HANDBOOK OF PROTOZOOLOGY

KUDO

HANDBOOK
OF
PROTOZOOLOGY

HANDBOOK
OF
PROTOZOOLOGY

BY

RICHARD ROKSABRO KUDO, D.Sc.

Assistant Professor of Zoology

University of Illinois

With one hundred and seventy-five illustrations

CHARLES C THOMAS · PUBLISHER

SPRINGFIELD, ILLINOIS BALTIMORE, MARYLAND

1931

THOMAS BOOKS
SYMBOL OF LEADERSHIP

"*The revelations of the microscope are perhaps not excelled in importance by those of the telescope. While exciting our curiosity, our wonder and admiration, they have proved of infinite service in advancing our knowledge of things around us.*" . . . . . LEIDY.

PREFACE

Study of Protozoa was formerly considered as belonging exclusively to the domain of graduate students in zoology, but as a result of the tremendous advance in our knowledge of protozoan parasites of man and domestic animals in the last fifteen years, a number of universities and colleges have begun to offer courses dealing with both free-living and parasitic Protozoa to advanced students. For some years the author has taught such a course at the University of Illinois. The classes are composed chiefly of advanced students who have had at least one year of zoology and are majoring in zoology, botany, bacteriology, entomology or premedical curriculum. Although some admirable works on protozoology have appeared in recent years, no one of them would afford adequate guidance throughout a course of this kind. Most modern publications on the subject emphasize the parasitic forms and do not give much space to the taxonomy, biology, and orientation of the free-living forms from which the parasitic group undoubtedly evolved.

The aim of the present work is, therefore, to provide a handbook of introductory information on the common and representative genera of all the groups of both free-living and parasitic Protozoa. The author claims little originality in the material employed, for it is mainly compiled from data already known.

The text is divided into two parts: The first part consists of three chapters giving a general account of the morphology, physiology and reproduction of Protozoa. The treatment here is brief, since there are several excellent treatises on this part of protozoology, such as Calkins' *The Biology of the Protozoa.* Furthermore, the student has neither time nor need for extended discussion at the beginning of the course. The second part, which is composed of thirty chapters, is concerned with the taxonomy, biology and development of common Protozoa. Differentiation of classes, orders and families is carried on by keys. In some genera which are of common occurrence, such as Amoeba, Entamoeba, Arcella, Euglena, Paramecium, Chilodon, Vorticella, etc., several species are mentioned.

For the convenience of those who wish to study more of the details and particular features of certain forms, there is appended to each chapter a list of important references which will serve as guides to a more comprehensive literature on the subject.

Since comprehensive monographs on different groups of Protozoa are widely scattered and often unavailable to the average worker, the author has attempted to gather here as much material from them as could be put together within limited space. This handbook is, therefore, believed to be suitable for practical use by biology teachers in colleges and universities, field workers in pure and applied biological sciences, veterinarians, physicians, public health workers, and others.

To facilitate the use of this handbook, a comparatively large number of illustrations are inserted; for students can comprehend the form, appearance and structure of a microscopic organism more thoroughly and satisfactorily by looking at its picture than by reading a lengthy description. All the illustrations have been especially prepared for this work. The majority have been redrawn from illustrations found in earlier works, and in all such cases the indebtedness of the author is indicated by references to the sources. The original illustrations are accompanied by scales of magnification only. In order to make the illustrations as useful as possible for practical purposes, the magnification in most cases is not more than five hundred times natural size, this being the maximum afforded by microscopes ordinarily used by students. Higher magnifications are used to show very small forms and to bring out some minute protoplasmic structures.

The author is indebted to numerous colleagues and investigators for their observations which have been included in the present work. Special thanks are due to Mr. H. C. Oesterling, Editor of the Illinois State Natural History Survey, for assistance in the revision of the manuscript and the correction of the proof sheets.

January, 1931. R. R. K.

CONTENTS

HANDBOOK
OF
PROTOZOOLOGY

CHAPTER I

INTRODUCTION

PROTOZOA are considered as single-celled organisms; that is to say, the body of a protozoan, no matter how small or large it may be, is morphologically a single cell. Yet Protozoa possess all the characteristics common to living things. The various functions which make up the phenomenon known as life are performed by differentiated parts within the body. These parts, being comparable to the organs of a metazoan which are composed of a large number of cells grouped into tissues, are called **organelles,** or cell-organs. Thus one sees the one-celled protozoan is a complete organism somewhat unlike the cells making up a metazoan, each of which is dependent on other cells and cannot live independently. From this viewpoint, certain students maintain that the Protozoa are noncellular, and not unicellular, organisms. Through the process of organic evolution, the Protozoa have undergone cytological differentiation and the Metazoa histological differentiation. It is beyond the scope of the present work to discuss these viewpoints in detail. It may, however, be added here that certain cells which compose the body of a metazoan, as for example the leucocyte, spermatozoon, etc., behave as if they were independent organisms.

In being unicellular, the Protozoa and the Protophyta are alike. The majority of the former are quite clearly distinguishable from the majority of the latter on the basis of nuclear condition, method of division, nutrition, etc. While the majority of the Protophyta appear to possess scattered nuclear material or none at all, the Protozoa contain at least one nucleus. It is generally considered that the binary fission of the Protozoa and the Protophyta is longitudinal and transverse, respectively. A great majority of Ciliata, however, multiply by transverse division. In general the nutrition of Protozoa is holozoic and of Protophyta holophytic. But there are large numbers of Protozoa which nourish themselves by holophytic and saprozoic methods. Thus no absolute and clean-cut separation is possible between them. Haeckel, therefore, proposed the term Protistan kingdom to include these organisms in a single group, but this is not generally adopted, since it includes undoubted animals and plants, thus creating an equal amount of confusion between it and the animal or plant kingdom. This intermingling of characteristics between the two groups of microorganisms shows clearly their close interrelationship and suggests strongly their common ancestry.

Although the majority of the Protozoa are solitary and the body is composed of a single cell, there are a few forms in which the body is made up of more than one cell. These forms, which are known as **colonial Protozoa,** are well represented by the members of Volvocidae, in which the individuals are either joined by cytoplasmic threads or embedded in a common matrix. The majority of these cells are alike both in structure and in function, although in several genera there may be differentiation of the individuals into reproductive and vegetative cells. Unlike the cells in a metazoan which form tissues, these vegetative cells of colonial Protozoa, however, are not dependent upon other cells; hence they do not form any tissue. The reproductive cells produce zygotes through fusion which subsequently undergo repeated division processes and may produce a stage comparable to the blastula stage of a metazoan, but never reaching the gastrula stage. Thus colonial Protozoa are only cell-aggregates without histological differentiation and may thus be distinguished from the Metazoa.

With regard to their habitat, the Protozoa may be divided into free-living forms and those living on or in other organisms. The vegetative, or trophic, stages of free-living Protozoa have been found in every type of fresh and salt water, in soil and in decaying vegetable matter. While the freshwater inhabiting forms are ordinarily unable to live in salt water, and *vice versa*, seemingly one and the same species has, in a number of cases, been found in both fresh and salt waters.

The factors which influence their presence in a given body of water are temperature, chemical composition, kind and amount of food, etc. Excessive cold seems to be less detrimental than excessive heat. In the polar regions or at extremely high altitudes, certain Protozoa occur at times in fairly large numbers. Although the majority are incapable of living in water containing large quantities of chemical substances, some forms such as the members of Epalcidae are said to live in water rich in sulphurous substances produced by decaying and decomposing organic matter. Acid or alkaline contents of the water influence also the distribution of Protozoa in various ways.

Numerous species of Protozoa are cosmopolitan in their occurrence, partly because of their early appearance as living organisms. *Amoeba proteus*, *Paramecium caudatum*, etc., have been observed in fresh waters nearly everywhere in the world. The wide distribution of Protozoa is in part to be attributed also to their ability to encyst. With a small number of exceptions, the vast majority of free-living protozoans become more or less rounded and inactive, and differentiate or secrete a resistant envelope around themselves to withstand temporary unfavorable conditions. The factors involved seem to be low or high temperature, lack of food material, evaporation and chemical changes of the water in which they live. In some cases, the organism encysts temporarily in order to undergo nuclear reorganization and multiplication. Because of this change and also of the failure of causing certain protozoans to encyst under experimental conditions, it is supposed that some internal factors may play as great a part as the environmental conditions in the phenomenon of encystment.

Ordinarily a single cyst wall seems to be sufficient to protect the protoplasm against unfavorable external conditions. In some cases, however, there may be a double cyst wall, the inner one usually being more delicate. The cyst wall, as a rule, is composed of homogeneous substance, but it may contain calcareous scales, as in Euglypha (Fig. 1). While chitin is the usual material of which the cyst wall is composed, cellulose makes up the cyst envelope of numerous Phytomastigina.

Some protozoans inhabit soil of various types and localities. Under ordinary circumstances, they occur near the surface, their maximum abundance being found at a depth of about 10 to 12 centimeters (Sandon). It is said that a very few occur in the subsoil. Here also one notices a very wide geographical distribution of apparently one and the same species. For example, Sandon found *Amoeba proteus* in samples of soil collected from Greenland, Tristan da Cunha, Gough Island, England, Mauritas, Africa, Argentina, and India. This amoeba is known to occur in various parts of Europe, North America, Japan, and Australia. Most of the Testacea live in moist soil in abundance. Sandon in his survey referred to above found *Trinema enchelys* (p. 242) in the soils of Spitzbergen, Greenland, England, Japan, Australia, St. Helena, Barbadoes, Mauritus, Africa, and Argentina.

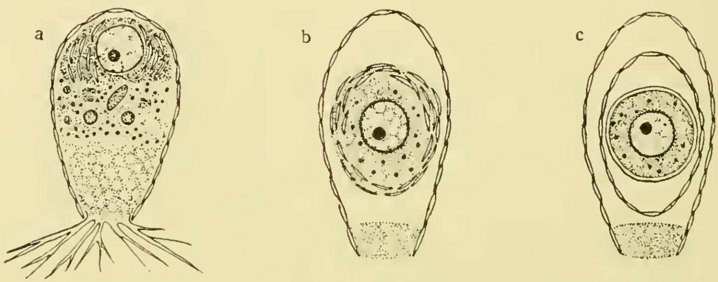


Fig. 1 Encystment of *Euglypha acanthophora.* ×320 (After Kühn).

Of the Protozoa living in close association with other animals, symbionts, commensals and parasites will here be considered. Certain Protozoa live within the bodies of other animals in a kind of association that is apparently of mutual benefit. They are called symbionts. The relation between termites and some Hypermastigida which inhabit the formers' intestine is a typical example of **symbiosis.** According to Cleveland, these flagellates digest the cellulose substances which are eaten by termites and transform them into glycogenous substances which are used as food by the insects. If deprived of these flagellates by being subjected to oxygen under pressure, the insects die, and if the wood diet of the termites is stopped, the flagellates die. In this connection, it may be mentioned that no one of the enormous number of species of the Hypermastigida has ever been found in encysted condition. It is presumed that the young termites become the hosts to the flagellates when they feed upon freshly voided fecal matter of the older ones already containing the flagellates.

Commensalism is an association in which one partner, the commensal, is benefited, while the other, the host, is neither injured nor benefited. A number of Protozoa live attached to other Protozoa or other animals. For example, numerous species of Suctoria are attached to the integument of active aquatic animals.

Parasitism is a somewhat different type of association. Here a protozoan lives at the expense of another organism. The former is the parasite and the latter the host. The injury to the host varies greatly according to circumstances. Parasitic Protozoa are found to occur in almost every phylum of the animal kingdom, including phylum Protozoa itself. A few forms are parasitic in plants. Some of the Suctoria are parasitic in various Ciliophora. Microsporidia parasitize Myxosporidia and Gregarinida, although they are ordinarily parasites of the Metazoa.

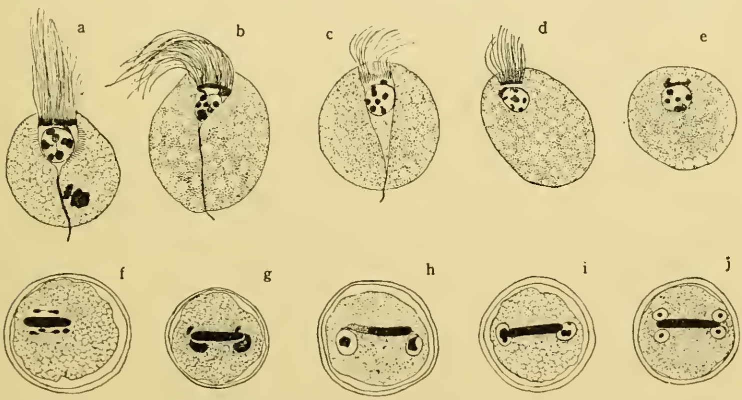


Fig. 2 Encystment of *Lophomonas blattarum* as seen in stained preparations. ×1150 (After Kudo).

A precise distinction between the commensal and the parasite is impossible, since in many cases there is no way to determine the exact effect of the presence of the organism concerned upon the host body. In its broad sense, the term **parasitic Protozoa** includes the commensals also. The Protozoa inhabiting the digestive tract of the host encyst under certain circumstances (Fig. 2). The cysts are voided in the fecal matter and become the source of new infection. In other gut-inhabiting parasites such as Gregarinida, Coccidia, etc., encystment is followed by the production of numerous spores which become the sources of infection when excreted. In the Protozoa which inhabit organs other than those of the digestive tract, the resistant spores may or may not be produced. *Plasmodium vivax*, one of the three species of malarial parasites of man, lives in the circulatory system and is transmitted from man to man by anopheline mosquitoes only. Therefore, it does not produce spores. Cnidosporidia, which are cell or tissue parasites, produce typical resistant spores, which become set free usually through wounds or disintegration of the host body after death and which serve for infection of new host animals.

