species.

Anoplophrya Stein, 1860 (syns. *Eliptophrya*, *Macrophrya*). Many to very many species. Pl. XIII, Fig. 1; XXVIII 2, 3.

Corlissiella de Puytorac, 1960. Single species.

Herpetophrya Siedlecki, 1902. Single species.

Lomiella de Puytorac, 1961. Few species.

Lubetiella de Puytorac, 1959. Few species.

Metastomum Georgévitch, 1941. Single species.

Paranoplophrya Rohrbach, 1936. Single species.

Perseia Rossolimo, 1926 (syn. *Persea*). Few species.
Prototravassosia Artigas & Unti, 1938. Single species.
Sigmophrya de Puytorac, 1971. Single species.
Incertae sedis: Orchitophrya Cépède, 1907. Single species. Pl. XXVIII, Fig. 5.

Family BUETSCHLIELLIDAE de Puytorac, n. fam.

With general characteristics of the Anoplophryidae (above), but with differences in the silverline system (kinetal patterns, "systèmes sécants," thigmotactic area, etc.) which especially set its genera apart; ciliature may be spiraled; macronucleus rod-like or dendritic; reproduction palintomic; in polychaete annelids. [Since de Puytorac is planning to establish this group as a new family, it is appropriate to credit him with its name, but as of the date of the present work where the taxon is first characterized (unless a diagnosis appears elsewhere while this book is still in press).]

Anoplophryopsis de Puytorac, 1954. Single species. Pl. XXVIII, Fig. 6.
Buetschliella Awerinzew, 1908 [*non* Jírovec, 1933]. Several species. Pl. XXVIII, Fig. 4.
Herpinella de Puytorac, 1954. Single species.
Rhizocaryum Caullery & Mesnil, 1907. Few species. Pl. XXVIII, Fig. 7.

Family HOPLITOPHRYIDAE Cheissin, 1930

(syn. Mesnilellidae)

Body elongate, cylindrical, tapered posteriorly; ectoplasm thickened at apical end, with insertion of some cytoskeletal fibers; body ciliation moderate to light; generally single row of contractile vacuoles; chain formation common in division; commensals of only fresh-water aquatic oligochaetes except for a few species in an occasional terrestrial annelid.

Akidodes Lom, 1959. Few species. Pl. XXVIII, Figs. 8, 9.
Anglasia Delphy, 1938. Single species.
Buetschliellopsis de Puytorac, 1954. Several species. Pl. XXVIII, Figs. 10, 11.
Delphyella de Puytorac, 1969. Single species. Pl. XXVIII, Fig. 12.
Hoplitophrya Stein, 1859 (syn. *Protoradiophrya*). Many species [some in terrestrial oligochaetes]. Pl. XXVIII, Figs. 14, 15.
Jirovecella Lom, 1957. Single species. Pl. XXVIII, Fig. 13.
Juxtamesnilella de Puytorac, 1954. Several species.
Juxtaradiophrya de Puytorac, 1954. Several species. Pl. XXVIII, Fig. 16.
Mesnilella Cépède, 1910. Several to many species. Pl. XXVIII, Figs. 17–19.
Mixtophrya de Puytorac, 1969. Single species.
Protoradiophryopsis Georgévitch, 1950. Single species.
Radiophryoides Lom, 1956. Few species. Pl. XXVIII, Fig. 22.

Family RADIOPHRYIDAE de Puytorac, 1972

Body generally ovoid and flattened, occasionally elongate; apical and dominated by prominent inverted "V"-shaped cytoskeletal organelle onto which numerous fibers converge; hooks or spines or other attachment fixtures often present; body ciliation dense; one or two rows of contractile vacuoles; chain formation not common; commensals of aquatic and terrestrial oligochaetes, a few polychaetes, and occasionally a fresh-water lamellibranch mollusc.

Acanthodiophrya de Puytorac & Dragesco, 1968. Single species. Pl. XXVIII, Fig. 21.
Anthonyella Delphy, 1936. Few species.
Cheissinophrya de Puytorac & Dragesco, 1969. Single species. Pl. XXVIII, Fig. 20.
Coelophrya de Puytorac & Dragesco, 1968. Single species. Pl. V, Fig. 12k.

Desmophrya Raabe, 1933. Single species.
Dicoelophrya de Puytorac & Dragesco, 1968. Few species.
Durchoniella de Puytorac, 1954. Few to several species. Pl. III, Fig. 9; XXVIII 27.
Eudrilophrya de Puytorac, 1971. Single species.
Helella Kaczanowski, 1961 (syns. *Hellela, Hellella*). Few species. Pl. XXVIII, Fig. 28.
Hovasseiella de Puytorac, 1955. Single species.
Metaracoelophrya de Puytorac & Dragesco, 1969. Single species.
Metaradiophrya Heidenreich, 1935. Many species. Pl. XXVIII, Fig. 25.
Mimophrya de Puytorac, 1969. Few species.
Mrazekiella Kijenskij, 1925. Few species. Pl. XXVIII, Fig. 26.
Ochridanus Georgévitch, 1941. Few species.
Paracoelophrya de Puytorac, 1969. Few species. Pl. IV, Fig. 12.
Radiophrya Rossolimo, 1926 (syns. *Cheissinella, Cheissiniella*). Many species. Pl. XIII, Fig. 2; XXVIII 23, 24.
Radiophryopsis Georgévitch, 1941. Single species.

Family CONTOPHRYIDAE de Puytorac, 1972

Body elongate-ellipsoidal; skeletal fibers little developed; circular area at apical end of body free of cilia; a single median (or two pair of) cytoskeletal hook(s); only two contractile vacuoles; in tropical earthworms.

Contophrya de Puytorac & Dragesco, 1968. Single species. Pl. XXVIII, Fig. 29.
Dicontophrya de Puytorac & Dragesco, 1968. Few species. Pl. XXVIII, Fig. 30.

Family MAUPASELLIDAE Cépède, 1910

Body cylindrical, rounded at both ends; skeletal fibers relatively short; small anterior spine, fixed or mobile; division equal or unequal, sometimes with catenulation; in terrestrial oligochaetes and leeches.

Acanthophrya Heidenreich, 1935. Single species.
Buchneriella Heidenreich, 1935. Few species.
Georgevitchiella de Puytorac, 1957. Single species.
Maupasella Cépède, 1910 (syn. *Schultzellina*). Many species. Pl. XIII, Fig. 3; XXVIII 31, 32.

Family INTOSHELLINIDAE Cépède, 1910

Body cylindrical, elongate; rather elaborate cytoskeletal "annulus" at anterior end; body ciliation dense, with kineties often loosely spiraled; division involves chain-formation; in aquatic oligochaetes. [I have removed *Spirobuetschliella* Hovasse, 1950, often included here, to an uncertain position within the apostome kinetofragminophorans.]

Intoshellina Cépède, 1910. Several species. Pl. XXVIII, Fig. 34.
Monodontophrya Vejdovsky, 1892 (syn. *Eumonodontophrya*). Few spp. Pl. XXVIII, Fig. 33.

Family HAPTOPHRYIDAE Cépède, 1923

(for Discophryidae Cépède [*non* Collin]; syns. Sieboldiellinae, Sieboldiellininae)

Body large, elongate (up to 2,000 μm in length, some species), densely ciliated; kineties converge anteriorly onto horseshoe-shaped suture line; conspicuous adhesive sucker at apical end of body, sometimes provided with two or more hooks or spines; long canal replaces row(s) of contractile vacuoles; anisotomic fission, with chain-formation common; hosts include marine and fresh-water turbellarians, anuran, and (especially) urodelean amphibians. [Should this, plus the following group, be separated from all preceding astome taxa at some suprafamilial (e.g., subordinal) level?]

Annelophrya Lom, 1959. Single species.

Cepedietta Kay, 1942 (syn. "*Haptophrya*," as widely *mis*used). Several species [all in amphibian hosts, especially salamanders]. Pl. I, Fig. 38; XIII 4; XXVIII 41–43.

Haptophrya Stein, 1867 (for *Discophrya* Stein [*non* Lachmann]; syn. *Sieboldiellina*). Several species [solely in turbellarian hosts]. Pl. XXVIII, Figs. 35–39.

Lachmannella Cépède, 1910. Single species. Pl. XXVIII, Fig. 46.

Steinella Cépède, 1910. Single species. Pl. IV, Fig. 15; XXVIII 44, 45.

Family CLAUSILOCOLIDAE de Puytorac, n. fam.

(syn. Proclausilocolidae)

Body comma-shaped or broadly ellipsoidal in form, flattened, and not especially elongate; thigmotactic area present at anterior end but weakly developed and without well-defined sucker; infraciliary pattern differs from that of the Haptophryidae; scattered contractile vacuoles; two species are commensals in the body cavity of certain land snails, with a third described from African earthworms. [Jankowski (1975) proposed a familial name, Proclausilocolidae, for the same group of genera but offered no description or characterization. Since de Puytorac has independently been planning for some years to establish the family as named here, I am crediting him with the taxon, but as of the date of the present work, where the group's characterization is apparently first appearing.]

Clausilocola Lom, 1959. Single species. Pl. XXVIII, Fig. 47.

Haptophryopsis de Puytorac, 1971. Single species [in earthworms]. Pl. XXVIII, Fig. 40.

Proclausilocola Lom, 1959. Single species.

Subclass (2) Peritricha Stein, 1859

(syns. Cyclohymenophora, Dexiotricha, Peritrichasina, Peritrichia, Peritrichidea, Peritrichorida, Stomatoda)

Body characteristically inverted bell- or goblet-shaped or conical-cylindrical; conspicuous buccal ciliature, winding counterclockwise, at apical pole and a scopula (plus prominent holdfast derivatives: usually contractile stalk or complex adhesive disc) at antapical pole; somatic ciliature reduced to subequatorial locomotor fringe (trochal band); a ciliated infundibulum, into which the contractile vacuole empties, leads to the cytostome; stomatogenesis buccokinetal, with plane of fission of body parallel to major axis; dimorphism (with migratory telotroch stage), colonies, loricae or thecae, and cysts common in the life cycle of many species; conjugation ("total") invariably involves fusion of a micro- with a macroconjugant; very widespread aquatic distribution, with species generally free-living or occurring as symphorionts on diverse hosts, but with some as commensals or even parasites on or in other organisms (ranging from protozoa to vertebrates).

Order PERITRICHIDA Stein, 1859

(syns.: see those of subclass, above)

With characteristics of subclass (above).

Suborder (1) Sessilina Kahl, 1933

(syns. Astylozoina, Loricina, Natantina, Scyphidiina, Sedentaria, Sessilia, Sessili[i]da, Stylophorina, Thigmodiscina; Aloricata + Loricata)

Sedentary or sessile (adults), commonly stalked (or with inconspicuous adhesive disc), with a few species secondarily mobile; many produce arboroid colonies; some entire groups loricate; mucocysts and pellicular pores universal; adults generally filter-feeding bactivores (larval stage mouthless); widely ranging habitats (fresh-water, brackish, marine), with animate substrata involving metazoa from many phyla (major exception: echinoderms); a few species live as endozoic forms.

Family VORTICELLIDAE Ehrenberg, 1838

(syn. Zoothamniidae)

With contractile stalk; all species colonial except in two genera (*Haplocaulus*, *Vorticella*); zooids not independently contractile among colonial forms (except in *Carchesium*); species all attached – to inanimate objects, plants, rotifers, crustaceans (amphipods, decapods, etc.), even turtles, etc. – in various fresh-water and marine habitats.

Carchesium Ehrenberg, 1830. Several to many species. Pl. IV, Fig. 16b; XXIX 13–18.

Entziella Stiller, 1951. Single species.

Haplocaulus Precht, 1935. Many species. Pl. XXIX, Figs. 24, 25.

Intranstylum Fauré-Fremiet, 1904 (syn. *Intrastylum*). Several species. Pl. XXIX, Figs. 21, 22.

Myoschiston Precht, 1935. Several species.

Parazoothamnium Piesik, 1975. Single species.

Pseudocarchesium Sommer, 1951. Several species. Pl. XXIX, Fig. 23.

Rugaecaulis Lom [unpublished]. Single species.

Tucolesca Lom, n. n. (for *Leptodiscus* Tucolesco, 1962 [hom. of *Leptodiscus* Hertwig, 1877 (dinoflagellate)]). Single (and type-) species, *T. mirabilis* (Tucolesco, 1962) n. comb. Pl. XXIX, Fig. 20.

Vorticella Linnaeus, 1767 (syn. *Vorticellopsis*). Very many (well over 150 described: but all bonafide?) species. Pl. I, Fig. 21; II 7; III 1; IV 16a; V 43, 44; XIV 1; XXIX 1–12.

Zoothamnium Bory de St. Vincent, 1826 (syn. *Zoothamnia*). Very many (*ca.* 50) species. Pl. XXIX, Figs. 26–28.

Incertae sedis: Craspedomyoschiston Precht, 1935, single species; *Monintranstylum* Banina, 1976, single species; *Pseudovorticella* Foissner & Schiffmann, 1975, few species. Pl. XXIX, Fig. 19.

Family ASTYLOZOIDAE Kahl, 1935

(syns. Astylozooidae, Astylozoonidae, Hastatellidae)

Stalkless, mobile, planktonic forms, with one or two rigid caudal bristles; organisms resemble zooids of *Vorticella* broken away from stalk; mature form swims with apical pole forward, telotroch with antapical end first; two or more prominent circlets of curious spines in second genus.

Astylozoon Engelmann, 1862 (syn. *Geleiella*). Several species. Pl. XXIX, Figs. 29–31.

Hastatella Erlanger, 1890. Few species. Pl. XXIX, Figs. 32, 33.

Family EPISTYLIDIDAE Kahl, 1933

(syn. Epistylidae – a misspelling all too commonly used!)

Generally stalked, with stalk often noncontractile (but body may be highly contractile); solitary or colonial; great range in sizes [some species of two genera (*Campanella*, *Epistylis*) may have zooids up to 600 μm]; abundant in fresh-water habitats (occasionally marine), free or as symphorionts associated with diverse hosts – from other peritrichs to molluscs, crustaceans (barnacle to crab and crayfish: body or gills), aquatic insects, lower vertebrates, etc. – with one genus (*Apiosoma*) especially widely found on the integument of fresh-water fishes.

Apiosoma Blanchard, 1885 (syn. *Glossatella*). Many species. Pl. XXV, Fig. 37; XXIX 34–36, 44.

Campanella Goldfuss, 1820. Few species. Pl. IV, Fig. 19; XXIX 37.

Epistylis Ehrenberg, 1830 (syns. *Allomeron, Nidula, Orthochona*). Very many (*ca.* 100) species. Pl. I, Figs. 4, 39; V 42, 45; XXIX 38–46.

Opisthostyla Stokes, 1886. Several species.

Rhabdostyla Kent, 1881. Many to very many species. Pl. V, Fig. 46; XXIX 47.

Incertae sedis: Systylis Bresslau, 1919. Single species.

Family OPERCULARIIDAE Fauré-Fremiet, n. fam.

Generally with stalk, noncontractile; solitary or colonial, with highly developed theca in many species; epistomial disc has characteristic appearance of an operculum at anterior end of body; found very commonly as epibionts on fresh-water insects or other arthropods, but one species (*Operculariella*) is endocommensal in esophagus of a beetle and another (*Orsomia*) associated with an oligochaete annelid. [Lom (personal communication) has suggested that Fauré-Fremiet – on the basis of unpublished notes seen by Lom – should be credited with this family: I concur. Jankowski (1975), working independently, has recently proposed the same name for the group, but provided no description or characterization.]

Ballodora Dogiel & Furssenko, 1921. Few species. Pl. XXIX, Fig. 58.

Heteropolaria Foissner & Schubert, 1977. Single species.

Opercularia Goldfuss, 1820 (syn. *Cochlearia* p.p., *Discotheca, Kindella*). Very many (perhaps 100?) species. Pl. XXIX, Figs. 48–52.

Operculariella Stammer, 1948. Single species.

Orbopercularia Lust, 1950. Very many (*ca.* 50) species. Pl. I, Fig. 34; XXIX 59.

Propyxidium n. n. (for *Pyxidiella* Corliss, 1960 [for *Pyxidium*]; syn. *Cochlearia* p.p.). Many species. Pl. XXIX, Fig. 64. [My 1960 replacement name for Kent's venerable, but preoccupied, *Pyxidium* was, it turns out, preoccupied itself by *Pyxidiella* Cookson & Eisenack, 1958, a protistan fossil of unknown affinities. Thus a second new name is required. For the many included species in their new combination, see Corliss' (1960b) list, substituting *Propyxidium* for *Pyxidiella* (with appropriate changes in endings of specific epithets); type-species, *P. cothurnoides* (Kent, 1882) n. comb.]

Incertae sedis: Orsomia Baer, 1952. Single species.

Family OPISTHONECTIDAE Foissner, 1976

(syns. Telotrochidiidae, Telotrochiidae)

Stalkless, planktonic, with aboral end of body in advance when swimming; "telotroch" stage permanent (capable of division, etc.); small group of rigid cilia present, separate from (other) oral ciliature and especially distinctive in first genus; cylindrical to bell-shaped body (oral end narrower), with nonstalk-producing scopula at aboral pole and permanent trochal band nearby. [Jankowski (1967a) mentioned the need for this separate family in listing a name, "Telotrochiidae" (apparently meaning Telotrochidiidae), for it, but offered no description or characterization.]

Opisthonecta Fauré-Fremiet, 1906. Few species. Pl. XIV, Fig. 2; XXIX 60, 61.

Telotrochidium Kent, 1881 (syn. *Telotrichidium*). Few species. Pl. XXIX, Figs. 62, 63.

Family SCYPHIDIIDAE Kahl, 1933

Solitary, stalkless (yet sessile) forms; adherence to substrata by scopulary organelles forming flattened disc often prominently distinct from rest of body; one group (*Ambiphrya*) with permanent posterior trochal band; large, gelatinous pseudocolony formed by one free-living planktonic species (*Gonzeella*); generally found as epibionts on (gills of) fresh-water or marine fishes, molluscs, or other invertebrates (e.g., leeches, marine worms, etc.).

Ambiphrya Raabe, 1952. Few species. Pl. XXIX, Fig. 57.
Gonzeella Kufferath, 1953. Single species.
Ophrydiopsis Penard, 1922. Single species.
Paravorticella Kahl, 1933. Few species.
Scyphidia Dujardin, 1841. Many species. Pl. XXIX, Figs. 53–56.
Incertae sedis: Pachystomos Rudzinska, 1952 (syn. *Pachystomus*). Single species [likely belongs in genus *Scyphidia*?].

Family OPHRYDIIDAE Ehrenberg, 1838

Body bottle-, vase-, or spindle-shaped, often with long and highly contractile neck, elongate macronucleus, and aborally located contractile vacuole; solitary (first genus) or forming often huge (up to 15 cm in diameter) gelatinous "spherical" colonies (green-colored from endosymbiotic zoochlorellae in the individual zooids); atypical stalk, sometimes of long peduncular fibers; bonafide species perhaps exclusively fresh-water forms.

Gerda Claparède & Lachmann, 1858 (resurrected genus). Few species. Pl. XXIX, Figs. 67–71.
Ophrydium Bory de St. Vincent, 1826. Few species. Pl. I, Fig. 40; XXIX 72–76.

Family ELLOBIOPHRYIDAE Chatton & Lwoff, 1929

Solitary, stalkless forms; fission anisotomic; members of type-genus are particularly distinguished by the remarkable production, on either side of the scopula, of elongate cylindrical projections which encircle a gill filament of their host and glue themselves together to form a closed circle in firm attachment; *Ellobiophrya* found only as commensal of a marine lamellibranch mollusc, while species of other two genera are associated with marine fishes. [I am indebted to Lom (personal communication) for suggesting that Chatton & Lwoff (1929), who proposed the status of "tribe" for their unusual genus, be credited with the familial name.]

Caliperia Laird, 1953. Few species. Pl. XXIX, Fig. 66.
Clausophrya Naidenova & Zaika, 1969. Single species.
Ellobiophrya Chatton & Lwoff, 1923. Single species. Pl. XXIX, Fig. 65.

Family TERMITOPHRYIDAE Lom, n. fam.

Scopula produces unique pad-like disc as organelle of attachment; body is of an inverted cone-shape, with reduced area of oral ciliature and long, helical infundibulum; endocommensals (in the intestine) of certain African termites. [Lom has for some time been planning establishment of this family; by coincidence, Jankowski (1975) also named it but included no description or characterization. The group is credited to Lom, as of the date of the present publication.]

Termitophrya Noirot & Noirot-Timothée, 1959. Single [maybe more: Gisler (1967)] species.

Family ROVINJELLIDAE Matthes, 1972

Colonial but with its few zooids in a "group-lorica," a curious structure opened widely at its upper end; the shared stalk is in two sections, one rigid, other highly contractile; found on a marine crustacean (a beach isopod).

Rovinjella Matthes, 1972. Single species. Pl. XXIX, Fig. 77.

Family VAGINICOLIDAE de Fromentel, 1874

(for Vaginiferidae)

Loricate, solitary, with or without a stalk (generally very short when present); oral region of body protrusible well beyond opening of lorica; division isotomic or anisotomic; some species with a true operculum (e.g., *Pyxicola*); macronucleus usually ribbon-like in form; found attached to plants or inanimate substrata or as symphorionts in both fresh-water and marine habitats.

Caulicola Stokes, 1894 (syn. of *Pyxicola*?). Few species. Pl. XXIX, Figs. 94, 95.

Cothurnia Ehrenberg, 1831. Very many (*ca.* 100?) species. Pl. I, Fig. 26; XXIX 78–83.

Cothurniopsis Entz, Sr., 1884 (syn. of *Cothurnia*?). Several species.

Pachytrocha Kent, 1882 (syn. of *Pyxicola*?). Single species.

Platycola Kent, 1882. Many species. Pl. XXIX, Figs. 99, 100.

Pseudothuricola Kahl, 1935. Few species.

Pyxicola Kent, 1882. Several species. Pl. I, Fig. 35; XXIX 96–98.

Thuricola Kent, 1881. Several species. Pl. XXIX, Figs. 84, 85.

Vaginicola Lamarck, 1816 (syn. *Miculopodium*). Very many (*ca.* 50) spp. Pl. XXIX 86–93.

Incertae sedis: *Cyclodonta* Matthes, 1958. Single species. Pl. I, Fig. 25.

Family LAGENOPHRYIDAE Bütschli, 1889

(syn. Lagenophryiidae)

Loricate, solitary, stalkless; relationship of organism's body to lorica unique: attachment is only at opening (loricastome), where complex elastic and contractile lips, collar, etc. are present; lorica in shape of flattened hemisphere, with surface "glued" to substratum (host's integument) called ventral and the oral end considered anterior; properties of lorica, macronucleus, and (controversially) host-specificity used to distinguish species; most common hosts (with gills as usual site of attachment) are fresh-water amphipods and decapods (especially the crayfish), but salt- and brackish-water shrimps and crabs have also been implicated.

Lagenophrys Stein, 1851. Very many (> 60) species. Pl. XXIX, Figs. 101–105.

Operculigera Kane, 1969. Few species.

Stylohedra Kellicott, 1884. Few to several species.

Incertae sedis: *Eilymophrys* n. n. (for *Cystophrys* Bresslau, 1922 [hom. of *Cystophrys* Archer, 1869 (heliozoon)]). Single (and type-) species, *E. gemmans* (Bresslau, 1922) n. comb.

Suborder (2) Mobilina Kahl, 1933

(syns. Mobilia, Mobilida, Mobiliida, Mobilorina)

Mobile forms, conical, cylindrical, or goblet-shaped, sometimes discoidal (orally-aborally flattened); dominant feature the aboral (basal) disc, a holdfast organelle of considerable complexity (denticulate ring, radiating myonemes, etc.); trochal band permanently ciliated; stalkless, with scopula generally vestigial (though producing cilia in some forms); all species associated with some other organism as "host", often fresh-water or marine invertebrates (on integument or gills), but other groups (ciliates, amphibians, especially fishes), and other locations (digestive and urogenital tracts) may also be involved; fish-gill forms pathogenic in heavy populations.

Family URCEOLARIIDAE Dujardin, 1840

Body cylindrical, often slightly tipped to one side; adoral spiral (buccal ciliature) turns *ca.* 400°, with wide radius; denticles of skeletal ring smoothly linked, *ca.* 20 in number; compact macronucleus; no cortical rings; ectosymbionts of fresh-water turbellarians and marine polychaetes and molluscs (gill surfaces). [The well-known generic name *Urceolaria* turns out to be a junior homonym, but the International Commission on Zoological Nomenclature will be petitioned to conserve it – even as the heterotrich *Stentor* has been preserved – because of its long-time usage and universal acceptance (the senior homonym is a little-known junior synonyn of the name of a rotifer). See brief comments on this intricate nomenclatural problem at the end of Chapter 13.]

Urceolaria Stein, 1854 (a *nomen conservandum*, pending). Few species. Pl. IV, Fig. 21a; XIV 3; XXIX 117–122, 128e.

Family LEIOTROCHIDAE Johnston, 1938

Body cylindrical or barrel-shaped, with slightly bulging apical end; adoral spiral of *ca.* 400°, with radius like that of aboral adhesive disc; denticles smoothly linked, *ca.* 20 in number; macronucleus bulbous with two arms (roughly H-shaped); cortical rings present; widespread symbiont on gills of marine molluscs and on scattered other invertebrates (e.g., on spines of sea urchins). [Some workers consider the genus *Leiotrocha* confamilial with *Urceolaria*, thus in the preceding family.]

Leiotrocha Fabre-Domergue, 1888. Few species. Pl. III, Fig. 15; XXIX 127, 128e.

Family POLYCYCLIDAE Poljansky, 1951

Body conical, tapered apically; adoral spiral of *ca.* 360°, with greatly reduced radius, and buccal ciliature relatively inconspicuous; denticles smoothly but densely linked, numerous (35–55); cortical rings in evidence; some scopulary cilia present, and two trochal bands; macronucleus ribbon-like, with thick "nodes" and L-shaped; endocommensals of holothurian echinoderms.

Polycycla Poljansky, 1951. Few species. Pl. XXIX, Figs. 126, 128f.

Family TRICHODINOPSIDAE Kent, 1881

Body conical, tapered apically; adoral spiral of *ca.* 360°, with greatly reduced radius, and buccal ciliature relatively inconspicuous; highly specialized infundibular area, with bulbous expansion posteriorly, etc.; denticles smoothly but densely linked, quite numerous (30–40); cortical rings and some scopulary cilia present; macronucleus compact, discoidal; intestinal symbionts of a terrestrial prosobranch snail.

Trichodinopsis Claparède & Lachmann, 1858. Single spp. Pl. IV 22b; XXIX 123–125, 128f.

Family TRICHODINIDAE Claus, 1874

Body cylindrical, barrel-, or goblet-shaped, occasionally slightly tapered apically or flattened into discoidal or hemispherical form; adoral spiral ranges from turn of 180° to 2–3 nearly full circles, always with wide radius (matching that of aboral adhesive disc); buccal ciliature conspicuous; denticles complex, often linked via hooks and/or spikes, generally 15–40 in number (but approaching 60 in several genera); no scopulary but often marginal cilia; macronucleus sausage- to horseshoe-shaped (sometimes compact); numerous species, widely distributed and found in diversity of hosts (e.g., *Trichodina*: others often with higher host-specificity): other ciliates and integument of various aquatic invertebrates, plus mantle cavity of land gastropod molluscs, to skin, urinary bladder, and especially gills of marine and fresh-water fishes and a few amphibians.

Dipartiella G. Stein, 1961 (syn. *Dogielina* [hom.]). Few species. Pl. XXIX, Fig. 128d.

Paratrichodina Lom, 1963. Several species.

Semitrichodina Kazubski, 1958. Few to several species. Pl. IV, Fig. 21c.

Trichodina Ehrenberg, 1830 (syns. *Anhymenia, Cyclochaeta, Cyclocyrrha, Paravauchomia, Poljanskina*). Very many (*ca.* 200) species described. Pl. IV, Figs. 21a, 22a, 46; V 47, 48; XIV 4; XXIX 106–114, 128a.

Trichodinella Šrámek-Hušek, 1953 (for *Brachyspira*; syn. *Foliella*). Several species. Pl. IV, Fig. 21b; XXIX 115, 128c.

Tripartiella Lom, 1959. Several species. Pl. IV, Fig. 21b; XXIX 128b.

Vauchomia Mueller, 1938. Few species. Pl. IV, Fig. 21d; XXIX 116.

Incertae sedis: Acyclochaeta Zick, 1928. Single species.

EXPLANATION OF FIGURES

PLATE XXVI (pages 279–281)

Page 279. Figs. 1–10. *Tetrahymena*. 1, 2. *T. pyriformis* (Furgason, Corliss). 3. *T. setosa* (Holz & Corliss). 4. *T. rostrata* (Corliss). 5, 6. *T. vorax*, macrostome [with *Colpidium* in food vacuoles] and microstome forms (Kidder et al., Corliss). 7a,b. *T. paravorax*, microstome and macrostome forms (Dragesco & Njiné). 8–10. *T. patula*, macrostome [with *Colpidium* in food vacuoles in first one] and microstome forms (Maupas, Schewiakoff, Corliss). 11–15. *Colpidium*. 11–13. *C. colpoda* (Kahl, Bary, Corliss). 14. *C. striatum* [syn. *C. kleini*] (Corliss). 15a,b. *C. campylum* (von Gelei & Horváth). 16–18. *Lambornella*. 16. *L. clarki* (Corliss & Coats). 17. *L. stegomyiae* (Corliss & Coats). 18. *L. clarki*: a, cuticular "invasion" cyst on larval mosquito cuticle; b, melanized ciliate under cuticle – example of an unsuccessful invasion (reconstructed from photomicrographs in Corliss & Coats). 19. *Monochilum* (Schewiakoff). 20. *Stegochilum* (Jankowski). 21, 22. *Curimostoma* (Kozloff, Corliss). 23, 24. *Deltopylum* (Fauré-Fremiet & Mugard, Corliss).

Page 280. Figs. 25–35. *Glaucoma*. 25–28. *G. scintillans* (Kahl, Kahl, Dragesco, Corliss). 29. *G. macrostoma* (Corliss). 30. Generalized AZM bases, as seen through buccal overture (Corliss). 31–33. *G. frontata* (Calkins & Bowling, Dragesco, Corliss). 34, 35. *G. dragescui* (Dragesco, Corliss). 36. *Glaucomella* (Grolière). 37–39. *Epenardia*, and its AZM bases (Kahl, Corliss, Corliss). 40–42. *Espejoia*, macrostome and microstome forms (Wang & Nie, Fauré-Fremiet & Mugard, Fryd-Versavel et al.). 43. *Turaniella* (Iftode & Versavel). 44–47. *Ophryoglena* (Mugard, Kahl, Canella & Rocchi-Canella, Canella & Rocchi-Canella). 48–50. *Ichthyophthirius*, trophont, reproductive cyst with emerging tomites (one enlarged), and theront (Bütschli, Fouquet, Canella & Rocchi-Canella). 51. *Cryptocaryon* (Sikama).

Page 281. Figs. 52–63. *Paramecium* [note: body outlines credited to Vivier are drawn to scale]. 52–55. *P. caudatum* (Kalmus-Wichterman, Kükenthal-Matthes in Grell, Vivier, von Gelei). 56, 57. *P. calkinsi* (Vivier, Agamaliev). 58. Member of "*aurelia*" complex (Vivier). 59. *P. trichium* (Vivier). 60. *P. multimicronucleatum* (Vivier). 61, 62. *P. bursaria* (Vivier, Klein). 63. Pre-20th-century portrayals of the celebrated "slipper animalcule," by: a, Hill; b, O. F. Müller; c, Ehrenberg; d, Dujardin; e, Stokes. 64–67. *Frontonia* (Tönniges, Agamaliev, Dragesco, Dragesco). 68, 69. *Disematostoma* (von Gelei, Dragesco). 70. *Wenrichia* (von Gelei). 71. *Clathrostoma* (Fauré-Fremiet). 72a,b. *Neobursaridium* (Dragesco). 73. *Lembadion* (Dragesco). 74. *Parastokesia* (Fauré-Fremiet). 75. *Marituja* (Wilbert). 76, 77. *Urocentrum* (Fauré-Fremiet, Klein). 78. *Stokesia* (Dragesco).

PLATE XXVII (pages 282–285)

Page 282. Figs. 1–3. *Philaster* (Mugard, Thompson, Coats & Small). 4, 5. *Porpostoma* (Mugard, Coats–unpub.). 6. *Metanophrys* (de Puytorac et al.). 7. *Madsenia* (Profant–unpub.). 8. *Paralembus* (Grolière). 9. *Parauronema* (Thompson). 10. *Potomacus* (Thompson). 11, 12. *Paranophrys* (Thompson & Berger, Mugard). 13–15. *Uronema* (Hoare, Párducz, Thompson & Evans). 16. *Miamiensis* (Thompson & Moewus). 17. *Uropedalium* (Thompson). 18. *Uronemopsis* (Kahl). 19. *Balanonema* (Penard). 20–23. *Cohnilembus* (Calkins, Kahl, Schewiakoff, Small–unpub.). 24, 25. *Cryptochilidium* (Profant–unpub., Florentin). 26. *Pectenita* (Jankowski). 27. *Entodiscus* (Powers). 28. *Entorhipidium* (Lynch). 29, 30. *Biggaria* (Profant–unpub., Powers). 31, 32. *Cryptochilum* (Powers, Maupas).

Page 283. Fig. 33. *Thyrophylax* [with mixture of other (unidentified) echinoid-inhabiting ciliates in food vacuoles] (Strelkow). 34–36. *Loxocephalus* (Fauré-Fremiet, Jankowski, Schewiakoff). 37–39. *Dexiotricha* (Stokes, von Gelei, Fauré-Fremiet). 40, 41. *Sathrophilus* (Jankowski, Grolière). 42, 43. *Cardiostomatella* (Kahl, Dragesco). 44. *Colpodopsis* (Fauré-Fremiet–unpub.). 45. *Urozona* (Jankowski). 46, 47. *Cinetochilum* (G. von Gelei, Kahl). 48. *Anophrys* (Mugard). 49. *Sertumia* (Tucolesco). 50–53. *Pseudocohnilembus* (Calkins, Hoare, Evans & Corliss, Profant–unpub.). 54, 55. *Thigmophrya* (Raabe, Fenchel). 56. *Myxophyllum* (Raabe). 57. *Cochliophilus* (Kozloff). 58. *Conchophyllum* (Kidder). 59. *Gullmarella* (Fenchel).

Page 284. Figs. 60–63. *Pleuronema* (Schewiakoff, Noland, Dragesco, Agamaliev). 64. *Pleurocoptes* (Fauré-Fremiet). 65–69. *Cyclidium* (Hoare, Calkins, Párducz, Jankowski, Grolière). 70. *Hippocomos* (Czapik & Jordan). 71a,b. *Schizocalyptra* (Dragesco). 72a,b. *Histiobalantium* (Dragesco). 73. *Histiobalantium*(?) or *Pleuronema*(?) or ? (Noland). 74–76. *Cristigera* (Fauré-Fremiet–unpub., Dragesco, Kahl). 77, 78. *Ctedoctema* (Kahl, Wilbert & Buitkamp). 79, 80. *Peniculistoma* (Kidder, Fenchel). 81. *Thigmocoma* (Kazubski). 82–84. *Conchophthirus* (Kidder, Raabe, Raabe).

Page 285. Fig. 85a,b. *Ancistrum* (Raabe). 86. *Ancistrumina* (Fenchel). 87. *Dragescoa* (Jankowski). 88. *Protophrya* (Chatton & Lwoff). 89, 90. *Hemispeira* (Fenchel, Chatton & Lwoff). 91, 92. *Boveria* (Fenchel, Issel). 93. *Plagiospira* (Chatton & Lwoff). 94. *Cheissinia* (Cheissin). 95, 96. *Hysterocineta* (Raabe, de Puytorac). 97. *Drilocineta* (de Puytorac). 98, 99. *Ptychostomum* (de Puytorac). 100, 101. *Protoptychostomum* (de Puytorac, Kaczanowski). 102. *Preptychostomum* (de Puytorac). 103, 104. *Protanoplophrya* (Raabe, Miyashita). 105a,b. *Taeniocineta* (Beers). 106. *Epicharocotyle* (Kozloff). 107. *Eminothigma* (de Puytorac). 108a,b. *Nucleocorbula* [inverted with respect to original orientation] (Santhakumari & Nair). 109. *Thurstonia* (de Puytorac). 110. *Kozloffia*, in nascent catenoid colony formation (de Puytorac). 111. *Kysthothigma* (Miyashita).