The cysts of both free-living and parasitic Protozoa are carried from place to place by the wind, very often attached to soil particles, decayed leaves, twigs, etc., or by insects, birds, and other animals. When the cysts encounter a proper environment in the water or in a specific host animal, the contents germinate and the organisms once more assume their active and trophic phase.

Relationship of Protozoology to Other Biological Sciences

A brief consideration of the relationship of protozoology to other branches of biology and its possible applications may not be out of place here. Since the Protozoa are single-celled animals manifesting the characteristics common to all living things, they have been studied by numerous investigators with a view to discovering the nature and mechanism of various phenomena, the sum-total of which is known collectively as vitality. Though the investigators generally have been disappointed in the results, inasmuch as the assumed simplicity of unicellular organisms has proved to be offset by the complexity of their cell-structure, nevertheless any discussion of biological principles today must take into account the information obtained from studies of Protozoa. It is now commonly recognized that adequate information on various types of Protozoa is prerequisite to a thorough comprehension of biology and a proper application of biological principles.

Practically all students agree in holding that the higher types of animals have been derived from organisms which existed in the remote past and which probably were somewhat similar to the Protozoa of the present day. Since there is no sharp distinction between the Protozoa and the Protophyta or between the Protozoa and the Metazoa, and since there are intermediate forms between the major classes of the Protozoa themselves, progress in protozoology contributes toward the advancement of our knowledge of the steps by which living things in general evolved.

Geneticists have undertaken studies on heredity and variation among Protozoa. Dimensional variation is encountered commonly in various species, as has been shown by Jennings, Jollos, Dobell, Hegner, and others. Whether the variation is due to germinal or to environmental conditions cannot easily be determined. The interesting case of the double form of *Uroleptus mobilis* observed by Calkins apparently involved germinal changes, since this form divided true for 367 generations through a period of 405 days. On the other hand, the environmental changes or acquired characteristics are not inherited. Changes due to differences in temperature or composition of the medium last through numerous generations as long as the differences are maintained, but thereafter the original characteristics reappear.

Parasitic Protozoa almost always are limited to one or more specific hosts. By studies of the forms belonging to one and the same genus or species, the phylogenetic relation among the host animals may be established or verified. The mosquitoes belonging to the genera Culex and Anopheles, for instance, are known to transmit *Plasmodium praecox* and human species of Plasmodium, respectively. They are further infected by specific microsporidian parasites. For instance, *Thelohania legeri* has been found widely in the many species of anopheline mosquitoes only; *T. opacita* has, on the other hand, been found in culicine mosquitoes, although the larvae of species belonging to these two genera live frequently in the same body of water. By observing some intestinal Protozoa in certain monkeys, Hegner has recently obtained evidence of the probable phylogenetic relationship between them and other higher mammals.

Study of a particular group of parasitic Protozoa and their hosts may throw light on the geographic condition of the earth in the remote past. The members of the genus Zelleriella are invariably found in the frogs of the family Leptodactylidae. By an extensive study of these amphibians from South America and Australia, Metcalf has found that the species of Zelleriella occurring in the frogs of the two continents are almost identical. He finds it more difficult to conceive of convergent or parallel evolution of both the hosts and the parasites, than to assume that there once existed between Patagonia and Australia a land connection over which frogs containing Zelleriella migrated.

Experimental studies of large Protozoa have thrown light on the relation between the nucleus and the cytoplasm and have furnished a basis for an understanding of regeneration in animals. In Protozoa we find various gradations of nuclear division ranging from a simple amitotic division to a complex process comparable in every detail with the typical metazoan mitosis, so that a great part of our knowledge of cytology is based upon studies of protozoan cells.

Through the studies of various investigators in the past thirty years, it has now become known that numerous parasitic Protozoa occur in man. *Entamoeba histolytica*, *Balantidium coli*, and three species of Plasmodium, all of which are pathogenic to man, are widely distributed throughout the world. In certain restricted areas are found other pathogenic forms, such as Trypanosoma and Leishmania. Since all parasitic Protozoa presumably have originated in free-living forms and since our knowledge on the morphology, physiology and reproduction of the parasitic forms has largely been obtained by study of the free-living organisms, a general knowledge of the entire phylum is necessary to an understanding of the parasitic forms.

Recent studies have further revealed that almost all domestic animals are hosts to numerous parasitic Protozoa, many of which are responsible for serious infectious diseases. Many of the forms found in domestic animals are morphologically indistinguishable from those in man. *Balantidium coli* is now generally considered as a parasite of swine, and man is its secondary host. Knowledge of protozoan parasites is useful to medical practioners, just as it is essential to veterinarians inasmuch as certain diseases in animals, such as Texas fever, dourine, nagana, cocciodiosis, blackhead, etc., are caused by protozoans.

Sanitary betterment and improvement are fundamental requirements in the modern civilized world. One of man's necessities is safe drinking water. The majority of Protozoa live in water and many of them seem to be responsible, if present in sufficiently large numbers, for giving certain colors or odors to the waters of reservoirs or ponds. For example, according to Whipple, the chrysomonad Synura, which produces an oily substance as a result of metabolic activities, was found to be the cause of "cucumber" odor in several water supplies, and Calkins found that the oil droplets which were developed in a large number of individuals of *Uroglenopsis americana* became the cause of an offensive odor of the water in which they lived. Bursaria, Ceratium, Dinobryon, Mallomonas, etc., if present in large numbers, may give a "fishy" odor.

But these Protozoa which are occasionally harmful are comparatively small in number compared with those which are beneficial to man. It is generally understood that bacteria feed on various waste materials present in polluted water, but that upon reaching a certain concentration, they would cease multiplying and would allow the excess organic substances to undergo decomposition. Numerous holozoic Protozoa, however, feed upon the bacteria and prevent them from reaching the saturation population. Protozoa thus help indirectly in the purification of the water. Protozoology therefore must be considered as an important part of modern sanitary science.

Young fish feed extensively on small aquatic organisms such as larvae of insects, small crustaceans, annelids, etc., all of which depend largely upon Protozoa and Protophyta as sources of food supply. Thus the fish are indirectly dependent upon Protozoa as food material. On the other hand there are numbers of Protozoa which prey upon fish. The Myxosporidia are almost exclusively parasites of fish and often cause death to large numbers of commercially important fish. Success in fish-culture, therefore, requires among other things a good knowledge of Protozoa.

Since Russel and Hutchinson suggested some twenty years ago that Protozoa are probably a cause of limitation of the numbers, and therefore the activities, of bacteria in the soil and thus tend to decrease the amount of nitrogen which is given to the soil by the nitrifying bacteria, several investigators have brought out the fact that in the soils of temperate climates Protozoa are present and active throughout the year. The exact relation between specific protozoans and bacteria in the soil is a matter which still awaits future investigations, although numerous experiments and observations have already been made. All soil investigators should be acquainted with the biology and taxonomy of free-living Protozoa.

It is a matter of common knowledge that the silkworm and the honey bee suffer from protozoan infection known as microsporidiosis. Sericulture in southern Europe suffered great damages in the middle of the nineteenth century because of the "pébrine" disease caused by the microsporidian, *Nosema bombycis*. During the first decade of the present century, another microsporidian, *Nosema apis*, was found to destroy occasionally a large number of honey bees. Methods of control have been developed and put into practice so that these microsporidian infections are at present not serious, even though they still occur. On the other hand, other Microsporidia are now known to infect certain insects, such as mosquitoes and lepidopterous pests, which, when heavily infected, die sooner or later. Methods of artificial destruction of these insects by means of chemicals are more and more used, but attention should be given to ultilization of the parasitic Protozoa and Protophyta for this purpose.

While the majority of Protozoa lack permanent skeletal structures and their fossil forms are unknown, there are two large groups in the Sarcodina which possess conspicuous shells and which are found as fossils. They are Foraminifera and Radiolaria. From early Palaeozoic times down to the present day, the carbonate of lime which makes up the skeletons of Foraminifera has been left embedded in various rock-strata. Although there is no distinctive foraminiferan fauna characteristic of a given geologic period, there are certain peculiarities of fossil Foraminifera which distinguish one formation from the other. From this fact one can understand that knowledge of foraminiferous rocks is highly useful in checking up logs in well drilling. The skeletons of the Radiolaria are the main constituent of the ooze of littoral and deep-sea regions. They have been found abundantly in silicious rocks of the Palaeozoic and the Mesozoic, and are also identified with the clays and other formations of the Miocene. Thus knowledge of these two orders of Sarcodina, at least, is essential for the student of geology and paleontology.

The History of Protozoology

Aside from the few large forms, Protozoa are unobservable with the naked eye, so that we can easily understand why they were unknown prior to the invention of the microscope. Antony van Leeuwenhoek (1632–1723) is commonly recognized as the father of protozoology. Grinding the lenses himself, Leeuwenhoek made more than four hundred microscopes, including one which, it is said, had a magnification of 270 times. Among the many things he discovered were various Protozoa. Between 1673 and 1703 he apparently observed Vorticella, Carchesium, Stylonychia, Volvox, Opalina, Nyctotherus, Polystomella, etc. Thus he was the first to see some of the well-known Protozoa.

Leeuwenhoek was followed by Buonanni (1691), who observed Colpoda; by Harris (1696), who discovered Euglena; and by an anonymous author (1703), who described Euplotes, Vorticella, and Paramecium. In 1718 there appeared a treatise on microscopic organisms by Joblot, in which the author emphasized the non-existence of abiogenesis by using boiled hay-infusions in which no Infusoria developed without exposure to the atomosphere. This experiment confirmed that of Redi who, twenty years before, had made his well-known experiments by excluding flies from decomposing meat. Trembly (1745) studied division in some Ciliata, including probably Paramecium. Noctiluca was first described by Baker (1753).

Rösel (1755) observed an amoeba, possibly *Amoeba proteus* or an allied form, which he called "die kleine Proteus," and also Vorticella, Stentor, and Volvox. Ledermüller is said to have coined the term "Infusoria" in 1763 (Bütschli). By using the juice of geranium, Ellis (1770) caused the extrusion of the "fins" (trichocysts) in Paramecium. Eichhorn (1783) observed the heliozoan, Actinosphaerium, which now bears his name. O. F. Müller described Ceratium a little later and published two works on the Infusoria (1786). Although he included unavoidably some Metazoa and Protophyta in his monographs, some of his descriptions and figures of Ciliata were so well done that they are of value at the present time.

At the beginning of the nineteenth century the cyclosis in Paramecium was brought to light by Gruithuisen. Goldfuss (1817) coined the term "**Protozoa,**" including in it the coelenterates. Ten years later there appeared d'Orbigny's systematic study of the Foraminifera, which he considered as microscopical cephalopods. In 1828 Ehrenberg began publishing his observations on Protozoa and in 1838 he summarized his contributions in "Die Infusionsthierchen als vollkommene Organismen," in which he diagnosed genera and species so well that many of them still hold good. He excluded Rotatoria and Cercaria from Infusoria. Through the studies of Ehrenberg the number of known Protozoa increased greatly; he, however, proposed the term "Polygastricha," under which he placed Mastigophora, Rhizopoda, Ciliata, Suctoria, Desmids, etc., since he believed that the food vacuoles present in them were stomachs. This hypothesis became immediately the center of controversy, which incidentally, together with the then-propounded cell theory and improvements in microscopy, stimulated researches on Protozoa.

Dujardin (1835) took pains in studying the protoplasm of various Protozoa and found it alike in all. He named it "sarcode." In 1841 he published an extensive monograph of various Protozoa which came under his observations. The term "Rhizopoda" was coined by this investigator. The commonly used term "protoplasm" was coined by Purkinje in 1840.

The term Protozoa was given a distinct definition by Siebold in 1845 as follows: "Die Thiere, in welchen die verschiedenen Systeme der Organe nicht scharf ausgeschieden sind, und deren unregelmässige Form und einfache Organization sich auf eine Zelle reduzieren lassen." This definition is still followed today. Siebold subdivided Protozoa into Infusoria and Rhizopoda. The sharp differentiation of Protozoa as a group certainly inspired numerous microscopists. As a result, various students brought forward group names, such as Radiolaria (J. Müller, 1858), Ciliata (Perty, 1852), Flagellata (Cohn, 1853), Suctoria (Claparède and Lachmann, 1858, 1859), Heliozoa, Protista (Haeckel, 1862, 1866), Mastigophora (Diesing, 1865). Of Suctoria, Stein failed to see the real nature (1849), but his two monographs on Ciliata and Mastigophora (1854, 1859–1883) contain concise descriptions and excellent illustrations of numerous species, several of which are inserted in the present work. Indeed, we owe to him much of the classification of the Ciliata which is most commonly adopted at present.

Haeckel (1873), who went a step further than Siebold and distinguished between Protozoa and Metazoa, devoted ten years to his study of Radiolaria, especially those of the Challenger collection, and described in his celebrated monographs more than 4000 species.

In 1879 the first comprehensive monograph on the Protozoa of North America was put forward by Leidy under the title of "Freshwater Rhizopods of North America," which showed the wide distribution of many known forms of Europe and revealed a number of new and interesting forms. This work was followed by Stokes' "The Fresh-water Infusoria of the United States," which appeared in 1888. Bütschli (1880) established Sarcodina and made an excellent contribution to the taxonomy of the then-known species of Protozoa, which is still considered as one of the most important works on general protozoology. The painstaking researches by Maupas, on the conjugation of ciliates, corrected erroneous interpretation of the phenomenon observed by Balbiani some thirty years before and gave impetus to a renewed cytological study of Protozoa. The variety in form and structure of the protozoan nuclei became the subject of intensive studies by several cytologists. Weismann (1881) put into words the immortality of the Protozoa. Schaudinn contributed much toward the cytological and developmental studies of Protozoa.