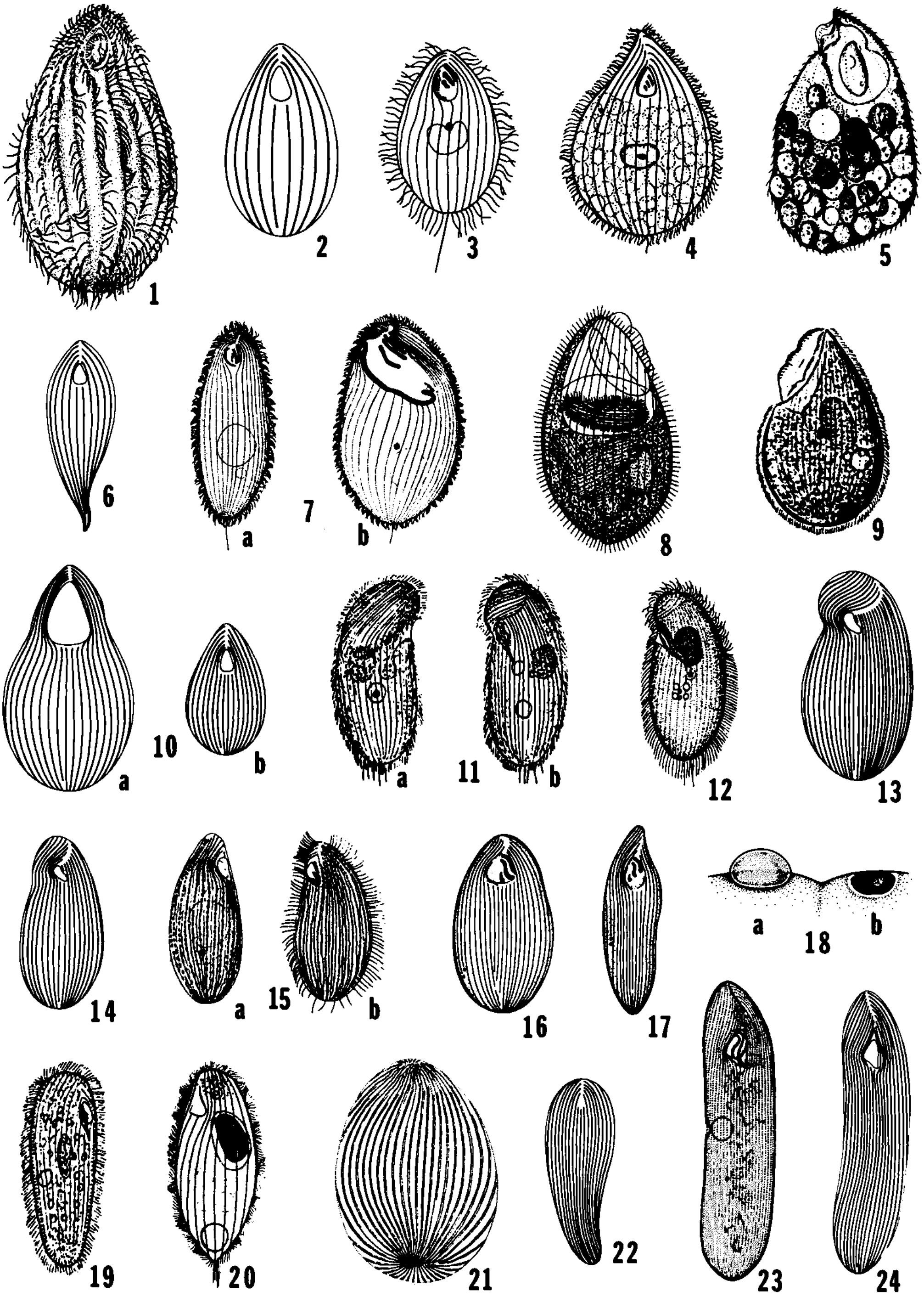

PLATE XXVI. Class Oligohymenophora, subclass Hymenostomata, order Hymenostomatida: selected genera. [See page 278 for figure explanations.]

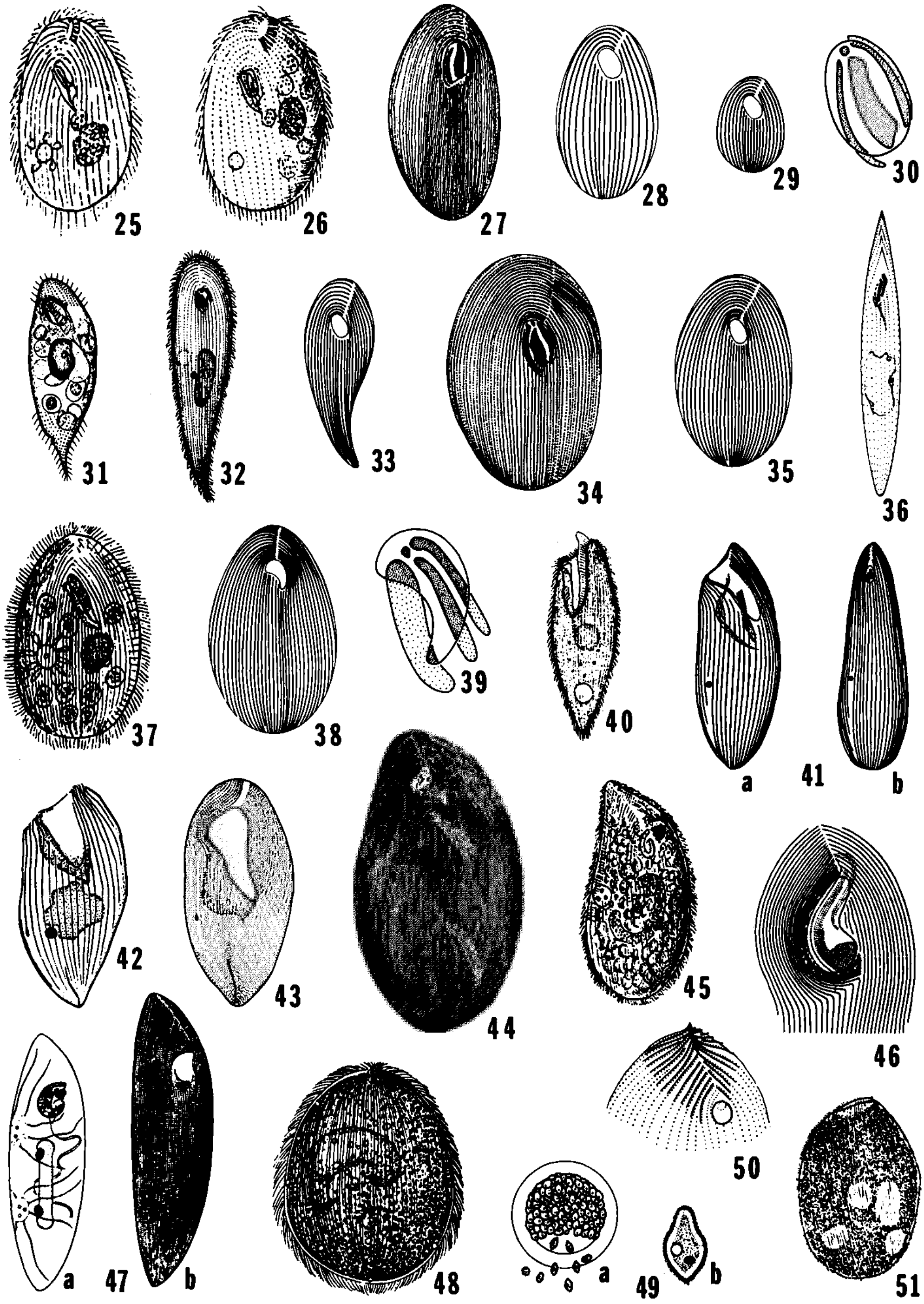

PLATE XXVI, continued. [See page 278 for figure explanations.]

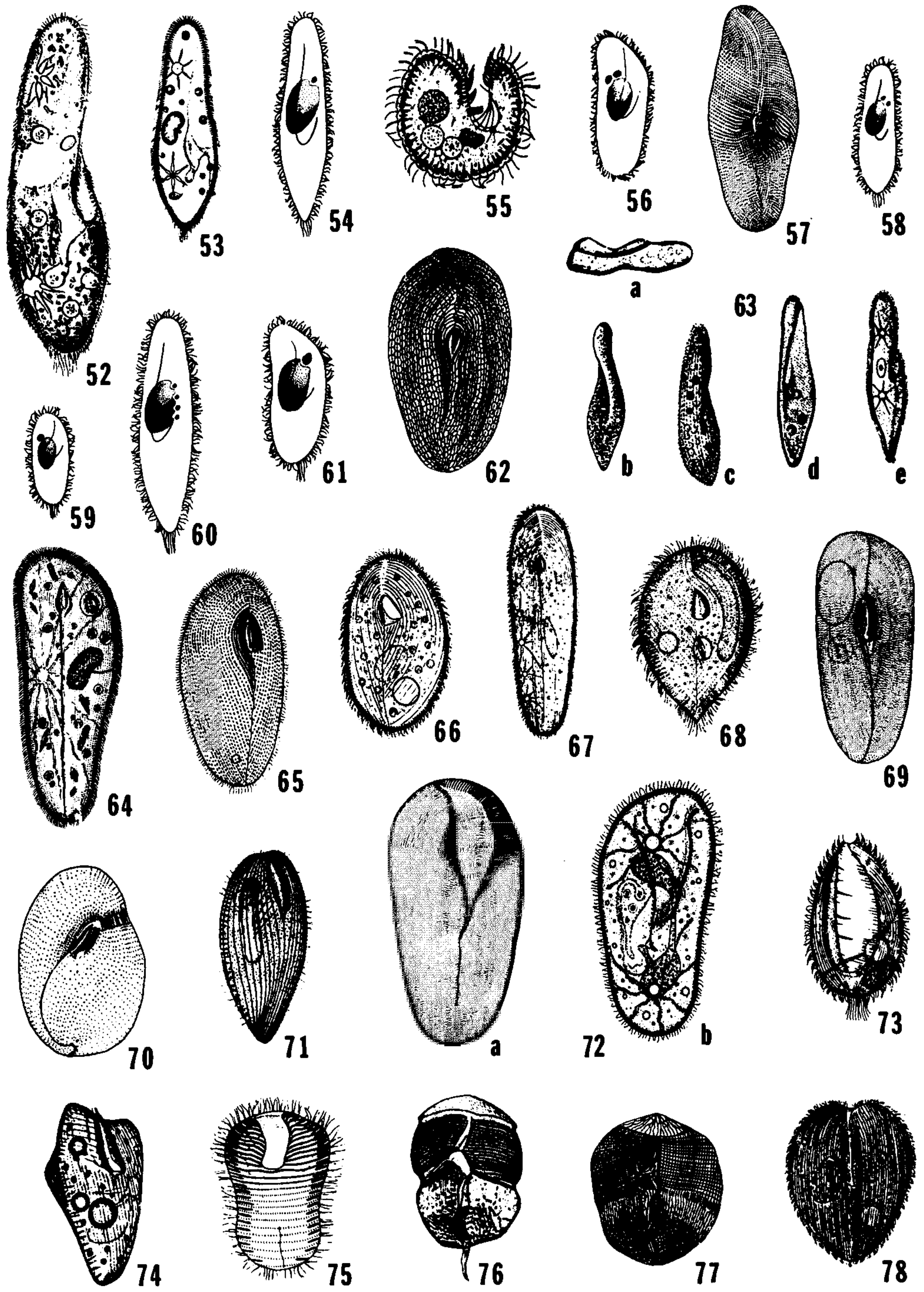

PLATE XXVI, concluded. [See page 278 for figure explanations.]

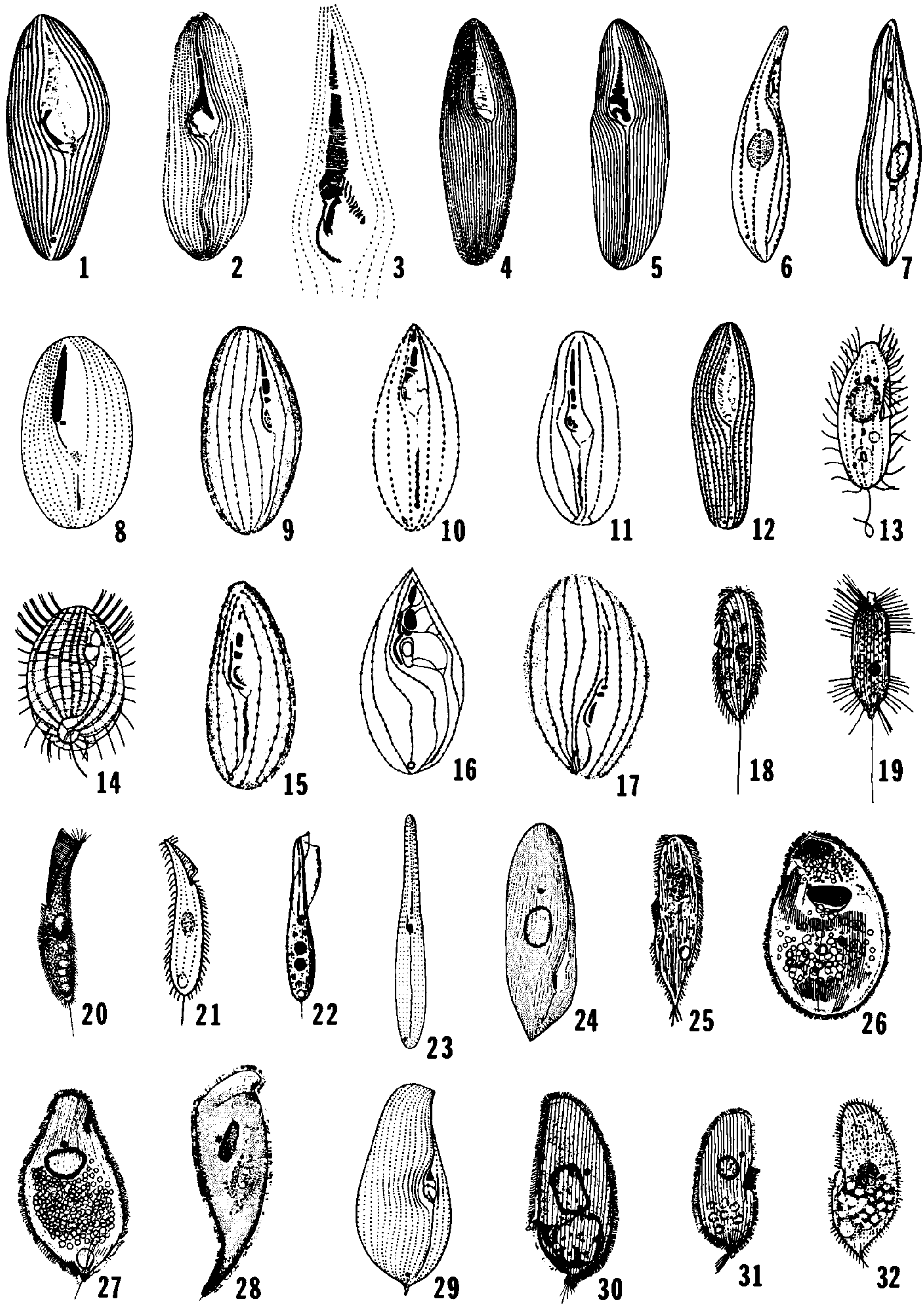

PLATE XXVII. Class Oligohymenophora, subclass Hymenostomata, order Scuticociliatida: selected genera. [See page 278 for figure explanations.]

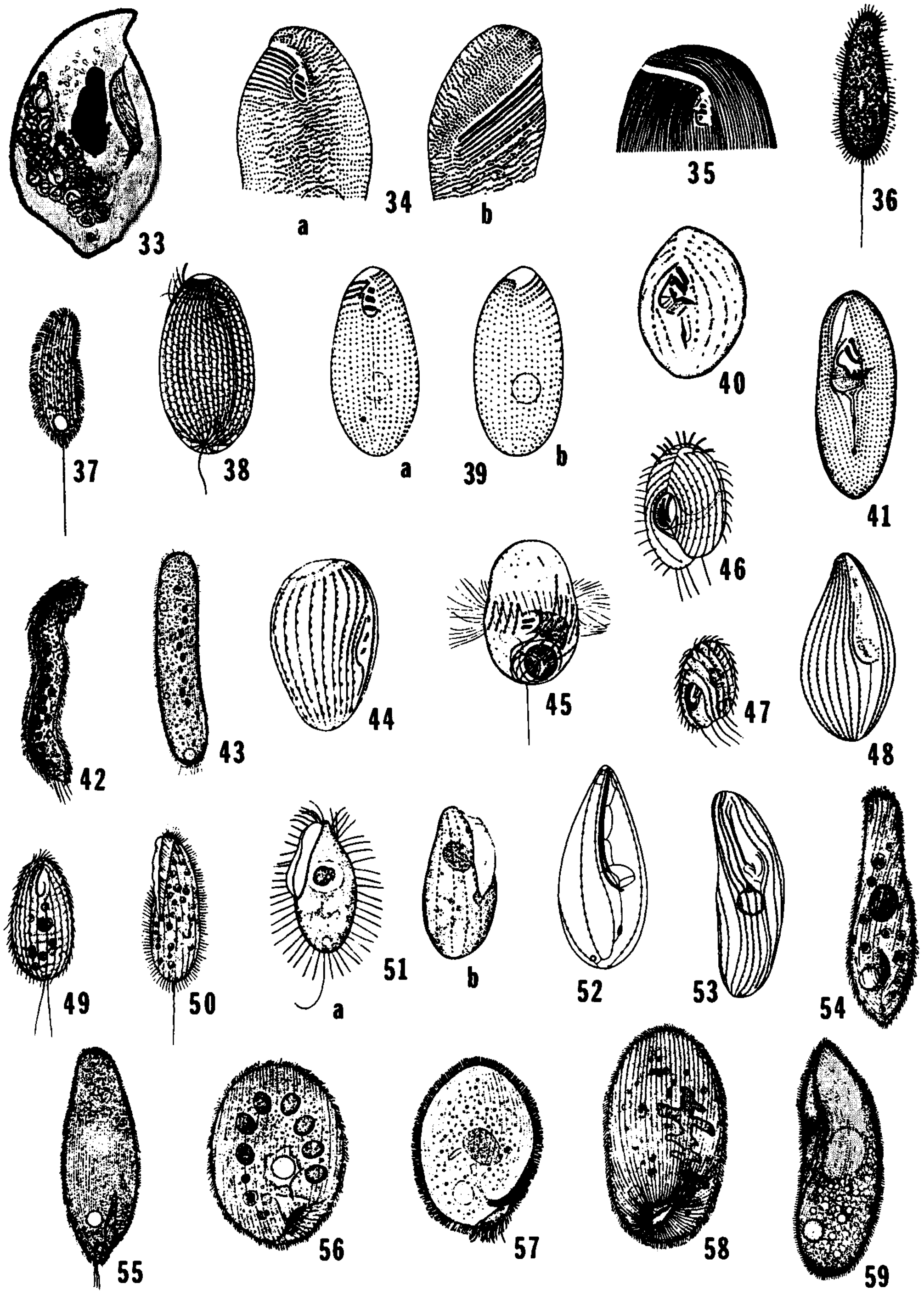

PLATE XXVII, continued. [See page 278 for figure explanations.]

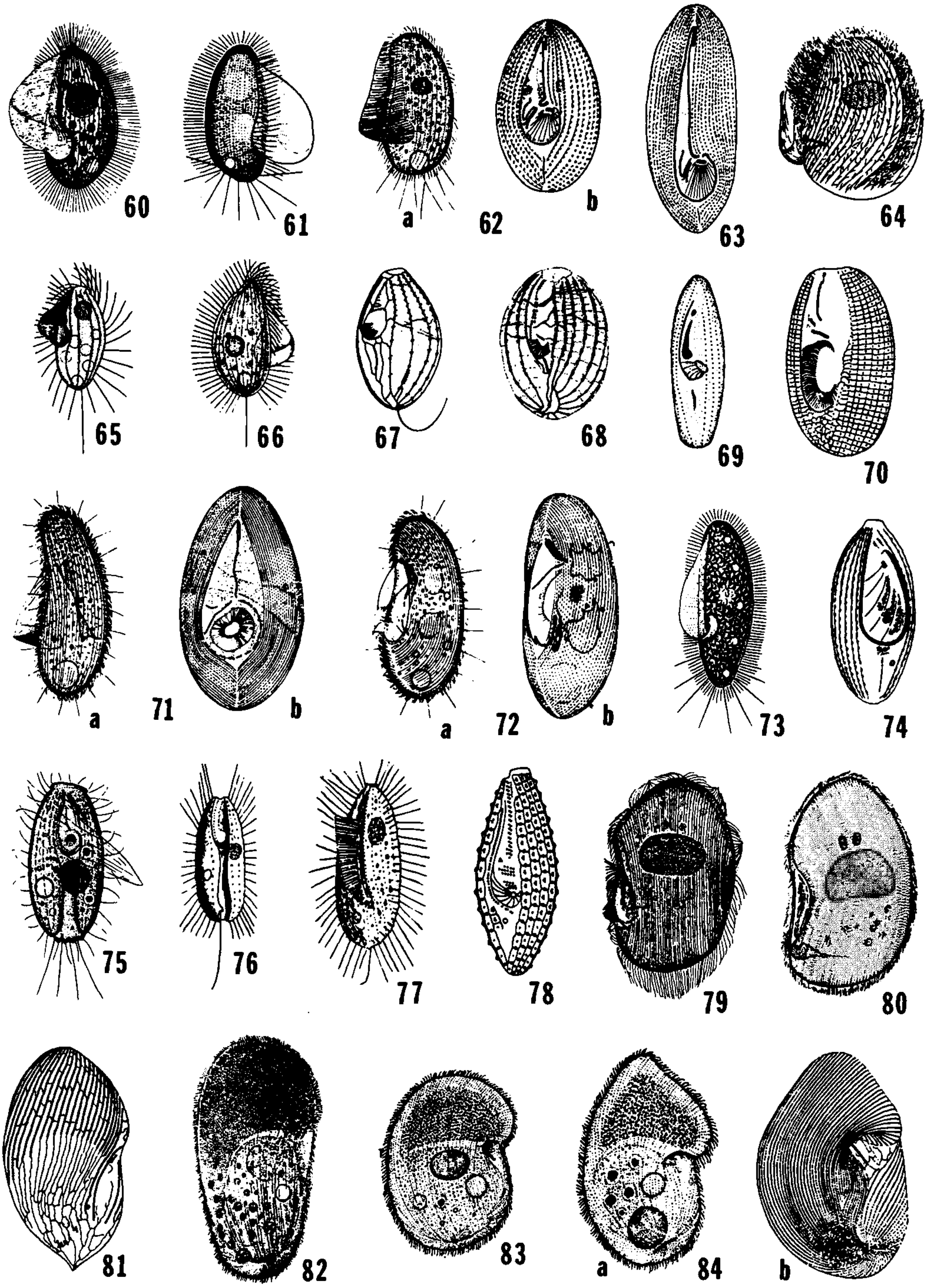

PLATE XXVII, continued. [See page 278 for figure explanations.]

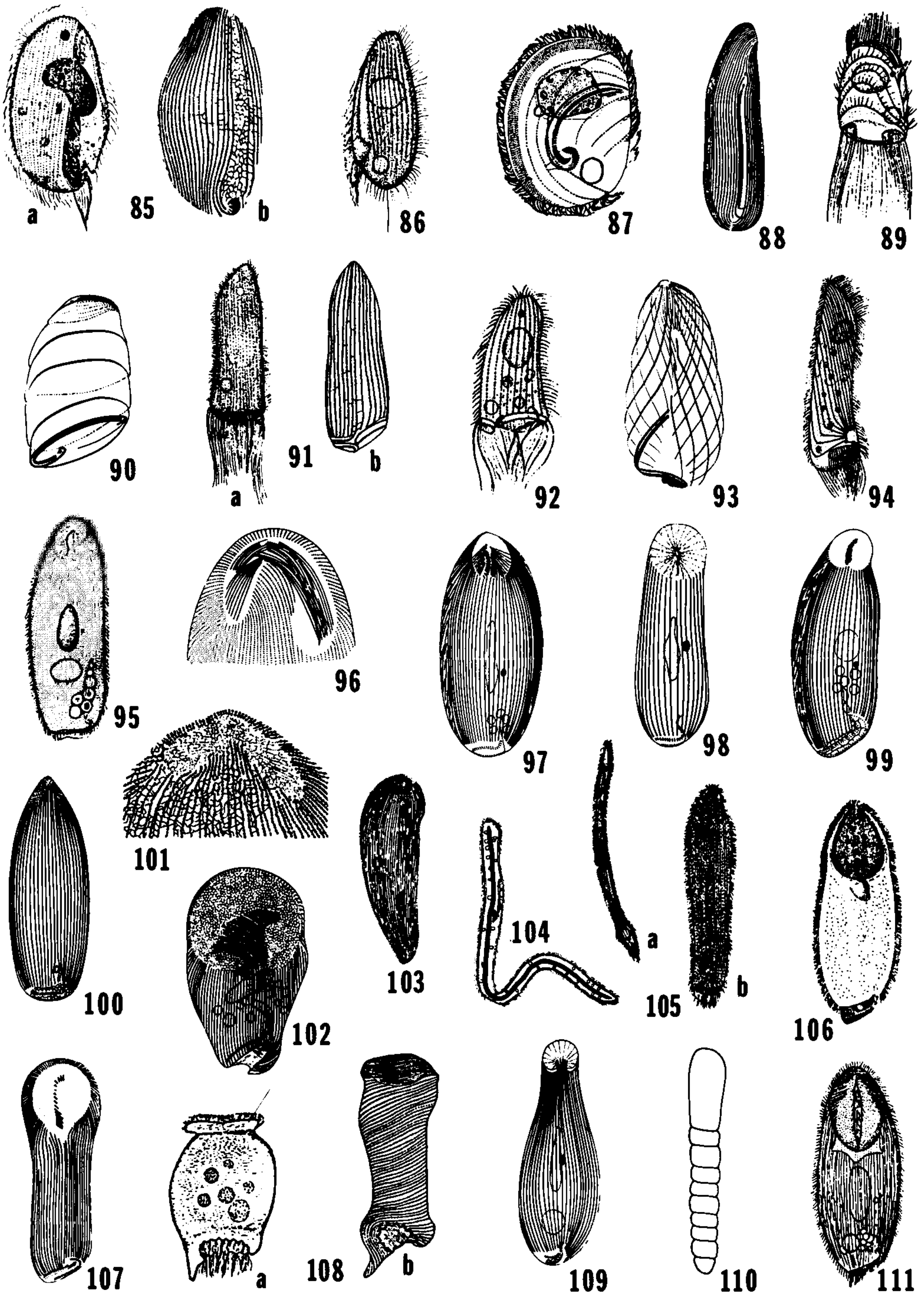

PLATE XXVII, concluded. [See page 278 for figure explanations.]

EXPLANATION OF FIGURES

PLATE XXVIII (pages 287, 288)

Page 287. Fig. 1. *Archiastomata* (Foissner). 2, 3. *Anoplophrya* (Mackinnon & Hawes, de Puytorac). 4. *Buetschliella* (Cépède). 5. *Orchitophrya* (Cépède). 6. *Anoplophryopsis* (de Puytorac). 7. *Rhizocaryum* (Cépède). 8, 9. *Akidodes* (Lom). 10, 11. *Buetschliellopsis* (Lom). 12. *Delphyella* (de Puytorac). 13. *Jirovecella* (Lom). 14, 15. *Hoplitophrya* (Bütschli, de Puytorac). 16. *Juxtaradiophrya* (de Puytorac). 17–19. *Mesnilella* (Bütschli, de Puytorac, Cheissin). 20a,b. *Cheissinophrya* (de Puytorac & Dragesco). 21a–c. *Acanthodiophrya* (de Puytorac & Dragesco). 22. *Radiophryoides*, nascent catenoid colony (Lom). 23, 24. *Radiophrya*, apical end, and beginning of catenoid colony formation (de Puytorac, Cheissin). 25a,b. *Metaradiophrya* (Beers). 26a,b. *Mrazekiella*, nascent catenoid colony (Cheissin).

Page 288. Fig. 27. *Durchoniella* (de Puytorac). 28. *Helella* (Kaczanowski). 29a,b. *Contophrya* (de Puytorac & Dragesco). 30. *Dicontophrya* (de Puytorac & Dragesco). 31, 32. *Maupasella*, whole organism and details of spine and its accessory components (Mackinnon & Hawes, de Puytorac). 33a,b. *Monodontophrya* (Cheissin). 34. *Intoshellina* (Cheissin). 35–39. [The "real"] *Haptophrya* [syn. *Sieboldiellina*] (von Siebold, Bütschli, Bishop, Corliss et al., Lom). 40. *Haptophryopsis* (de Puytorac). 41–43. *Cepedietta* [formerly often mistakenly called *Haptophrya*], with mature catenoid colony in 42b (Maupas, Woodhead, Kay). 44, 45. *Steinella* (Bütschli, Sikora). 46. *Lachmannella* (Claparède & Lachmann). 47a,b. *Clausilocola* (Lom).

PLATE XXIX (pages 289–293)

Page 289. Figs. 1–12. *Vorticella*, stalked form (extended, contracted, or free-swimming), and occasional telotroch (Bütschli, Leeuwenhoek, O. F. Müller, d'Udekem, Kent, Kent, Kent, Noland & Finley, Fauré-Fremiet, Fauré-Fremiet, Fauré-Fremiet, Noland & Finley). 13–18. *Carchesium* (Leeuwenhoek, O. F. Müller, Kent, Kent, Stein, Matthes). 19. *Pseudovorticella* (Foissner & Schiffmann). 20. *Tucolesca* (Tucolesco). 21, 22. *Intranstylum* (Stiller). 23. *Pseudocarchesium* (Sommer). 24, 25. *Haplocaulus*, telotroch and adult form (Stiller, Nenninger).

Page 290. Figs. 26–28. *Zoothamnium* (Summers, Stein, Kent). 29–31. *Astylozoon* (Dingfelder, Wang & Nie, Dingfelder). 32, 33. *Hastatella* (Jarocki & Jakubowska, Wang & Nie). 34–36 [see also 44]. *Apiosoma* (Lom). 37. *Campanella* (Schröder). 38–46. *Epistylis*. 38. On left, attached to *Acineta* (suctorian); on right, another individual captured by the suctorian (Fauré-Fremiet). 44. On left, attached to another peritrich, *Apiosoma*; on right, suctorian *Erastophrya*, attached to same *Apiosoma* (Fauré-Fremiet). 39–43, 45, 46. Other species (Stiller, Sommer, Ehrenberg, Stiller, Fauré-Fremiet, Stiller, Kent). 47. *Rhabdostyla* (Nenninger).

Page 291. Figs. 48–52. *Opercularia* (Nenninger, Collin, Sommer, Kent, Fauré-Fremiet). 53-56. *Scyphidia*, with a telotroch in 54a (Fauré-Fremiet, Thompson et al., Quennerstedt, Stiller). 57a,b. *Ambiphrya*, adult and telotroch (Raabe). 58. *Ballodora* (Matthes). 59. *Orbopercularia* (Matthes). 60, 61. *Opisthonecta* (Fauré-Fremiet, Foissner). 62, 63. *Telotrochidium* (Fauré-Fremiet, Foissner). 64. *Propyxidium* (Nenninger). 65a–c. *Ellobiophrya*, attached and unattached [to host gill tissue] adult forms with a telotroch in 65b (Chatton & Lwoff). 66a,b. *Caliperia*, similarly [see preceding figure] attached and unattached adult forms (Laird). 67–71. *Gerda*, telotroch and various adults (Claparède & Lachmann, Stokes, Penard, Kahl, Kent). 72–76 [with last figure on following page]. *Ophrydium*, individual zooids and colonies (Stein, Wrzesniowski, Ehrenberg, Penard, Kent). [The two "spherical" colonies of Fig. 74 are shown at what could be an actual size. They can become much larger still, though the (then) tens of thousands of contained zooids remain microscopic, of course, and/but give a green coloration (via their symbiotic zoochlorellae) to the entire mass.]

Page 292. Fig. 76a,b [see explanation above]. 77. *Rovinjella* (Matthes). 78–83. *Cothurnia* (Hamilton, Stiller, Entz, Stokes, Vuxanovici, Penard). 84, 85. *Thuricola* (Sommer). 86–93. *Vaginicola* (Sommer, d'Udekem, Kent, Stokes, Stokes, Penard, Ehrenberg, de Fromentel). 94, 95. *Caulicola*(?), with operculum shown [surely mistakenly] as attached to rim of lorica-opening (d'Udekem, Stokes). 96–98. *Pyxicola* (Kent). 99, 100. *Platycola* (de Fromentel). 101–105. *Lagenophrys* (Penard).

Page 293. Figs. 106–114. *Trichodina* (Uzmann & Stickney, Clark, Busch, Bovee, Padnos & Nigrelli, Jackson, Lom, MacLennan, Fulton). 115. *Trichodinella* (Lom). 116. *Vauchomia* (Mueller). 117–122. *Urceolaria* (Zick, Johnston, Wallengren, Jankowski, Claparède & Lachmann, Fenchel). 123–125. *Trichodinopsis* [note attached spirochaetes, originally described as cilia] (Claparède & Lachmann, Issel, Raabe). 126. *Polycycla* (Fauré-Fremiet & Czapik). 127a–c. *Leiotrocha* (Fenchel). 128a–f. Denticles of aboral ring representative of selected mobiline peritrich genera, as indicated (all after Raabe): a, *Trichodina*; b, *Tripartiella*; c, *Trichodinella*; d, *Dipartiella*; e, *Urceolaria* and *Leiotrocha*; f, *Polycycla* and *Trichodinopsis*.

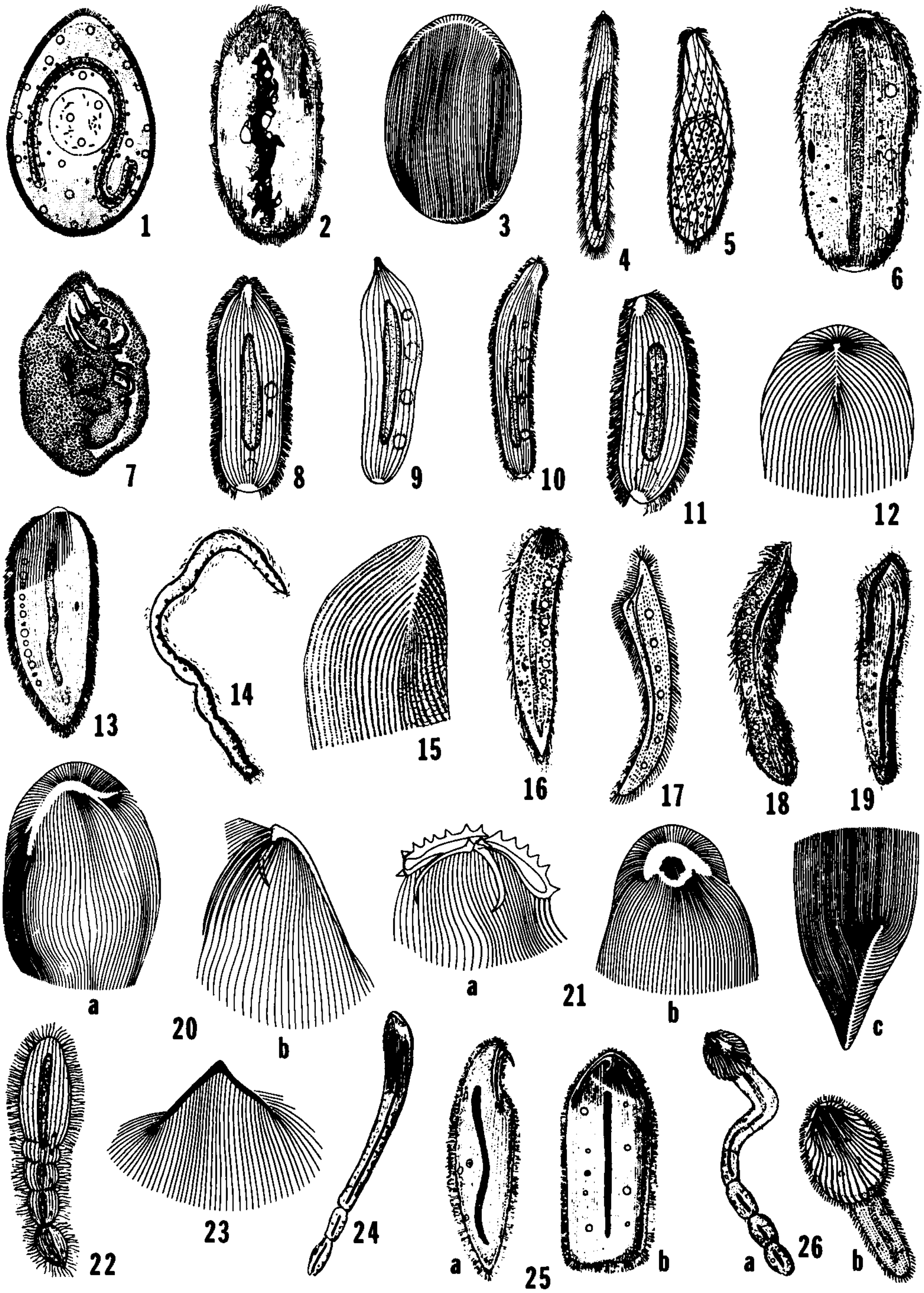

PLATE XXVIII. Class Oligohymenophora, subclass Hymenostomata, order Astomatida: selected genera. [See page 286 for figure explanations.]

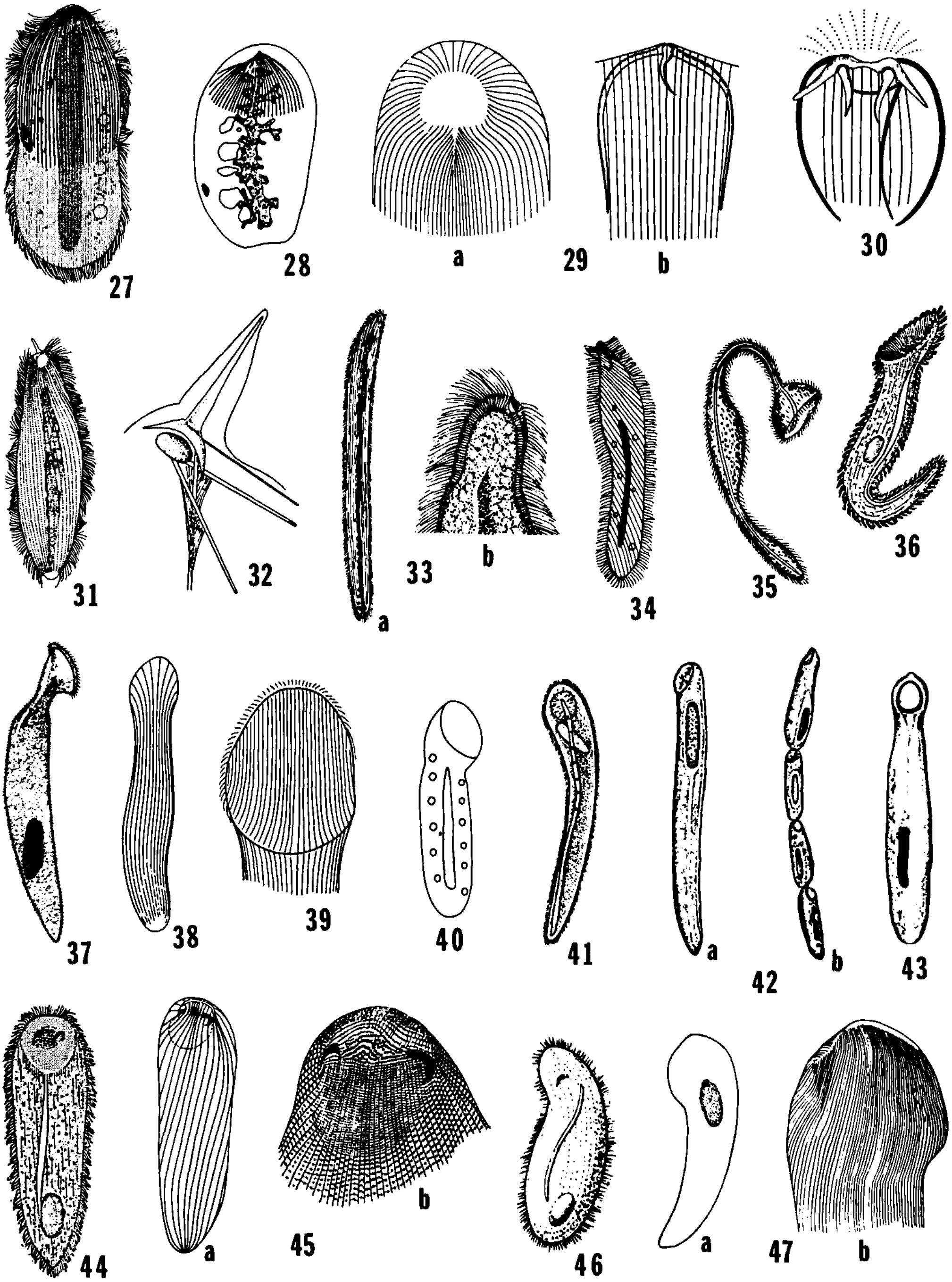

PLATE XXVIII, concluded. [See page 286 for figure explanations.]

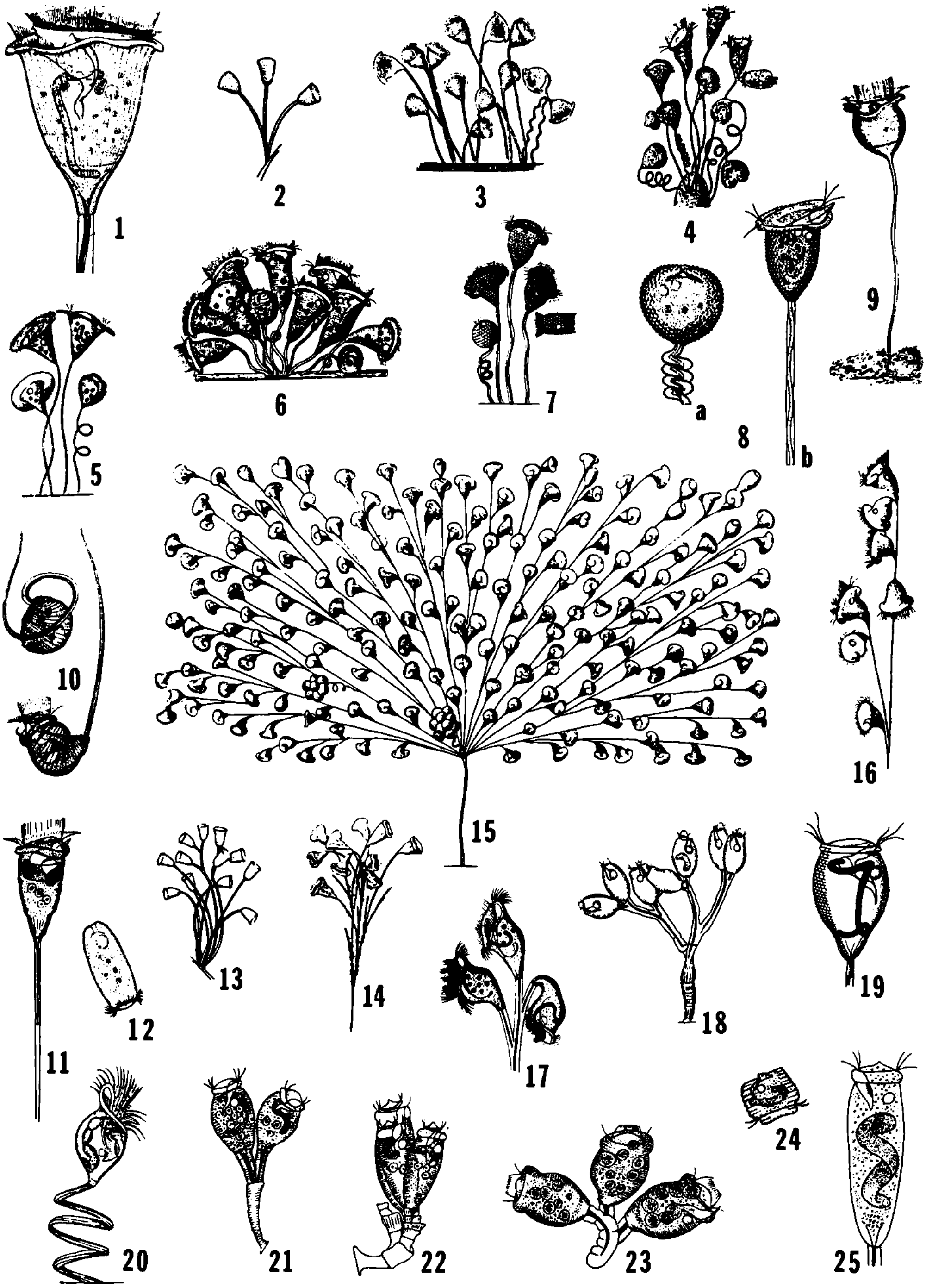

PLATE XXIX. Class Oligohymenophora, subclass Peritricha, order Peritrichida: selected genera. [See page 286 for figure explanations.]

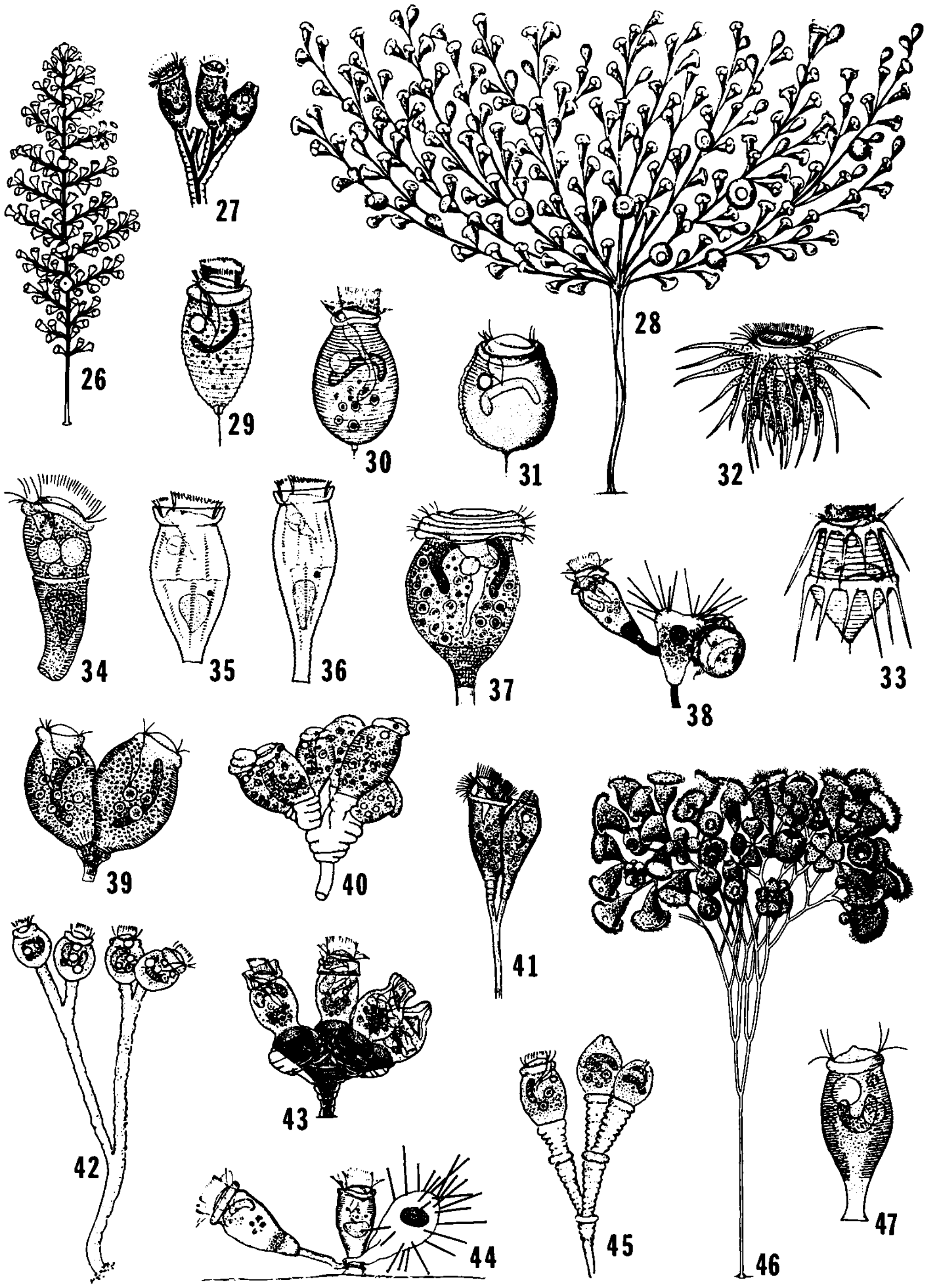

PLATE XXIX, continued. [See page 286 for figure explanations.]

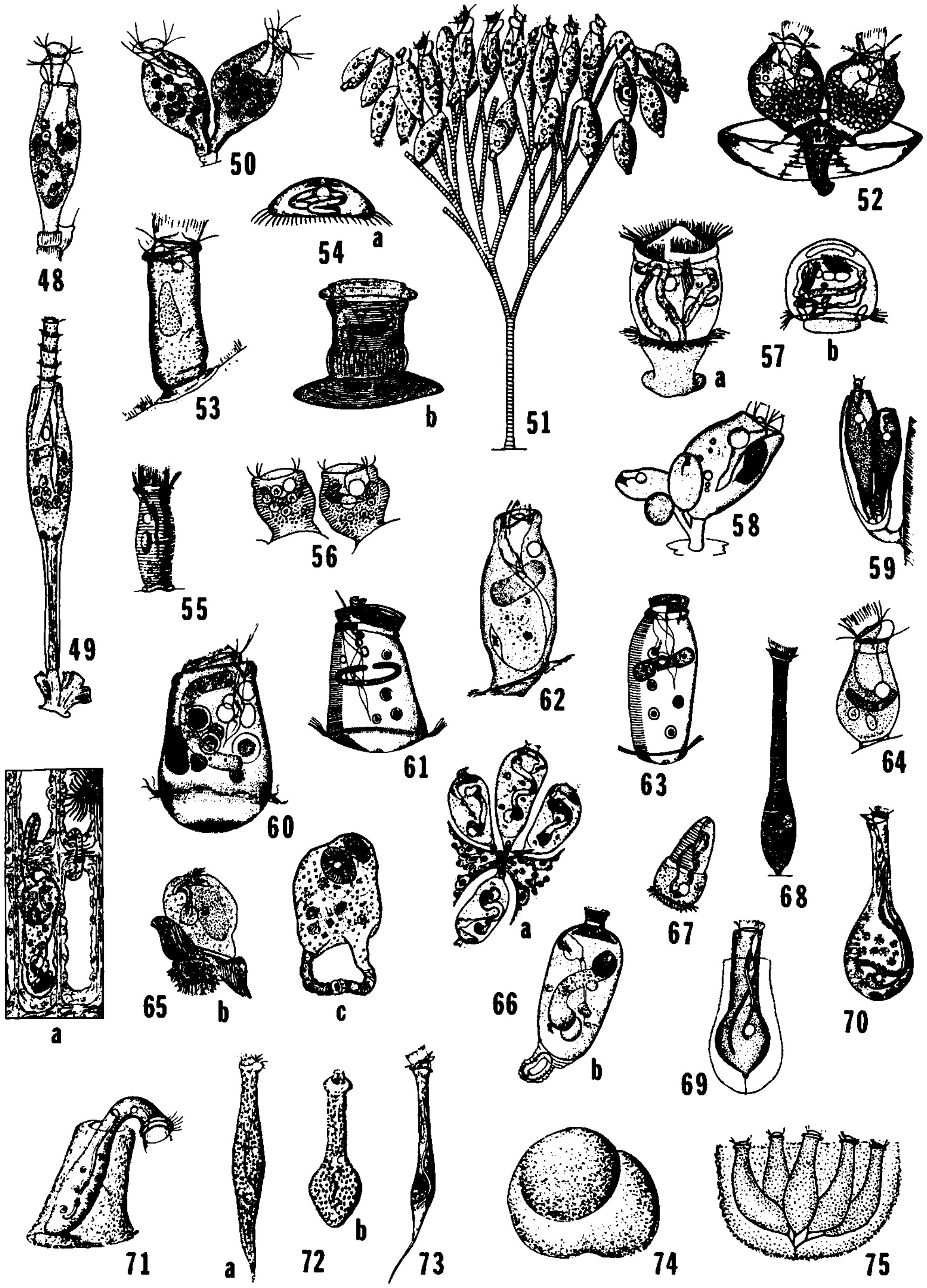

PLATE XXIX, continued. [See page 286 for figure explanations.]

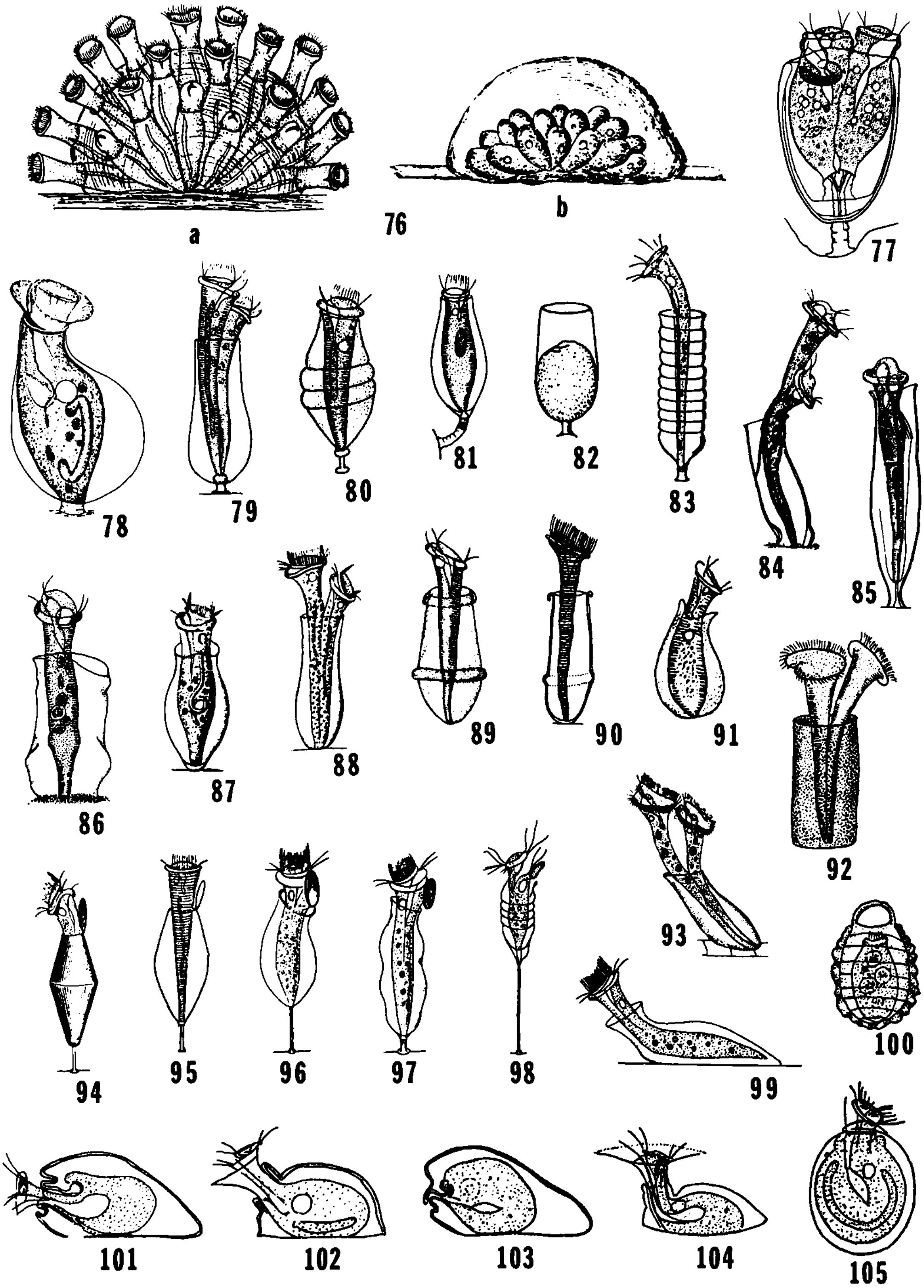

PLATE XXIX, continued. [See page 286 for figure explanations.]

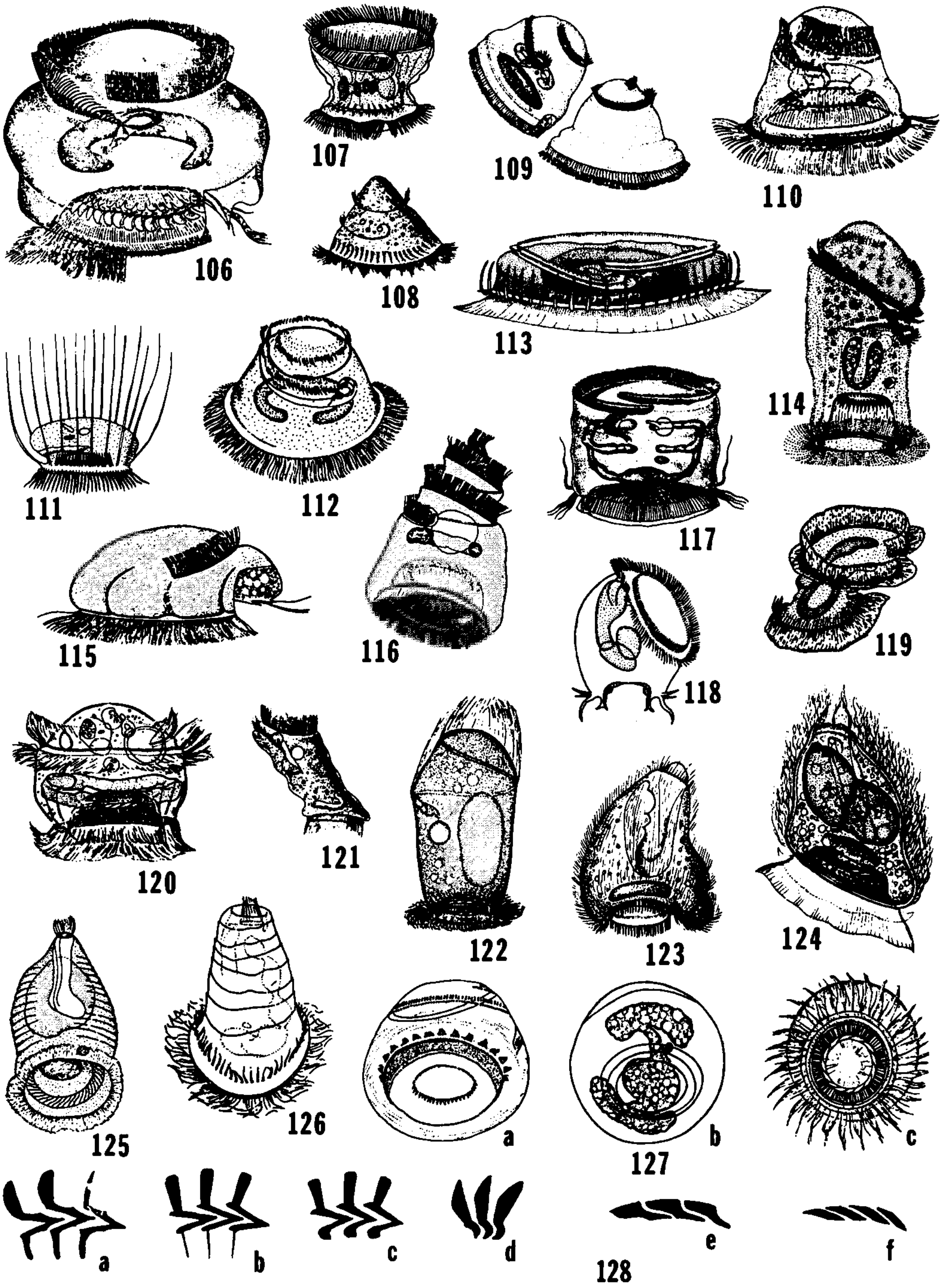

PLATE XXIX, concluded. [See page 286 for figure explanations.]

Class III. POLYHYMENOPHORA Jankowski, 1967

(syns. Membranellata *p.p.*, Membranellophora *p.p.*; Polytrichidea + Oligotrichidea, Postciliodesmatophora *p.p.*)

Oral ciliature conspicuous, with adoral zone of multiple membranelles (generally paramembranelles) especially prominent and often extending out of buccal cavity onto and/or around anterior end of body; one or more paroral membranes on the right; paucity of simple somatic ciliature (except in one major group) or with its replacement by cirri (in another group); stomatogenesis parakinetal or apokinetal; kinetodesmata rare, toxicysts and trichocysts absent; postciliodesmata common and prominent; fission almost always isotomic; conjugation temporary and isogamontic; species widely distributed, generally of large body size and diverse feeding habits, and (with one or two subgroup exceptions) very commonly free-living, free-swimming forms.

Subclass **Spirotricha** Bütschli, 1889

(syns. Blepharismina, Bursari[i] na, Condylostomatina, Stentorina)

With characteristics of class (above).

Order 1. HETEROTRICHIDA Stein, 1859

(syns. Heterotricha, Heterotrichorida, Heterotrichorina)

With characteristics of subclass *s.s.* (above). Body generally large to very large, sometimes highly contractile; somatic ciliation frequently holotrichous, with regular, even dense, rows of simple cilia (though not true of all suborders); wide distribution, both free-living and symbiotic forms.

Suborder (1) Heterotrichina Stein, 1859

(syns. Blepharismina, Bursariina, Condylostomatina, Stentorina)

With characteristics of order *s.s.* (above). Somatic ciliature well developed, but buccal organelles (paramembranelles) also numerous and prominent; of large body size, often contractile; single conspicuous contractile vacuole at posterior end of body; mucocysts in abundance, and pigment vesicles common in many species; no loricae, but cysts common; essentially all free-living forms [endosymbiotic families formerly included here now comprise separate suborder: see below], widely distributed in great variety of habitats.

Family SPIROSTOMIDAE Stein, 1867

(syns. Blepharismidae, Spirostomatidae)

Large, often elongate, cylindrical forms, some highly contractile, some pigmented; long, narrow peristomial field, sometimes with buccal ciliature relatively inconspicuous; somatic ciliation uniform, often dense, and typically complete; contractile vacuole posterior, frequently large, and may have lengthy collecting canal; macronucleus compact, ovoid to elongate-moniliform; free-living in fresh-water (predominantly), marine, or edaphic habitats. [I am removing the controversial genus *Protocruzia* from this family, where it is customarily placed, provisionally considering it (*sensu stricto*) to be a philasterine scuticociliate (class Oligohymenophora). But quite possibly two or three *totally different* organisms have been included over the years under the same name! Thus, I am here resurrecting (with a large degree of uncertainty) Mansfeld's genera *Diplogmus* and *Propygocirrus*, suggesting that they may represent the "heterotrichine" moiety of the *Protocruzia (sensu lato)* of the literature.]

Anigsteinia Isquith, 1968. Several species. Pl. XXX, Figs. 5, 6.

Blepharisma Perty, 1849. Many species (all valid?). Pl. V, Figs. 19, 49; XXX 1–4.

Gruberia Kahl, 1932. Few species. Pl. I, Fig. 10; XXX 7.

Parablepharisma Kahl, 1932. Few species. Pl. XXX, Figs. 8, 9.

Pseudoblepharisma Kahl, 1926. Few species.

Spirostomum Ehrenberg, 1833. Several to many species. Pl. V, Fig. 121; XXX 13–15.

Incertae sedis: Diplogmus Mansfeld, 1923, Pl. XXX, Fig. 12; and *Propygocirrus* Mansfeld, 1923, Pl. XXX, Fig. 11: resurrected genera, each with single (or more?) species.

Family PHACODINIIDAE n. fam.

Body ovoid in shape, compressed laterally, with rigid and ribbed pellicle (= cuirass); cytoplasm nonpigmented; lengthy peristomial field, with conspicuous membranelles, terminating very near posterior pole of organism; somatic ciliature, in widely spaced rows, occurs in little packets of 6-8 delicate cilia each; macronucleus horseshoe-shaped; these hypotrich-like organisms show world-wide distribution, found mainly in edaphic habitats (e.g., moss on trees). [Supported by modern redescriptions by Didier & Dragesco (1978), Dragesco (1970), Gellért (1950b), and Roque (1971) – though Penard's (1922) observations also remain excellent – plus unpublished notes of my own, I decided some time ago to separate this group at the familial level from the rather different Spirostomidae. In the meantime, Jankowski (1975) has independently suggested the same familial name, but without description or characterization.]

Phacodinium Prowazek, 1900. Single species. Pl. IV, Fig. 33; XXX 10.

Transitella Gellért, 1950. Single species.

Family METOPIDAE Kahl, 1927

Anterior part of body uniquely twisted to left, and posterior part sometimes tailed and/or bearing tuft of longer (caudal) cilia; buccal membranelles large, yet rather inconspicuous; uniform somatic ciliation, but often not dense; macronucleus compact, centrally located; widely distributed as fresh-water polysaprobic forms, but some also marine and psammophilic or inquilinic in echinoids. [Note that *Caenomorpha* has now been removed to a separate suborder (below): Kahl (1932b) and Corliss (1961), as well as others – until the work of Jankowski (1964a,b) – failed to recognize the cardinal differences between it and *Metopus*.]

Bothrostoma Stokes, 1887. Few species. Pl. XXX, Fig. 24.

Brachonella Jankowski, 1964. Several species. Pl. III, Fig. 26; XV 4; XXX 25.

Metopus Claparède & Lachmann, 1858 (syn. *Metopides* [hom.]). Very many (> 50) species. Pl. V, Fig. 50; XV 3; XXX 29–33.

Palmarella Jankowski, 1975 (for *Palmarium* Gajewskaja, 1925 [hom.]). Few species. Pl. XXX, Fig. 27.

Spirorhynchus da Cunha, 1915 (syn. of *Metopus*?). Few species. Pl. XXX, Fig. 34.

Tesnospira Jankowski, 1964. Single species. Pl. XXX, Fig. 26.

Tropidoatractus Levander, 1894. Single species. Pl. XXX, Fig. 28.

Family CONDYLOSTOMATIDAE Kahl in Doflein & Reichenow, 1929

(syns. Bryometopidae, Condylostomidae)

Body typically large, heavily ciliated, contractile; buccal ciliature, including paroral membrane, prominent; macronucleus long and moniliform in type-genus; body very elongate in some forms, nearly ellipsoidal in others; contractile vacuole often with long feeding canal; in various habitats: fresh-water, edaphic, and especially marine.

Bryometopus Kahl, 1932. Few species. Pl. XXX, Fig. 45.

Condylostoma Bory de St. Vincent, 1826 (originally written as *Kondyliostoma*, then, for a few more years, as *Kondylostoma*). Many species. Pl. II, Fig. 12; XV 2; XXX 37–40.

Copemetopus Villeneuve-Brachon, 1940. Single species. Pl. XXX, Fig. 43.

Incertae sedis: Dellochus Corliss, 1960 (for *Lochus*). Single species.

Family REICHENOWELLIDAE Kahl, 1932

Body ellipsoidal, with narrowed peristomial field; somatic ciliation uniform, occasionally slightly spiraled; macronucleus elongate but not moniliform; in fresh-water or edaphic habitats.

Balantidioides Kahl, 1930 (for *Balantidiopsis* Pen. [*non* Büt.]). Few spp. Pl. XXX, Fig. 35.

Reichenowella Kahl, 1932. Single species. Pl. XXX, Fig. 36.

Family CLIMACOSTOMIDAE Repak, 1972

(syn. Pediostom[at]idae)

Body large, ovoid, with very prominent peristomial field (buccal cavity) occupying much of anterior part of body; stomatogenesis parakinetal; paramembranelles conspecuous; somatic ciliation dense; macronucleus usually in form of thick ribbon, often coiled and lengthy; symbiotic zoochlorellae in some species; fresh-water and marine forms.

Climacostomum Stein, 1859. Few to several species. Pl. XV, Fig. 1; XXX 44.

Fabrea Henneguy, 1890 (syn. *Bursalinus*). Single species. Pl. XXX, Figs. 41, 42.

Pediostomum Kahl, 1932. Single species.

Family STENTORIDAE Carus, 1863

Majestic in size and movement; trumpet-shaped, elongate, uniformly ciliated, highly contractile; oral ciliature spirals clockwise nearly 360° around flared-out anterior end; stomatogenesis apokinetal; often pigmented and/or with symbiotic zoochlorellae; a few species with mucilaginous loricae; macronucleus commonly moniliform; typically in fresh-water habitats only. [The validity of *Parastentor* and the taxonomic position of the curious fish parasite *Stentoropsis* remain questionable. The latter genus may well belong in the following suborder, with the bulk of the other endocommensalistic heterotrichs.]

Stentor Oken, 1815 (a *nomen conservandum*; syns. *Stentorella, Stentorina*). Many species. Pl. III, Fig. 20; V 13, 51; XXX 16–23.

Incertae sedis: Parastentor Vuxanovici, 1961, and *Stentoropsis* Dogiel & Bychowsky, 1934: each with single species.

Family BURSARIIDAE Dujardin, 1840

(syn. Thylakidiidae)

Body large and broad, with rounded posterior (though tailed in one species) end and truncate anterior end; buccal cavity prominent, funnel-like, opening at apical end of organism and remaining open down onto ventral surface for some distance; elongate, rod-like macronucleus, with up to 35 micronuclei; heavy-walled cyst; predominantly fresh-water forms.

Bursaria O. F. Müller, 1773. Few species. Pl. I, Fig. 20; XXX 46–50.

Bursaridium Lauterborn, 1894. Several species. Pl. XXX, Fig. 51.

Thylakidium Schewiakoff, 1892 (syn. *Thylacidium*). Single species.

Family CHATTONIDIIDAE Villeneuve-Brachon, 1940

Body large and somewhat rotund, with gently pointed posterior end; buccal cavity opens apically and bears full circle of strong membranelles; stomatogenesis apokinetal, with new infraciliary bases developing in oligotrich-like pouch; macronucleus very long, with loops; a unique "posteroaxial cavity," containing cilia, opens at posterior pole; in polluted brackish waters.

Chattonidium Villeneuve, 1937. Single species. Pl. XXX, Fig. 53.

Family PERITROMIDAE Stein, 1867

Body ellipsoidal, dorsoventrally flattened, with regular ciliation on ventral surface only; lateral edges and dorsal surface bear short stiff spines, associated in latter location with curious wart-like prominences; buccal membranelles conspicuous at apical end of organism, curving down left side to cytostome located in anterior third of body; pair of ovoid-to-spherical macronuclei present; like hypotrichs (where formerly classified) in number of characteristics; generally in marine habitats, including salt marshes.