In the first year of the present century, Calkins in the United States and Doflein in Germany wrote modern textbooks on protozoology dealing with the biology as well as the taxonomy. Calkins initiated the so-called isolation pedigree culture of ciliates in order to study the physiology of conjugation and other phenomena connected with the life history of the ciliates. The application of this method has been wide.

Today the Protozoa are more and more intensively studied from both the biological and the parasitological sides, and important contributions appear continuously. Since all parasitic Protozoa must have originated in free-living forms, the comprehension of the morphology, physiology and development of the latter group obviously is fundamentally important for a thorough understanding of the former group.

Compared with the advancement of our knowledge on free-living and large Protozoa, that on parasitic forms has been very slow. This is to be expected, of course, since the vast majority of them are so minute that the discovery of their presence has been made possible only through improvements in the microscope and in technique.

Here again Leeuwenhoek, in 1681, seems to have been the first to observe a parasitic protozoan, for he found *Giardia intestinalis* in his own diarrhoeic stools. There is no record of anyone having seen Protozoa living in other organisms until 1828, when Dufour's account of the gregarine from the intestine of coleopterous insects appeared. Some ten years later, Hake observed the oocyst of the coccidian, *Eimeria stiedae*, of rabbits, without realizing its real nature. A flagellate was observed in the blood of salmon by Valentin in 1841, and the frog trypanosome was discovered by Gluge and Gruby (1842), the latter author creating the genus Trypanosoma for it.

The gregarines were a little later given attention by Siebold (1839), Kölliker (1848) and Stein (1848). The year 1849 marks the first record of an amoeba being found in man, for Gros then observed *Entamoeba gingivalis* in the human mouth. Five years later, Davaine found in the stools of cholera patients two flagellates (Trichomonas and Chilomastix). Kloss in 1855 observed the coccidian, *Klossia helicina*, in the excretary organ of Helix. Eimer (1870) made an extensive study of Coccidia occurring in various animals. *Balantidium coli* was discovered by Malmsten in 1856. Lewis in 1870 observed *Entamoeba coli* in India and Lösch in 1875 found *Entamoeba histolytica* in Russia. At the beginning of the nineteenth century, an epidemic disease, pébrine, of the silkworm appeared in Italy and France, and a number of biologists became engaged in its investigation. Foremost of all, Pasteur (1870) made an extensive report on the nature of the causative organism, now known as *Nosema bombycis*, and also on the method of control and prevention. Perhaps this is the first scientific study of a parasitic protozoan to result in an effective practical method of control of its infection.

Lewis in 1878 saw an organism which is known since as *Trypanosoma lewisi* in the blood of rats. In 1879 Leuckart created the term "Sporozoa," including in it the gregarines and coccidia. Other groups of Sporozoa were soon definitely designated. They are Myxosporidia (Bütschli, 1881), Microsporidia (Balbiani, 1882) and Sarcosporidia (Balbiani, 1882).

Parasitic protozoology received a far-reaching stimulus when Lavern (1880) discovered the malarial parasite in the human blood. Smith and Kilborne (1893) demonstrated that the Babesia of the Texas fever of cattle in the southern United States was transmitted by cattle ticks from host to host and thus brought to light for the first time the close relationship between an insect and a parasitic protozoan. Two years later, Bruce discovered *Trypanosoma brucei* in the blood of horses and cattle suffering from "nagana" disease in Africa, and in the following year he showed by experiments that the tsetse fly transmits the trypanosome from host to host. Studies of malarial diseases continued and several important contributions appeared. Golgi (1886, 1889) studied the schizogony and its relation to the occurrence of fever and was able to distinguish two types of fever. MacCallum (1897–1898) found in the United States the union of a microgamete and a macrogamete of Haemoproteus of birds. Almost at the same time, Schaudinn and Siedlecki (1897) showed that anisogamy results in the production of zygotes in Coccidia. The latter author then (1898, 1899) published correct observations upon the life-cycle of Coccidia. Ross (1898) showed how *Plasmodium praecox* was carried by *Culex fatigans* and described its life-cycle. Since that time several investigators have brought to light important observations concerning the biology and development of these organisms and their relation to man. In the present century, Forde and Dutton (1901) observed that the sleeping sickness in Africa is also due to an infection by *Trypanosoma gambiense.* In 1903 Leishman and Donovan recognized Leishmania of "kala-azar."

Artificial cultivation of bacteria had contributed toward a very rapid advancement in bacteriology, and it was natural, as the number of known parasitic Protozoa rapidly increased, that attempts to cultivate them *in vitro* should be made. Musgrave and Clegg (1904) cultivated, on bouillon-agar, small free-living amoebae from old fecal matter. In 1905 Novy and McNeal cultivated successfully the trypanosome of birds in blood-agar medium, which remained free from bacterial contamination and in which the organisms underwent multiplication. Almost all species of Trypanosoma and Leishmania have since been cultivated in a similar manner. This serves for detection of a mild infection and also identification of the species involved. It was found, further, that the changes which these organisms underwent in the culture media were imitative of those that took place in the invertebrate host, thus contributing toward the life-cycle studies of them.

Bass (1911) and Bass and Johns (1912) demonstrated that Plasmodium of man could be cultivated *in vitro* for a few generations. During and since the world war, it became known that numerous intestinal Protozoa of man are widely present throughout the tropical, subtropical and temperate zones. Taxonomic and developmental studies on these forms have, therefore, appeared in an enormous number. Cutler (1918) seems to have succeeded in cultivating *Entamoeba histolytica*, though his experiment was not repeated by others. Barret and Yarborough (1921) cultivated *Balantidium coli* and Boeck (1921) also cultivated *Chilomastix mesnili*. Boeck and Drbohlav (1925) succeeded in cultivating *Entamoeba histolytica*, and their work was repeated and improved upon by several investigators. While the cultivation has not yet thrown any new light on the life-history of the amoeba, it seems to have some value for diagnosing an infection. Since that time, almost all intestinal Protozoa of both vertebrates and invertebrates have been cultivated *in vitro*.

References

Bütschli, O. 1887–1889 Protozoa. Bronn's Klassen und Ordnungen des Thier-reichs. Vol. 1, Part 3.

Calkins, G. N. 1926 The biology of the Protozoa. Philadelphia.

Cole, F. J. 1926 The history of protozoology. London.

Dobell, C. 1911 The principles of protistology. Archiv für Protistenkunde, Vol. 23.

———. 1920 The discovery of the intestinal Protozoa of man. Proc. Roy. Soc. Med., Vol. 13.

Doflein, F. and E. Reichenow. 1929 Lehrbuch der Protozoenkunde. Jena.

Nordenskiöld, E. 1928 The history of biology. New York.

Sandon, H. 1927 The composition and distribution of the protozoan fauna of the soil. Edinburgh.

Whipple, G. C. (revised by G. M. Fair and M. C. Whipple) 1927 The microscopy of drinking water. Fourth ed. New York.

CHAPTER II

MORPHOLOGY AND PHYSIOLOGY OF PROTOZOA

PROTOZOA range in size from less than 5 microns to more than 1 cm. in diameter. On the whole, however, they are microscopic. The parasitic forms, especially the cytozoic parasites, are generally small, while the free-living forms are of much larger dimensions. Leishmania (Fig. 52) and Plasmodium (Fig. 121) may be taken as examples of minute Protozoa. There are numerous species of free-living ciliates which can be seen with the unaided eye, and these are among the largest Protozoa.

The fundamental components of the protozoan body are the nucleus and the cytoplasm. Not a single protozoan is known which does not possess at least one nucleus. Experimental evidence indicates clearly that when a protozoan is deprived of its nucleus it degenerates sooner or later. On the other hand, if the loss is in the cytoplasmic portion, the organism is capable of regenerating its lost part. Thus the nucleus controls both anabolic and catabolic activities of the organism. Furthermore, the nucleus contains chromatin substance in which are lodged "genes," or factors, characteristic of each species.

The Nucleus

The nucleus is of various form, size, and structure. At one extreme there is a small compact nucleus and at the other a large moniliform or elongated one. In between is found every conceivable variety of form. The majority of Protozoa contain a single nucleus. During the process of division, however, there may be two or more nuclei. There are, moreover, forms which regularly contain two or more nuclei throughout the greater part of their life-cycle. In several widely scattered species, each individual possesses two similar nuclei, for example, in *Pelomyxa binucleata*, *Arcella vulgaris* (Fig. 4), *Giardia intestinalis* (Fig. 62), *Dientamoeba fragilis* (Fig. 87), etc. In several groups of the Ciliata, two different nuclei, a macronucleus and a micronucleus, are normally present. The **macronucleus** is much the larger and controls the metabolic or trophic activities of the organism, while the **micronucleus** is very minute and is concerned with the reproductive activity. Some species have two or more nuclei of each kind, but the majority possess only one of each kind. In Mycetozoa (Fig. 69), some other Sarcodina such as Actinosphaerium (Fig. 98), *Pelomyxa palustris*, Protociliata, and numerous Sporozoa, there occur many nuclei of similar structure. These multinucleate forms result either from repeated divisions of a single nucleus or from fusion of numerous uninucleate individuals.

Although protozoan nuclei manifest various structures they may be put under two types: compact, or massive, and vesicular (Fig. 3). The **compact** nucleus, which is most frequently found in ciliates, is filled more or less compactly with minute

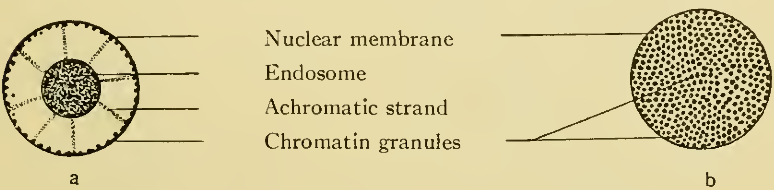


Fig. 3 a. Vesicular nucleus. b. Compact nucleus.

chromatin granules. The macronucleus of *Paramecium caudatum* represents this type (Fig. 16). The **vesicular** nucleus consists of a nuclear membrane, achromatic strands or network, chromatin granules and nuclear sap. Besides there is an intranuclear body, which is usually spherical in form, and which appears to be of different make-up, as judged by its staining reaction, among different nuclei. In some it seems to be composed almost exclusively of chromatin, while in others it shows varying proportions of chromatin and plastin materials. This chromatic body is often called the karyosome, but the use of this term has been attended with much confusion. The term **endosome** is, therefore, employed in the present work, in agreement with Minchin and Calkins, to designate one or more conspicuous intranuclear bodies.

While chromatin granules are usually confined to the intranuclear space, they are in some cases scattered throughout the cytoplasm either temporarily or permanently. These extranuclear chromatin granules are known as **chromidia**. In Testacea, such as Arcella (Fig. 4) and Euglypha (Fig. 1), there are chromidia surrounding the nuclei. They have been found by some investigators to give rise to secondary nuclei through reorganization, the original nuclei degenerating in the meantime. According to Calkins, in *Dileptus anser* (Fig. 4) there occur a large number of small spheroidal chromidia, each of which is composed of a plastin core and a chromatin cortex.

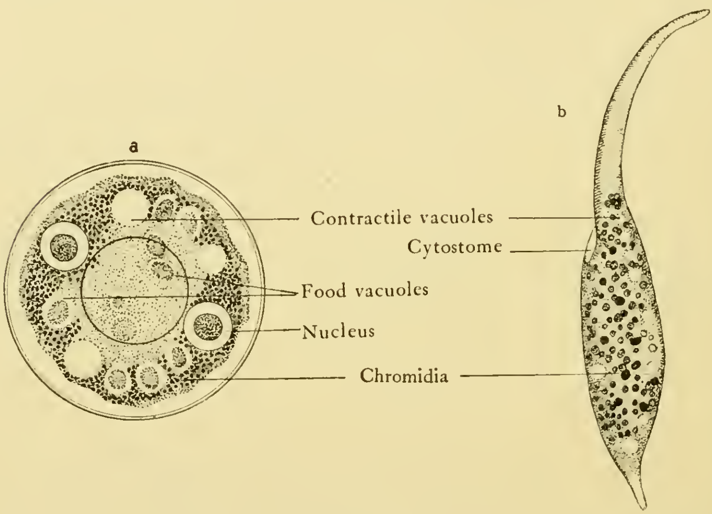


Fig. 4 a. A stained *Arcella vulgaris* showing the two nuclei and chromidia. ×350.
b. A stained *Dileptus anser* with scattered nuclei or chromidia. × about 100 (After Calkins).

In Mastigophora or in other groups in which flagellate stages occur, the body possesses a structure which is directly or indirectly connected with the basal portion of the flagellum (Fig. 5). This body has sometimes been called the kinetonucleus, but there is no evidence to indicate that it is a nuclear structure, although in some forms it is connected with the nucleus by a filamentous structure known as the **rhizoplast**. The term **blepharoplast**, or kinetoplast, is to be used to designate such a structure. Closely related to this is the **parabasal body,** or apparatus, found in certain Mastigophora, such as Polymastigida and Hypermastigida. It occurs in a close association with the nucleus. Its function is not well understood, but in some forms it appears to be a cell-organ of protection for the nucleus, while in others it may be a storing organelle of material used by the kinetic cell-organs.