Peritromus Stein, 1862. Several species. Pl. XXX, Figs. 34, 35.

Suborder (2) Clevelandellina de Puytorac & Grain, 1976

As in preceding suborder, somatic ciliature well developed, buccal organelles numerous and prominent (though here unique as heteromembranelles), and body size often above average (i.e., > 150 μm). But additionally, here, are kinetodesmal (as well as cathetodesmal and retrodesmal) fibers in some species; complex "systèmes sécants," characteristic of specific kinetal patterns; macronuclear karyophore in many species; sometimes conspicuous dorsoanterior sucker; cilia-lined cytoproct in several forms; and all species endosymbionts in digestive tract of either insects (or certain related arthropods) and lower vertebrates or, less often, in oligochaetes and molluscs. [Most important taxonomic step, recognition of this separate suborder!]

Family NYCTOTHERIDAE Amaro, 1972

Body ovoid to slightly reniform, plump; buccal ciliature running from near-apical to subequatorial position, in a sigmoid-like curve as it enters conspicuous infundibulum of the buccal cavity *sensu lato*; single, large, compact macronucleus, in anterior half of body, supported by more or less well-developed karyophore; systèmes sécants vary significantly with included genera; endosymbionts in wide variety of hosts: from oligochaetes, insects (cockroach), and myriapods (centipede, millipede) to molluscs (shipworm), amphibians (frog, toad), and reptiles, but not fishes.

Metanyctotherus Albaret, 1970. Few species. Pl. XXX, Fig. 58.

Nyctotheroides Grassé, 1928 (syns. *Kudoella, Pseudonyctotherus*). Many to very many (> 50?) described species. Pl. IV, Fig. 11; XV 5; XXX 59–62.

Nyctotherus Leidy, 1849. Many to very many (> 50?) described species. Pl. I, Fig. 18; III 3; XXX 56, 57.

Pronyctotherus Albaret & Njiné, 1976. Few species.

Family SICUOPHORIDAE Amaro, 1972

Body plump-ovoid to ellipsoidal, occasionally tailed; sucker (often extensive) typically present on concave surface of body, uniquely reinforced with polysaccharide skeletal elements (which are also elsewhere on body); buccal ciliature and macronucleus similar to those of preceding family; kinetal sutures vary with genus; endosymbionts in vertebrate hosts only: amphibians, reptiles, and (if *Ichthyonyctus* remains here) certain fresh-water fishes.

Geimania Albaret, 1975. Few species. Pl. XXX, Fig. 66.

Metasicuophora Albaret, 1973. Single species.

Parasicuophora Albaret, 1968. Few species.

Prosicuophora de Puytorac & Oktem, 1967. Single (more?) species. Pl. IV, Fig. 13.

Sicuophora de Puytorac & Grain, 1969 (syn. *Wichtermania*). Several species. Pl. V, Fig. 12m; XXX 63, 64.

Incertae sedis: *Ichthyonyctus* Jankowski, 1974. Several species. Pl. XXX, Fig. 65.

Family CLEVELANDELLIDAE Kidder, 1938

(for Clevelandiidae)

Body basically ovoid or elongate-ovoid, with posterior pole oddly shaped because of bearing entire buccal cavity and its (infundibular) opening; macronucleus and systèmes sécants reminiscent of Nyctotheridae; endosymbionts in certain insects (termites, wood-feeding roaches) only.

Clevelandella Kidder, 1938 (for *Clevelandia*; syn. *Emmaninius*). Many species. Pl. XV, Fig. 6; XXX 67, 68.

Metaclevelandella Uttangi & Desai, 1963. Single species.

Paraclevelandia Kidder, 1937. Few species. Pl. XXX, Fig. 69.

Family INFEROSTOMATIDAE Ky, 1971

Body roughly ovoid in shape, but distorted somewhat by huge sucker on right side at anterior end and by position of buccal cavity *sensu stricto* (infundibulum only) directly at the (truncate) posterior pole; other features generally similar to those of the Sicuophoridae, although a transverse suture is unique here (except for its presence in *Ichthyonyctus*); found only in intestine of certain fresh-water fishes.

Inferostoma Ky, 1971. Single species. Pl. XXX, Fig. 70.

Incertae sedis in suborder Clevelandellina:

Family NATHELLIDAE Singh, 1953

(syn. Nathelliidae)

Body relatively large, uniformly ciliated; the adoral ciliature and "peristome" course from anterior to posterior end of body in a gentle sigmoidal curve; compact macronucleus; single contractile vacuole; organisms found in digestive tract of fresh-water siluroid fishes. [More and better data needed! Possibly these ciliates are congeneric with *Inferostoma*; in which case, the names of the preceding family and genus would have to fall as junior synonyms of Nathellidae and *Nathella*, respectively.]

Nathella Singh, 1953. Few species. Pl. XXX, Fig. 71.

Suborder (3) Armophorina Jankowski, 1964

(syn. Armophorida)

Body generally small, top-shaped (often with very long caudal spine), with somatic ciliature absent except for caudal tuft and several anteriorly located cirri; buccal ciliature (accompanied by a "ciliary stripe") extensive, encircling body and spiraling posteriad, with cytostome thus near antapical pole; pellicle rigid; large ovoid macronucleus, multiple in several species; free-living polysaprobic forms, typically in fresh-water habitats.

Family CAENOMORPHIDAE Poche, 1913

(syns. Gyrocoridae, Gyrocorycidae, Gyrocorythidae, Ludiidae)

With characteristics of suborder (above).
Caenomorpha Perty, 1852 (syns. *Gyrocoris*, *Gyrocorys*). Many spp. Pl. XV 7; XXX 72–74.
Cirranter Jankowski, 1964 (for *Trochella*). Single species. Pl. XXX, Fig. 76.
Ludio Penard, 1922. Single species. Pl. XXX, Fig. 75.

Suborder (4) Coliphorina Jankowski, 1967

Universally loricate, sessile forms, with vermiform migratory larval stage; body large and elongate, especially in neck region in some species, with conspicuous pair of "peristomial wings" extending from the lorica (a structure generally cylindrical, with a definite bend in some species) and bearing the prominent buccal ciliature; somatic ciliation uniform and holotrichous; body highly contractile and often pigmented; stomatogenesis parakinetal; widely distributed in marine habitats (few species, fresh-water), with loricae attached to algae, higher aquatic plants, or integument or shells of invertebrates (molluscs, various crustaceans, bryozoa, coelenterates, etc.).

Family FOLLICULINIDAE Dons, 1914

(syn. Claustrofolliculinidae)

With characteristics of suborder (above).
Ampullofolliculina Hadži, 1951. Single species.
Ascobius Henneguy, 1884 (syn. *Semifolliculina* p.p.). Several species. Pl. XV, Fig. 8.
Atriofolliculina Hadži, 1951. Few species.
Aulofolliculina Hadži, 1951. Single species.
Botticula Dioni, 1972. Single (fresh-water) species.
Claustrofolliculina Hadži, 1951. Single species.
Diafolliculina Hadži, 1951. Few (one fresh-water) species.
Donsia Hadži, 1951 [*non* Jankowski, 1967] (syn. *Semifolliculina* p.p.). Single species.
Echinofolliculina Dons, 1934. Single species.
Epifolliculina Hadži, 1951. Single species.
Eufolliculina Hadži, 1951. Few species. Pl. XXX, Fig. 85.
Folliculina Lamarck, 1816. Few (races of one in fresh-water) species. Pl. XXX, Figs. 77–79.
Folliculinopsis Fauré-Fremiet, 1936 (syn. *Alexandrina*). Few species.
Halofolliculina Hadži, 1951 (syn. *Freia* [*Freya*] p.p.). Few species.
Lagotia Wright, 1858 (syns. *Angustofolliculina*, *Semifolliculina* p.p.). Many species. Pl. XXX, Figs. 80, 81.
Latifolliculina Hadži, 1951. Single species.
Magnifolliculina Uhlig, 1964. Few species. Pl. XXX, Fig. 82.
Metafolliculina Dons, 1925 (syn. *Freia* [*Freya*] p.p.). Several spp. Pl. I, Fig. 32; XXX 83, 84.
Mirofolliculina Dons, 1927 (syn. *Microfolliculina*). Single species.
Pachyfolliculina Hadži, 1951. Single species.
Parafolliculina Dons, 1914. Several species.
Pebrilla Giard, 1888. Single species.
Pedifolliculina Hadži, 1951. Single species.
Perifolliculina Hadži, 1951. Single species.
Planifolliculina Hadži, 1951. Single species.
Platyfolliculina Hadži, 1938. Few species.

Priscofolliculina Deflandre & Deunff, 1957 (syn. *Prisofolliculina*). Several (all fossil) species.
Pseudofolliculina Dons, 1914. Single species.
Splitofolliculina Hadži, 1951. Few species.
Stentofolliculina Hadži, 1938. Single species.
Tapetofolliculina Andrews & Nelson in Hadži, 1951. Single species.
Valletofolliculina Andrews, 1953. Single species.

Suborder (5) Plagiotomina Albaret, 1974

Body laterally flattened, elongate-ovoid, with right side slightly concave; somatic ciliation uniform, but cilia in small, cirrus-like groups; no adhesive sucker; buccal ciliature extensive, coursing from apical end to subequatorial position; stomatogenesis parakinetal; macronucleus dendritic, with no karyophore; no mucocysts; endocommensals solely in certain species of lumbricid oligochaete annelids.

Family PLAGIOTOMIDAE Bütschli, 1887

With characteristics of suborder (above).
Plagiotoma Dujardin, 1841. Few species. Pl. III, Fig. 12; V 12m; XV 9; XXX 86, 87.

Suborder (6) Licnophorina Corliss, 1957

(syns. Licnophorida, Scaiotricha *p.p.*)

Body in form of hour-glass, with prominent oral disc apically and conspicuous basal disc at posterior pole; essentially without cilia except for buccal organelles and posterior ciliary rings; stomatogenesis apokinetal; basal disc, fiber-rich and quite complex, serves as organelle of attachment; macronucleus moniliform or fragmented; ectocommensals on a variety of marine organisms ranging from an alga (substratum for one unique species) to tunicates, with coelenterates, annelids, molluscs, and echinoderms (sea cucumber) also involved.

Family LICNOPHORIDAE Bütschli, 1887

With characteristics of suborder (above).
Licnophora Claparède, 1867 (syn. *Lichnophora*). Several spp. Pl. XV, Fig. 10; XXX 88–90.

Order 2. ODONTOSTOMATIDA Sawaya, 1940

(for Ctenostomata, Ctenostom[at]ida, Ctenostomina; syn. Odontostomata)

Body small, laterally compressed, wedge- or helmet-shaped (nearly as wide as long), with armor-like cuirass and often short posterior spines or, occasionally, cirri; somatic ciliature reduced; buccal membranelles inconspicuous, < 10 in number; one to several rounded macronuclei; no cytoproct; fresh-water (rarely marine) polysaprobic forms.

Family EPALXELLIDAE Corliss, 1960

(for Epalcidae and Epalxidae)

"Chunky" forms, generally with short posterior spines and no cirri; somatic ciliature relatively dense (in its short anterior and posterior kinetal segments); some species with well-developed "tooth" (spine) overhanging hidden buccal cavity; macronuclear number variable; found in polysaprobic habitats, principally fresh-water, but a few *Epalxella* in marine biotopes.

Epalxella Corliss, 1960 (for *Epalxis*). Several species. Pl. XV, Fig. 12; XXX 91, 92.

Pelodinium Lauterborn, 1908. Single species. Pl. XXX, Fig. 94.

Saprodinium Lauterborn, 1908. Several species. Pl. XV, Fig. 11; XXX 93.

Family DISCOMORPHELLIDAE Corliss, 1960

(for Discomorphidae [for Ctenostom[at]idae])

Body discoidal, smooth in outline except for prominent anterior spine(s) and protruding "ciliary stripe" overhanging buccal cavity; posteriorly, several conspicuous cirri and a single spine; macronucleus single; found in fresh water, under polysaprobic conditions.

Discomorphella Corliss, 1960 (for *Discomorpha*). Single species (possibly with several varieties or races). Pl. XXX, Fig. 95.

Family MYLESTOMATIDAE Kahl in Doflein & Reichenow, 1929

(syns. Atopodiniidae, Mylestomidae)

Body discoidal, with very sparse somatic ciliation; posterior end either rounded or with four spines (spineless forms have pair of conspicuous cirri there); macronucleus single; like preceding groups, predominantly in polysaprobic fresh-water habitats (but a few *Mylestoma* are marine).

Atopodinium Kahl, 1932. Single species. Pl. XXX, Fig. 96.

Mylestoma Kahl, 1928. Several species. Pl. XXX, Figs. 97, 98.

Order 3. OLIGOTRICHIDA Bütschli, 1887

(syns. Oligotricha, Oligotrichorida)

Body form ovoid to elongate, sometimes tailed, with thickened pellicle; commonly reduced somatic ciliature; buccal paramembranelles extensive and conspicuous, often in two sections – one inside buccal cavity proper, other ("somatic" portion) out onto body surface encircling anterior pole of organism; infraciliary base of paroral membrane composed of single, nonzigzag row of kinetosomes (monostichomonad); stomatogenesis apokinetal in a below-surface pouch; a perilemma present external to the cell (plasma) membrane in many species; possibly no cytoproct; macronucleus with reorganization bands; mainly (but not exclusively) marine, pelagic organisms, and free-swimming (even when loricate, as in suborder Tintinnina); all free-living except for two oligotrichine species associated with echinoids. [Some workers would raise this order to the level of an independent subclass.]

Suborder (1) Oligotrichina Bütschli, 1887

(syn. Strombidiina)

Body typically small, rounded or gently pointed posteriorly (though several species with lengthy tail or caudal cilium); somatic ciliature typically reduced to a few short rows of cirri-like bristles or an equatorial belt of very short "sensory" cilia (but one genus holotrichous); "bipartite" adoral zone of membranelles, with the more conspicuous "somatic" portion ("open" or "closed") used in locomotion; perilemma in some species, not others; pellicle may be strengthened by skeletal elements, especially in posterior half of body; predominantly marine organisms, but several well-known and widely distributed species live solely in fresh-water habitats, and at least one is strongly edaphic. [Third family is controversially included here.]

Family HALTERIIDAE Claparède & Lachmann, 1858

(syn. Meseridae [for Lieberkuehnidae])

Small, active forms; circle of apical membranelles "open"; somatic ciliature present, though generally reduced to a few bristles; predominantly fresh-water forms, but also a few are edaphic; marine forms poorly known. [The genera *Metastrombidium* and *Parastrombidium*, erected before 1931, are valid despite the highly unusual situation of their containing no named species.]

Cephalotrichium Meunier, 1910. Single species.

Halteria Dujardin, 1841. Several species. Pl. IV, Fig. 20a; XVI 1; XXXI 1–4.

Halterioforma Horváth, 1956. Single species [solely edaphic].

Meseres Schewiakoff, 1893. Few species [holotrichous ciliation].

Metastrombidium Fauré-Fremiet, 1924. *No* species.

Parastrombidium Fauré-Fremiet, 1924. *No* species. Pl. XXXI, Fig. 5.

Incertae sedis: Jeannellia Tucolesco, 1962, single [cavernicolous] species; *Octocirrus* Rao, 1928, single species [very inadequately described]; *Spelaeonecta* Jankowski, 1975 (for *Faureia* Tucolesco, 1962 [hom.]), several [cavernicolous] species.

Family STROMBIDIIDAE Fauré-Fremiet, 1970

(syn. Tontoniidae)

Free-swimming (rarely loricate), pelagic forms; circlet of apical membranelles "open"; somatic ciliature greatly reduced or even absent altogether; pellicle, especially in posterior half of body, made rigid by presence of both "trichites" (in a band) and polysaccharide plaques (over a broad area); perilemma present in some species; predominantly in marine habitats, with one species an ectosymbiont of echinoids, though several very common planktonic fresh-water forms.

Buehringa Busch, 1921. Few (perhaps only one) species.

Laboea Lohmann, 1908 (syn. *Conocylis*). Single (or more?) species. Pl. XXXI, Fig. 12.

Strombidium Claparède & Lachmann, 1859 (syn. *Strombidion*). Very many (*ca.* 50) species. Pl. II, Fig. 16; IV 20a; XVI 2; XXXI 6–10.

Tontonia Fauré-Fremiet, 1914. Few species. Pl. XXXI, Fig. 11.

Family STROBILIDIIDAE Kahl in Doflein & Reichenow, 1929

(syn. Torquatellidae)

Peristomial field entirely apical, with uniquely "closed" circlet of apical membranelles; somatic ciliature, though not conspicuous, present (e.g., in slightly spiraled, widely spaced longitudinal rows in some species); found in both fresh-water and marine habitats, with one species an inquiline of echinoids. [Fauré-Fremiet's (1970a) recent resurrection of "*Torquatella*" has complicated matters nomenclaturally, since that name has been not only a junior synonym for 100 years but also a junior homonym! I am here proposing the generic replacement name of *Patronella* (in honor of my one-time "Patron," the late "Monsieur Fauré"), but am suggesting that we leave the homonym-based (and, therefore, invalid), ancient familial name of (Kent's) Torquatellidae unreplaced, carrying it simply as a "synonym" of Strobilidiidae. *Strobilidium* itself, incidentally, seems to show very close affinity to members of the following suborder. Although I am provisionally leaving it in the present suborder, Oligotrichina, it is thought to be more like a tintinnine than a halteriid or a strombidiid by a number of workers (e.g., Deroux).]

Patronella n. n. (for *Torquatella* Lankester, 1874 [hom. of *Torquatella* Held, 1837 (mollusc)]). Single (and type-) species, *P. typica* (Lankester, 1874) n. comb. Pl. XXXI, Fig. 13.

Strobilidium Schewiakoff, 1893 (syns. *Strombilidium, Turbilina*). Many species. Pl. IV, Fig. 20b; XXXI 14, 15; and in *Frontispiece.*

Strombidinopsis Kent, 1881. Few species. Pl. XXXI, Fig. 16.

Incertae sedis: Ciliospina Leegaard, 1915, single species; *Lohmanniella* Leegaard, 1915, few species; *Sphaerotrichium* Wulff, 1919 (syns. *Sphaerotrichum, Spherotrichum*), single species.

Suborder (2) Tintinnina Kofoid & Campbell, 1929

(syns. Tintinnida, Tintinnoida, Tintinnoidea, Tintinnoina, Tintinnoinea)

Body cylindrical or cone-shaped, highly contractile, often with elongate posterior end; all loricate; ciliature dominated by apically located buccal paramembranelles (sometimes with interspersed tentaculoids) in a "closed" arrangement; a perilemma presumably universally present; loricae range 25–1,000 μm in length, up to 3,000 μm if certain aberrant questionable fossil material included (but usual size, 100–200 μm); widespread members of marine pelagic and neritic plankton (with fossil evidence for past aeons), but several forms found abundantly in fresh-water habitats; form, size, and composition of the universally possessed lorica most important diagnostically at all infrasubordinal taxonomic levels. [I do not accept the all-fossil families Calpionellidae Bonet, 1956 and Colomiellidae Bonet, 1956, distributing their genera among other families. Highly doubtful all-fossil genera are listed at the bottom of page 307.]

Family TINTINNIDIIDAE Kofoid & Campbell, 1929

(syn. Tintinnididae)

Lorica tubular or flaring; collar typically absent; wall gelatinous, with agglutinated particles and spiral structure; found in marine, brackish, and (occasionally) fresh-water habitats; no fossil species known (to date).

Leprotintinnus Jörgensen, 1900. Several species. Pl. XXXI, Fig. 29.

Tintinnidium Kent, 1881. Several to many species. Pl. XXXI, Figs. 17, 18, 28.

Family CODONELLIDAE Kent, 1881

(syn. Calpionellidae *p.p.*)

Lorica tubular to cup-shaped, with aboral end sometimes pointed; with or without collar; wall commonly reticulate and may be agglutinated; predominantly marine (neritic and eupelagic) forms, but a few species (e.g., of *Codonella* and *Tintinnopsis*) abundant in the plankton of fresh-water lakes, rivers, and ponds; numerous fossil as well as widespread contemporary forms.

Amphorellina Colom, 1948. Single (or two?) species.

Chitinoidella Doben, 1963. Several to many species. Pl. XXXI, Fig. 112.

Claretinella Keij, 1974. Single (or two?) species.

Codonaria Kofoid & Campbell, 1939. Several species.

Codonella Haeckel, 1873. Many to very many species. Pl. XXXI, Figs. 25, 26, 35–37.

Codonopsis Kofoid & Campbell, 1939. Single species.

Coxliellina Colom, 1948. Several species.

Crassicollaria Remane, 1962. Several species. Pl. XXXI, Fig. 110.

Dicloeopella Eicher, 1965. Single species.

Durandella Dragastan, 1972. Single species.

Lorenziella Knauer & Nagy, 1964. Few species. Pl. XXXI, Fig. 111.

Parachitinoidella Trejo, 1972. Single species.

Poroecus Cleve, 1902 (for *Porella;* syns. *Poraecus, Porecus*). Several species.

Praetintinnopsella Borza, 1969. Single species.
Pseudarcella Spandel, 1909 (syn. *Arpseudarcelloum*). Few species. Pl. XXXI, Fig. 107.
Remanellina Tappan & Loeblich, 1968. Single species. Pl. XXXI, Fig. 109.
Remaniella Catalano, 1965. Single species.
Salpingellina Colom, 1948. Several species.
Spinarcella Keij, 1969. Single species.
Spinophenia Szczechura, 1969. Single species.
Tintinnopsella Colom, 1948. Many species. Pl. XXXI, Fig. 114.
Tintinnopsis Stein, 1867 (syn. *Coniocylis*). Very many (> 100) species. Pl. I, Fig. 31; III 17; IV 20b, 52; V 53; XXXI 19–24, 30–34.
Tytthocorys Tappan & Loeblich, 1968. Single species. Pl. XXXI, Fig. 108.
Urnulella Szczechura, 1969. Single species.
Vautrinella Cuvillier & Sacal, 1963. Few species.
Yvonniellina Tappan & Loeblich, 1968 (syns. *Conicarcella, Pseudarcella* p.p.). Few species.

Family CODONELLOPSIDAE Kofoid & Campbell, 1929

(syns. Calpionellidae *p.p.*, Colomiellidae)

Lorica top-shaped, with aboral end rounded to apiculate; collar delicate but sometimes ridged, with wall of bowl thicker and reticulate or agglutinated; all species marine (neritic and eupelagic); many fossil as well as extant forms.

Calpionella Lorenz, 1902. Several species. Pl. XXXI, Figs. 103, 104.
Calpionellites Colom, 1948. Several species. Pl. XXXI, Figs. 105, 106.
Calpionellopsella Trejo, 1975. Single species.
Calpionellopsis Colom, 1948. Few species. Pl. XXXI, Figs. 101, 102.
Codonellopsis Jörgensen, 1924. Very many (> 50) species. Pl. XXXI, Figs. 38, 39.
Colomiella Bonet, 1956. Few species. Pl. XXXI, Fig. 113.
Deflandronella Trejo, 1975 (for *Deflandrella*). Single species.
Laackmanniella Kofoid & Campbell, 1929. Few species. Pl. XXXI, Fig. 40.
Praecalpionellopsis Borza, 1971. Single species.
Stenosemella Jörgensen, 1924. Many species. Pl. XVI, Fig. 4; XXXI 41.
Stenosemellopsis Colom, 1948. Several species.

Incertae sedis: Luminella Kofoid & Campbell, 1939. Few species.

Nomen inquirendum: Micropoculum Dons, 1922. Few species. [This genus has been completely overlooked by tintinnine specialists. It was erected, with two species, by Dons (1922) as a new peritrich genus "near *Cothurnia*." But, as Kahl (1935a) judiciously pointed out, it (its loricae) was (were) probably (those of) a tintinnine; however, his suggestion, in effect, that *Micropoculum* should fall as a (junior) synonym of *Codonellopsis* Jörgensen (1924) is impossible, since the latter name is the more recent of the two. If some future taxonomic expert on the group decides that Kahl's conclusion is correct (that species of the two nominal genera are congeneric), then a petition to the International Commission on Zoological Nomenclature would be in order, asking for preservation of the much better known name of the junior synonym.]

Family METACYLIDIDAE Kofoid & Campbell, 1929

(for Coxliellidae; syns. Calpionellidae *p.p.*, Metacyclidinae, Metacylin[e]ae)

Lorica tubular or goblet-shaped, delicate and with spirally wound lamina; aboral end sometimes with horn; wall may have prismatic structure and/or be agglutinated with coccoliths; practically all marine (eupelagic and neritic) forms, though occasionally one found in fresh water;

a number of fossil species. [The genus *Coxliella* – via its type-species, at least – may actually have no reality: as Laval-Peuto (1977) has very recently pointed out, there is a "coxlielliform" stage in the life cycle of many tintinnines, including species from a number of families. Thus I am here tentatively placing the generic name in a "questionable" status (see below) and replacing the former familial name (Coxliellidae) with the next name available for the group, *viz.*, Metacylididae (originally the second included subfamily).]

Climacocylis Jörgensen, 1924. Several species. Pl. XXXI, Fig. 43.
Favelloides Colom, 1939. Few species.
Helicostomella Jörgensen, 1924. Several species. Pl. XXXI, Fig. 48.
Metacylis Jörgensen, 1924 (syn. *Metacyclis*). Several to many spp. Pl. I, Fig. 30; XXXI 42.
Pseudometacylis Balech, 1968. Single species.
Rhabdonelloides Colom, 1939. Several species.
Spiroxystonellites Knauer, 1969. Single species.
Incertae sedis: Rhizodomus Strelkov & Virketis, 1950; *Stylicauda* Balech, 1951: each with single species.
Nomen inquirendum: Coxliella Brandt, 1906. Many species [but see discussion, above.] Pl. XXXI, Figs. 44–47.

Family EPIPLOCYLIDIDAE Kofoid & Campbell, 1939

(syns. Epiplocyclididae, Epiplocylidae)

Lorica short, acorn-shaped, sometimes with suboral shelf; aboral end blunt, acuminate, or with horn; wall thin, hyaline, reticulate; all forms marine (eupelagic); no fossil species.

Epicancella Kofoid & Campbell, 1929. Single species. Pl. XXXI, Fig. 50.
Epiplocylis Jörgensen, 1924. Many species. Pl. XXXI, Fig. 51.
Epiplocyloides Hada, 1938 (syn. *Epiorella*). Several species.

Family CYTTAROCYLIDIDAE Kofoid & Campbell, 1929

(syns. Cyttarocylidae, Petalotrichidae)

Lorica bell- or kettle-shaped, sometimes elongate; collar flared above constriction; wall may be reticulate; all forms marine (predominantly eupelagic). No fossil species.

Cyttarocylis Fol, 1881. Several to many species. Pl. XXXI, Fig. 49.
Parapetalotricha Hada, 1970. Few species [better located in following family?].
Petalotricha Kent, 1881. Several species. Pl. XXXI, Figs. 52, 53.

Family ASCAMPBELLIELLIDAE Corliss, 1960

(for Craterellidae)

Lorica cup-shaped, not elongate, with smooth to denticulate oral rim; one or two collars; some species with agglutinated coccoliths; all forms marine (mainly eupelagic); no fossil species. [I am indebted to Mme. Laval-Peuto (personal communication) for suggestions that this family be split off from the (former) Petalotrichidae and that *Petalotricha* is confamilial with *Cyttarocylis* (with Cyttarocylididae having priority over Petalotrichidae): see preceding family.]

Acanthostomella Jörgensen, 1927 (syn. *Acantostomella*). Several species.
Ascampbelliella Corliss, 1960 (for *Craterella*). Several to many species. Pl. XXXI, Fig. 54.
Luxiella Lecal, 1953. Few species.
Incertae sedis: Niemarshallia Corliss, 1960 (for *Marshallia*); *Wailesia* Kofoid & Campbell, 1939: each with single species.

Family DICTYOCYSTIDAE Haeckel, 1873

Lorica with dense bowl; collar with open arched frames or windows (latter with or without panes); wall of bowl reticulate and, in some species, agglutinated; all forms marine (eupelagic); no true fossil species [some radiolarian fossils are superficially very similar in appearance].

Dictyocysta Ehrenberg, 1854. Many to very many spp. Pl. I, Fig. 29; V 52; XXXI 55, 56.
Wangiella Nie, 1934. Single species.

Family PTYCHOCYLIDIDAE Kofoid & Campbell, 1929

(syns. Ptychocyclidae, Ptychocyclididae, Ptychocylidae)

Lorica bell- or kettle-shaped, with elongate bowl; oral rim toothed or with lip; wall trilaminated, alveolar in midsection; all forms marine (mostly eupelagic); no fossil species.

Cymatocylis Laackmann, 1910 (syn. *Cymatocyclis*). Very many (*ca.* 50) species. Pl. XXXI, Figs. 60–64.
Favella Jörgensen, 1924. Many spp. [Genus not well assigned here?] Pl. XXXI, Figs. 58, 59.
Protocymatocylis Kofoid & Campbell, 1929 (syn. *Protocymatocyclis*). Few species.
Ptychocylis Brandt, 1906 (syns. *Pthocylis, Ptychocyclis*). Several species. Pl. XXXI, Fig. 57.

Family RHABDONELLIDAE Kofoid & Campbell, 1929

Lorica conical to chalice-shaped; opening rimmed; aboral horn in some species; wall with vertical ribs; all forms marine (mostly eupelagic); no fossil species.

Epirhabdonella Kofoid & Campbell, 1939 (syn. *Epirrhabdonella*). Few species.
Protorhabdonella Jörgensen, 1924 (syn. *Protorrhabdonella*). Several species.
Rhabdonella Brandt, 1906. Many species. Pl. XXXI, Figs. 65–67.
Rhabdonellopsis Kofoid & Campbell, 1929. Several species. Pl. XXXI, Fig. 68.

Family XYSTONELLIDAE Kofoid & Campbell, 1929

(syn. Xistonellidae)

Lorica elongate, chalice-shaped; aboral end long and narrow; wall reticulate; all species marine (mainly eupelagic); a few fossil forms known.

Parafavella Kofoid & Campbell, 1929. Many to very many species. Pl. XXXI, Figs. 69, 70.
Parundella Jörgensen, 1924. Many species.
Xystonella Brandt, 1906 (syn. *Xistonella*). Several species. Pl. XXXI, Figs. 71, 72.
Xystonellopsis Jörgensen, 1924. Very many (but < 50) species. Pl. XXXI, Fig. 73.
Incertae sedis: Parafavelloides Deflandre & Deflandre-Rigaud, 1949. Single or a few (fossil) species (but never properly described?).

Family UNDELLIDAE Kofoid & Campbell, 1929

Lorica goblet-shaped, occasionally elongate and sometimes with suboral ledge; an inner collar may be present; wall trilayered; all forms marine (eupelagic); no fossil species. [Some genera should be combined? See Balech (1975).]

Amplectella Kofoid & Campbell, 1929. Several species. Pl. XXXI, Fig. 79.
Amplectellopsis Kofoid & Campbell, 1929. Few species. Pl. XXXI, Fig. 80.
Cricundella Kofoid & Campbell, 1929 (syn. *Circundella*). Few species. Pl. XXXI, Fig. 81.
Micrundella Busch, 1949. Few species.

Proplectella Kofoid & Campbell, 1929 (syn. *Proplecta*). Many species. Pl. XXXI, Fig. 82.
Undella Daday, 1887. Many species. Pl. XXXI, Figs. 74–76.
Undellopsis Kofoid & Campbell, 1929. Many species. Pl. XXXI, Figs. 77, 78.
Incertae sedis: Rotundocylis Kufferath, 1952. Single species.

Family TINTINNIDAE Claparède & Lachmann, 1858

Lorica elongate; oral end flared; in some species, *both* ends of lorica open; wall hyaline; primarily marine (eupelagic) forms, but few found in brackish habitats; no fossil species.
Albatrossiella Kofoid & Campbell, 1929. Few species. Pl. XXXI, Fig. 98.
Amphorellopsis Kofoid & Campbell, 1929. Several species.
Amphorides Strand, 1926 (for *Amphorella*). Several species. Pl. XXXI, Figs. 27, 86, 87.
Brandtiella Kofoid & Campbell, 1929. Single species.
Bursaopsis Kofoid & Campbell, 1929. Several species. Pl. XXXI, Fig. 88.
Buschiella Corliss, 1960 (for *Imperfecta*). Single species.
Canthariella Kofoid & Campbell, 1929. Few species.
Clevea Balech, 1948. Single species.
Dadayiella Kofoid & Campbell, 1929. Several species.
Daturella Kofoid & Campbell, 1929. Many species. Pl. XXXI, Figs. 89, 90.
Epicranella Kofoid & Campbell, 1929. Several species. Pl. XXXI, Fig. 91.
Eutintinnus Kofoid & Campbell, 1939. Very many (but < 50) species, all with lorica open at both ends. Pl. I, Fig. 27; XVI 3; XXXI 83–85.
Odontophorella Kofoid & Campbell, 1929. Single species.
Ormosella Kofoid & Campbell, 1929. Several species. Pl. XXXI, Fig. 99.
Proamphorella Kofoid & Campbell, 1939. Single species.
Prostelidiella Kofoid & Campbell, 1939 (syn. *Prostellidiella*). Single species.
Rhabdosella Kofoid & Campbell, 1929 (syns. *Epirhabdosella, Epirrhabdosella*). Few species. Pl. XXXI, Figs. 93, 94.
Salpingacantha Kofoid & Campbell, 1929. Several species. Pl. XXXI, Fig. 95.
Salpingella Jörgensen, 1924. Many species. Pl. I, Fig. 28; XXXI 96, 97.
Salpingelloides Campbell, 1942. Few species.
Steenstrupiella Kofoid & Campbell, 1929. Several species. Pl. XXXI, Fig. 100.
Stelidiella Kofoid & Campbell, 1929. Few species. Pl. XXXI, Fig. 92.
Tintinnus Schrank, 1803. Few to several species.

Incertae sedis in suborder Tintinnina:

Genera considered by some authorities as containing forms which are only parts of the body of fossil molluscs: *Campbelliella* Radoičić, 1959, few species; *Daturellina* Radoičić, 1959, several species; *Hadziina* Radoičić, 1969 (for *Hadziella*), single species; *Metacyclina* Radoičić, 1965, several species; *Zetella* Radoičić, 1965, single species.

Genus labeled as a crinoid by some workers: *Patelloides* Leischner, 1959, single species.

Genera representing a group of "stomiosphaerid" fossils of unknown affinities, though occasionally listed in the literature as "uncertain tintinnines": *Bonetocardiella* Dufour, 1968, few species; *Cadosina* Wanner, 1940, several to many species; *Cadosinopsis* Scheibner, 1967, single species; *Carpistomiosphaera* Nowak, 1968, few species; *Colomisphaera* Nowak, 1968, few species; *Hemistomiosphaera* Nowak, 1968, single species; *Parastomiosphaera* Nowak, 1968, single species; *Stomiosphaera* Wanner, 1940, many species.

Special comment: There appear to be three main problems in the taxonomy of tintinnines: the need for differential characters other than those of the lorica; the desirability of knowing the range of variability within a given species (or genus); and the difficulty of identifying certain microfossil material which seems to bear a resemblance to tintinnine loricae.

Order 4. HYPOTRICHIDA Stein, 1859

(syns. Hypotricha, Hypotrichina, Hypotrichorida)

Dorsoventrally flattened, oval or elongate, medium-sized forms, occasionally tailed; unique cursorial mode of locomotion; prominent zone of generally numerous adoral (para)membranelles on left-anterior portion of the ventral surface, bordering a broad peristomial field and sometimes continuing over apical end of body onto the dorsal surface; paroral membrane may be multiple (diplo- or polystichomonad condition); somatic ciliature commonly represented by rows or localized groups of cirri, conspicuous on the ventral surface, and rows of widely spaced pairs of short cilia ("sensory bristles") dorsally; a perilemma present in some species; stomatogenesis generally apokinetal, but apparently parakinetal in more primitive forms; macronuclear reorganization bands common; cytoproct, as well as a contractile vacuolar system, always present, and mucocysts plentiful; widely distributed free-living forms in many and diverse habitats, with a few ectocommensalistic on various invertebrates and one inquilinic in an echinoid. [It is extremely difficult to arrange families, genera, and even species of the hypotrichs into their proper taxonomic groupings until we have available many more data of a comparative nature, especially with respect to the morphogenetics of their binary fission. Thus the classification presented below must, in many instances, be considered provisional.]

Suborder (1) Stichotrichina Fauré-Fremiet, 1961

Body often elongate, sometimes very drawn out posteriorly; ventral cirri generally small and quite inconspicuous (occasionally as few as 2–3 cilia per cirrus) and typically arranged in 3–12 longitudinal (sometimes spiraled) rows; marginals common, transverse cirri sometimes absent; stomatogenesis parakinetal in the allegedly primitive forms studied to date; several species produce loricae, with a few of these exhibiting colony-formation; found free-living in diverse habitats, with one well-known species (*Kerona*) an ectocommensal on *Hydra*.

Family SPIROFILIDAE von Gelei, 1929

(syns. Atractidae, Hypotrichidiidae, Kahliellidae)

Ventral cirri inconspicuous and in quite numerous and/or helically spiraled rows; zone of adoral membranelles not highly prominent; various body shapes, with some forms tailed and others more elongate at the anterior end; lorica produced by some species; stomatogenesis parakinetal in primitive genera (e.g., *Hypotrichidium* and *Kahliella*). [Nomenclatural note: although the generic name *Spirofilum* must, by the law of priority, fall as a junior synonym of the older *Hypotrichidium*, it is perfectly legitimate to maintain the *familial* name founded on it: thus Spirofilidae *is* correct, and Jankowski's (1975) recent "replacement" name of Hypotrichidiidae must be treated as a (junior) synonym.]

Atractos Vörösváry, 1950. Single species.

Hypotrichidium Ilowaisky, 1921 (syn. *Spirofilum* von Gelei, 1929 [*non* von Gelei, 1944]). Few to several species. Pl. XXXII, Fig. 7.

Kahliella Corliss, 1960 (for *Kahlia*). Several species. Pl. XXXII, Figs. 1–3.

Plesiotricha Dragesco, 1970 (syn. *Uroleptopsis* p.p.). Single species. Pl. XXXII, Fig. 4.

Spiretella Borror, 1972 (for *Spiretta*; syns. *Microspiretta*, *Spiratella* [hom.]). Single species. Pl. XXXII, Fig. 6.

Spirofilopsis Corliss, 1960 (for *Spirofilum* von Gelei, 1944 [*non* von Gelei, 1929]). Single species. Pl. XXXII, Fig. 5.

Stichotricha Perty, 1949. Several species. Pl. I, Fig. 37; XVII 2; XXXII 8–11.

Urospinula Corliss, 1960 (for *Urospina*). Few species.

Incertae sedis: *Kahliela* Tucolesco, 1962. Single species. [Though poorly described, this was erected as a separate genus, despite the fact that the name gives the appearance of being merely a misspelling of *Kahliella*.]

Family STRONGYLIDIIDAE Fauré-Fremiet, 1961

(correction for Strongylidae; syn. Chaetospiridae)

Elongate forms, with reduced number of spiraled rows of ventral cirri; some species loricate; found in marine, fresh-water, and edaphic habitats.

Chaetospira Lachmann, 1856 (syn. *Stichospira*). Several species. Pl. XXXII, Fig. 18.
Strongylidium Sterki, 1878. Several species. Pl. XXXII, Figs. 14, 15.
Urostrongylum Kahl, 1932. Few species. Pl. XXXII, Figs. 16, 17.

Incertae sedis: *Cladotricha* Gajewskaja, 1926, possibly several species, Pl. XXXII, Figs. 12, 13; *Klonostricha* Vuxanovici, 1963, few species.

Family UROSTYLIDAE Bütschli, 1889

(syn. Banyulsellidae)

Ventral cirri in straight rows (of variable number), generally with only transverse cirri (near posterior end) morphologically distinct and conspicuous; body elongate-elliptical in outline, but quite broad, and often of large size (up to 800 μm). [*Banyulsella* may well be out of place here.]

Banyulsella Dragesco, 1953. Single species. Pl. XXXII, Fig. 29.
Hemicycliostyla Stokes, 1886 (syn. *Hemiciplostyla*). Few species. Pl. XXXII, Fig. 25.
Isosticha Kiesselbach, 1936. Single species.
Paraholosticha Kahl, 1932. Several species. Pl. XXXII, Figs. 26 –28.
Paraurostyla Borror, 1972. Few species. Pl. XXXII, Figs. 23–24.
Urostyla Ehrenberg, 1830. Several to many species. Pl. XVII, Fig. 1; XXXII 19–22.

Family HOLOSTICHIDAE Fauré-Fremiet, 1961

Right and left marginal cirri present, with variable number of rows of other ventral cirri; transverse and frontal cirri often differentiated; body elongate; macronuclei two to many in number. [The family seems overlarge; perhaps *Uroleptus* and close relatives should be removed. And do *Gonostomum* and *Trachelostyla* (with others?) belong even in the following suborder, family Oxytrichidae? *Uroleptoides* also represents a problem. Etc.!]

Amphisiella Gourret & Roeser, 1888. Several to many species. Pl. XXXII, Figs. 35, 36.
Bakuella Agamaliev & Alekperov, 1976. Few species. Pl. XXXII, Fig. 46.
Balladyna Kowalewski, 1882 (syn. *Balladina*). Few species. Pl. XXXII, Figs. 49, 50.
Balladynella Stiller, 1974 (syn. *Balladinella*). Few species.
Gonostomum Sterki, 1878. Few species. Pl. XXXII, Figs. 59, 60.
Holosticha Wrzesniowski, 1877 (syn. *Amphisia*). Many species. Pl. XXXII, Figs. 30–34.
Keronopsis Penard, 1922. Many species. Pl. XXXII, Figs. 53–58.
Lamtostyla Buitkamp, 1977. Single species.
Laurentiella Dragesco & Njiné, 1971 (for *Laurentia*). Single species. Pl. XXXII, Fig. 51.
Paruroleptus Kahl, 1932. Several species. Pl. XXXII, Fig. 44.
Parurosoma von Gelei, 1954. Single species.
Psammomitra Borror, 1972 (for *Micromitra* [for *Mitra*]). Few species. Pl. XXXII, Figs. 65–67.
Pseudourostyla Borror, 1972. Few species. Pl. XXXII, Figs. 47, 48.
Trachelochaeta Šrámek-Hušek, 1954. Single species.

Trachelostyla Kahl, 1932 (syn. *Stichochaeta*). Several species. Pl. XXXII, Figs. 61–63.
Trichotaxis Stokes, 1891. Several species. Pl. XXXII, Fig. 52.
Uncinata Bullington, 1940. Single species. Pl. XXXII, Figs. 64, 79.
Uroleptoides Wenzel, 1953. Single species. Pl. XXXII, Fig. 45.
Uroleptopsis Kahl, 1932. Several species. Pl. XXXII, Fig. 43.
Uroleptus Ehrenberg, 1831. Several species. Pl. III, Fig. 2; XXXII 37–42.
Wallackia Foissner, 1977. Single species.

Family PSILOTRICHIDAE Bütschli, 1889

Cirri long and sparse and in a few curving ventral rows; no differentiated frontals and no transverse cirri; peristomial area limited to anterior third of organism; body oval to elliptical in outline, small, often with zoochlorellae in cytoplasm; two macronuclei; exclusively fresh-water forms. [Does it deserve independent familial status?]

Hemiholosticha von Gelei, 1954. Single species. Pl. XXXII, Fig. 74.
Psilotricha Stein, 1859 (syn. *Pigostyla*). Few species. Pl. XXXII, Figs. 70–73.

Family KIITRICHIDAE Nozawa, 1941

Cirri relatively uniform, in 7–10 curving ventral rows; body small, rounded-elliptical in outline, with conspicuous peristomial field extending from apical end to well below the equatorial zone of the organism; macronucleus single, marine forms. [First genus possibly a heterotrich?]

Caryotricha Kahl, 1932. Single species. Pl. XXXII, Fig. 68.
Kiitricha Nozawa, 1941. Single species. Pl. XXXII, Fig. 69.

Family KERONIDAE Dujardin, 1840

(syn. Lacazeidae)

Cirri generally in several oblique rows across the ventral surface of the body; body shape variable, from broad to elongate, even tailed in some species; transverse cirri present; found in various habitats, including sand, and one species well-known ectocommensal on *Hydra*. [Nomenclatural note: it is Ehrenberg's *Kerona* which has been accepted here for more than 125 years, although the generic name was actually first proposed by O. F. Müller (see further remarks under the family Oxytrichidae, below). *Eschaneustyla* may be out of place here.]

Eschaneustyla Stokes, 1886. Several species. Pl. XXXII, Fig. 76.
Kerona Ehrenberg, 1835 [*non* O. F. Müller, 1773]. Single species. Pl. XXXII, Figs. 83, 84.
Lacazea Dragesco, 1960. Single species. Pl. XXXII, Fig. 82.
Incertae sedis: Epiclintes Stein, 1862. Few species [one an *Uncinata*?]. Pl. XXXII, Figs. 75, 77–79.

Incertae sedis in suborder Stichotrichina:

Balladinopsis Ghosh, 1921 (syn. *Balladynopsis*); *Prooxytricha* Poche, 1913 (for *Trichogaster*); *Psilotrix* Gourret & Roeser, 1888; *Stylonethes* Sterki, 1878: each with single species.

Suborder (2) Sporadotrichina Fauré-Fremiet, 1961

(syn. Sporadotrichorina)

Body sometimes elongate, even tailed, but often oval to elliptical in outline; ventral cirri typically heavy and conspicuous and arranged in specific, localized groups; marginal cirri often absent or else reduced; stomatogenesis apokinetal; found in widely diverse habitats (fresh-water, edaphic, marine, interstitial, etc.); a few species are symbiotic, either as ectocommensals on integument (or in branchial cavity) of several invertebrates or as inquilines of echinoids.

Family OXYTRICHIDAE Ehrenberg, 1838

(syn. Pleurotrichidae)

Clear-cut rows of right and left marginal cirri; frontoventral and transverse cirri typically heavy and distinctive; zone of adoral membranelles generally restricted to anterior third or quarter of relatively elongate body. [Nomenclatural note: although O. F. Müller's *Kerona* is, strictly speaking, a *senior* synonym of Ehrenberg's *Stylonychia*, protozoologists have been unanimously favoring the latter name for more than 125 years; it seems advisable to leave matters that way (see also remarks under Keronidae, above). Taxonomic note: perhaps this family deserves a (separate) subordinal standing of its own? See comment on page 174, Chapter 16.]

Actinotricha Cohn, 1866. Single species. Pl. XXXII, Fig. 116.
Ancystropodium Fauré-Fremiet, 1907. Single species. Pl. XXXII, Figs. 80, 81.
Gastrostyla Engelmann, 1862. Several species. Pl. XXXII, Figs. 90–93.
Histriculus Corliss, 1960 (for *Histrio*). Several species. Pl. XXXII, Figs. 121–123.
Onychodromus Stein, 1859 (syn. *Peritromoides*). Single species. Pl. XXXII, Fig. 111.
Opisthotricha Kent, 1882 (syn. *Opistotricha*). Several to many species. Pl. XXXII, Figs. 94–97.
Oxytricha Bory de St. Vincent, 1825 (syns. *Oxitricha*, possibly *Rhabdotricha*?). Very many (*ca.* 50) species. Pl. I, Fig. 22; XXXII 85–89.
Parahistriculus Grolière, 1976 (syn. *Parahistricus*). Single species. Pl. XXXII, Fig. 124.
Parastylonychia Dragesco, 1963. Single species. Pl. III, Fig. 23; XXXII 110.
Pleurotricha Stein, 1859. Few to several species. Pl. XXXII, Figs. 113–115.
Steinia Diesing, 1866. Many species. Pl. XXXII, Figs. 98–102.
Stylonychia Ehrenberg, 1830 (syns. *Kerona* O. F. Müller [*non* Ehrenberg], *Stylonichia*). Many species. Pl. IV, Fig. 34; XXXII 103–109.
Tachysoma Stokes, 1887. Several species. Pl. XXXII, Figs. 117, 118.
Urosoma Kowalewski, 1882 (syn. *Pseudostrombidium*). Several spp. Pl. XXXII, Figs. 119, 120.

Family ASPIDISCIDAE Ehrenberg, 1838

(syn. Paraeuplotidae)

Generally small forms, with flattened, oval to rounded body; no marginal cirri, but strikingly prominent ventral group(s); reduced number of oral membranelles, located centrally and inconspicuously on ventral surface of body, with apparently no paroral membrane(s); dorsal surface often distinctly ribbed, ridged, or humped; widely distributed in variety of habitats, including echinoid gut and ascidian branchial cavity.

Aspidisca Ehrenberg, 1830 (syn. *Aspidiscopsis*). Very many (but < 50) species. Pl. III, Fig. 25; IV 32; XXXII 126–130.
Euplotaspis Chatton & Séguéla, 1936. Single species. Pl. XXXII, Fig. 135.
Onychaspis Stein, 1859 (syn. of *Aspidisca*?). Single species, Pl. XXXII, Fig. 125.
Incertae sedis: Paraeuplotes Wichterman, 1942. Single species. Pl. XXXII, Fig. 136.

Family EUPLOTIDAE Ehrenberg, 1838

(syns. Ploesconiidae, Uronychiidae)

Marginal cirri absent or greatly reduced in number; transverse and frontoventrals often tremendously developed, heavy, and very conspicuous; oral ciliature also prominent, usually extending more than half the length of the body; intercirral tracts of microtubules; kinetodesmata reported; many species, widely distributed, predominantly marine; *Euplotes* has been found in sea urchins, and *Uronychia* in mollusc mantle cavity. [*Discocephalus*, a curious genus with an equally curious taxonomic history, is tentatively included here. *Swedmarkia* reminds one strongly of *Gastrocirrhus*, a member of the following family.]

Certesia Fabre-Domergue, 1885. Few species.
Cytharoides Tuffrau, 1975. Single species. Pl. XXXII, Fig. 148.
Diophrys Dujardin, 1841. Many species. Pl. XVII, Fig. 4; XXXII 149–152.
Discocephalus Ehrenberg in Hemprich & Ehrenberg, 1828 (syn. *Polycoccon*). Several species. Pl. XXXII, Figs. 131, 132.
Euplotes Ehrenberg, 1830 (syns. *Ploesconia*, possibly *Crateromorpha*?). Very many (perhaps > 50) species. Pl. I, Figs. 12, 16; II 8; III 22; IV 10, 47, 48; V 54, 57; XVII 3; XXXII 137–147.
Swedmarkia Dragesco, 1954. Single species. Pl. XXXII, Figs. 133, 134.
Uronychia Stein, 1859 (syn. *Euronychia*). Several species. Pl. V, Fig. 58; XXXII 153–155.

Family GASTROCIRRHIDAE Fauré-Fremiet, 1961

No marginal cirri; other cirri large and in unusual patterns; expansive buccal cavity or peristomial field, with anterior end of body remarkably truncate (most pronounced in *Gastrocirrhus*); all marine or psammophilic forms.

Cirrhogaster Ozaki & Yagiu, 1941. Single species. Pl. XXXII, Fig. 159.
Euplotidium Noland, 1937. Few species. Pl. XXXII, Fig. 160.
Gastrocirrhus Lepşi, 1928. Few species. Pl. XXXII, Figs. 156–158.

Incertae sedis in suborder Sporadotrichina:

Allotricha Sterki, 1878, single species; *Cinetoconia* Renault & Roche, 1898, single (fossil!) species [very likely not a ciliate at all?]; *Gruberella* Corliss, 1960 (for *Stylocoma*), few species; *Onychodromopsis* Stokes, 1887, few species, Pl. XXXII, Fig. 112.

NOTE ON PLATES XXII–XXXII [concluded from page 242]

Multiple pictures under the same name may or may not be of different species in that genus. I have tried to select forms representative of ciliate diversity; the variability exhibited within genera can seldom be illustrated with the number of figures allowable. The use of "a," "b," etc., incidentally, is restricted to drawings of the same ciliate by the same author. Species of some genera are depicted elsewhere in this book: deliberately, such drawings are not repeated here, nor has space permitted cross-reference to them. However, such data are included in the lists of genera following each familial characterization and also in the Systematic Index.

It has not been feasible to present the drawings adjusted to a single scale of size; nevertheless, the tintinnine loricae *are*, with only a few exceptions, drawn to scale; and, when reasonable, smaller species are depicted at a reduced size relative to any nearby larger forms. Supplying actual dimensions of each organism portrayed could be misleading, since the range within a genus or family – not to mention the species itself – may be so considerable. Some of the more familiar or more commonly encountered ciliates are purposely shown relatively larger to reveal various structural details shared by numerous species.

Helpful though I hope these figures will prove to be, they cannot serve as substitutes for those usually appearing in the specialized taxonomic monographs prepared by experts on given genera or families. The latter *must* be consulted by the serious student of any particular group.

EXPLANATION OF FIGURES

PLATE XXX (pages 314–317)

Page 314. Figs. 1–4. *Blepharisma* (Dragesco, Suzuki, von Gelei, Dingfelder). 5, 6. *Anigsteinia* (Dragesco, Anigstein). 7. *Gruberia* (Dragesco). 8, 9. *Parablepharisma* (Kahl, Villeneuve-Brachon). 10. *Phacodinium* (Dragesco). 11. *Propygocirrus*(?) (Jankowski). 12. *Diplogmus*(?) (Villeneuve-Brachon). 13–15. *Spirostomum*, extended, partially contracted, fully contracted (Noland–unpub., Stein, Villeneuve-Brachon). 16–23. *Stentor* (O. F. Müller, Ehrenberg [picture supplied by Lynn B. Graves], Stein, Dragesco, Kent, Tartar, Dragesco, Stein).

Page 315. Fig. 24. *Bothrostoma* (Jankowski). 25. *Brachonella* (Jankowski). 26. *Tesnospira* (Jankowski). 27. *Palmarella* (Jankowski). 28. *Tropidoatractus* (Kahl). 29–33. *Metopus* (Dragesco, O. F. Müller, Borror, Dragesco, Powers). 34. *Spirorhynchus* (Kirby). 35. *Balantidioides* (Wenzel). 36. *Reichenowella* (Kahl). 37–40. *Condylostoma* (Fauré-Fremiet, Dragesco, Bullington, Wrzesniowski). 41, 42. *Fabrea*, trophont and cyst (Villeneuve-Brachon, Kirby). 43. *Copemetopus* (Villeneuve-Brachon). 44. *Climacostomum* (Stein). 45. *Bryometopus* (Grolière). 46–50. *Bursaria* (O. F. Müller, Schuberg, Kahl, Bary, Tuffrau). [Note relative size of the metazoan rotifer detectable inside the ciliate depicted in Fig. 48!]

Page 316. Fig. 51. *Bursaridium* (Fauré-Fremiet). 52. *Thylakidium* (Schewiakoff). 53. *Chattonidium* (Villeneuve-Brachon). 54, 55. *Peritromus* (Bütschli, Tuffrau). 56, 57. *Nyctotherus* (Stein, Albaret). 58a,b. *Metanyctotherus* (Albaret). 59–62. *Nyctotheroides* (Stein, Wenyon, Villeneuve-Brachon, Jankowski). 63, 64. *Sicuophora* (Albaret). 65. *Ichthyonyctus* (Ky). 66a,b. *Geimania* (Albaret). 67, 68. *Clevelandella* (Albaret). 69a,b. *Paraclevelandia* (Albaret). 70. *Inferostoma* (Ky). 71. *Nathella* (Singh).

Page 317. Figs. 72–74. *Caenomorpha* (Blochmann, Jankowski, Villeneuve-Brachon). 75. *Ludio* (Jankowski). 76. *Cirranter* (Jankowski). 77–79. *Folliculina* (Kent, O. F. Müller, Hamilton). 80, 81. *Lagotia* (Stein, Fauré-Fremiet). 82. *Magnifolliculina* (Uhlig). 83, 84. *Metafolliculina* (Fauré-Fremiet, Wright). 85. *Eufolliculina* (Fauré-Fremiet). 86, 87. *Plagiotoma* (Stein, Albaret). 88–90. *Licnophora* (Calkins, Fauré-Fremiet, Villeneuve-Brachon). 91, 92. *Epalxella* (Jankowski, Kahl). 93. *Saprodinium* (Jankowski). 94. *Pelodinium* (Jankowski). 95,a,b. *Discomorphella* (Jankowski). 96. *Atopodinium* (Jankowski). 97, 98. *Mylestoma* (Jankowski, Kahl).

PLATE XXXI (pages 318–320)

Page 318. Figs. 1–4. *Halteria* (Noland–unpub., Szabó, Dragesco, Fauré-Fremiet). 5. *Parastrombidium* (Fauré-Fremiet). 6–10. *Strombidium* (Fauré-Fremiet, Fauré-Fremiet, Dragesco, Borror, Dragesco). 11. *Tontonia* (Fauré-Fremiet). 12. *Laboea* (Fauré-Fremiet). 13. *Patronella* (Fauré-Fremiet). 14, 15. *Strobilidium* (Deroux, Fauré-Fremiet). 16. *Strombidinopsis* (Fauré-Fremiet). 17, 18. *Tintinnidium* (Fauré-Fremiet, Claparède & Lachmann). 19–24. *Tintinnopsis* (Brownlee–unpub., Brownlee–unpub., Haeckel, Wang & Nie, Fauré-Fremiet, Calkins). 25, 26. *Codonella* (Claparède & Lachmann, Fauré-Fremiet). 27. *Amphorides* (Fauré-Fremiet).

Page 319. Figs. 28–100. Tintinnine loricae, all [on this and following page] – *except* for (enlarged) Figs. 42, 54, 98 – drawn to same scale, in endorsement of helpful method of presentation used by Kofoid & Campbell (1929, 1939). 28. *Tintinnidium* (Daday). 29. *Leprotintinnus* (Jörgensen). 30–34. *Tintinnopsis* (Daday, Daday, Daday, Claparède & Lachmann, Claparède & Lachmann). 35–37. *Codonella* (Haeckel, Entz, Jr., Kofoid & Campbell). 38, 39. *Codonellopsis* (Laackmann, Brandt). 40. *Laackmanniella* (Laackmann). 41. *Stenosemella* (Brandt). 42. *Metacylis* (Meunier). 43. *Climacocylis* (Kofoid & Campbell). 44–47. "*Coxliella*" (Claparède & Lachmann, Jörgensen, Laackmann, Laackmann). 48. *Helicostomella* (Mereschowsky). 49. *Cyttarocylis* (Brandt). 50. *Epicancella* (Brandt). 51. *Epiplocylis* (Ostenfeld & Schmidt). 52, 53. *Petalotricha* (Brandt, Jörgensen). 54. *Ascampbelliella* (Ostenfeld). 55, 56. *Dictyocysta* (Haeckel, Brandt). 57. *Ptychocylis* (Meunier). 58, 59. *Favella* (Jörgensen). 60–64. *Cymatocylis* (Laackmann). 65–67. *Rhabdonella* (Kofoid & Campbell, Kofoid & Campbell, Entz, Sr.). 68. *Rhabdonellopsis* (Kofoid & Campbell). 69, 70. *Parafavella* (Brandt, Jörgensen).

Page 320. Figs. 71, 72. *Xystonella* (Kofoid & Campbell). 73. *Xystonellopsis* (Kofoid & Campbell). 74–76. *Undella* (Daday, Daday, Laackmann). 77, 78. *Undellopsis* (Kofoid & Campbell, Laackmann). 79. *Amplectella* (Kofoid & Campbell). 80. *Amplectellopsis* (Kofoid & Campbell). 81. *Cricundella* (Kofoid & Campbell). 82. *Proplectella* (Laackmann). 83–85. *Eutintinnus* (Kofoid & Campbell). 86, 87. *Amphorides* (Claparède & Lachmann). 88. *Bursaopsis* (Daday). 89, 90. *Daturella* (Kofoid & Campbell). 91. *Epicranella* (Kofoid & Campbell). 92. *Stelidiella* (Brandt). 93, 94. *Rhabdosella* (Kofoid & Campbell). 95. *Salpingacantha* (Kofoid & Campbell). 96, 97. *Salpingella* (Brandt, Merkle). 98. *Albatrossiella* (Laackmann). 99. *Ormosella* (Kofoid & Campbell). 100. *Steenstrupiella* (Kofoid & Campbell). 101–114. Sections or reconstructions of *fossilized* tintinnine loricae, *not* drawn to scale. 101, 102. *Calpionellopsis* (Remane). 103, 104. *Calpionella* (Colom, Remane). 105, 106. *Calpionellites* (Colom, Remane). 107. *Pseudarcella* (Tappan & Loeblich). 108. *Tytthocorys* (Tappan & Loeblich). 109. *Remanellina* (Tappan & Loeblich). 110. *Crassicollaria* (Remane). 111. *Lorenziella* (Remane). 112. *Chitinoidella* (Remane). 113. *Colomiella* (Remane). 114. *Tintinnopsella* (Remane).

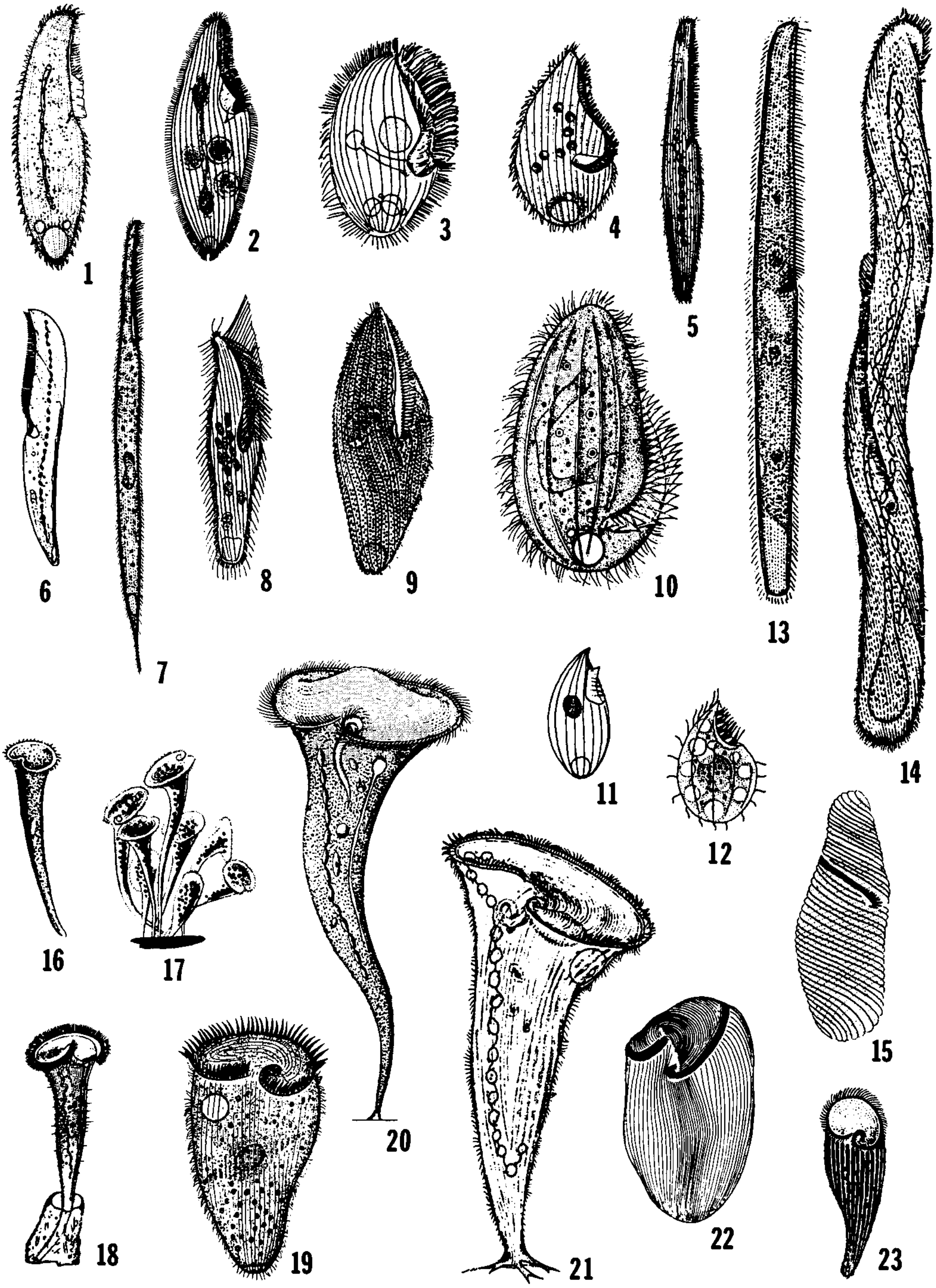

PLATE XXX. Class Polyhymenophora, subclass Spirotricha, orders Heterotrichida and Odontostomatida: selected genera. [See page 313 for figure explanations.]

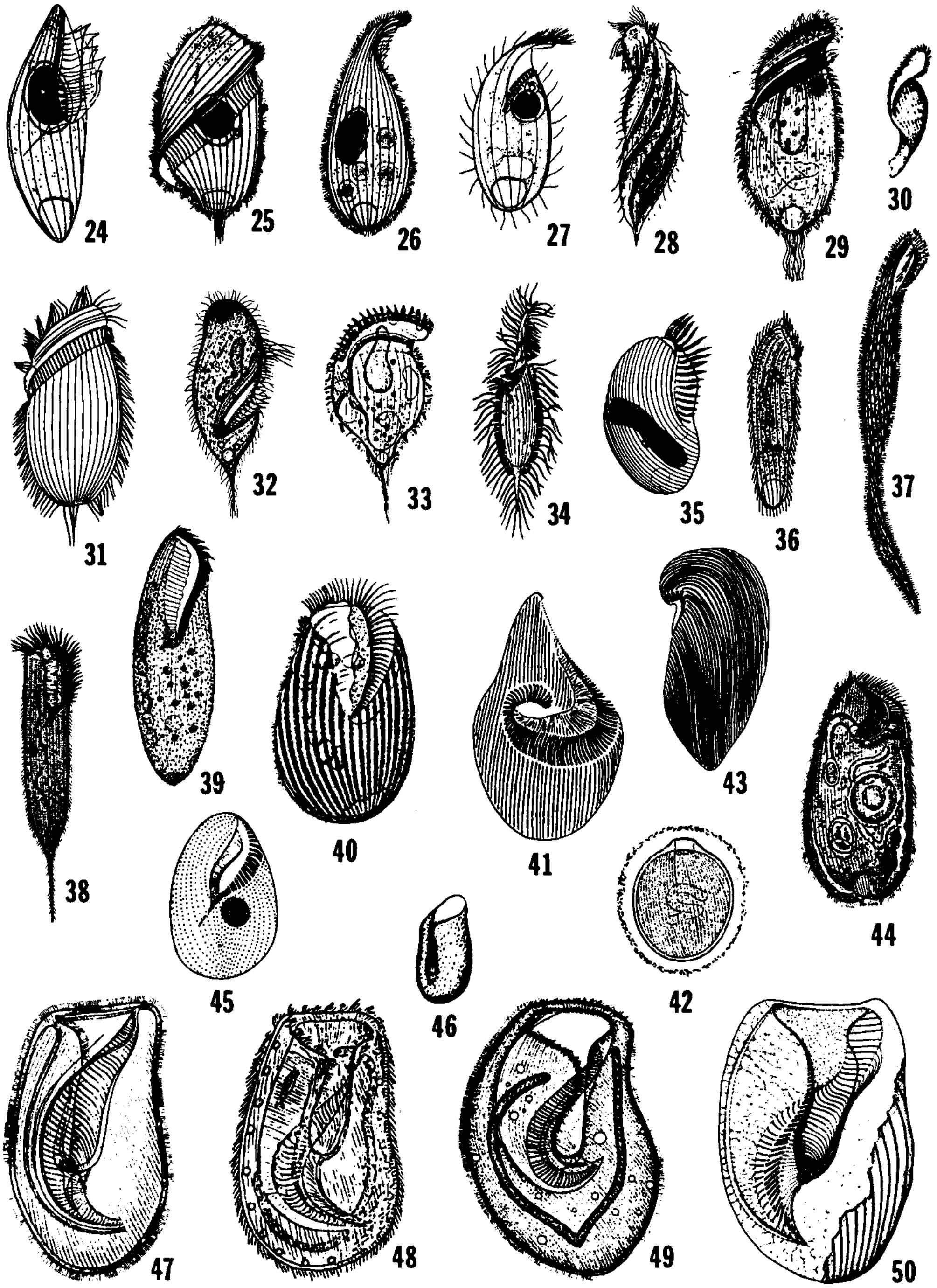

PLATE XXX, continued. [See page 313 for figure explanations.]

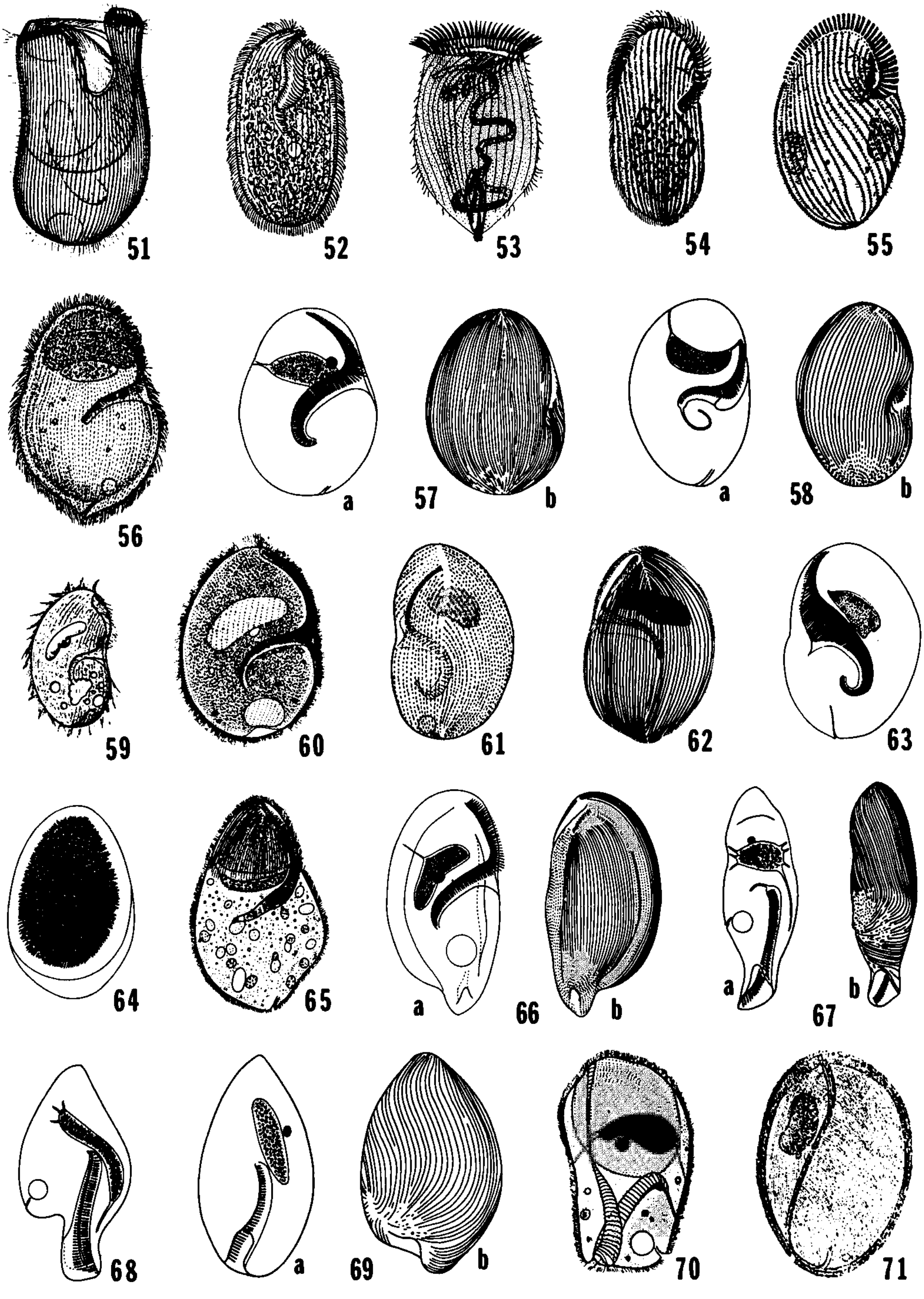

PLATE XXX, continued. [See page 313 for figure explanations.]