The Cytoplasm

The bulk of the body of a protozoan is made up of the cytoplasm, which is almost always colorless. Certain Protozoa encased in a test, or lorica, may show coloration due to the color

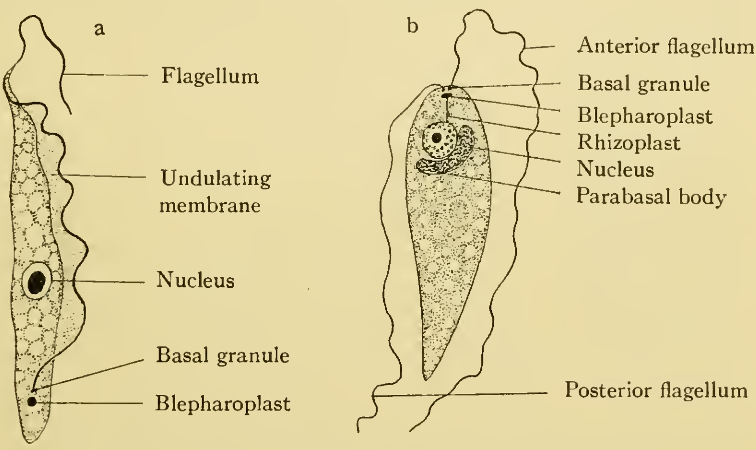


Fig. 5 Diagrams of two flagellates showing their structures.
a. *Trypanosoma brucei*
b. *Prowazekella lacertae* (After Kühn).

of the latter. Chromatophore-bearing forms, of course, appear colored, but the cytoplasm itself is usually colorless. There are, however, a few exceptions. One of them is the heterotrichous ciliate, *Blepharisma lateritia* (Fig. 160), which is frequently colored pink. Arcichovskij found a special pigment in this protozoan and called it **zoopurpurin.**

The extent and nature of the cytoplasmic differentiation differs greatly among various groups. In a number of forms the cytoplasm is differentiated into two parts: ectoplasm and endoplasm. The **ectoplasm** appears on the periphery as a hyaline and homogeneous zone. The **endoplasm** is greater in volume and more fluid and may be granulated or alveolated. These two parts, however, are not distinctly separated parts of the cytoplasm. They are freely interchangeable with each other. A protozoan may show a conspicuous ectoplasmic zone at one time, and may not show it at all at other times. This is true as a rule in Sarcodina. In pellicle-possessing Protozoa, as in the Ciliata, the ectoplasm and the endoplasm appear to be permanently differentiated during the trophic life of the individual.

The majority of Protozoa possess a definite membrane which surrounds the body. This is commonly called the **pellicle,** or periplast, and fits the body surface more or less closely. The

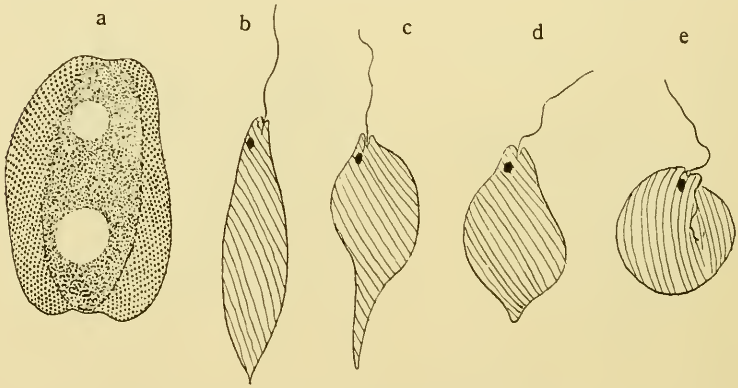


Fig. 6 a. *Paramecium caudatum* treated with alcohol, showing somewhat distended pellicle with its pores for cilia. × about 150.
b–e. Changes in body-form of *Euglena viridis*. × about 350.

presence of a pellicle is easily demonstrated by treating a ciliate with a dehydrating reagent. The protoplasm shrinks and pulls away from the pellicle, and the latter becomes somewhat distended by the accumulation of a watery fluid and to a certain extent by the pressure of the cover glass (Fig. 6). In life the pellicle is elastic and expansible to a considerable extent, as will be noted by examining *Euglena viridis* (Fig. 6). In some forms, the pellicle is marked by striation as in Phacus (Fig. 40), by ridges, by furrows, or by nodules arranged in definite rows, as in *Euglena spirogyra* (Fig. 40). In others, again, the pellicle may be composed of characteristic plates, as in Coleps (Fig. 148). The pellicle, in many cases, may thicken locally and produce spinous projections or hooks which serve as protective or attaching cell-organs. Gelatinous substances are sometimes secreted by Protozoa for protection of the body.

Some Protozoa secrete a test, or lorica, which encases the protoplasmic body. The **test** may be composed of chitin, pseudochitin, silicious or calcareous substances. An example of this is the homogeneous chitinous shell of Arcella (Fig. 4). In others the test is made up of scales produced in the cytoplasm and cemented together around the body; and again the shell is formed by cementing together foreign materials such as sand grains, sponge skeletons, diatom shells and others. Various Foraminifera seem to possess a remarkable selective power in the use of foreign materials for the construction of their tests. According to Cushman, *Psammosphaera fusca* uses sand grains of uniform color but of different sizes, while *P. parva* uses grains of more or less uniform size but adds, as a rule, a single large acerose sponge spicule, which is built into the test and which extends out both ways considerably. Cushman thinks that this is not accidental, since the specimens without the spicules are few and those with a short or broken spicule are not found. *P. bowmanni*, on the other hand, uses only mica flakes which are found in a comparatively small amount, and *P. rustica* uses acerose sponge spicules for the framework of the test, skilfully fitting smaller broken pieces into polygonal areas.

Closely associated with the body surface are the cell-organs of locomotion, the pseudopodia, flagella and cilia. **Pseudopodia** are usually temporary or semi-permanent cytoplasmic projections which serve for locomotion and food-capturing. According to their form and structure, four types are distinguishable:

Lobopodia. These are temporary cytoplasmic projections ordinarily composed of both ectoplasm and endoplasm, as in *Amoeba proteus* (Fig. 80). They are more or less broad with rounded ends.

Filopodia. These are also temporary cytoplasmic projections, but are usually made up of the hyaline ectoplasm only. They are more or less rod-like or filamentous, as in several Testacea (Fig. 93).

Rhizopodia. These are branching (reticulopodia) or anastomosing (myxopodia) temporary cytoplasmic projections. They are commonly found in Foraminifera (Fig. 76) and Testacea (Fig. 94).

Axopodia. These are more or less straight, filamentous, and usually radiating, semi-permanent pseudopodia widely present in Heliozoa (Fig. 98) and Radiolaria (Fig. 104). They possess an axial filament which is surrounded by a thin layer of cytoplasm. The latter undergoes a constant movement. The axial filament may originate in the "central granule," a special basal body, or in the general cytoplasm.

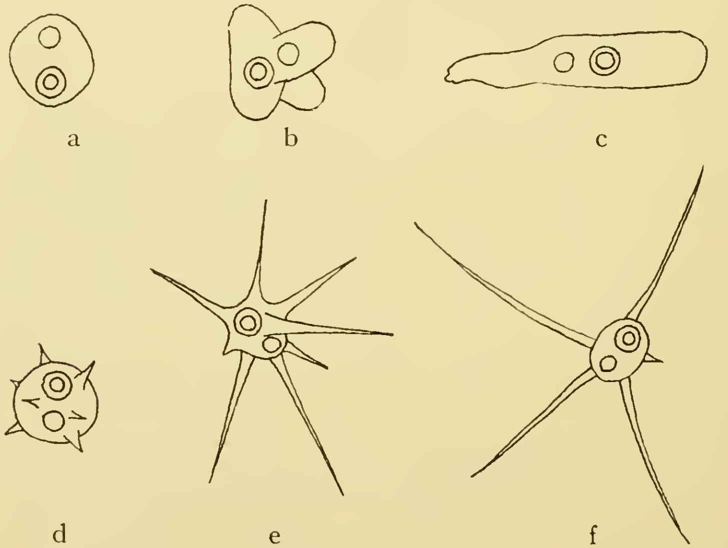


Fig. 7 *Vahlkampfia limax*, showing different pseudopodia. (After Verworn). a, b, contracted forms; c, individual showing typical appearance; d–f, "radiosa" forms, after addition of potassium hydrate solution to the water.

While the pseudopodia formed in an individual are usually of characteristic form and appearance, they may show an entirely different appearance under certain circumstances. According to the often-quoted experiment of Verworn, "limax" amoebae change into "radiosa" amoebae upon addition of potassium hydrate to the water (Fig. 7). In some cases during and after certain internal changes an amoeba may show conspicuous differences in pseudopodia (Neresheimer). Pseudopodia occur widely in forms which are placed under classes other than Sarcodina during a part of their life-cycle. Care, therefore, should be exercised in using them in taxonomic consideration of the Protozoa.

Flagella are filamentous extensions of the cytoplasm. Ordinarily they are extremely fine and highly vibratile, so that it is difficult to see them in life under the microscope with a moderate magnification. In a comparatively small number of species the flagellum can be seen distinctly in life as a long filament, as for example in Peranema (Fig. 42). As a rule, the number of flagella present in a single individual is small, varying from one to

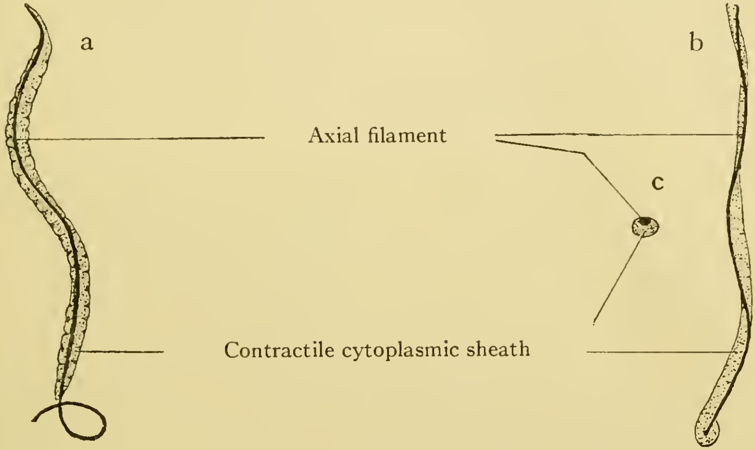


Fig. 8 Diagrams of flagella. a, flagellum of Euglena (After Bütschli); b, optical longitudinal; and c, transverse section of flagellum of Trachelomonas (After Plenge).

eight. In Hypermastigida there are numerous flagella (Fig. 12). Instead of being composed of a homogeneous substance, a flagellum appears to be made up of at least two parts (Fig. 8). An axial filament which is highly elastic, takes its origin directly, or indirectly through the basal granule, in the blepharoplast. Surrounding this filament there is a sheath of contractile cytoplasm which varies in thickness alternately on either side. The flagellum ordinarily tapers toward the free end.

The flagellum is usually inserted near the anterior end and directed forward. Its movement will pull the organism toward the front. Combined with this there may be a trailing flagellum which, as the name implies, is directed posteriorly. It serves to steer the course of movement or it may push the body forward to a certain extent. In a small number of flagellates, the flagellum is inserted near the posterior end of the body. In such cases its movement will push the body forward. The pulling and pushing flagella were called tractella and pulsella, respectively, by Lankester.

In some parasitic Mastigophora such as Trypanosoma (Fig. 5), Prowazekella (Fig. 5), Trichomonas (Fig. 61), etc., there is a very delicate membrane along one side of the body and a flagellum makes its outer margin. When this membrane vibrates, it presents a characteristic undulating movement, as will easily be seen in *Trypanosoma rotatorium*. This structure is called the **undulating membrane.**

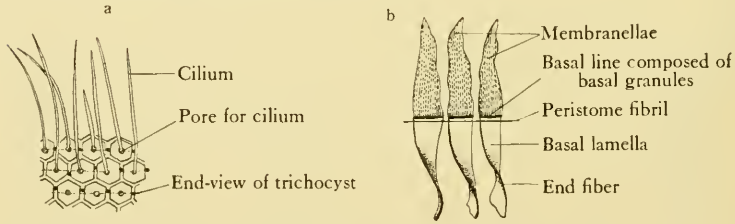


Fig. 9 a. Part of the pellicle of *Paramecium caudatum*, showing the arrangement of cilia. ×1100 (After Schuberg)
b. Portion of the adoral zone of *Stentor coeruleus* showing three membranellae. (After Dierks).

Cilia are the cell-organs of locomotion found chiefly in the Ciliophora. They are fine and short cytoplasmic projections and originate in the ectoplasmic portion of the body (Fig. 13). Ordinarily they are very numerous in holotrichous ciliates and uniform in length, as in Opalina, or they may be longer at the extremities, in the peristome or around the cytostome. They undergo alternate movements of contraction and relaxation. Some investigators believe that there is a layer of contractile element at one side of the axial filament which arises from a minute granule embedded in the ectoplasm, and that its contraction results in bending of the cilium and its relaxation in straightening of it. The cilia are generally arranged in longitudinal, oblique or spiral rows. In young Suctoria, the ciliary rows are transverse (Fig. 173, *c*, *d*). Although cilia are primarily the cell-organs of locomotion, they serve directly or indirectly for food-capture also.

In some ciliates, there are much stouter and considerably longer cytoplasmic projections, known as cirri (Fig. 10). They may occur with the cilia or completely replace them. A **cirrus** is composed of a number of cilia whose roots produce a basal plate, and from this thick base it tapers gradually to a point. In some cases, the end of a cirrus may show two or more branches (Fig. 167). The cirri usually are confined to the ventral surface of the organism and are called frontal, marginal, ventral, anal, and caudal cirri according to their location (Fig. 10). Unlike cilia, cirri may move in any direction, so that organisms possessing them show various ways of locomotion.

In all ciliates except the Holotrichida, there occurs an **adoral zone** on the left margin of the peristome, which consists of a number of triangular or plate-like membranellae (Fig. 9). Each **membranella** is composed of numerous cilia which are completely fused into one mass. The adoral zone seems to serve primarily for bringing food particles to the cytostome. Still more common is the **undulating membrane** which is composed of one or more rows of longitudinally placed cilia (Fig. 10). It is, therefore, different in structure from the so-called undulating membrane found in some Mastigophora mentioned above. The undulating membrane in the cytopharynx of Paramecium and that in the peristome of Pleuronema (Fig. 158) are typical examples.