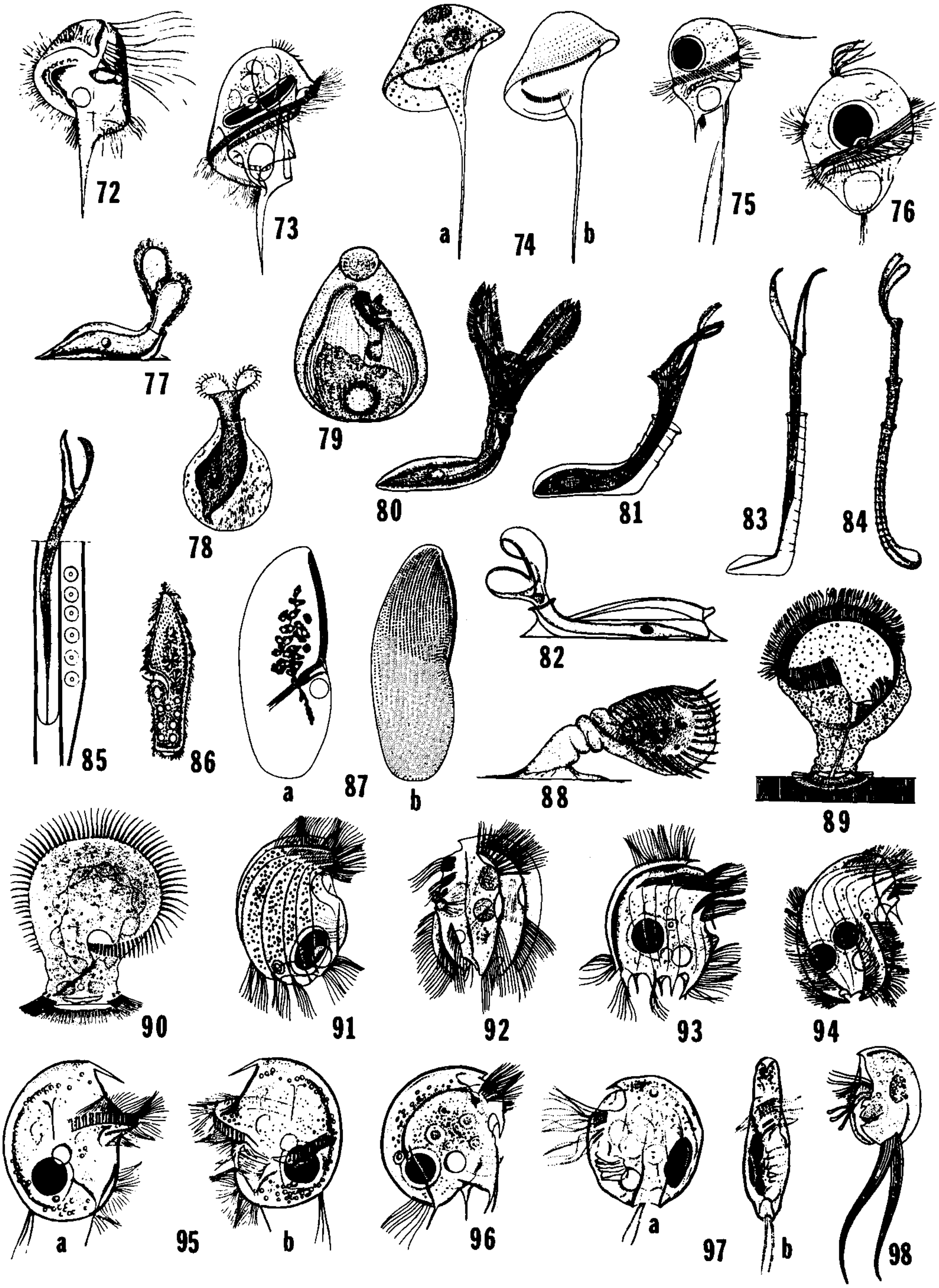

PLATE XXX, concluded. [See page 313 for figure explanations.]

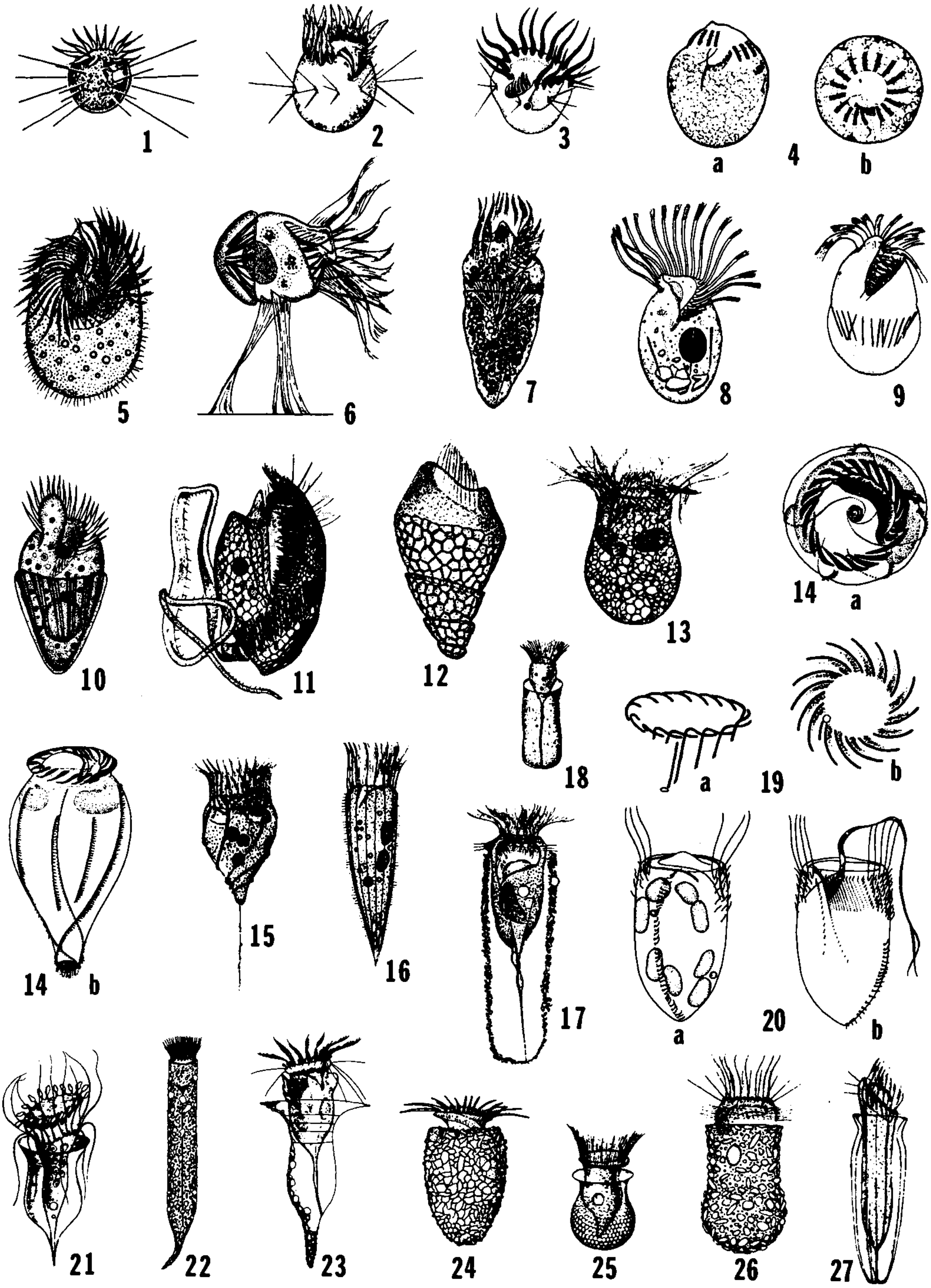

PLATE XXXI. Class Polyhymenophora, subclass Spirotricha, order Oligotricha: selected genera. [See page 313 for figure explanations.]

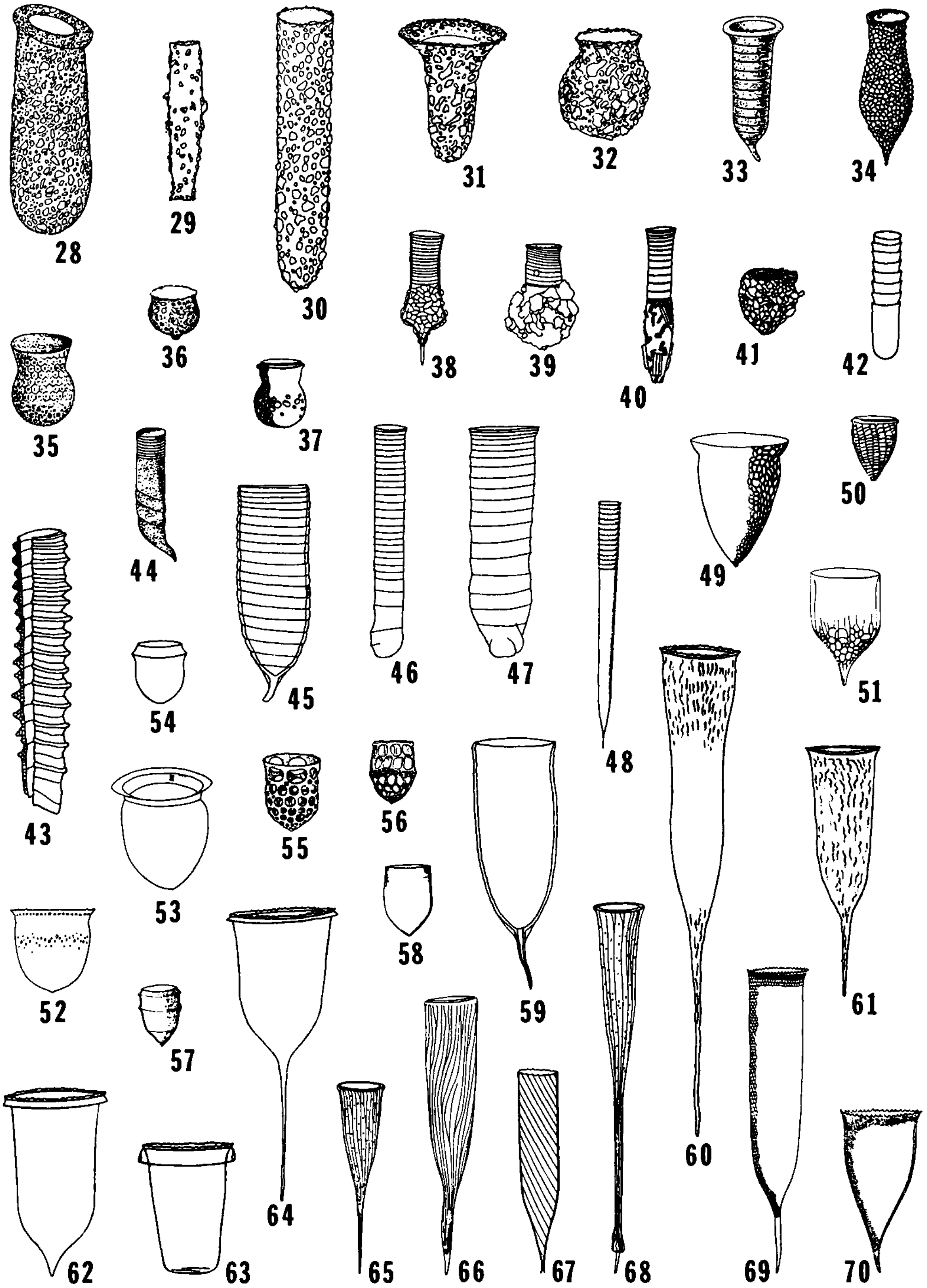

PLATE XXXI, continued. [See page 313 for figure explanations.]

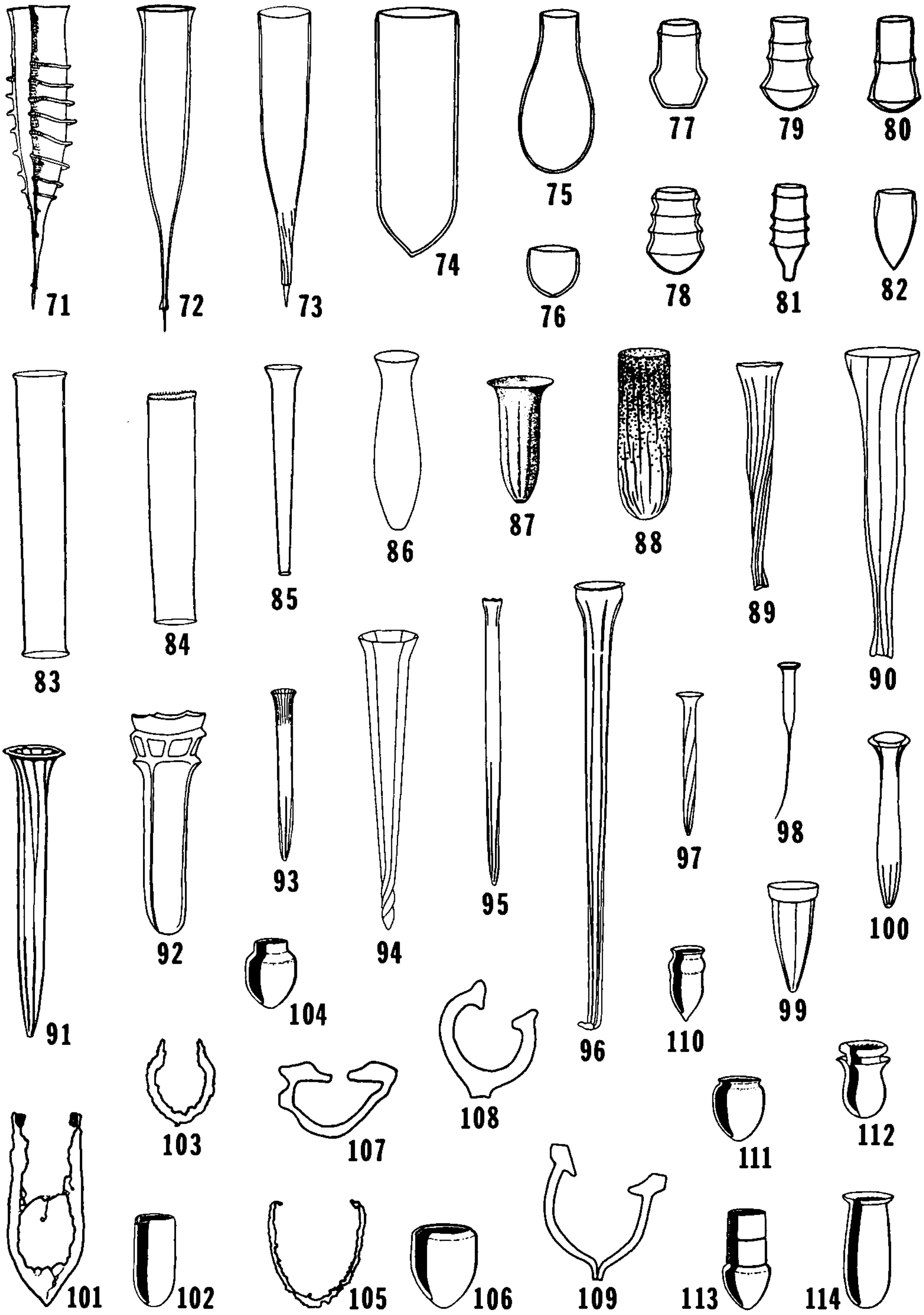

PLATE XXXI, concluded. [See page 313 for figure explanations.]

EXPLANATION OF FIGURES

PLATE XXXII (pages 322–326)

Page 322. Figs. 1–34. Presumably the "more primitive" hypotrichs are represented here. 1–3. *Kahliella* (Dragesco, Dragesco, von Gelei). 4. *Plesiotricha* (Dragesco). 5a,b. *Spirofilopsis* and its tube-like lorica (Dingfelder). 6. *Spiretella* (Dingfelder). 7a,b. *Hypotrichidium* (Dragesco). 8–11. *Stichotricha*, with a "colony" of sorts in 10 (Stein, von Gelei, von Gelei, Borror–unpub.). 12, 13. *Cladotricha* (Gajewskaja). 14, 15. *Strongylidium* (Calkins, Kahl). 16, 17. *Urostrongylum* (Kahl, Kattár). 18. *Chaetospira* (Froud). 19–22. *Urostyla* (Stokes, Fauré-Fremiet, Wang & Nie, Gellért & Tâmas). 23, 24. *Paraurostyla* (Dragesco). 25. *Hemicycliostyla* (Gellért & Tâmas). 26–28. *Paraholosticha* (Borror, Gellért & Tâmas, Dragesco). 29. *Banyulsella* (Dragesco). 30–34. *Holosticha* (Dragesco, Grolière, Bullington, Grolière, Borror).

Page 323. Figs. 35, 36. *Amphisiella* (Fauré-Fremiet, Dragesco). 37–42. *Uroleptus* (Engelmann, Kahl, Calkins, Dragesco, Dragesco, Grolière). 43. *Uroleptopsis* (Kahl). 44. *Paruroleptus* (Grolière). 45. *Uroleptoides* (Wenzel). 46. *Bakuella* (Agamaliev & Alekperov). 47, 48. *Pseudourostyla* (Jerka-Dziadosz, Takahashi). 49, 50. *Balladyna* (Roux). 51. *Laurentiella* (Dragesco). 52. *Trichotaxis* (Dragesco). 53–58. *Keronopsis* (Dragesco, Dragesco, Dragesco, Agamaliev, Grolière, Maupas). 59, 60. *Gonostomum* (Wenzel, Lepşi). 61–63. *Trachelostyla* (Wang & Nie, Gellért, Borror). 64 [see also 79, on following page]. *Uncinata* (Bullington). 65–67. *Psammomitra* (Wright, Claparède & Lachmann, Kahl). 68. *Caryotricha* (Kahl). 69. *Kiitricha* (Nozawa).

Page 324. Figs. 70–73. *Psilotricha* (Stein, Dingfelder, Dingfelder, Grolière). 74. *Hemiholosticha* (von Gelei). 75, 77–79. *Epiclintes* (Borror, Bullington, Claparède & Lachmann, Bütschli). 76. *Eschaneustyla* (Stokes). 77–79. [see above: but is 79 possibly an *Uncinata* (see 64, on preceding page)?]. 80, 81. *Ancystropodium* (Fauré-Fremiet). 82. *Lacazea* (Dragesco). 83, 84. *Kerona* (Stein, Wang & Nie). 85–89. *Oxytricha* (Stein, Dragesco, Dragesco, Grolière, Agamaliev). 90–93. *Gastrostyla* (Grim, Calkins, Borror, Dragesco). 94–97. *Opisthotricha* (Dragesco, Stokes, Gellért, Grolière). 98–102. *Steinia* (Dragesco, Dragesco, Dingfelder, Grolière, Grolière).

Page 325. Figs. 103–109. *Stylonychia* (Stein, Stein, Lang, Jahn & Jahn, Machemer in Grell, Maupas, Dragesco & Njiné). 110. *Parastylonychia* (Dragesco). 111. *Onychodromus* (Stein). 112. *Onychodromopsis* (Gellért & Tâmas). 113–115. *Pleurotricha* (Stein, Dragesco, Dragesco). 116. *Actinotricha* (Dragesco). 117, 118. *Tachysoma* (Gellért & Tâmas, Grolière). 119, 120. *Urosoma* (Stokes, Dragesco). 121–123. *Histriculus* (Stokes, Gellért & Tâmas, Wenzel). 124. *Parahistriculus* (Grolière). 125. *Onychaspis* (Stein). 126–130. *Aspidisca* (Stein, Wang & Nie, Calkins, Dragesco, Agamaliev). 131, 132. *Discocephalus* (Dragesco). 133, 134. *Swedmarkia* (Dragesco). 135. *Euplotaspis* (Chatton & Séguéla). 136. *Paraeuplotes* (Wichterman).

Page 326. Figs. 137–160. Presumably the more or most "advanced" hypotrichs are represented here. 137–147. *Euplotes* (Dragesco, Stein, Stein, Calkins, Dragesco, Borror, Curds, Tuffrau, Carter, Agamaliev, Tuffrau). 148. *Cytharoides* (Tuffrau). 149–152. *Diophrys* (Wallengren, Calkins, Fauré-Fremiet, Fauré-Fremiet). 153–155. *Uronychia* (Calkins, Calkins, Fenchel). 156–158. *Gastrocirrhus* (Fauré-Fremiet, Fauré-Fremiet, Bullington). 159. *Cirrhogaster* (Ozaki & Yagiu). 160. *Euplotidium* (Noland).

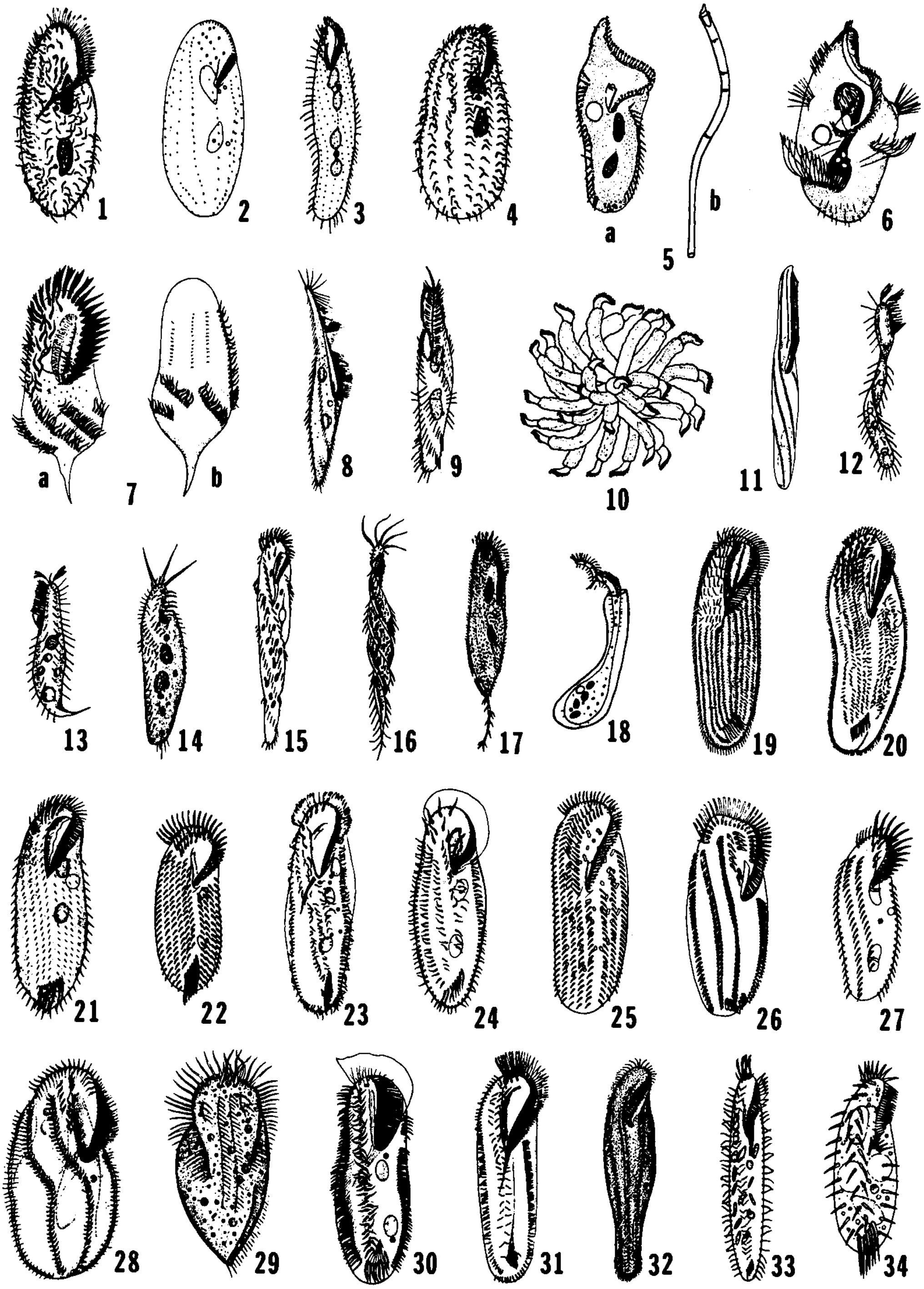

PLATE XXXII. Class Polyhymenophora, subclass Spirotricha, order Hypotrichida: selected genera. [See page 321 for figure explanations.]

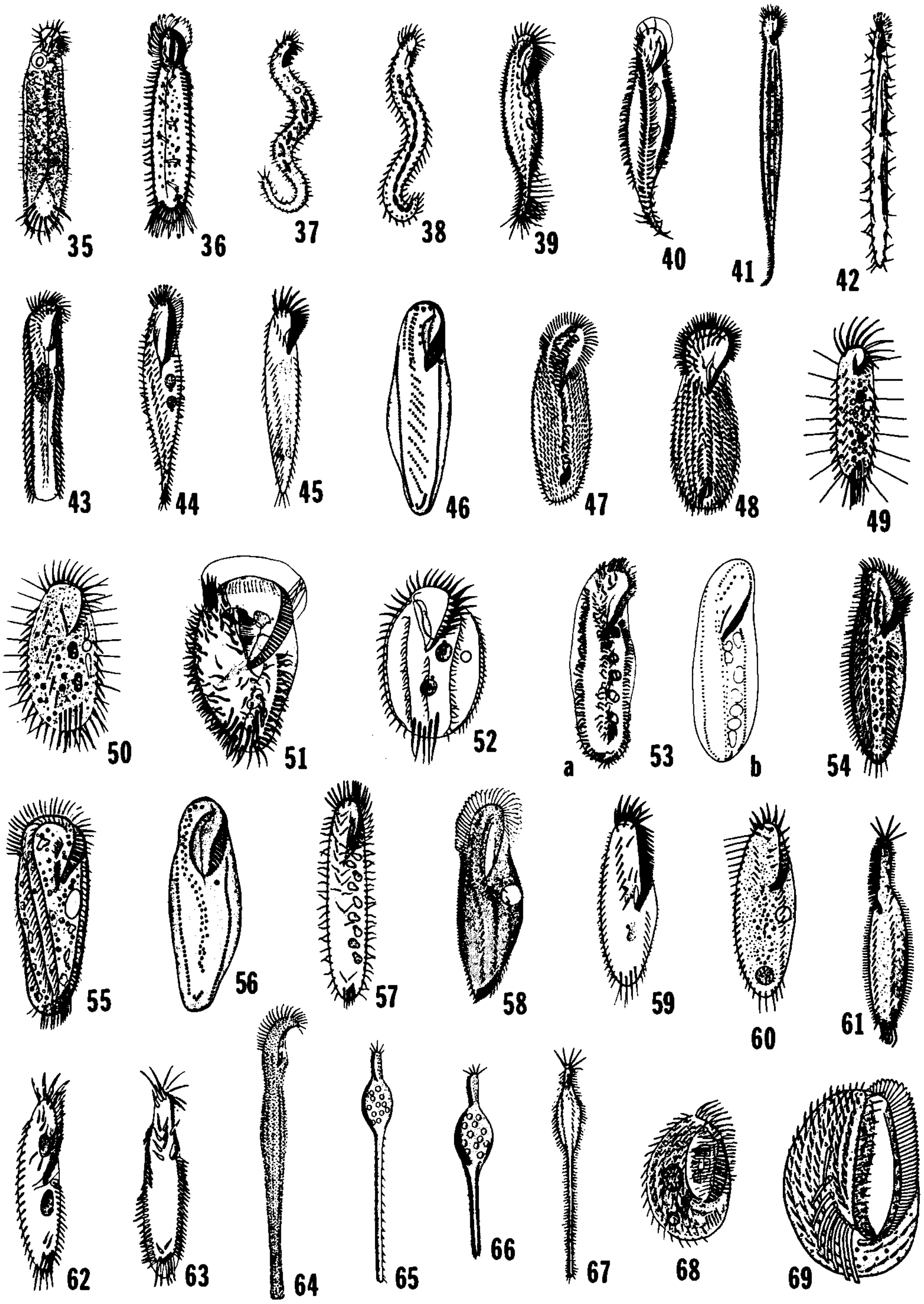

PLATE XXXII, continued. [See page 321 for figure explanations.]

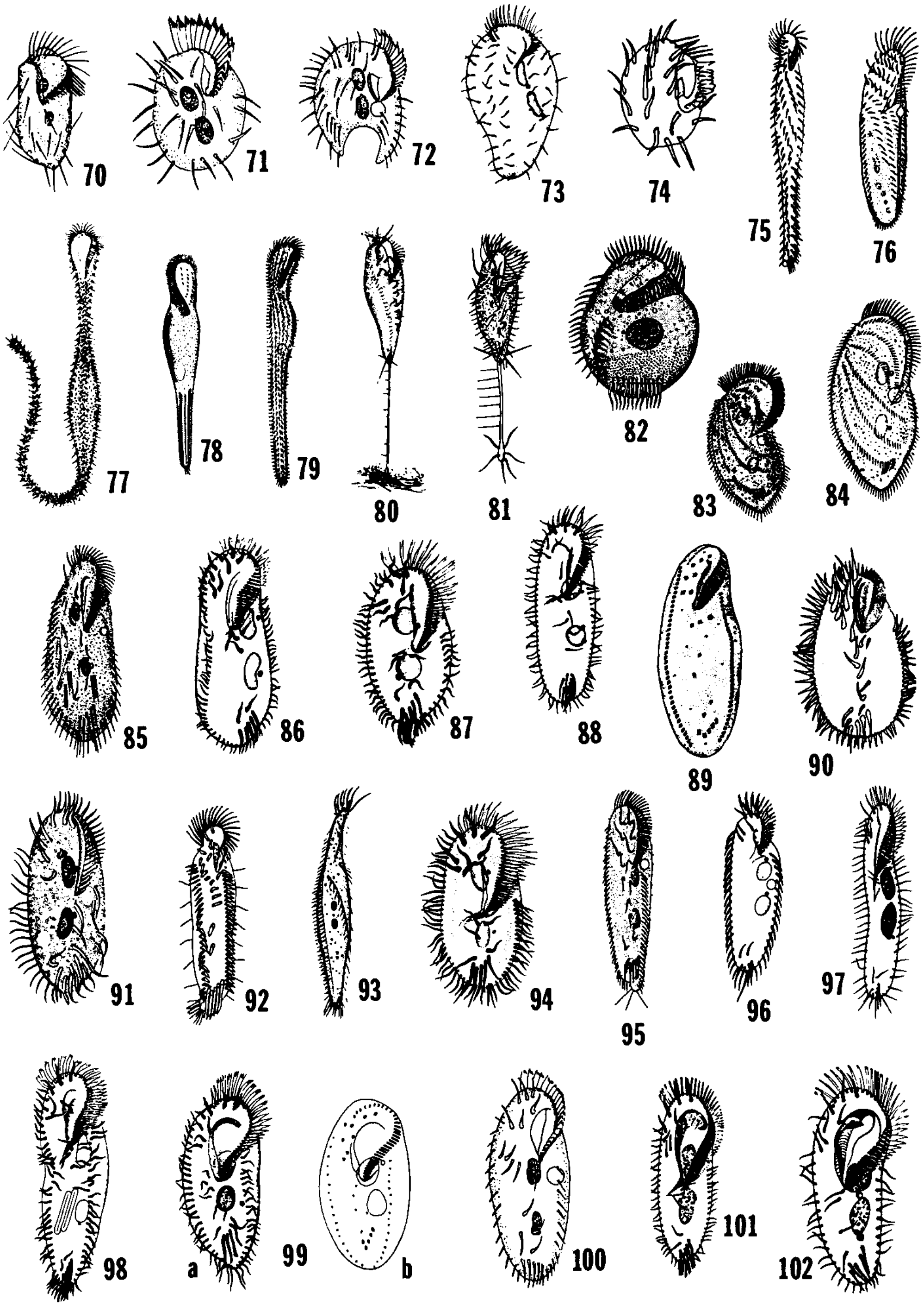

PLATE XXXII, continued. [See page 321 for figure explanations.]

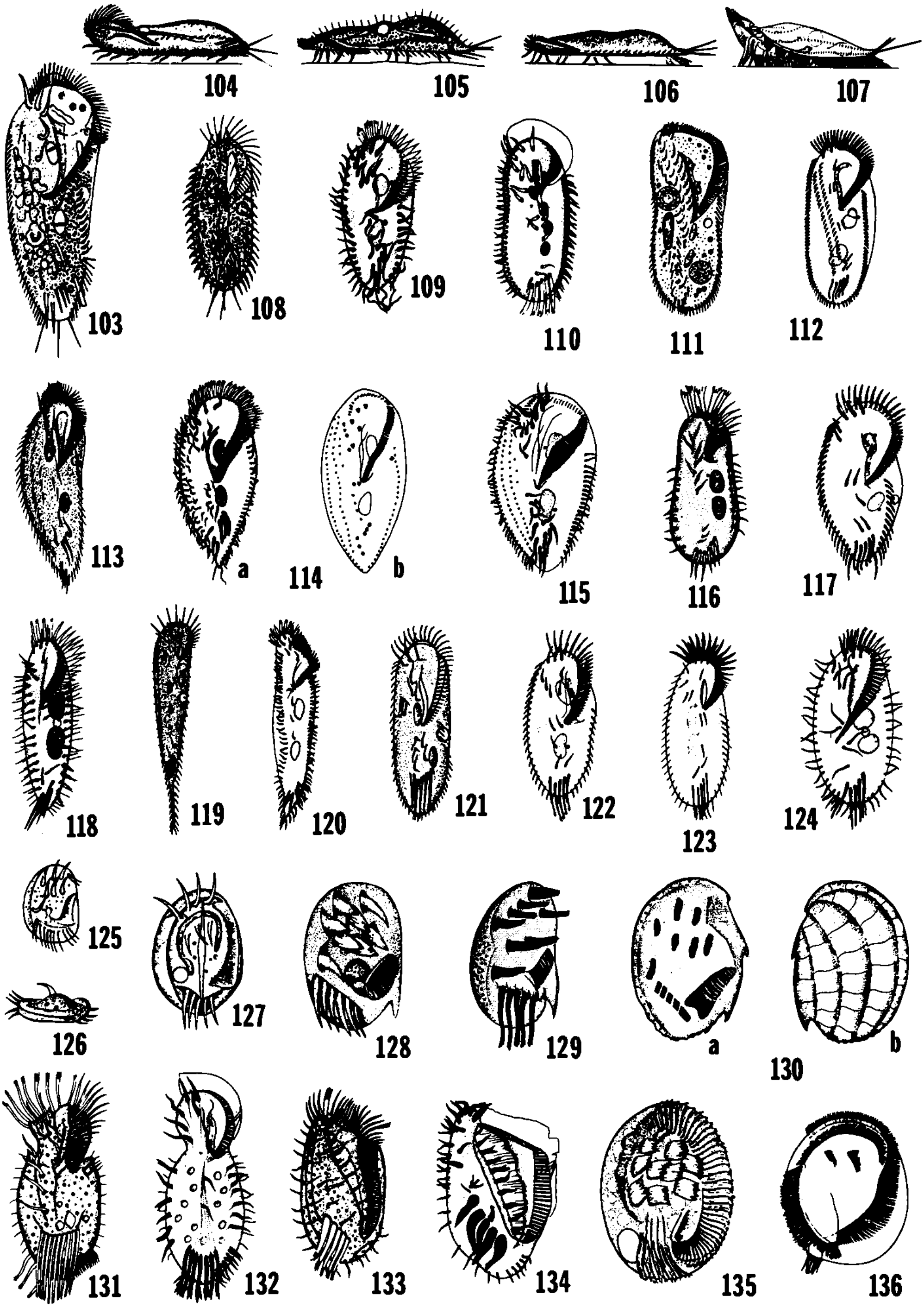

PLATE XXXII, continued. [See page 321 for figure explanations.]