In Suctoria, except one genus, cilia are present only during developmental stages, and as the organisms become mature, **tentacles** are formed. The latter are either suctorial or prehensile in function and are often very long. Each contains a highly contractile axial filament. In a few instances the tentacle is tubular, and this type is interpreted by Collin as possibly derived from a cytostome and cytopharynx of the ciliate (Fig. 11).

Although the vast majority of Protozoa, possess only one of the three cell-organs of locomotion mentioned above, a proto-

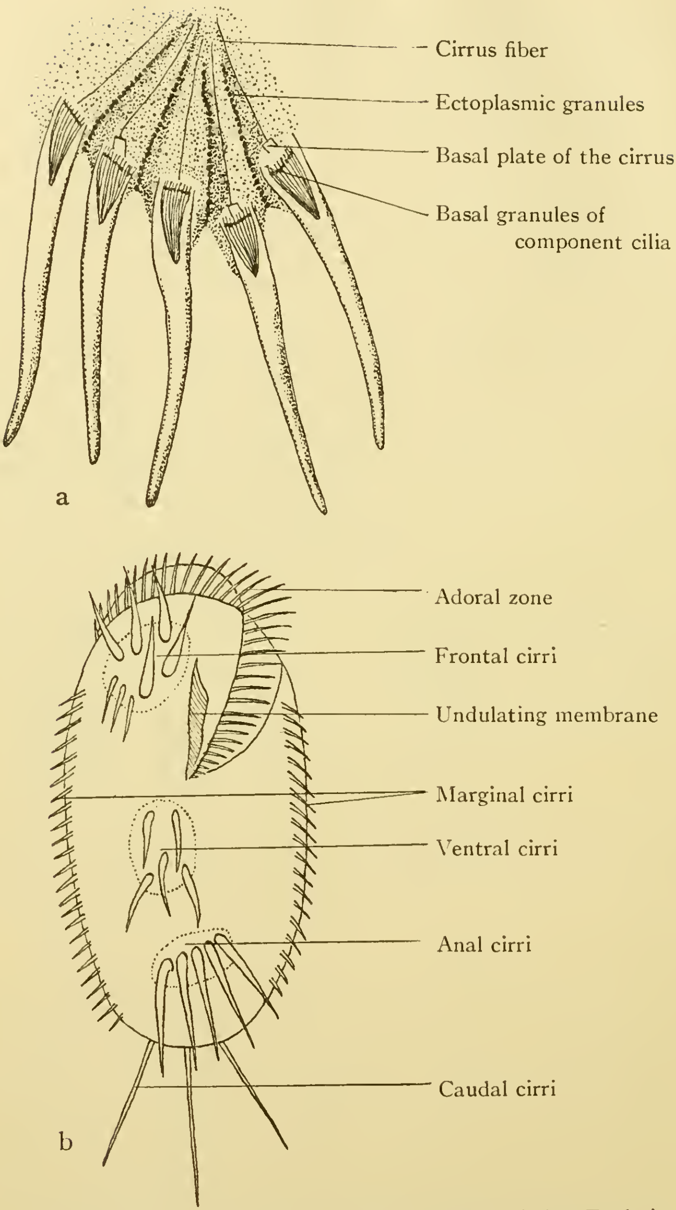


Fig. 10 a. Five anal cirri of *Euplotes patella*. (After Taylor).
b. Schematic ventral view of Stylonychia to show the distribution of cirri.

zoan may possess pseudopodia at one phase and flagella at another phase during its life-cycle. Among numerous examples, Naegleria (Fig. 79) and Trimastigamoeba (Fig. 79) may be mentioned. Furthermore, pseudopodia and flagella may occur at the same time, as in Dimorpha (Fig. 44), Actinomonas and Ciliophrys (Fig. 44). In other cases such as Monomastix (Fig. 147), a flagellum and cilia are present at the same time.

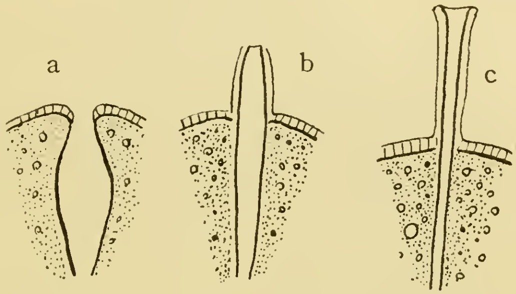


Fig. 11 Diagrams showing possible development of a suctorian tentacle from a cytostome and cytopharynx of a ciliate. (After Collin).

Various types of cell-organs are present in the cytoplasm. In Mastigophora, Ciliata and the majority of Sporozoa which possess a definite body form due to the presence of a pellicle, there occur in the cytoplasm highly contractile filaments known as **myonemes.** In large forms they are noted in life, while in smaller forms staining is required to show their presence. In the hypermastigid Trichonympha, Kofoid and Swezy observed longitudinal and transverse myonemes (Fig. 12). In the Ciliata they are usually arranged parallel to the rows of cilia. In Stentor, which is highly contractile, Schröder found that the myonemes are lodged in canals located just below the alveolar layer. Each myoneme is band-form and is said to be composed of alternating light and dark parts. In some Sporozoa such as the gregarines, the myonemes take chiefly a transverse course, and in the parasitic Mastigophora such as Trypanosoma, they are usually parallel to the undulating membrane.

In numerous ciliates, there occur characteristic structures

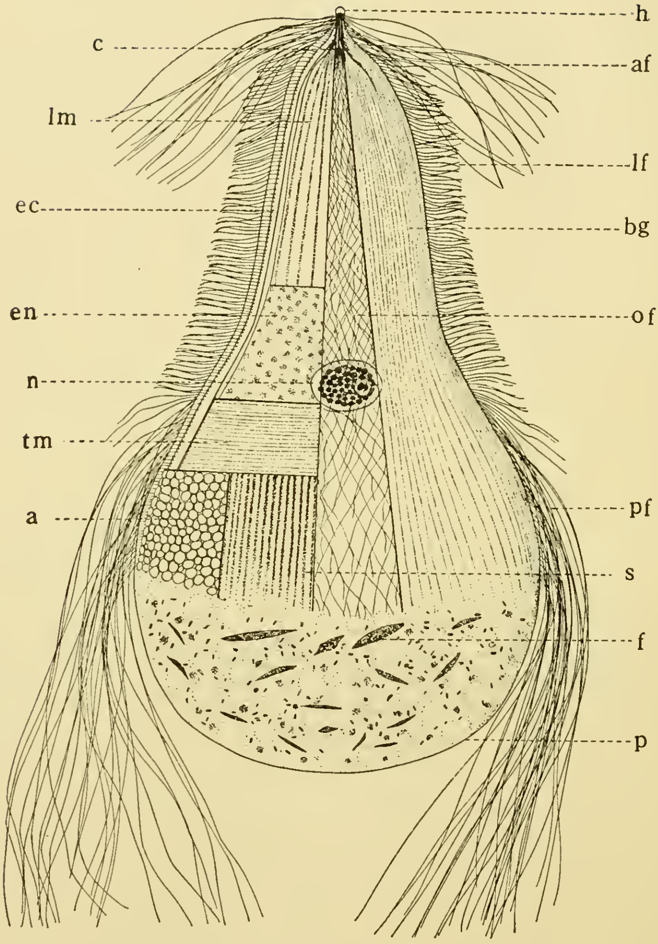


Fig. 12 Schematic drawing of *Trichonympha campanula.* ×450 (After Kofoid and Swezy).

a, alveolar layer; af, anterior zone of flagella; bg, basal granules; c, centroblepharoplast; ec, ectoplasm; en, endoplasm; f, food particles; h, head-organ; lf, lateral flagella; lm, longitudinal myonemes; n, nucleus; of, oblique fibers; p, pellicle; pf, posterior flagella; s, surface ridges; tm, transverse myonemes.

known as the **trichocysts** (Fig. 13), which are apparently defensive cell-organs. As seen in a living Paramecium, the refractile trichocysts are embedded in the ectoplasm and arranged at right angles to the body surface. Each trichocyst is a spindle-shaped body with a round end which is prolonged into a fine projection facing the body surface. Trichocysts take a nuclear stain intensely. Brodsky (1924) believes that they are made up of colloidal excretory substances and are first formed around the

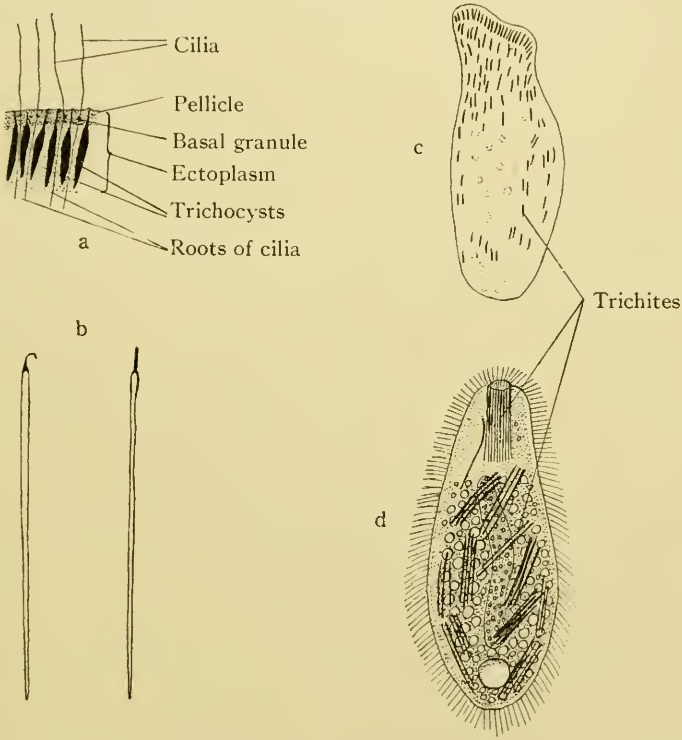


Fig. 13 a. Portion of section of *Paramecium caudatum* showing ectoplasmic structure. ×1530.
b. Two completely extruded trichocysts of *Paramecium caudatum.* ×1530.
c. *Spathidium spatula* as seen in stained section, showing trichites. ×200 (After Woodruff and Spencer).
d. *Enchelyodon farctus* from life. × about 180 (After Blochmann from Doflein).

macronucleus, becoming fully formed during the course of their migration toward the periphery of the body. The extrusion of trichocysts is easily induced by means of mechanical pressure or chemical stimulation, though the mechanism of the extrusion is not well understood. Brodsky maintains that the fundamental force is not the mechanical pressure, but that the expansion of the colloidal substances results under certain stimuli in the extrusion of the trichocysts through the pellicle. The fully extruded trichocyst is an elongated structure with a drawn-out free end and with a small cap-like structure and a fine filament at its base. The fully extruded trichocysts of *Paramecium caudatum* are as much as 40 microns in length.

In certain ciliates there occur rod-like **trichites** which ordinarily surround the cytopharynx (Fig. 13). Reserve trichites are scattered throughout the endoplasm. They apparently serve to strengthen the cytostome and cytopharynx and to capture and hold actively motile Protozoa on which the organisms live. In the spores of Cnidosporidia there is a characteristic filamentous structure known as the **polar filament,** which is spirally coiled in an envelope, the **polar capsule** (Fig. 133). Under a suitable stimulation, the filament extrudes and serves probably for temporary anchoring of the spore to the gut-epithelium of the host. A similar structure is also found in some Dinoflagellida.

In the pellicle-bearing Protozoa there is always a definite **cytostome** which varies considerably in size, form and location in different forms. In those that feed continuously, such as Paramecium, the cytostome is permanently open, and in others, it is closed except at the time of food-taking. These forms also have a **cytopyge,** or cell-anus, through which undigested solid particles or waste bodies are extruded to the exterior. It is usually closed and difficult of observation except during the actual defecation (Fig. 14).

The cytostome leads into a tubular widening of the endoplasm, known as the **cytopharynx,** or gullet. The cytopharynx may possess an undulating membrane or cilia. It may be surrounded by trichites as has been stated. At the end of the cytopharynx the food vacuole is first formed.

The mode of nutrition is considered as an important means in distinguishing between animals and plants. The Protozoa nourish themselves by various methods as follows:

1. **Holozoic** (zootrophic, heterotrophic) nutrition. This is the animal-like nutrition. The organism obtains nourishment by taking in other animals or plants and digesting them as does a typical metazoan.

2. **Holophytic** (autotrophic, phytotrophic) nutrition. The Protozoa possessing chlorophyll or allied substances are capable of obtaining necessary nourishment by using water, carbon dioxide and other inorganic substances. This nutrition is truly plant-like and is common among the Phytomastigina. In a

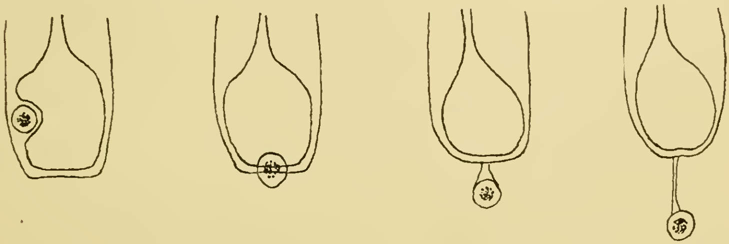


Fig. 14 Outline sketches showing the defecation process in *Spirostomum ambiguum*. (After Blättner).

number of cases, the organism itself is without chromatophores, but is apparently not holozoic because of the presence of chlorophyll-bearing foreign organisms. For example, in Paulinella (Fig. 96) in which occur no food particles, chromatophores of peculiar shape are always present. They appear to be a species of Alga which holds a symbiotic relationship with this testacean. Perhaps they act as the true chromatophores of Euglenidae.

3. **Saprozoic** (saprophytic) nutrition. Certain Protozoa are able to derive materials necessary for building up their body from dissolved organic substances in water. The actual acquisition is done by osmosis through the body surface.

4. **Parasitic** nutrition. Many Protozoa living in other animals absorb by osmosis the body fluid, digested food material or cell-substances of the host. This is somewhat similar to the saprozoic nutrition, but substances used here are those which have been produced in the host body. Other parasites, for exam-

ple *Entamoeba histolytica*, may be holozoic, since they ingest the host tissue cells.

Certain ciliates seem to be able to live in water rich in sulphurous substances produced by putrefying vegetable and animal matter. Lauterborn called them **sapropelic forms.**

Many Protozoa apparently nourish themselves by more than one method at the same or different times. Many chromatophore-bearing Protozoa are known to nourish themselves by holophytic as well as saprozoic methods under changed environmental conditions. This mode is sometimes known as **mixotrophic** (Pfeiffer).

In the major groups of the Protozoa except the Sporozoa, there occur one or more vacuoles known as **contractile,** or pulsating, **vacuoles.** As a rule, the fresh-water inhabiting Protozoa contain contractile vacuoles, and those of the salt water or of parasitic habitat do not, although exceptions are noted here and there. In the Protozoa which do not possess a pellicle, the vacuole is formed by accumulation of watery substance in one or more droplets, which increase in size and unite into one. Thus the vacuole enlarges slowly but continuously, until it reaches a certain size, which may vary even within one individual, and finally bursts through the thin ectoplasm to the outside. Aside from Protociliata, contractile vacuoles occur generally in the ciliates even among the parasitic forms. They show in many cases a more conspicuous and complicated structure than those found in other groups. In them the vacuoles are more or less definitely located in the superficial portion of the endoplasm, although there is no delimiting membrane around them. In a number of species there are accessory canals known as **radiating canals.** These canals, which are easily seen in Paramecium, are spaces in the endoplasm through which fluid matter becomes collected and flows toward the central vacuole. When the vacuole is fully formed, its contents are discharged to the exterior through the ectoplasm and pellicle. In forms such as Stentor or Spirostomum, the contractile vacuole is fed by a long longitudinal canal. In some forms there is a definite permanent pore in the pellicle through which the expulsion takes place (Figs. 156 and 160).

In many Mastigophora such as Euglena, there occur several minute contractile vacuoles around the reservoir into which their contents are discharged. The **reservoir** apparently gets rid of the waste matter through a canal, commonly known as the cytopharynx, which leads to the outside. Somewhat similar to this is the contractile vacuole of Vorticellidae. Here a contractile vacuole discharges its contents by a short canal. In Nyctotherus, Balantidium, etc., the contractile vacuole voids its contents through a special canal at the posterior end of the body. In the ciliates, the number, appearance and location of the contractile vacuoles are usually constant and highly characteristic, so that they have a taxonomic value.

As to the function of the vacuole, it seems probable that it adjusts the water contents of the cytoplasm by throwing out from time to time a certain amount of water from the body, and that in doing so it carries out dissolved waste products. The pulsation of the contractile vacuole is, according to Bütschli, not due to the active contraction of the cytoplasm, but to the physical attraction of the small droplet of fluid by the water which surrounds the organism.

Other cell-organs present in the cytoplasm vary a great deal in different groups. **Food vacuoles** are conspicuously present in holozoic Protozoa. These are droplets of fluid, usually water in which are suspended food particles such as Protophyta, other Protozoa or small Metazoa ingested as food. In the amoeboid Protozoa which do not possess a cytostome, the food particles are of variable dimensions, and when the particles are large it is difficult to make out the thin film of water which surrounds them. When minute food-particles are taken in through a cytostome and cytopharynx, the food vacuoles are usually of the same size. In saprozoic Protozoa and the majority of parasitic forms, in which dissolved food is absorbed by osmosis through the body surface, food vacuoles containing solid particles do not occur.

Holophytic Protozoa possess in their endoplasm **chromatophores,** or chromoplasts (Fig. 15), which are made up of chlorophyll. The color of the chromatophores may be yellow, orange, brown, grass-green, blue-green, or even red, due to the pigments which envelop them. Ordinarily they have definite shape, *e.g.*, band-form, stellate, ovoid, ring-form, discoidal, or cup-like; but may occasionally occur in an irregularly diffused or reticulate condition. The number of chromatophores present in an individual varies in different species.

In association with the chromatophores are found one or more **pyrenoids** which are usually embedded in them. A pyrenoid may be naked or covered by amylaceous substance. It

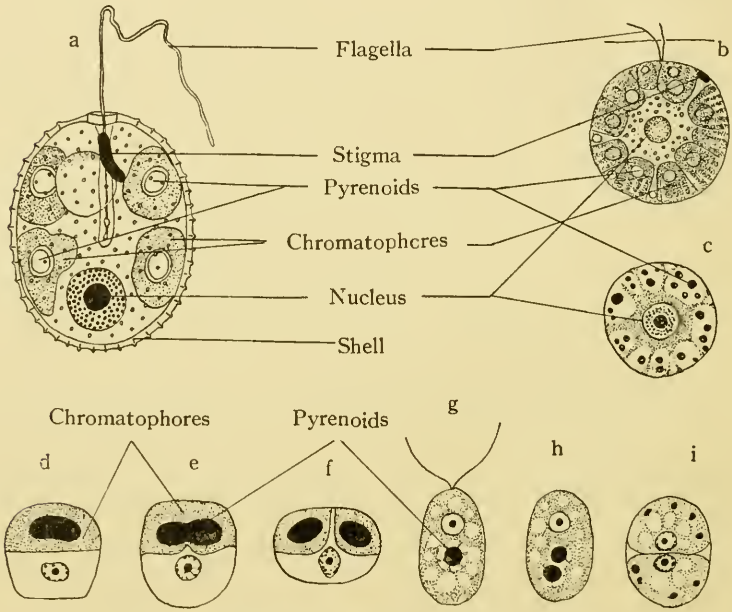


Fig. 15 a. *Trachelomonas hispida* from life. ×530. (After Doflein). b,c. Propagative cells of *Pleodorina illinoisensis*. ×1000. (After Merton). b, from life; c, from stained preparation. d–f. Terminal cells of *Hydrurus foetidus*, showing the division of chromatophore and pyrenoid. (After Geitler). g–i. *Chlamydomonas* sp., showing the division of pyrenoids. (After Geitler).

multiplies during cell-division. As Geitler showed, the pyrenoid in Euglena and allied forms is naked and may or may not be in the chromatophore; while in Volvocidae or Cryptomonadida it is encased in a starch envelope. The pyrenoid seems to become the center in the formation of paramylum bodies and allied reserve food materials.

Chromatophore-bearing forms usually contain also a red-pigmented spherical, ovoid, or elongated body known as the **stigma,** or eye-spot (Fig. 15), which is a cell-organ that responds to light stimulation. The stigma is composed of an oily substance (lipochrome) and in a number of cases possesses a secondary structure made of a paramylum body which seemingly functions as a lens system.

Oils and **fats** are widely distributed among various Protozoa. In some cases they serve not only as reserve food material but also for other purposes. Their function may be hydrostatic, as in Radiolaria, or photogenic, as in various Dinoflagellida. In some cases the oil droplets which are liberated into the water by the disintegration of the protozoan body result in an objectionable odor, as was reported by Calkins in the case of *Uroglenopsis americana* (Fig. 30).

Pigments and **crystals** are also commonly observed in various Protozoa. These are, as a rule, products of catabolism. Not infrequently a common ciliate such as Paramecium may contain a number of crystals in the endoplasm. According to Schaeffer, these crystals in *Amoeba proteus*, *A. discoides* and *A. dubia*, are characteristic to each species (Fig. 80). In malarial organisms brownish granules, known as **melanin** pigment, are formed as a result of absorption and digestion by the organisms of the haemoglobin of the erythrocyte. The coloration of *Blepharisma lateritia* is due to the presence of a specific pigment, as was stated above.

Certain groups have an endoskeleton. In Trichomonas and allied Mastigophora, there is a conspicuous rod-like structure which makes the axis of the body. It is commonly known as the **axostyle** and is understood to serve as a supporting and strengthening cell-organ of the body (Fig. 61). In other forms a number of filamentous structures known as **axial filaments** may be present to form an endoskeleton (Fig. 63). These structures are especially noted in the Mastigophora which inhabit the digestive tract of animals.

References

Bullington, W. E. 1925 Study of spiral movement in the ciliate Infusoria. Arch. f. Protistenk., Vol. 50.

Calkins, G. N. 1926 The biology of the Protozoa. Philadelphia.

Dierks, K. 1926 Untersuchungen über die Morphologie und Physiologie der *Stentor coeruleus* mit besonderer Berücksichtigung seiner kontraktilen und konduktilen Elemente. Arch. f. Protistenk., Vol. 54.

Doflein, F. and E. Reichenow. 1929 Lehrbuch der Protozoenkunde. Jena.

Gray, J. 1928 Ciliary movement. Cambridge.

Jennings, H. S. 1906 Behavior of the lower organisms. New York.

Schaeffer, A. A. 1920 Amoeboid movement. Princeton.

CHAPTER III

REPRODUCTION IN PROTOZOA

THE MODE of reproduction in the Protozoa is highly variable among different groups, and even in the same group it varies with differences in habitat. It will here be briefly considered under asexual and sexual reproduction.

Asexual Reproduction

Nuclear Division

Between a simple direct division on the one hand and a complicated indirect division which is comparable to the mitosis of a typical metazoan cell on the other hand, all kinds of nuclear division are to be encountered.

Direct nuclear division. While not so widely found as was thought in former years, amitosis occurs without doubt in the macronuclear division of the Ciliophora and in the nuclear division of several Cnidosporidia and others. The macronucleus elongates itself without any noticeable changes in internal structure and becomes constricted through the middle, resulting in the formation of two daughter nuclei. A typical example is the division of the macronucleus as observed in *Paramecium caudatum* (Fig. 16). When the macronucleus is an elongated beaded form, as in *Spirostomum ambiguum*, the whole becomes condensed into a rounded mass prior to the division. In *Uroleptus mobilis*, which contains normally eight or more nuclei, the macronuclei, according to Calkins, after throwing off fine granules and losing the nuclear cleft, fuse into one, preparatory to a direct division (Fig. 17). The nucleus then divides twice or three times before the cytoplasmic division occurs; the fourth nuclear division appears after the daughter cells have become separated completely. In *Dileptus anser* (Fig. 4), with scattered nuclei or chromidia, Calkins has shown that the individual granules become elongated and divide where they happen to lie. In *Endamoeba blattae*, the nucleus of the trophozoite divides amitotically (Fig. 18). In Cnidosporidia the minute nucleus frequently undergoes a division which could be considered only as amitosis (Fig. 18). In the case of external budding in the

Fig. 16 Macronuclear, and subsequent cytoplasmic, division in *Paramecium caudatum* as seen in stained specimens. Cytoplasmic cell-organs are entirely omitted. ×260.

Suctoria, as for instance, Ephelota, the macronucleus branches out a small portion of its body into each of the developing buds, and nuclear constrictions result in the forming of many young individuals (Fig. 18).

Indirect nuclear division. The indirect division which occurs in Protozoa is of manifold types as compared with the mitosis in the cells of Metazoa, in which, aside from minor variations, the change is of a uniform pattern. There are, however, instances of indirect nuclear division in Protozoa which are similar to the typical mitosis of multicellular animals. Chatton, Alexeieff and others have proposed several terms to designate the various types of indirect nuclear division, but no one of these

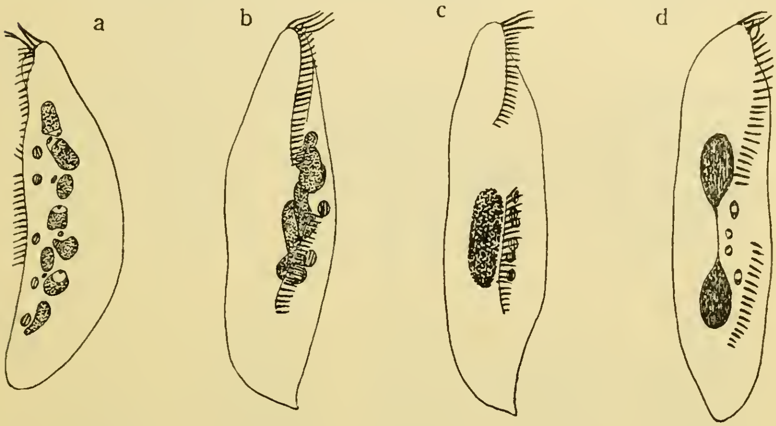


Fig. 17 Stages in macronuclear division in *Uroleptus mobilis.* ×300. (After Calkins).

a. A stage in the fusion of the macronuclei; the micronuclei in mitosis.

b. A much later stage in the macronuclear fusion.

c. The stage in which the macronuclei became fused into one mass prior to amitosis.

d. A stage in the amitosis of the macronuclear material.

types is sharply defined, since there are intermediate forms between any two of them. For our purpose, mention of the chief types will suffice.