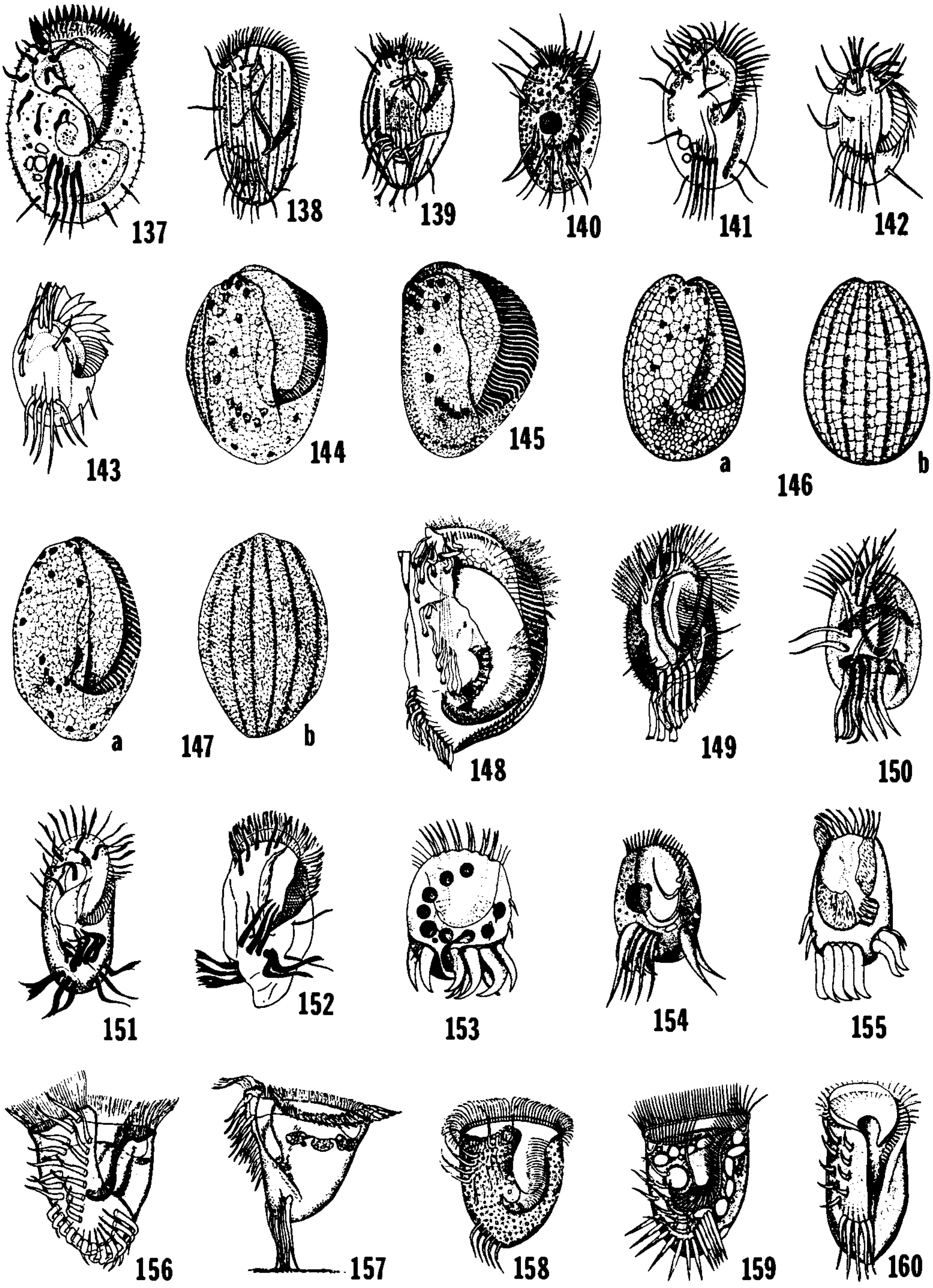

PLATE XXXII, concluded. [See page 321 for figure explanations.]

Chapter 21

Major Monographs, Books, and Review Articles — and Principals in Ciliatology

In 1961, I estimated, perhaps conservatively, that some 10–12,000 original papers had appeared within the past 200 years on topics directly concerned, in whole or in significant part, with one or more species of ciliates. And now, just a decade and a half later, in view of the flood of scientific literature in general and the fact that more and more biologists seem to be turning to protozoa for their experimental material, I suppose the figure should read closer to 18–20,000. Here my principal aim is to provide a selective guide to these writings, over and above the citation of many of them in preceding chapters. The bulk of the 2,925 references directly included in the bibliography (Chapter 22) bear post-1960 dates. On the other hand, important monographs and classical papers of decades (or centuries) past are not excluded. In order to find reference to key older works, the reader is not obliged to return to the first edition (Corliss, 1961), with its total of some 1,700 citations; nor, indeed, to Kahl (1930–1935: see especially 1935c, his "bibliography" for all sections of this great series), with its nearly 900 selectively cited papers; nor even to Bütschli (1887–1889: see pages 1196–1227, 1839–1841), among whose 886 chronologically arranged works one finds reference to practically all of the notes and minor observations – as well as the significant contributions – of the interesting earliest decades in the history of ciliatology. Such older works, if truly noteworthy, are (also) included in this edition.

Perhaps it would be helpful to mention, very briefly, the nature of papers which have generally been excluded. Shorter papers or brief reports, of any vintage and especially if part of a series, are seldom all included; the first or last, as appropriate, may be. Also abstracts are exceedingly rarely cited. They are included only if a major taxon (of familial or suprafamilial rank) is described or some other highly significant contribution never published later elsewhere (yet) is being made there. Sometimes (too frequently) new generic names appear in abstracts and/but are then called "new" a *second* time in subsequently published full papers, occasionally even with change in authorship! Although the "author-and-date" of such a name must be that of the abstract, I may *cite* only the longer description in this book. Unpublished doctoral dissertations (whether or not available on microfilm) are deliberately excluded wholesale – there are too many of them and usually most of the important material incorporated in them has seen the light of day through subsequent publication of one or more major papers on the subject. Finally, minor works of limited scope, even if new species or occasionally new genera are described in them, are not usually included; and scores of nonexceptional papers on subjects unrelated to ciliate systematics, evolution, or phylogenetics are deliberately (and justifiably) excluded, regardless of their date. (Some, mostly older, works serving solely as sources of figures are not cited in the text proper.)

The great bulk of my direct references to the literature occurs in the individual chapters of Part I, as mentioned above. But several hundred publications are mentioned for the first time in the present chapter; and quite a number of others are repeated here, for the special reasons apparent in the treatment of topics included in the following sections. The reader interested in a specific area of research using ciliate material rather than in a given taxonomic group is also enabled to find the literature of pertinence by one or more of the following means: by having knowledge of the name(s) of worker(s) in the field (he or she should then go directly to the alphabetized bibliography and scan the titles of the works listed); by knowing the name(s) of the genus or genera of ciliates involved (go to the index, where reference to all pages including data on its or their species will be given); by being willing to glance over the literature section(s) of each chapter in Part I – set off from other text material by a short line of asterisks – where a guide to the papers on specific topics is often clearly included; and/or by turning to a later section of the present chapter, where a number of area-review works of substance and recent vintage appear. The chapter ends with references to techniques for handling ciliates.

Older Monographs and Textbooks

Unfortunately, this is not the place for even an abbreviated history of protozoology or ciliatology, despite the need for it. Cole's (1926) account is quite incomplete and now very much out of date; Dobell's (1932) exquisite footnotes sorely require fleshing out; Goldschmidt's (1956) charming glimpses of a few 19th century "giants" only whets the appetite; and Woodruff's (1938, 1939a,b) and Wenrich's (1956) papers are most restricted in their coverage. I *am* tempted to make one or two brief remarks here about the very earliest "philosophers in little things" (using Woodruff's apt phrase): and see Corliss (1978b).

First of all, Antony van Leeuwenhoek's (1674) discovery of the protozoa with his most remarkable hand lens must be mentioned (see Corliss, 1975a, for a very recent – tricentennial – tribute to this "founding father"). The Dutchman saw, and described in words (but proposed no taxonomic names), various species of ciliates before the turn of the 18th century; and he figured the parasitic heterotrich *Nyctotherus* in 1683. Buonnani (1691) is probably correctly to be credited with publishing the first drawing of a free-living ciliate (possibly *Colpidium*), although Christiaan Huygens had sketched *Paramecium*, and others, in a letter dated 1678 (not actually published until 210 years later). King (1693), soon after, produced several ciliate drawings. Leeuwenhoek's now well-known figures (see reproductions in Corliss, 1975a; Dobell, 1932) of *Coleps, Cothurnia*, and *Vorticella* appeared a bit later, in 1702. Joblot (1718), Hill (1752), and Wrisberg (1765) were the next pioneers of note in the early years of ciliatology. Works of other late 17th and early 18th century microscopists who observed ciliates (e.g., Ellis, 1769; Harris, 1696; Hooke, 1665; Rösel von Rosenhof, 1755; and Trembly, 1744) are included, without comment, in an addendum to the bibliography of this book, as is also the interesting historical note by (another person with name of) Cole (1853). The only ciliate genus named by Linnaeus (1767, 12th ed.) was *Vorticella*.

The first taxonomic monographs in protozoology, however, had to await the arrival on the scene of the Danish zoologist O. F. Müller (1773, 1776, 1786), in the second half of the 18th century. His great posthumous publication (1786), written entirely in Latin, treated scores of ciliate species (though they were assigned to no more than a dozen genera). A few of his names and observations still hold good today: note his abiding generic names scattered throughout my classification system (Chapter 20). But, as Dobell (1932) has pointed out, Müller's *animalcula infusoria* "were a motley crew of microscopic creatures," including not only protozoa and bacteria but also algae, rotifers, worms of various sorts, etc. [It might be noted, in passing, that "O.F.M.'s" contributions to biology overall have not been fully appreciated: an often overlooked assay of his impact on science is contained in a sensitive and perceptive booklet by Anker (1950).]

The 19th century brought a relative flood of monographs and papers, although – with respect to the ciliates – fewer than half a dozen workers were outstanding in original work in the first half of that century, *viz.*, Ehrenberg (e.g., 1830, 1831, 1833, 1835, 1838, 1840, 1854, to cite the bulk of the works in his magnificent series); Dujardin (1838, 1840, 1841); the often-overlooked Eichwald (1844–1852); and von Siebold (1848), with his invertebrate textbook (recalling the earlier "Handbuch" of considerable value by Goldfuss, 1820, and the authoritative works by Lamarck, 1801, 1815). Although Ehrenberg's ill-fated Polygastrica Theory was overthrown by his French contemporary Dujardin, both of these well-known researchers contributed unforgettably to the comparative morphology and taxonomy of ciliates, leaving names and descriptions a number of which are valid still. What might be called the first textbook of protozoology appeared in the early 1800's as well, the work of the enterprising Englishman Pritchard (1834–1861), who, with colleagues, produced a voluminous compendium running into several editions, the later ones with even colored plates. As was true of practically all early works, it contained accounts of algae, bacteria, rotifers, and a few other micrometazoa as well as ciliates

PLATE XXXIII. Pre- and early 20th-century principals in protozoology and leaders in ciliatology. [See page 352 for identifications.]

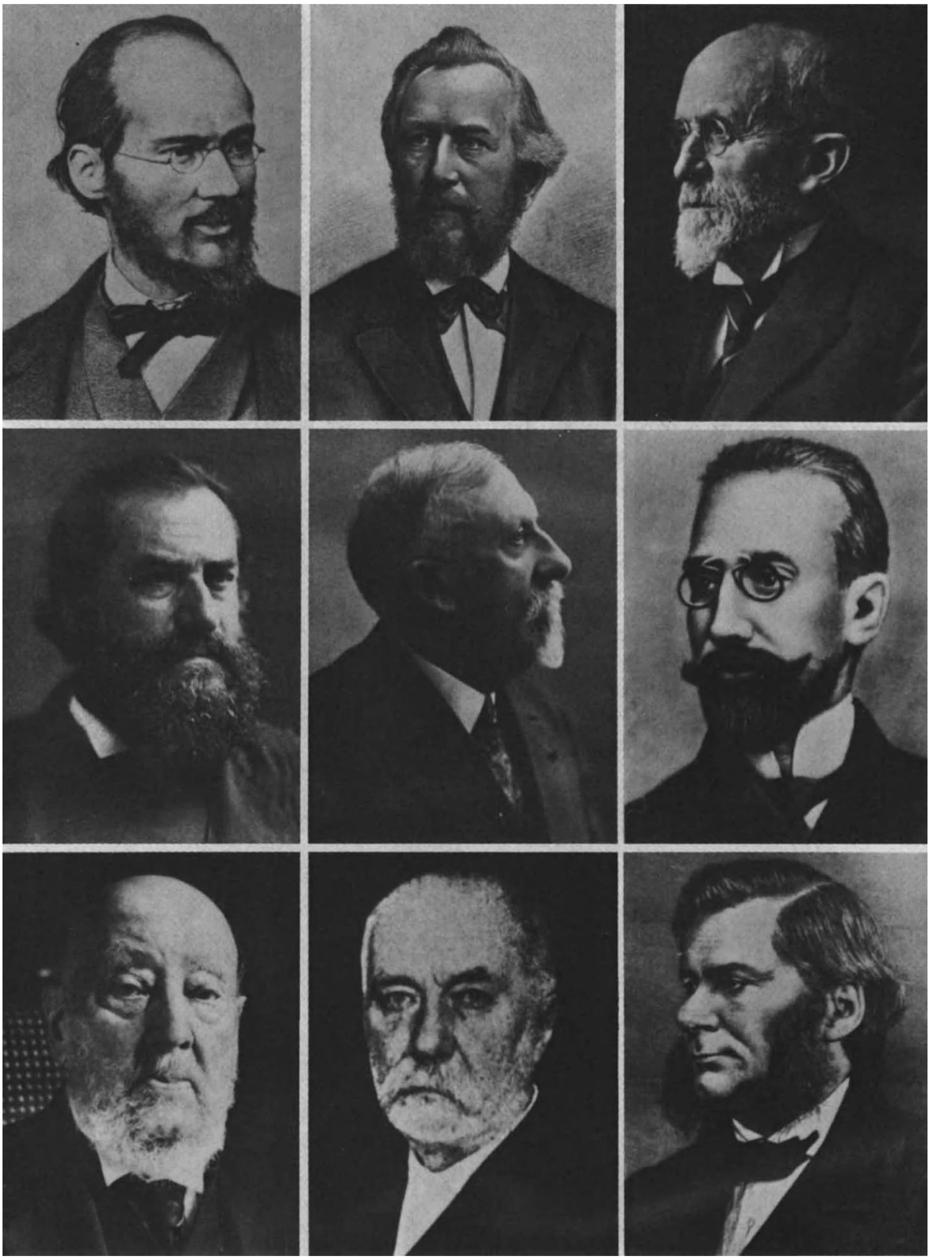

PLATE XXXIII, continued. [See page 352 for identifications.]

PLATE XXXIII, continued. [See page 352 for identifications.]

PLATE XXXIII, concluded. [See page 352 for identifications.]

and other protozoa, and favored free-living, fresh-water forms. Finally, Bory de St. Vincent's (1826) early effort at classification of microorganisms should not be omitted from mention. Incidentally, Mandl's (1839) vest-pocket-sized "Ehrenberg 1838" – an extraction of the taxonomic section but only of the diagnoses in French (leaving aside the German and Latin descriptions and using a greatly reduced page- and print-size) – is a boon to the systematist unable to obtain use of the original rare and gigantic tome.

In the latter half of the 19th century (and spilling over into the early 1900's), concomitant with the appearance of improved methods of microscopy, with the development of interest in cellular biology and in "microbes" of possible medical interest, and with a new emphasis on evolution and phylogeny of the so-called higher forms of life, the exciting field of protistology truly came of age. There occurred literally an explosion of knowledge in ciliatology, with descriptions of scores of new species, expansion of taxonomic schemes of classification, exploration of many new habitats, investigations of symbiotic associations of all kinds, etc. For example, Thompson's (1885) *Bibliography* included some 350 original papers on the "Infusoria" alone during the prolific period 1861–1883. If I were to be limited to citation of fewer than 150 memorable ciliate works of the years 1849–1914 – out of the many hundreds of respectable papers and books which appeared on all aspects of their biology during that expanse of time – I would choose the following, presented below in two groups.

(1) These two dozen truly classical monographs, often superbly illustrated: Balbiani (1861, 1888, 1892–1893), Bütschli (1876, 1887–1889), Claparède & Lachmann (1858–1861), Delage & Hérouard (1896), Fabre-Domergue (1888), Haeckel (1866), Hertwig (1876, 1877, 1889), Kent (1880–1882), Maupas (1881, 1883, 1888, 1889), Schewiakoff (1889, 1893, 1896), Stein (1854, 1859c, 1867), and Stokes (1888). Of all these, the most admirable from the point of view of ciliate systematics can be none other than the exhaustive treatise by Bütschli (1887–1889), "architect of protozoology" (Dobell, 1951) and historian of the field up to his time. He established – with particular dependence on Stein – a scheme of ciliate classification destined to last for 50 years, with the only major early modifications coming from Schewiakoff (1896), a follower of Stein. [Schewiakoff's monograph, in Russian, is not widely available; but Hoare (1927a) has provided an excellent English translation of his taxonomic keys to the "holotrich" ciliates; and Schouteden (1906) has, in effect, presented the entire work in the French language.]

(2) Plus these additional highly significant contributions, usually long papers, occasionally books, generally of a systematic-ecological nature but also including some pioneering experimental observations: André (1912), Bergh (1882), Binet (1889), Blochmann (1886), Brandt (1907), Brodsky (1908), Brumpt (1913), Brumpt & Joyeux (1912), Bundle (1895), Bürger (1905, 1908), Buschkiel (1910), Calkins (1901, 1902a,b), Calkins & Cull (1907), Cépède (1910), Clark (1866), Cohn (1866), Collin (1909b, 1911, 1912), Conn (1905), Cuénot (1891), von Daday (1887, 1910), Dobell(1911), Doflein (1901, 1902), Dons (1913–14), Edmondson (1906), Eichwald (1844–52), Engelmann (1862, 1876), Enriques (1907), Entz, Jr. (1909), Entz, Sr. (1884, 1892), Eyferth (1885), Fauré-Fremiet (1905, 1910a,b, 1912), Foettinger (1881), Fol (1883), Fraipont (1877–1878), de Fromentel (1874–1876), Gourret & Roeser (1886, 1888), Greeff (1870–1871), Gruber (1884), Haeckel (1873a), Hamburger & von Buddenbrock (1911, 1913), Hartog (1906), Henneguy (1890), Hertwig (1902, 1903), Hickson (1903), Hickson & Wadsworth (1902, 1909), Jennings (1897, 1904, 1908a,b), Johnson (1893), Koltzoff (1912), Laackmann (1910), Lachmann (1856), Lanessan (1882), Lankester (1885), Levander (1893, 1894), Lorenz (1902), Maier (1903), Mast (1909), Mereschkowsky (1879), Mermod (1914), Métalnikow (1912), Meunier (1910), Neresheimer (1903), Pearl (1907), Penard (1914), Perejaslawzewa (1886), Perty (1852), Plate (1886, 1889), Prowazek (1898–1903), Quennerstedt (1865–1869), Rees (1884), Rhumbler (1888), Robin (1879), Root (1914), Roux (1899, 1901), Sand (1895, 1899–1901), Schuberg (1888, 1890), Sharp (1914), Stein (1849, 1851), Sterki (1878), Stevens (1901, 1904), Stokes (1885, 1894), Thon (1905), d'Udekem (1864), Verworn (1889), Wallengren (1894, 1895, 1897), Woodruff (1905, 1912), Woodruff & Erdmann (1914), and Wrzesniowski (1870, 1877). The paper by Stokes (1894) was one of the very last of the three dozen notes or generally short papers of this

prolific early American pioneer in ciliatology whose 1888 monograph has been listed in the preceding paragraph. See also the notes by his contemporary Kellicott (1884, 1885, 1889) and see Wenrich (1956) for a brief history of other early American protozoologists, in general so overshadowed by their European contemporaries in those times (see Corliss, 1978b).

Twentieth Century Works, to 1960

The outstandingly important works of the 20th century (post-1914) have generally been cited in place – that is, in appropriate locations in preceding chapters. But the major textbooks (or comprehensive taxonomic reviews or an occasional all-ciliate treatise) in protozoology published during the period 1900–1960 ought to be mentioned here, since many of them were quite significant in bringing the Ciliophora to the attention of the world of biologists and are not cited elsewhere (for similar books *since* 1961, see Chapter 18 or below). Following the historic efforts of protozoologists such as Calkins (1901), Doflein (1901), Hartog (1906), Hickson (1903), and Minchin (1912) – only the first and last of which were truly textbooks and treated all taxonomic groups of the protozoa quite evenly and quite fully – there came the greatly enlarged and improved editions of Doflein's (1909, 1911, 1916) text and subsequent printings or editions of Hartmann's handbook or "practicum" of protozoology (which was actually the second part of Kisskalt & Hartmann's *Praktricum der Bacteriologie und Protozoologie*, but was bound separately and always appeared a year later than Kisskalt's section, with its own pagination, etc., following the single first edition of 1907: e.g., see Hartmann, 1915, third edition, and 1928, fifth and last edition). Poche's (1913) classification of the protozoa also appeared in the interim, as did the section on ciliates by Conn & Edmondson (1918) in the first edition of Ward & Whipple's celebrated *Fresh-Water Biology*.

Then, in the 1920's and 1930's, another spate of textooks (or of other special monographs or series of papers) was published: Bělař's (1926) classical work on nuclei; Bhatia's (1936) ciliate volume of his fauna of British India (with nearly 1,000 full references to the pre-1935 literature); Calkins' (1926, 1933) completely new series; Chatton & Lwoff's (1935a) incomparable monograph on apostomes; Doflein & Reichenow's (1927–1929) continuation of the Doflein series; Dogiel's (1925, 1927) classics on ophryoscolecids; Fauré-Fremiet's (1924) masterful treatise on planktonic ciliates; E. Fernández-Galiano's (1921) unique work, the first protozoological textbook in Spanish; J. von Gelei's (1933, 1934e, 1938, 1939b) fine series on ciliate "sense-organs"; Grandori & Grandori's (1934) monograph on protozoa of the soil; Hartmann's (1928) fifth edition; Hegner's (1938) clever booklet (reprinted without change, but as "Hegner, 1968," by Dover Publications), mostly concerned with parasitic forms; Hegner & Taliaferro's (1924) human protozoology (first of its kind but little on ciliates); Jennings' (1920, 1929, 1931) well-known volumes on the heredity, genetics, and behavior of unicellular organisms; Jollos' (1921) highly influential work on "inheritance" in ciliates; Krüger's (1936) classic on trichocysts studied by the technique of darkfield illumination; Kudo's (1931, 1939) first two editions of what was destined to become a very popular text; Penard's (1922, 1938) perceptive treatment of fresh-water ciliates and his protozoological treatise with philosophical overtones; Poljansky's (1934) monograph on conjugation in *Bursaria*; Power's (e.g., 1933, 1935) series on sea-urchin ciliates (also see Lucas, 1934, 1940; Lynch, 1929, 1930; Madsen, 1931; Nie, 1934; Uyemura, 1934; Yagiu, 1940; and papers by still others); Pratt's (1935) handy illustrated manual on invertebrates, including protozoa; Prenant's (1935) slim volume on ciliates; Sandon's (1927, 1932) important works on soil protozoa and food of protozoa; Schoenichen's (1927) totally ignored taxonomy of the "Infusoria"; Wang's taxonomic-morphological series on the protozoa (principally ciliates) of China (Wang, 1925, 1930a,b, 1940; Wang & Nie, 1932, 1933, 1935); and Wenyon's (1926) celebrated and timeless two-volume treatise (which served as a model for a number of very similar subsequent works, including Knowles, 1928, and Thomson & Robertson, 1929, the latter printed by Wenyon's publisher).

In the same period (1920–1940), Lepşi's (1926) helpful little volume appeared; as did Chatton's (1938) rare and invaluable "Titres et Travaux Scientifiques" (and see Lwoff, 1948).

This was the decade, too, of Kahl's (1930–1935) monumental effort, which still – despite its age – stands as the single best source of an illustrated taxonomic guide to ciliate genera and species (exclusive of marine tintinnines, all suctorians, and certain parasitic groups: the last two, however, were largely treated in Kahl, 1933, 1934a,b; and the tintinnines, through the 1930's, in Jörgensen, 1924, 1927, Jörgensen & Kahl, 1933, and Kofoid & Campbell, 1929, 1939). Among the scores of important papers published on species of the ever-popular *Paramecium* in the 1920's and 1930's, several outstanding ones are singled out for mention here which are not cited elsewhere in the book. G. von Gelei (1937, 1939a), J. von Gelei (1934a,c, 1939a), and Lund (1933) presented early classics on the "silverline system," producing data relevant even in the current era of ultrastructural research. In the broad field of genetics and inheritance, Jennings' works (cited above), Jollos' (1934) stimulating hypothesis of "Dauermodifikationen," and then Sonneborn's (1937: and see 1938, 1939) exciting announcement of the discovery of mating types in *P. aurelia* led to several continuing series of major studies in the area on various species of the genus and established the ciliate Protozoa as significant experimental organisms in modern genetic research. Deserving of inclusion here are also Jennings' (1939a,b: and see 1941, 1942) pioneering accounts of mating types in *P. bursaria*; Gilman's (1939, 1941) similar work on *P. caudatum*; Diller's (1934, 1936) exceedingly important recognition of the sexual phenomenon of autogamy in *P. aurelia*; and Wichterman's (1939, 1940) discovery of cytogamy, "autogamy in pairs," in *P. caudatum.*

In the 1940's, Hyman's (1940) important first volume in her incomparable series on the invertebrates appeared, dealing in part with the protozoa (and see Hyman, 1959, for an "updating" of the work); Doflein & Reichenow's (1949–1953) sixth (last) edition came out; Kudo's (1946) – still to be followed by Kudo (1954, 1966) – third edition was published, as was Jahn & Jahn's (1949) popular and ever-useful "picture-guide" to the protozoa. Lwoff's (1943) monograph on protozoan physiology appeared, recalling his pioneering work of the preceding decade (Lwoff, 1932). Z. Raabe's (1947) long and important paper on means of adaptation by ciliates to a symbiotic mode of life might well be included here, and Kirby's (1941a,b) invaluable chapters on protozoa and other organisms (in roles of both host and parasite). Klein's (1943) major "summarizing" monograph on the "Silberliniensystem," containing a plethora of beautiful photomicrographs mostly garnered from his earlier original observations (e.g., Klein, 1926, 1927, 1928, 1929, 1930), was published. A group of medical and veterinary protozoology texts also suddenly blossomed forth in this period of the forties. For example, see Beltrán (1948), Curasson (1943), Das Gupta (1944), Hoare (1949), Morgan & Hawkins (1948), Neveu-Lemaire (1943), and Richardson & Kendall (1948: latest edition, 1963). Understandably, only small sections were devoted to ciliates, since *Balantidium, Buetschlia, Dasytricha, Isotricha, Nyctotherus,* and especially *Ophryoscolex* (and its many relatives in the rumen of ruminants: *Diplodinium, Entodinium,* etc., etc.) are practically the only ciliate genera ever mentioned, with *Balantidium* alone found in man. Many general or medical parasitology books, whether of broad scope or limited primarily to tropical diseases, were also widely available by this time, but do not warrant citation here.

In the last decade of this brief pre-1960 coverage, the following quartet of important new textbooks of protozoology appeared: Dogiel (1951), Grell (1956), Hall (1953), Jírovec et al. (1953). Copeland's (1956) classification of the protists, including protozoa, also might be mentioned here. Important taxonomic-ecological guides to fresh-water protozoa were included in works by Noland (1959) and Pennak (1953). Klein, the isolated Austrian worker whose silver-impregnation technique has basically revolutionized ciliate taxonomy, published his last two papers (Klein, 1955, 1958; and see Corliss, 1969b), still defending his unpopular conviction (though revived today by Foissner, 1969b,c, and Foissner & Simonsberger, 1975a,b) that the silverline system itself functions as a "nervous system" with "reproductive and formative potentialities." Lwoff's (1950) classic on ciliate morphogenesis made its appearance (see the fine tribute to Lwoff, still active today, in Monod & Borek, 1971), as did Grell's (1953) valuable review of the protozoan nucleus. The posthumous major work by von Gelei (1954) was published in this important decade, marking the end of a most active career (see complete list of his works, the majority in Hungarian, in Gellért & Müller, 1954). It was one of Fauré-Fremiet's most active 10-year periods on ciliates,

PLATE XXXIV. Greatest European leaders in ciliatology in (predominantly) the first half of the 20th century. [See page 352 for identifications.]

PLATE XXXV. Chez "Monsieur Fauré," 9 rue Thénard (en face de Collège de France), Paris. [See page 352 for further explanation.]

PLATE XXXVI. Additional 20th-century leaders in (diverse aspects of) the biology of ciliates. [See page 352 for identifications.]

PLATE XXXVI, concluded. [See page 353 for identifications.]

with production of nearly five dozen full papers (*ca.* 25% of which are included in the bibliography of this book) in the areas of morphogenesis, fine structure, ecology, nuclear phenomena, and systematics. His succinct reviews of "morphology" and "finer morphology" of protozoa (Fauré-Fremiet, 1953b, 1957a) were closely followed by a third in the series (1961h) on cilia and flagella. The man with the greatest impact of any single worker on modern ciliate systematics (see Frontispiece and Plates XXXIV, XXXV), Fauré-Fremiet's professional "publishing" life spanned the incredibly long period of nearly 70 years (see Corliss, 1972c; Willmer, 1972)!

Principals in Ciliatology

Before turning to the prolific literature of post-1960 years, I should like to spend a bit more time with the persons behind the early princi*ples* of protozoology, *viz.*, the princi*pals* who have been involved. The treatment, for want of space, has to be *very* brief; but I should like to emphasize the debt of ciliate systematics to the "giants in the field" who peered through their far-from-elegant microscopes back in "the good old days." Major contributions of 18th- and 19th-century leaders have already been cited in preceding pages and "by their works ye shall know them." Thus, in a way, proper – though sparse – homage has already been paid to such great individuals or teams as Balbiani, Bütschli, Claparède & Lachmann, Delage & Hérouard, Dujardin, Ehrenberg, Entz (junior and senior), Gourret & Roeser, Haeckel, Hertwig, Huxley, Kent, Levander, Maupas, Mereschkowsky, O. F. Müller, Plate, Pritchard, Roux, Sand, Schewiakoff, Schuberg, von Siebold, Stein, Stokes, Wallengren, and Wrzesniowski. See a few selected photographs in Plate XXXIII.

When considering the first half of the present century, it is clear that the number of "principals" has grown considerably. Any grouping should, minimally, include the following major contributors to our knowledge of some highly significant aspect of ciliatology *sensu lato* – both directly and also often in the training of students who became leaders in the next generation: Beltrán, Calkins, Cépède, Chatton, Cheissin, Doflein, Dogiel, Fauré-Fremiet, von Gelei, Grell, Hall, Hartmann, Hegner, Jahn, Jennings, Jírovec, Kahl, Kidder, Klein, Kofoid, Kudo, Lepşi, Lwoff, Metcalf, Noland, Penard, Poljansky, Raabe, Sonneborn, Šrámek-Hušek, Stammer, Stiller, Strelkow, Taylor, Wang, Wenrich, Woodruff, and Yagiu. Yet such a list fails to give proper recognition to an additional 90–100 investigators (demonstrating especially the upsurge of protozoology in America) whose impact on the diverse fields involved has also been considerable: Alverdes, E. André, Andrews, Awerinzew, Balamuth, Becker, Beers, Bhatia, Bishop, Brandt, Bresslau, Bretschneider, von Buddenbrock, Bullington, Bundle, Bush, Campbell, Chen, Child, Collin, Colom, da Cunha, von Daday, Dawson, De Morgan, Dewey, Diller, Dobell, Dons, Elliott, Enriques, Evans, E. Fernández-Galiano, Finley, Furgason, Gajewskaja, Garnjobst, Gassovsky, Georgévitch, Giese, Hadži, Hamburger, Heidenreich, Hoare, Horváth, Hovasse, Hsiung, Hyman, Ivanić, W. H. Johnson, Jollos, Jörgensen, Kalmus, Kay, Kimball, King, Kirby, Kitching, Kormos, Kozloff, Krüger, Lackey, Lauterborn, Loefer, Lucas, Lund, Lynch, MacDougall, MacLennan, Madsen, Mangold, Mast, Minchin, Muniz, Nie, Nigrelli, Noble, Párducz, Peschkowsky, Pickard, Powers, Prowazek, Reichenow, Rossolimo, Sandon, Schwartz, Sharp, Stevens, Summers, Swarczewsky, Tartar, Turner, Villeneuve-Brachon, van Wagtendonk, Weisz, Wenyon, Wetzel, and Wichterman. See a few selected photographs in Plates XXXIII–XXXVI.

Principals existed not only in the "good old days." But it is difficult – and perhaps a bit unwise – to attempt to single out the great, or potentially great, leaders on the current scene. Many of the "pre-1950" ciliatologists listed above were (or are still) productive well beyond that artificial half-century cut-off point, of course; in fact, some of our contemporary leadership is to be found among persons also very active 30 or more years ago. In this "Age of Ultrastructure," however, the major fields of ciliatology are beginning to depend more and more on the sophisticated approaches of the cell biologist and the molecular geneticist, and on the persons who apply them most effectively. In an earlier paper (Corliss, 1974a), I have acknowledged the debt of ciliate systematics to a group of relatively young workers around the world, and the lists of laboratories and people involved need not be repeated here. The productivity of such ciliatologists is easily verified by perusal of the bibliography of this book and – perhaps better – by noting the multiplicity and deserved repetitiveness of references to their works in citations throughout the pages of preceding chapters. A few selected photographs (all of which are *not* of recent vintage!) of persons comprising this last category appear in Plate XXXVII.

Recent (post-1960) Books and Review Articles

Although nearly every one of the preceding chapters includes citation of works of a review nature with respect to the group of organisms under consideration (reviews not only of taxonomic aspects but generally also of various other fields involved in the total biology of those ciliates), it may be helpful to offer here – in a single location – references to the principal books and review papers concerned primarily with ciliates (as cells *or* organisms!) and published in recent years, at least since 1960 and often since 1970. The combined bibliographies of all the works mentioned in the next few pages will lead the interested reader to many times the number of specific papers which space has permitted me to cite directly.

Textbooks or similar works of protozoology devoting a sizable section to the ciliates – or books or chapters which treat only ciliates – which have appeared since the first edition of this book include: Bick (1972), Borror (1973a), Curds (1969), Curtis (1968), Grell (1968, 1973), Hall (1964), A. R. Jones (1974), Kozloff (1972), Kudo (1966), Lepşi (1965), Mackinnon & Hawes (1961), Manwell (1961, 1968), Matthes & Wenzel (1966), Nikoljuk & Geltzer (1972), Poljansky & Cheissin (1962, 1965), Poljansky et al. (1963), Raabe (1964c), Raikov (1967, 1969, 1972a, 1976b: recalling – to an extent – such predecessors as Bělař, 1926; Grell, 1953, 1962, 1964), Sandon (1963), Sleigh (1973), Vickerman & Cox (1967), Westphal (1974, 1976), and Yagiu (1962). Many of these represent a splendid "take-off point," especially for the student or nonspecialist in any of a myriad of fields of interest, if background information is desired or a guide to the as-current-as-possible research literature is being sought.