A veritable mitosis was noted by Dobell in the heliozoan *Oxnerella maritima* (Fig. 19), which possesses an eccentrically located nucleus containing a large endosome and a central granule ("centroplast") from which radiate many axopodia (*a*). The first sign of the nuclear division is the slight enlargement, and migration toward the central granule, of the nucleus. The granule first divides into two (*c*, *d*) and the nucleus becomes

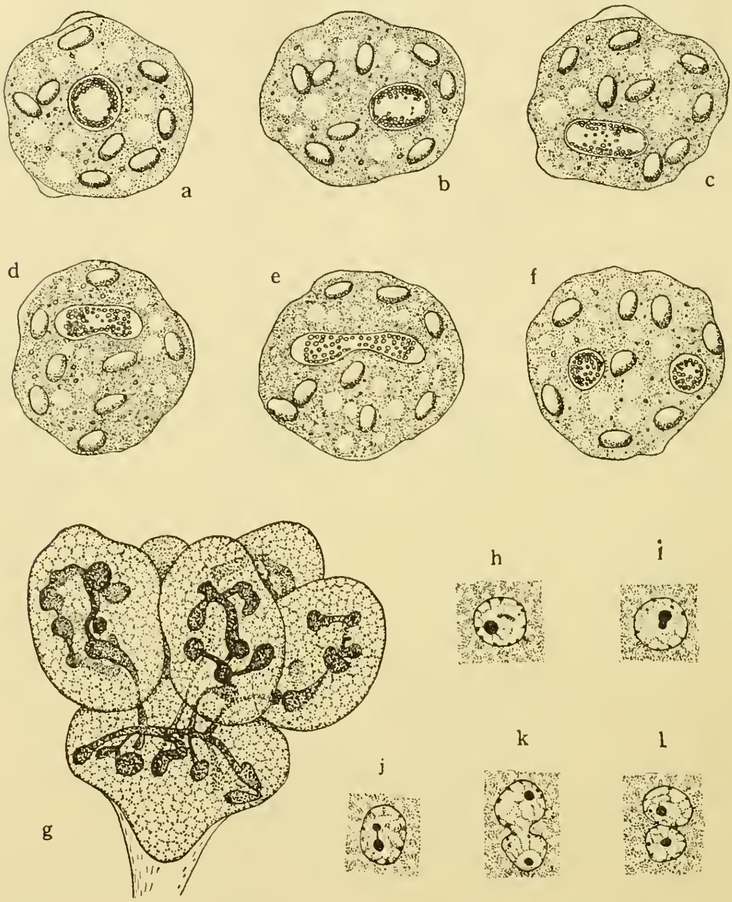


Fig. 18 a–f. Amitosis in *Endamoeba blattae* as seen in life. ×665. (After Kudo).

g. Budding in *Ephelota bütschliana.* (After Calkins).

h–l. Amitosis in trophozoite of *Myxosoma catostomi.* ×1500. (After Kudo).

located between the two granules (*e*). Presently spindle fibers are formed and the nuclear membrane disappears (*f*, *g*). After passing through an equatorial-plate stage, the two groups of chromosomes move toward the opposite granules (*g–i*). As the spindle fibers become indistinct, radiation around the central

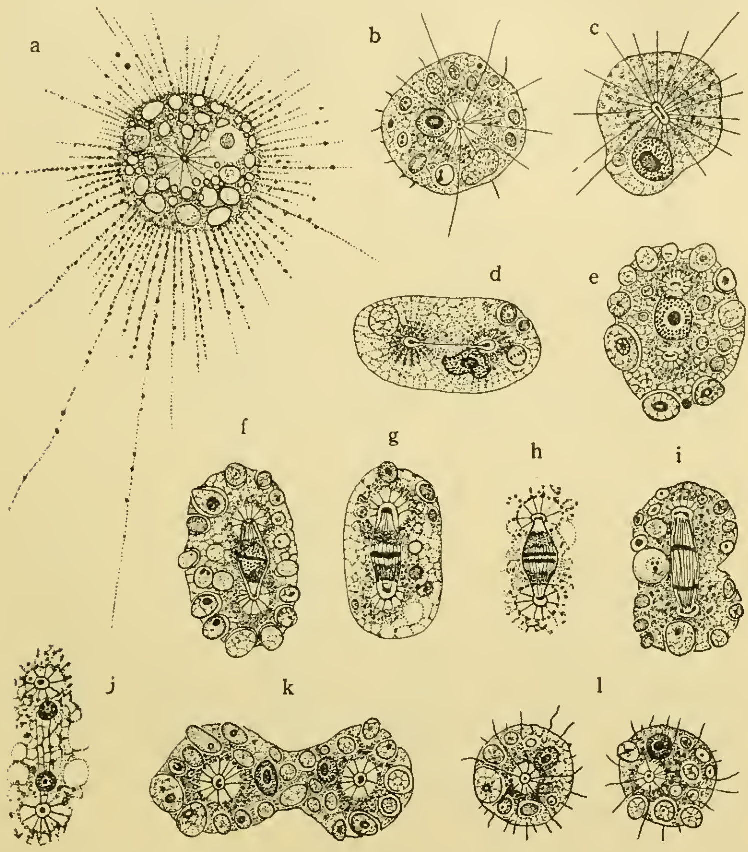
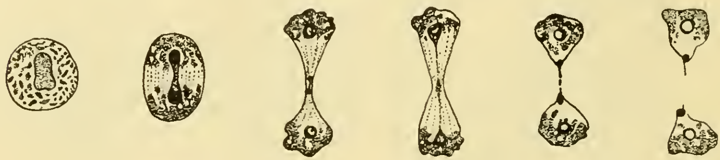


Fig. 19 *Oxnerella maritima* and stages of mitosis. × about 1000. (After Dobell).

a, a living individual; b, a stained specimen; c–g, prophases; h, metaphase; i, anaphase; j, k, telophase; l, complete division of the body into two daughter individuals.

granules becomes conspicuous and the two daughter nuclei are completely reconstructed to assume the resting phase (*j-l*).

In the asexual, or schizogonic, reproduction of the coccidian, *Eimeria schubergi* (Fig. 20), Schaudinn observed a division which is a good example of the type commonly called promitosis. In this the endosome becomes elongated and then divided into two masses; the chromatin granules are assembled in two groups



a

b

c

Fig. 20 a. Nuclear division of schizont of *Eimeria schubergi*. ×1500. (After Schaudinn).
b. Nuclear division of *Chilomonas paramecium*. ×1500. (After Doflein).
c. Nuclear division in sporont of *Thelohania legeri*. ×2100. (After Kudo).

with spindle fibers. In the nucleus of *Chilomonas paramecium* (Fig. 20), the nuclear elongation takes place at right angles to the axis of the body. The endosome breaks up and the chromatin granules become collected into larger rounded chromosomes which are then arranged in the equatorial plane. At about this time, fibers become distinct; two groups of chromosomes move toward the opposite ends and finally divide into two daughter nuclei. In these two cases the nuclear membrane persists.

In the microsporidian, *Thelohania legeri* (Fig. 20), the sporont nucleus divides mitotically. Formation of spireme and spindle fibers and disappearance of the nuclear membrane are distinctly observable, although whether the chromosomes split

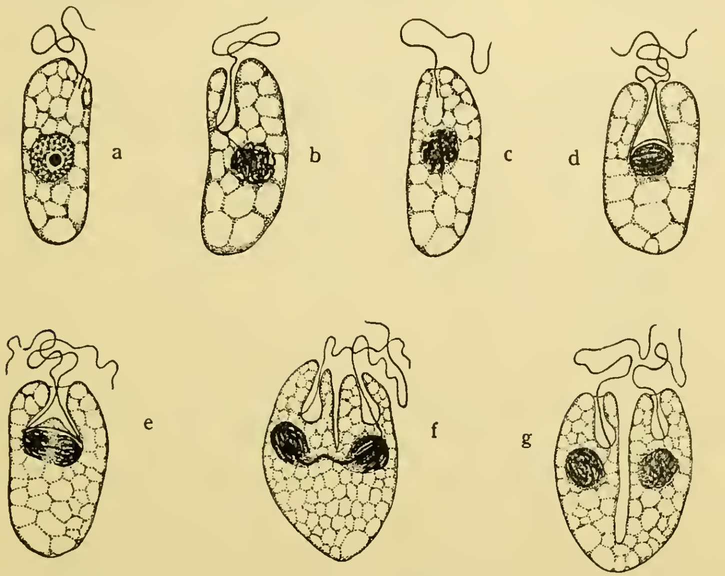


Fig. 21 Nuclear division in *Menoidium incurvum*. × about 1400. (After Hall). a, resting phase; b, c, prophase; d, "equatorial plate;" e, f, anaphase; g, telophase.

or not cannot be made out. In Mastigophora, which possess, as a rule, a blepharoplast from which a flagellum arises and which behaves in a manner somewhat comparable to that of the central granule of Oxnerella or of the centrosome in a metazoan mitosis, the blepharoplast divides and produces a strand between the divided parts in close association with the nucleus. This strand is known as the **paradesmose,** or centrodesmose (Figs. 21, 22). In several Mastigophora, a clear picture of the metaphase has been observed by numerous investigators.

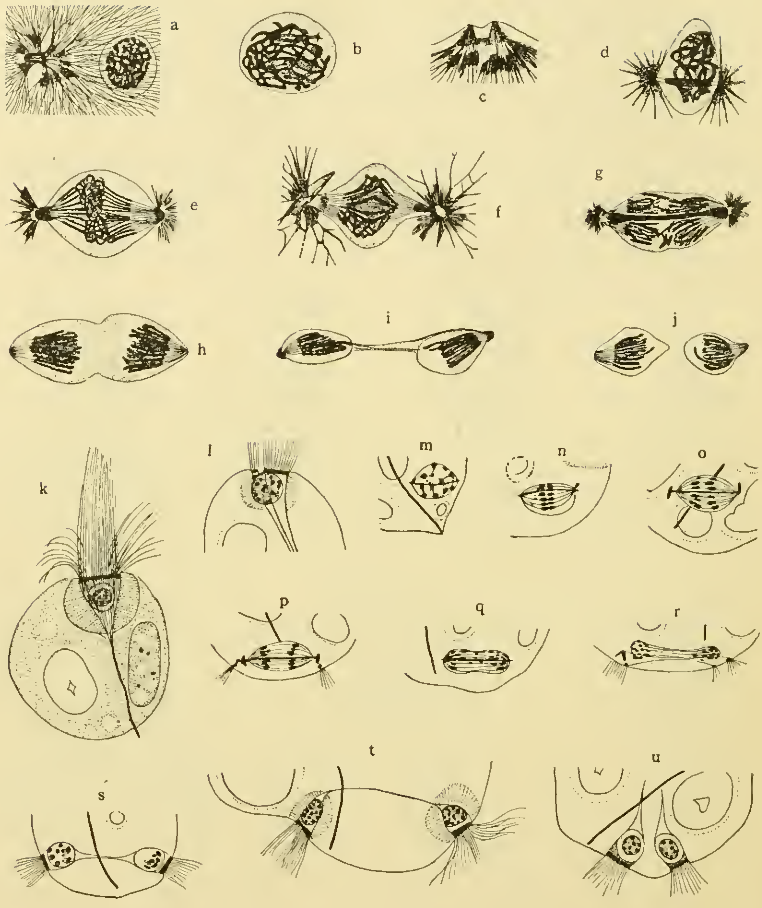


Fig. 22 a–j. Nuclear division in *Trichonympha campanula.* ×400. (After Kofoid and Swezy). a, beginning of division of the centroblepharoplast, the nucleus in prophase; b, nucleus in prophase; c, two centroblepharoplasts and the paradesmose between them; d, close association of the nucleus and paradesmose; e, formation of spindle fibers; f, metaphase, the paradesmose is on the opposite side of the nucleus; g, anaphase; h–j, telophase.

k–u. Nuclear division in *Lophomonas blattarum.* ×1150. (After Kudo). k, resting nucleus; l, m, prophase, n, metaphase; o–r, anaphase; s–u, telophase.

Cytoplasmic Division

Binary fission. As in metazoan cells, binary fission occurs very widely among the Protozoa. It is the division of the body into two nearly equal daughter cells. In the Amoebaea the body divides simply into two daughter individuals. In Testacea, as a rule, one of the daughter individuals occupies the old test, while the other moves out and forms a new one, as in Arcella and Euglypha. However, in some forms, such as Cochliopodium and Pseudodifflugia, the division is longitudinal, the test dividing also into two parts.

In the majority of the Mastigophora, the division is longitudinal (Fig. 21). The nucleus and the blepharoplast divide first. The old flagellum may or may not be absorbed during the division. The new flagellum or flagella develop from the blepharoplasts. In a few forms, such as *Oxyrrhis marina* and *Lophomonas striata*, the cytoplasmic division is transverse. In the latter species the second daughter individual develops its anterior end directed posteriorly. The two almost completely divided daughter individuals may remain together for some time, being connected by a filamentous strand.

In the Ciliophora the division is usually transverse (Fig. 16). The macro- and micro-nucleus each divide into two, and then the cytoplasmic organelles, such as the cytostome, contractile vacuoles, etc., are regenerated before the body divides into two. Incomplete division of the stalk results in producing arboroid colonies in many Peritrichida.

Budding. Multiplication by budding, which is less frequently found in Protozoa than binary fission, is the formation of one or more smaller individuals from the large parent organism. It is either endogenous or exogenous, depending upon the location of the developing bud. Exogenous budding is noted in Noctiluca (Fig. 35), Myxosporidia (Fig. 23), Telosporidia, Suctoria (Fig. 18), etc. Endogenous budding is found in certain Suctoria (Fig. 173), although it does not seem to occur either in the Ciliata or in the Mastigophora. In Testacea such as Arcella, endogenous budding is said to take place. It occurs quite commonly in numerous members of the Sporozoa.