Another source of data and references, often at a level slightly more sophisticated than that involved in most of the works cited above, is the "topical-review" series becoming so popular throughout fields of biological research. Some older "continuing series" seem temporarily to have been halted – for example, the celebrated Lwoff-Hutner set on biochemistry and physiology of protozoa (Lwoff, 1951; Hutner & Lwoff, 1955; Hutner, 1964a) – but others have simply been replaced: for instance, Calkins & Summers (1941), the "blue bible," – itself preceded by Hegner & Andrews (1930) – by Chen (1967–1972). And new ones have sprung up: for example, Kidder (1967a) and Prescott (e.g., 1964, first in the series, and 1975, one of the most recent volumes); the *Actualités Protozoologiques*, a summary of the Round Table sessions at the fourth International Congress of Protozoology (see de Puytorac & Grain, 1974), might be mentioned here, too. Then there are the compendia or authoritative papers on a variety of specific subjects: ultrastructure (Grain, 1969; Pitelka, 1963, 1969, 1974); contractility (Amos, 1975; Huang & Mazia, 1975); cilia and ciliary movement (Dryl, 1975; Dryl & Zurzycki, 1972; Naitoh, 1974; Naitoh & Eckert, 1974, Párducz, 1967; Satir, 1965; Sleigh, 1962, 1974a; Warner, 1972); trichocysts *sensu lato* (Hausmann, 1978; Hovasse, 1965; Hovasse & Mignot, 1975); nucleic acids (Salvano, 1975b); microbial communities (Cairns, 1971a; Patrick et al., 1967; and see some of the textbooks or monographs listed above); holozoic ciliate nutrition (Dive, 1973; Hutner et al., 1973); scanning electron microscopy (Kessel & Shih, 1974); and behavior of microorganisms (Pérez-Miravete, 1973). Important summaries of recent protozoological research progress in the U.S.S.R. appear in papers by Cheissin (1963a, 1967) and Poljansky (1973).

At the same time, in the modern explosion of scientific literature, a number of most useful books or monographs, often multi-authored, have appeared which are concerned solely with a series of topics on the biology of a selected group of ciliates, with the generic or other (higher-level) taxonomic name appearing in the title. For example, see Elliott (1973a), Hill (1972), and Nilsson (1976), on *Tetrahymena* (with emphasis on the biochemically popular *T. pyriformis*); Jurand & Selman (1969) and van Wagtendonk (1974), fulfilling a 20-year cycle on *Paramecium*:

recall Kalmus (1931) followed by Beale (1954) plus Wichterman (1953) in preceding periods; Tartar (1961) and Uhlig (1960), on *Stentor*; Eberhardt (1962), Giese (1973), and Wilfert (1972), on *Blepharisma*; Canella & Rocchi-Canella (1976), on ophryoglenine hymenostomes (and kindred groups); Didier (1971) and Roque (1961a), on peniculine hymenostomes; Jankowski (1964b, 1973b), on polysaprobic heterotrichs and chonotrichs, respectively; Albaret (1975), on endosymbiotic heterotrichs; Noirot-Timothée (1960), on entodiniomorphids; Stiller (1971, 1974a), on peritrichs and hypotrichs, respectively; Haider (1964), on mobiline peritrichs; Lom (1964), on peritrich mouthparts; Loeblich & Tappan (1968), Marshall (1969), and Tappan & Loeblich (1968), on tintinnines; Raabe's (1972: last one) thorough series on thigmotrichs; and, reasonably included here, Borror's (1972a) revision of the hypotrichs and de Puytorac's (1972a) concluding monographic paper on several families of astomes.

Furthermore, we are now seeing a great increase in monographs or sometimes handbooks on ciliates of a given geographical location, or, more often, of a given biotope or ecological niche *sensu lato* (Corliss, 1973a). Among many possible recent examples, let me list the following, a few of which have already been cited, in a different context, in preceding paragraphs: Balech (1962, 1971a,b), on the pelagic tintinnines; Bick (1972) and Curds (1969, 1975b), on ciliates in activated sludge or as pollution indicators, recalling the pioneering works of Lackey (1925), Lauterborn (1916), Wetzel (1928), and, later, Šrámek-Hušek (e.g., 1957); Borror (1973a, 1975), on marine ciliates of coastal and estuarine waters of New England; Cairns (1971a,b, 1977), Maguire (1971), Patrick et al. (1967), Salt (1971), and Taub (1971), and others, on fresh-water microbial communities; Chorik (1968), on the ciliates in the Moldavian basin; Dragesco (1970), on the free-living ciliates of the Cameroons; Fenchel (1967, 1968a,b, 1969; Fenchel & Riedl, 1970), on ciliates of the marine microbenthos; E. E. Jones (1974a), on the protozoa of Mobile Bay; Dietz (1964) and Reuter (1961), on species from brackish ponds and rockpools; Dingfelder (1962), of the Stammer school (see Matthes, 1974; Stammer, 1963), on ciliates in a fresh-water pond (recalling von Gelei, 1954); Gittleson & Hoover (1969) and Tucolesco (1962c), on cave-dwelling species; Hartwig (1973a,b), on the ecology and systematics of interstitial ciliates from the North Sea (for references to papers on such ciliates from other seas, see Corliss & Hartwig, 1977); Jankowski (1973b, and earlier papers), on the totally epibiotic and mostly marine chonotrichs, but including those on gammarids from fresh-water Lake Baikal; Kattar (1970) on psammophilic forms from the coast of Brazil; López-Ochoterena (1966), on mesosaprobic ciliates from a park in Mexico City; Lundin & West (1963), on the protozoa of northern Michigan; Nusch (1970), Pätsch (1974), Spoon (1976), and Wilbert (1969), on aufwuchs ciliates from sources near Bonn and [Spoon] from the upper Potomac estuary; J. C. Thompson (1972) and Thompson & Croom (1977), on ciliates from Antarctica; and Watson (1946), an aging but unique review, on coprozoic forms.

In the same broad category, one might place such works as the monograph by Grain (1966a) on the ciliates in the "biotope" provided by the digestive tract of certain ruminants and horses, reminiscent of classics of old (Buisson, 1923; Bundle, 1895; Hsiung, 1930; Kopperi, 1937; Strelkow, 1939; and others). Wang (1928), Webb (1956), and others, incidentally, set the "model" decades ago for many of the more recent ecological studies or surveys selectively cited in the preceding paragraph. Perhaps two of the most thorough earlier investigations of this kind were those by Gajewskaja (1933) and Swarczewsky (1928a–f, 1930) on the free-living ciliates and those associated with the gammarid fauna of the ancient Lake Baikal in southern Siberia (a locale to which Jankowski, 1973b, has recently returned).

Reviews of a general cytological nature or of cytoplasmic organelles are often directly or indirectly covered in citations made on immediately preceding pages or in earlier chapters. But special mention might be made here of several quite recent discussions, rich in references. For example, see Dutta (1974) – recalling Grimstone (1966) and other earlier reviews – on advances in the cytochemistry and ultrastructure of cytoplasmic inclusions found specifically in ciliates. In a much shorter work restricted to consideration of Golgi apparatus alone – an organelle even the existence of which was once questioned in these protozoa – Estève (1972) offers a compre-

PLATE XXXVII. New or emerging leaders in ciliate systematics (or in more or less impinging fields) in the second half of the 20th century. [See page 353 for identifications.]

PLATE XXXVII, continued. [See page 353 for identifications.]

PLATE XXXVII, continued. [See page 353 for identifications.]

PLATE XXXVII, concluded. [See page 353 for identifications.]

hensive if succinct review, giving evidence for the widespread distribution of Golgi in species of ciliates from the major taxonomic groups. Still in press at this time is the anticipated major review on extrusomes by Hausmann (1978). Finally, Müller's (1975) very recent paper on the biochemistry of protozoan microbodies might be cited, although ciliates are not the principal subject of the review.

Still another way to have a guide to "what's going on" in modern fields of ciliatology around the world is to follow the abstracts and proceedings of the International Congresses of Protozoology (five held to date), published copies of all of which are probably still available. For example, contact might be made with Drs. J. Ludvík, J. Lom, or J. Vávra, with respect to the first Congress, held in Prague in 1961; with Prof. P. C. C. Garnham or Dr. R. S. Bray, for the London meetings of 1965; with Profs. G. I. Poljansky, A. A. Strelkow, or Dr. I. B. Raikov, for Leningrad, 1969; with Prof. P. de Puytorac or Dr. J. Grain for Clermont-Ferrand (Aubière), 1973; and with Drs. B. M. Honigberg, S. H. Hutner, J. J. Lee, or W. Trager for New York City, June–July 1977. [The *Actualités* of the 1977 (fifth) Congress is expected in 1978.]

There are many important papers or reviews by (generally) nonsystematically oriented ciliatologists, or by cell biologists working with ciliates, which could be cited, particularly works containing stimulating ideas in the fields of genetics, cytogenetics, morphogenesis, and evolution, areas to which protozoan taxonomists might pay more attention. Selected contributions of recent appearance, including works by a few persons who are also active in systematics (shown in other papers of theirs), are: S. L. Allen (1967), Beisson (1972), Canella (1964a), Canella & Rocchi-Canella (1976), De Terra (1974), Dippell (1968), Ehret (1960, 1967, 1974), Ehret & de Haller (1963), Ehret & McArdle (1974), Fauré-Fremiet (1948b, 1953a, 1954b, 1961e,h, 1967c, 1970b), Frankel (1974, 1975b), Génermont (1975, 1976), Grain & Bohatier (1977), Grell (1962, 1964, 1967, 1973), Grimstone (1959, 1961), de Haller (1969, 1977), Hanson (1963, 1967, 1977), Hanson & Jerka-Dziadosz (1974), Miyake (1974), Moshkowski (1963, 1969), Nanney (1958, 1968a,b, 1972, 1974, 1977a,b), Ng & Frankel (1977), Orias (1976), Pitelka (1969, 1970), Poljansky (1973), Poljansky & Raikov (1976), Preer (1969), Prescott & Murti (1974), de Puytorac (1972b), de Puytorac & Grain (1976), Raikov (1969, 1972a, 1976b), Sonneborn (1957, 1963, 1964, 1970b,c, 1974a, 1975b), Tartar (1961, 1967), Tilney (1968, 1971), Vivier (1960), and Wolfe (1972).

Primarily for reasons of space, few references have been made directly to the nonciliate literature, and particularly to nonprotozoan works. But appreciation of ideas and advances in the broad fields of systematics, evolutionary biology, and classification (including sophisticated statistical approaches to handling taxonomic data) – with all sorts of other organisms (prokaryotic monerans, other protists, fungi, or higher plants and animals) involved – can be helpful in the formulation and application of principles in the case of the Ciliophora, as I have stressed in Chapter 3. From the vast literature available, some of which I have cited elsewhere (e.g., in Corliss, 1968, 1972e, 1974c, 1976), I shall single out the following: Anderson (1973), Ashlock (1971, 1974), Baker (1965), Ball (1974), Blackith & Reyment (1971), Blackwelder (1967), Bock (1970, 1974), Bronowski (1970), Brundin (1968), Buchanan & Gibbons (1974), Cain (1959), Cain & Harrison (1960), Clifford & Stephenson (1975), Crowson (1970), Darlington (1971), De Ley (1974), Dillon (1963), Dobzhansky (1970), Dougherty et al. (1963), Farris et al. (1970), Ghiselin (1977), Gould (1977), Hadži (1963), Hanson (1977), Hennig (1966, 1974), Honigberg (1963), Hull (1967, 1970), Huxley (1958), Inglis (1970), Jahn et al. (1974), Jardine (1967), Jardine & Sibson (1971), Jermy et al. (1973), Johnson (1970), Kavanaugh (1972), Kerkut (1960), Klein & Cronquist (1967), Leedale (1974), Lwoff & Tournier (1966), Margulis (1970, 1974a,b, 1975), Marx & Rabb (1970), Mayr (1965, 1969, 1970, 1974), Michener (1970), Nelson (1974), Olive (1975), Page (1976), Pickett-Heaps (1975), Remane (1956), Rensch (1959), Ross (1974), Schaefer (1976), Schaeffer et al. (1972), Simpson (1945, 1961, 1964), Sneath & Sokal (1973), Sokal & Sneath (1963), Stanier (1970), Stebbins (1971, 1974), Taylor (1976), Thorne (1963), Van Valen (1973), Whittaker (1959, 1969, 1977), and Wright (1974).

Finally in this day and age of an overwhelming flood of printed material on all subjects, sophisticated information retrieval systems must be relied on as indispensable sources of data in any field. Thus, for the ciliates, the modern worker should be aware of the mushrooming abstracting and indexing services available, running all the way from *Current Contents* through *Microbiology Abstracts* (Section C) and *Protozoological Abstracts* (Commonwealth Institute of Helminthology) to the "new" *Zoological Record*.

Techniques in Handling Ciliates

It is becoming increasingly difficult to give direct advice – or even appropriate literature references – of *general application* on methods of handling ciliates, for two main reasons. The first is best expressed in the words of Minchin who, over 65 years ago, perceptively pointed out, with respect to fixing and staining of protozoa, that every species or strain "requires its own special technique, which must be established empirically by trial, and can be discovered only to a very limited extent and with great uncertainty by analogy." The second is that because so many of the techniques today are the sophisticated methods of cell biology or molecular biochemistry they are neither restricted to the protozoa nor possible to explain in an abbreviated treatment. The best general advice to students is to find and study the papers on the species of organism with which they wish to work (with special attention to the "materials and methods" section), and then, by "trial and error," discover how to handle their own particular strain(s). Hundreds of the papers and monographs cited throughout this book can be helpful in such a way. Fortunately, with respect to hints on general collecting and laboratory handling, some specific books or manuals or chapters in books have been published, in addition to the advice or guidelines included in many general textbooks of protozoology: Bělař (1928), Galigher & Kozloff (1971), Goodrich (1950), Kirby (1950), Wenrich & Diller (1950); and see various modern handbooks of cytology and of microtechnique. The novel series on methods in cell biology edited by Prescott (first volume, 1964; tenth, 1975; but see now – just available – Cummings, 1977) contains numerous articles on how to handle protozoa in physiological-biochemical research. Electron microscopical techniques are considered below.

The problems of methods of collecting need to be stressed here. General guidelines are available – see appropriate sections in a number of the references already cited elsewhere in this chapter; but, as field work has (also) become more sophisticated, the techniques involved have required more attention. I am thinking particularly of the marine interstitial biotope, because of the growing interest in it and the necessity for quantification of collection data, etc., as the cytology-taxonomy moiety of the work intermingles with the ecological aspects of many of the problems being undertaken there today. For guidance in collecting material from this ecosystem, the reader is referred to relevant monographic researches, such as those of Dragesco (1960) and Fenchel (e.g., 1967, 1969); to the highly successful techniques of Deroux and colleagues (e.g., see Deroux, 1970) and of Uhlig (e.g., 1964a, 1966, 1968); and to general treatises on meiofauna (e.g., Hulings & Gray, 1971). Just out is another ecological "methods" paper: Wilbert (1977b).

Culturing methods, so basic to most work on ciliates, have now essentially been taken out of the hands of the general protozoologist and are to be found in works by the cell physiologist or biochemist (e.g., see the references to Prescott, cited above). Remaining of value, however, are such straightforward "old-fashioned" hints on culturing, feeding, and maintenance of various species as those available in the booklets written years ago by Needham et al. (1937) and Sandon (1932); and note some general suggestions in such more recent papers as Burbanck & Spoon (1967), Fauré-Fremiet (1961f), and Tuffrau (1967b). Also, for certain specific organisms (as indicated), see: Hanson (1974), Sonneborn (1950, 1970a), and van Wagtendonk & Soldo (1970b), on methods of handling *Paramecium*; Everhart (1972), Stone & Cameron (1964) – and many other works on synchronous-division techniques (see references in Corliss, 1973a,b, and Elliott, 1973a) – on *Tetrahymena*; and Prescott & Carrier (1964) on *Euplotes*. Tartar (1961, 1964) and Giese (1973) might be included here on behalf of *Stentor* and *Blepharisma*, respectively. Preservation of "reference-strain" material in a frozen state is now becoming possible with ciliates (e.g., see McGrath et al., 1977; Simon, 1971, 1972; and references therein), a technical advance long awaited.

Because of the great – really revolutionary – importance of methods of silver impregnation in the study of cortical features of ciliates, with subsequent impact on several major fields of research including morphogenetics as well as systematics, a brief listing of papers containing specific directions on how to use the several techniques available today (some briefly reviewed in Corliss, 1973c,d) are the following: Chatton & Lwoff (1930, 1936b), Corliss (1953a), Deroux & Dragesco (1968), Deroux & Tuffrau (1965), Diller (1966), Dragesco (1962c), Dragesco & Njiné (1971), Fernández-Galiano (1966, 1976), Foissner (1967), Foissner & Simonsberger (1975a), Frankel (1973b), Frankel & Heckmann (1968), G. von Gelei (1939b), J. von Gelei (1932, 1934d), von Gelei & Horváth (1931a,b), Honigberg & Davenport (1954), Horváth (1938), Jerka-Dziadosz & Frankel (1969), Klein (1926, 1958), Kozloff (1964), Lom (1964), Lynn & Berger (1972, 1973), Madrazo-Garibay & López-Ochoterena (1974), Ng & Nelsen (1977), Nie (1950), Repak & Cribbins (1966), del Rio-Hortega (1926), Tuffrau (1964b, 1965, 1967a, 1968), Uhlig (1972), Wilbert (1975), Williams & Scherbaum (1959), Yusa (1957), and Zagon (1970). Which silver technique is espoused in which publication will generally be clear from the titles of the papers (see Chapter 22). The value of such methods in preparation of type-specimen material has been stressed elsewhere (Corliss, 1972b). Other techniques – for example, nigrosin staining (recent papers: Borror, 1969; Deroux & Faidy, 1966), use of haemotoxylin, etc. – are often also excellent: but space prohibits direct citation of multiple specific references to them here.

Scattered figures throughout this book may serve in illustration of the superior results – in comparative morphology and systematics of ciliates – made possible through use of silver methods. Although most of these are drawings based on examination of silver-impregnated specimens (rather than original photomicrographs), they still support well my sincere plea for wider usage by taxonomic ciliatologists of one or more of the techniques currently available. The figures referred to include those on the several pages comprising Plates II, VII, and especially IV (in Part I of this book) and various drawings throughout Plates XXII-XXXII of Chapter 20 (Part II).

Electron microscopy, the use of which has been hailed as so important to systematics throughout this book, involves techniques of fixation, sectioning, counterstaining, etc. which are well beyond treatment here. For TEM, dozens of books exist on methodologies; and, once again, specific papers of recent vintage on ciliates should be sought out for counsel. For SEM, the same advice is appropriate; but the rather landmark note of Small & Marszalek (1969), in *Science*, might be cited here as a good starting place for the interested reader (see also Hausmann, 1974b; Kessel & Shih, 1974; Ruffolo, 1974; Zagon, 1971). A general book which relates SEM and TEM to problems of systematics and evolution is that by Heywood (1971); and Cole & Behnke (1975) recently reviewed the usage of electron microscopy in plant taxonomy. Badly needed is a full and comprehensive SEM-TEM "atlas" (or, preferably, set of atlases!) on features of the surface of ciliates and on the subpellicular, cortical, and deeper cytoplasmic structures and organelles of these fascinating creatures as well.

IDENTIFICATIONS OF PRINCIPALS IN CILIATOLOGY

PLATE XXXIII (pages 331–334)

Page 331

Row 1: Antony van Leeuwenhoek (1632–1723), Sir John Hill (1716–1775), Otto Friderich Müller (1730–1784).
Row 2: Jean Baptiste Pierre Antoine Lamarck (1744–1829), Christian Gottfried Ehrenberg (1795–1876), Félix Dujardin (1801–1860).
Row 3: [S.] Friedrich [N. von] Stein (1818–1885), W. Saville Kent (1845–1908), Otto Bütschli (1848–1920).

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Row 1: [J. L. R. A.] Édouard Claparède (1832–1871), Ernst [H. P. A.] Haeckel (1834–1919), Richard Hertwig (1850–1937).
Row 2: Joseph Leidy (1823–1891), Félix Mesnil (1868–1938), W [for Vladimir]. Schewiakoff (1859–1930).
Row 3: Eugène Penard (1855–1954), Émile [F.] Maupas (1842–1916), Thomas Henry Huxley (1825–1895).

Page 333

Row 1: Franz [J. T.] Doflein (1873–1924), Max Hartmann (1876–1962), V. A. Dogiel (1882–1955).
Row 2: Charles Atwood Kofoid (1865–1947), Harold Kirby [Jr.] (1900–1952), [C.] Clifford Dobell (1886–1949).
Row 3: Gary Nathan Calkins (1869–1943), Robert W. Hegner (1880–1942), Eduard Reichenow (1883–1960).

Page 334

Row 1: Herbert Spencer Jennings (1868–1947), Lorande Loss Woodruff (1879–1947), Charles Morley Wenyon (1878–1948), Henryk Raabe (1882–1951).
Row 2: Maynard M. Metcalf (1868–1940), Karl Bělař (1895–1929), Muriel Robertson (1883–1973), Charles Vincent Taylor (1885–1946).
Row 3: Richard Roksabro Kudo (1886–1967), Josif Lepşi (1895–1966), Libbie Henrietta Hyman (1888–1969), Harold Sandon.
Row 4: Elery R. Becker (1896–1962), Ann Bishop, Cecil A. Hoare, Sergei W. Awerinzew.

PLATE XXXIV (page 338)

Row 1: Emmanuel Fauré-Fremiet (1883–1971), Édouard Chatton (1883–1947), André Lwoff.
Row 2: József [von] Gelei (1885–1952), Alfred Kahl (1877–1946), Bruno M. Klein (1891–1968).
Row 3: Zdzisław Raabe (1909–1972), Georg I. Poljansky, Eugene M. Cheissin (1907–1968).

PLATE XXXV (page 339)

Four views of the compact living room or parlor, serving also as his study, where "Monsieur Fauré" worked and entertained guests for many decades in Paris, a very short distance from his laboratory at the Collège de France. Though measuring less than 20 X 20 ft in size (< 36 m^2), the room was a treasure-house of riches, a few of which may be pointed out: painting of (the first) Mme Fauré-Fremiet by M. Fauré, a piano of Saint-Saëns; model of grandfather E. Fremiet's Jeanne d'Arc, with bust of the sculptor by M. Fauré; flags of France, Great Britain, U.S.A. (in little vase on desk), well-used microscope, photograph of father Gabriel Fauré, stuffed bull-dog mascot of Yale University; bust of father-in-law L.-F. Henneguy by M. Fauré, reprint collection of (only) papers on ciliates. [Bust of Gabriel Fauré, other paintings, etc., not visible in these particular views.]

PLATE XXXVI (pages 340, 341)

Page 340

Row 1: Pierre-P. Grassé, Raymond Hovasse, David H. Wenrich (1885–1968), Schabsai M. D. Moshkowski.
Row 2: Lowell Evan Noland (1896–1972), Aleksandr [A.] Strelkow, C. Dale Beers (1901–1976), Otto Jírovec (1907–1972).
Row 3: Ludwig H. Bretschneider (1899–1964), Georges Deflandre (1897–1973), Sir John T. Randall, Mario F. Canella.
Row 4: B. R. Seshachar, Enrique Beltrân, Viktor Schwartz, Béla Pârducz (1911–1964).

PLATE XXXVI (continued)

Page 341

Row 1: Karl G. Grell, Waldo Hamlet Furgason (1902–1975), Arno Wetzel (1890–1977), Theodore Louis Jahn, Ryôzô Yagiu, Ralph Wichterman.
Row 2: Dorothy R. Pitelka, William Balamuth, Harold Eugene Finley (1905–1975), William F. Diller, Gordon H. Ball, Frederick R. Evans.
Row 3: Tracy M. Sonneborn, Vance Tartar, Seymour H. Hutner, J. A. Kitching, Arthur C. Giese, George W. Kidder.
Row 4: Richard P. Hall (1900–1969), Tze-Tuan Chen (1906–1976), Robert L. King (1896–1968), Paul B. Weisz, William D. Burbanck, Robert E. Hungate.
Row 5: Alfred M. Elliott, Willem J. van Wagtendonk, Willis H. Johnson, Karl Ernst Wohlfarth-Bottermann, Erik Zeuthen, Heinz Holter.
Row 6: Richard F. Kimball, Geoffrey H. Beale, Maria A. Rudzinska, John B. Loefer, Marshall Laird, John R. Preer, Jr.
Row 7: Theodore von Brand (1899–1978), Reginald D. Manwell.

PLATE XXXVII (pages 345–348)

Page 345

Row 1: Pierre de Puytorac, Anatol W. Jankowski, Jean Dragesco.
Row 2: Jean Grain, Michel Tuffrau, Gilbert Deroux.
Row 3: Jiří Lom, Igor B. Raikov, John O. Corliss.

Page 346

Row 1: Eugene B. Small, Maria Wolska, Eugene N. Kozloff, Stanlisław L. Kazubski.
Row 2: Jacques Berger, Phyllis C. Bradbury, Ayere Yusa, Tom Fenchel.
Row 3: Hélène Mugard-Rouyer, Jesse C. Thompson, Jr., Madeleine Roque, Cécile Noirot-Timothée.
Row 4: Arthur C. Borror, Colin R. Curds, Hartmut Bick, Eucario López-Ochoterena.

Page 347

Row 1: Pierre Didier, Jacques Bohatier, Claude-Alain Grolière, Adrien Batisse.
Row 2: Denis H. Lynn, Portia A. Holt, Michèle Laval-Peuto, Robert K. Peck.
Row 3: Jean-Louis Albaret, Wilhelm Foissner, Eike Hartwig, Gregory A. Antipa.
Row 4: Jerome J. Paulin, Janina Dobrzańska-Kaczanowska, Anna Czapik, Helen Tappan-Loeblich.

Page 348

Row 1: Dimas Fernândez-Galiano, Milden Rodrigues de Santa Rosa, Gotram Uhlig, Émile Vivier, Stuart S. Bamforth, John D. Stout.
Row 2: Earl D. Hanson, Charles F. Ehret, Gérard de Haller, Michael A. Sleigh, Sally L. Allen, David L. Nanney.
Row 3: L. Evans Roth, Robert W. Hull (1924–1970), John Tyler Bonner, Andrzej Kaczanowski, Albert Savoie, Chandra K. Pyne.
Row 4: Jytte R. Nilsson, George G. Holz, Jr., Stanisław Dryl, Miklós Müller, Robert L. Conner, Otto H. Scherbaum (1925–1969).
Row 5: Richard D. Allen, Christian F. Bardele, Klaus Hausmann, Lothar Schneider, David J. Patterson, Joseph Frankel.
Row 6: Gerald R. Seaman, Kenneth Gold, Norman E. Williams, Maria Jerka-Dziadosz, John Cairns, Jr., Guido Persoone.
Row 7: Howard E. Buhse, Jr., Donald M. Spoon.

Chapter 22

References Cited: a Selected Bibliography, with Emphasis on Works Published since 1960

Introductory Remarks

No paper or book is included in this bibliography which has not been cited directly in one or more of the preceding chapters. References are given uniformly and in full – to avoid the understandable frustration and inconvenience to the reader when titles are incomplete or lacking altogether or end-pages are missing – and have been carefully checked fo ccuracy against the original sources. Names of journals and periodicals, however, are abbreviated, but using a widely accepted style with consistency. More than 2,900 works are included here; the basis for selection of these from the many thousands potentially available has been discussed in the preceding chapter. Deliberately excluded, with rare exception, are abstracts, and other very short notes, and unpublished Master's theses or doctoral dissertations.

Having the proper date of publication of a paper is very important, particularly in the field of taxonomy. Unfortunately, certain numbers of some journals, on occasion, appear in the year following the supposed time of their appearance. When I have been able to determine that this has happened, I show *two* dates for the papers of authors so "trapped": the true date, following the author's name, plus the journal's earlier (incorrect) cover-date in parentheses after the volume number (just before the pagination). The date of a work is also indirectly involved in two other ways. In order to save space and to make the reading easier, I have generally *not* – in the text – included the initials of authors who have the same surnames *unless* the dates of their works are identical. Similarly, for multiple authorships with the same first or senior author, "et al." is used in the text unless there would be confusion because of an identical year of appearance of the two (or more) papers implicated (in the latter case, names of the first *two* authors are cited).

The date of a taxonomic *name* is not to be confused with date(s) of citation of *paper(s)* by the author of that name. There has not been space enough to include all original papers (often only notes or even abstracts) in which new taxa (particularly ciliate genera, more than eleven hundred of which I consider bonafide) have first been described. For example, mention of a genus "*X--us* Smythe, 1973" does *not* mean that the publication so indicated appears in the bibliography. If it *is* to be included, then that *particular* "Smythe (1973)" or "(Smythe, 1973)" must also appear in the text elsewhere, separate from combination with the generic name.

For those readers interested in "statistics" – and to save anyone (including reviewers!) the time and labor of counting – there are, on the following pages, more than 1, 950 references (a number greater than the entire bibliography of the first edition and *ca.* 67% of the present one) which bear a date in the sixties or seventies. In fact, well over half of such recent works have appeared within the past six or seven years (i.e., since the turn of the present decade).

Special Note. I have appended a section of several pages of "Additional References" to accommodate some 230 entries not to be found in the main bibliography. They represent: (1) A number of recent works available too late for inclusion in the regular section, which was, curiously enough, set in "camera-ready" type for the printer earlier than the text proper of the book; appropriate insertion of such references has been made in preceding chapters. (2) Several older references added tardily for various reasons; these are also now cited on earlier pages. (3) Some 40 papers selected to serve only as sources for figures in plates of Chapter 20: authors of these works are mentioned solely in the figure explanations (and without dates). The reader is urged to check *both* sections of the bibliography when searching for a desired paper by a given worker.

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1831. Über die Entwicklung und Lebensdauer der Infusionsthiere; nebst ferneren Beiträgen zu einer Vergleichung ihrer organischen Systeme. Abh. Akad. Wiss. Berlin, year 1831, pp. 1–154. (See note following entry on Ehrenberg, 1830, above; similar situation, with "final" appearance again in 1832, but with initial availability in 1831 in this case.)

1833. Dritter Beiträgen zur Erkenntniss der grosser Organisation in der Richtung des kleinsten Raumes. Abh. Akad. Wiss. Berlin, year 1833, pp. 145–336. (See note following entry on Ehrenberg, 1830, above; similar situation, except "final" appearance in 1835, in this case, but with initial availability in 1833.)

1835. Zusätze zur Erkenntniss grossen organischer Ausbildung in den kleinsten thierischen Organismen. Abh. Akad. Wiss. Berlin, year 1835, pp. 151–180. (See note following entry on Ehrenberg, 1830, above; similar situation, except "final" appearance in 1837, in this case, but with initial availability in 1835.)

1838. *Die Infusionsthierchen als Vollkommene Organismen.* Leipzig. 612 pp.

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Systematic Index

Included on the following pages are 2,362 scientific names associated, at one time or another, with the uninomial ciliophoran taxa treated in the pages of this book. The great bulk of them occur in the formal classification section of Chapter 20, but many are to be found also throughout all chapters, in the glossary (Chapter 2), the tables, etc. Nearly half of the names are of "good" or valid genera (1,125); the rest are either acceptable (to the author) as names at the familial, ordinal, or class levels or are (junior) synonyms or homonyms at generic and suprageneric levels. The majority of all names indexed fall, alas, into the unacceptable categories: all the more important, perhaps, to have them in the book, so that their proper status may be recognized when they are seen elsewhere in the literature.

Deliberately not included in the index, with rare exception, are sub- and supergeneric, sub- and superfamilial, superordinal, and superclass names. The levels or categories indicated by such names – somewhat paralleling the situation with respect to the subspecies taxon, in my opinion – are considered as either generally unnecessary or premature at our present state of taxonomic sophistication in protozoology. In actual practice, few ciliatologists have proposed such taxa; thus their names are relatively few in number.

No other "subject index" is offered, since description, characterization, and classification of named taxa form the prime goal of this book. However, a further kind of such index is represented by the glossary of Chapter 2, in which some 700 ciliate descriptive terms and concepts are defined or characterized in alphabetical sequence. Additionally, I have appended a supplementary "Host Index" to the final pages of the present index proper. Employing common or vernacular names, I have included there more than 150 entries involving hosts or host-groups or taxa with which species of ciliates have been reported to have an "association" ranging from endoparasitism and various kinds of commensalism to ectosymbiosis *sensu lato*. It may be found surprising both that so many ciliates are not purely free-living and that such a diversity of hosts is involved. No other writer has attempted compilation of such important information.

No author index is given, since hundreds of persons' names – many repeatedly – are involved, often dozens to a single page, in a work of the present kind. The nearly 3,000 literature citations are, of course, arranged alphabetically (Chapter 22). A "name index" of sorts is offered for the 185 ciliatologists whose photographs appear in the plates of Chapter 21, by purposely grouping their "figure identifications" together on pages 352, 353.

As an aid to the user, various styles of print are used on subsequent pages to indicate "good" and "bad" names, taxonomic levels, sections of the book being referred to, location of figures, etc.

Bonafide (valid, acceptable, "good" – in my judgment) generic names appear in a "regular" style of print (i.e., Roman type, with upper and lower case lettering); *invalid* generic names (junior homonyms or synonyms or misspellings) are given in *italics*. Bonafide familial names are in "regular" boldface print, whereas *synonymous* familial names appear in ***boldface*** italics. Acceptable names of the suprafamilial taxa (subordinal, ordinal, subclass, class, phylum) are printed in "regular" CAPITAL letters, while *rejected* names at those higher levels are in *CAPITAL* italics.

With respect to page numbers, those in "regular" (Roman) print are perhaps the most important, since they indicate location(s) of the taxon in the detailed classification section of (but *not* elsewhere in) Chapter 20; such a group of page numbers is often the second in line, as will be apparent. Numbers in *italics* indicate location of the taxonomic name in all other parts of the book, including the several tables; they may occur on either side of the special Chapter 20 entries. [For specific location of the multi-page overall treatment of a given class, subclass, or order (Chapters 5–16), the reader should refer to the Table of Contents.]

Finally, the whereabouts of drawings or micrographs selected as "representative" of over 50% of the genera recognized as valid are indicated by supplying plate and figure numbers in **boldface** print. Such data are the final entries for those particular generic names.

HOST INDEX

This index is comprised of vernacular or common names (with rare exception) of organisms serving as living substrata – "hosts," in the broadest sense – for various groups of ciliates associated with them more or less intimately as endo- or ectosymbionts (including symphorionts). For the larger and more popular groups of hosts, such as crustaceans or mammals, subgroup names are also used, with cross-referencing (to avoid space-wasting repetition) as appropriate. Page numbers given here are deliberately restricted (with one exception: the suctorian hosts referred to on page 236 actually appear on page 107 of Chapter 9) to locations containing mention of host names in the classification section of Chapter 20 (in Part II). Many host groups are, naturally, also referred to in various other chapters of the book; but such information – often less complete, anyway, than that given for the same ciliate groups in Chapter 20 – is not covered in this brief index. Page locations are generally to ciliate family diagnoses; and should the host names appear more than once on a given page, such multiplicity of appearance is not indicated (again, to conserve space) below. Names of most of the larger, "inclusive" taxa of hosts are arbitrarily written in the plural; smaller host group-names, in the singular.

The coverage below – completely dependent as it is on the information supplied in the succinct diagnoses of Chapter 20 – is inevitably far from exhaustive. Numerous small marine invertebrate groups, especially, have often, regretfully, been implicated only by "etc." as additional hosts of various ciliate species. But, nevertheless, as well as serving as a specific guide of sorts, this index should give the reader a definitive awareness of two important facts, *viz.*, that a good many ciliates are *not* purely "free-living," as is often intimated in textbooks; and that the taxonomic diversity of the involved hosts is considerable. Nowhere else in the published literature is such information available in a single place – this has been the chief motivation for my compiling the list which follows.