Multiple division. In multiple division the body divides into a number of daughter individuals completely, with or without degenerating remains of the parent body. In this process the nucleus may undergo either simultaneous multiple division, as in Aggregata, or more commonly, repeated binary fission, as in Plasmodium, to produce large numbers of daughter nuclei. The number of daughter individuals varies, not only among the

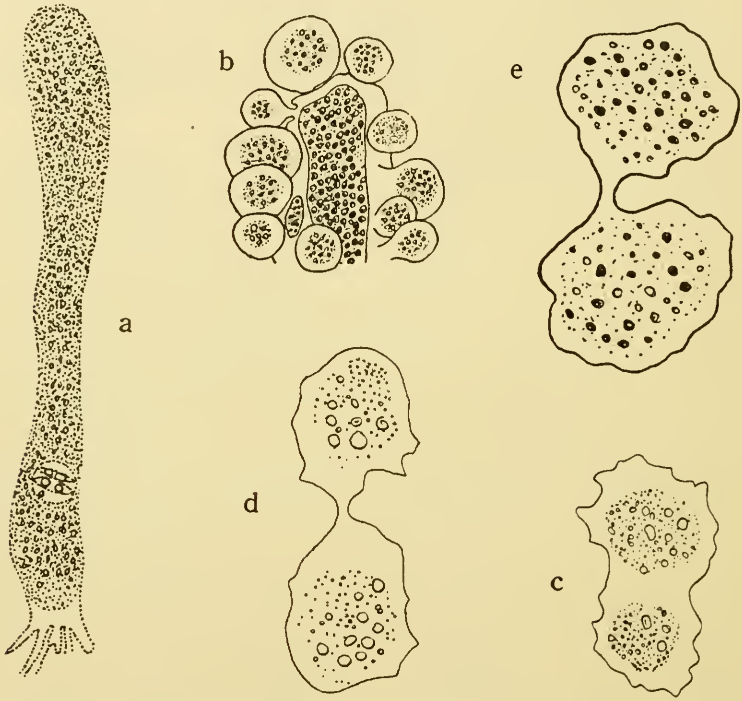


Fig. 23 Asexual reproduction in Myxosporidia. (From Kudo after several authors).

a, trophozoite of *Myxidium lieberkühni;* b, budding in the same myxosporidian; c, d, plasmotomy of trophozoite of *Chloromyxum leydigi;* e, plasmotomy of a trophozoite of *Sphaeromyxa balbianii.*

different groups, but also within one and the same species. Multiple division occurs commonly in Foraminifera, Radiolaria, Sporozoa, etc. Asexual multiple division, which is called **schizogony,** takes place widely in Sporozoa. In Mastigophora it is not of common occurrence but has been noted in cultures of *Trypanosoma lewisi, T. cruzi, Lophomonas blattarum,* etc.

Plasmotomy. In certain Myxosporidia which inhabit organ-cavities of the host fish, the multinucleate trophozoite has been found to divide into two or more smaller, still multinucleate bodies (Fig. 23). Doflein called this process plasmotomy. A similar division is also noted in some Mycetozoa and occasionally in Protociliata.

Colony formation. When the division is repeated without complete separation of the daughter individuals, various types of colonies are produced. Based upon the arrangement of the component individuals, these are usually placed under three types: catenoid, arboroid, and spheroid.

Catenoid (linear) colony. The daughter individuals are attached endwise, forming a chain of several individuals. Examples: the astomous ciliate, Haptophrya, and the dinoflagellate, Ceratium.

Arboroid (dendritic) colony. The daughter individuals remain connected with one another through attachment to stalks or tests, producing a tree-like appearance. Examples: Dinobryon, Hyalobryon, Hydrurus (Fig. 31), Phalansterium (Fig. 45), Anthophysa (Fig. 55), Epistylis (Fig. 170), Carchesium (Fig. 169), etc.

Spheroid colony. The individuals are embedded in a gelatinous matrix which is more or less rounded. Examples: Volvox, Eudorina, Pleodorina (Fig. 39), Syncrypta, Uroglena, Uroglenopsis (Fig. 30). Some are rosette-form, as in Gonium (Fig. 38); others are plate-form, as in Platydorina (Fig. 38).

The **gregaloid** colony, which also is sometimes spoken of is a group of individuals of one and the same species, usually of Sarcodina, which become attached to one another by means of pseudopodia. Such a colony can hardly be said to be due to incomplete division of the parent body.

Sexual Reproduction

Some Protozoa reproduce themselves in a manner comparable to the sexual reproduction which occurs universally in the Metazoa. Complete fusion of two gametes is here called **copulation** and is to be seen in various groups. A temporary union of two individuals for the exchange of nuclear material is designated as **conjugation** and is common among the Ciliophora.

Copulation

In the process of copulation two gametes take part. If the two gametes are morphologically alike, they are called **isogametes**; and if unlike, **anisogametes.**

Isogamy, or hologamy, is typically represented by the flagellate *Copromonas subtilis* (Fig. 24), in which there occurs,

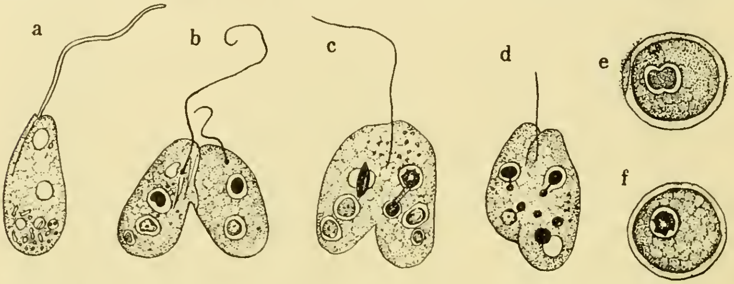


Fig. 24 Copulation in *Copromonas subtilis.* ×1300. (After Dobell).

according to Dobell, complete nuclear and cytoplasmic fusion between two individuals. Each nucleus, after casting off a portion of its nuclear material, fuses with the other nucleus. The process is comparable to fertilization among the Metazoa. The zygote thus formed encysts instead of carrying on an active trophic life. Among the Sporozoa, isogamy is commonly found in the gregarines such as Lankesterella (Fig. 123), Schizocystis (Fig. 126), etc. It is also quite common in the Foraminifera

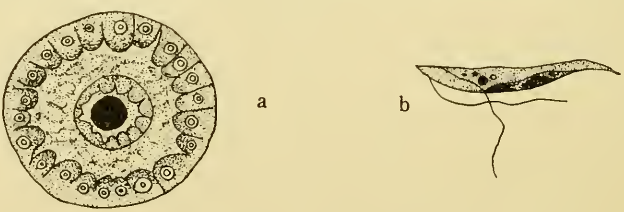


Fig. 25 Macrogamete and microgamete of *Volvox aureus.* ×1000. (After Klein).

(Figs. 73, 76). It perhaps occurs in the Radiolaria, although positive evidence is yet to be presented (Fig. 102).

Anisogamy seems to be more widely distributed. On the whole the differences between the microgametes and macrogametes are comparable to those which exist between the spermatozoa and ova of the Metazoa. The **microgametes** are actively motile, relatively small and numerous, while the **macrogametes** are non-motile as a rule, much larger but fewer (Fig. 25). In Chlamydomonas (Fig. 37), according to Goroschankin, the two gametes begin to fuse at their anterior ends. The flagella are lost and the cytoplasmic and nuclear fusions take place. A new body wall is secreted around the whole. In Volvox, the two gametes may be produced in the same colony, as in *Volvox globator*, or in different colonies, as in *V. aureus* and *V. perglobator*. The union of gametes results in the formation of a **zygote**. Pandorina and Eudorina show similar changes. In the Sporozoa, anisogamy has been observed in numerous species of Eimeria (Fig. 109), Plasmodium (Fig. 120), etc. In the Cnidosporidia, some cases of anisogamy have been reported by certain investigators, while others report negative findings. Anisogamy has been suggested to occur in some Amoebaea, particularly in *Endamoeba blattae*, by Mercier, but this awaits confirmation.

Conjugation

Conjugation is a temporary fusion of two individuals of one and the same species for the purpose of nuclear exchanges. This process is found almost exclusively in the Ciliophora. The two individuals may be similar or dissimilar morphologically. The former case is called **isogamous** conjugation, and the latter **anisogamous** conjugation. The former appears to occur more commonly than the latter.

In *Paramecium caudatum* (Fig. 26) two individuals come in contact on their oral surfaces. The micronucleus in each conjugant divides twice (*b–e*), forming four micronuclei, three of which degenerate and do not take active part during further changes (*f–h*). The remaining micronucleus divides once more, producing a wandering nucleus and a stationary nucleus (*f*, *g*). The wandering nucleus in each of the conjugants enters the other conjugant and fuses with its stationary nucleus (*h*, *r*). The two zygotes thus formed become separated from each other and are called exconjugants. In each of them, the micronucleus divides three times in succession (*i–m*) and produces eight nuclei (*n*), four of which remain as micronuclei, while the other four develop into macronuclei (*o*). Cytoplasmic fission follows then,

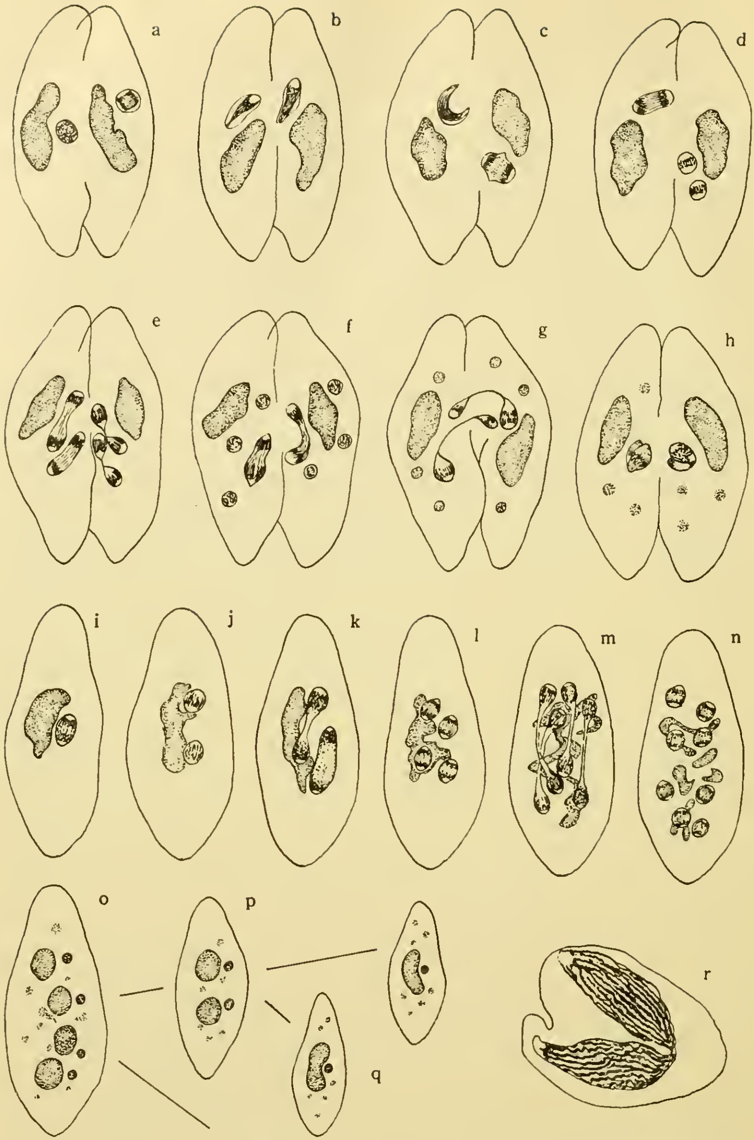


Fig. 26 Diagrammatic representation of conjugation in *Paramecium caudatum*. × about 130. (After Calkins).

a–f, micronuclear divisions; g, exchange of micronuclear material; h, fertilization; i–n, stages in three successive divisions of the nucleus; o, differentiation of four macronuclei and micronuclei; p, one of the products of the first cytoplasmic division, containing two macronuclei and two micronuclei; q, the products of the second and last cytoplasmic division, each possessing one macronucleus and one micronucleus; r, nuclear fusion such as shown in h, under higher magnification (×1200 after Dehorne).

producing, first, two with four nuclei (*p*) and, then, four small individuals, each containing a macronucleus and a micronucleus (*q*).

Anisogamous conjugation is essentially the same except that the conjugants are dissimilar in size and in some cases in structure. In Chilodon (Fig. 27), the conjugants are unequal in size. According to Dogiel, in *Cycloposthium bipalmatum* (Fig. 27)

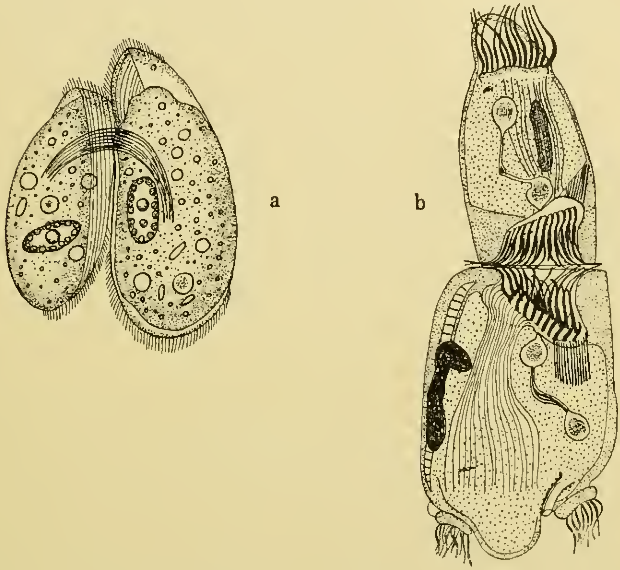


Fig. 27 a. Anisogamous conjugation in *Chilodon cucullulus.* ×140. (After Engelmann). b. Anisogamous conjugation in *Cycloposthium bipalmatum.* ×245 (After Dogiel).

conjugation takes place between two similar individuals or between two unequal ones.

A sexual process which is somewhat intermediate between copulation and conjugation is noted in certain ciliates. According to Maupas' classical work on *Vorticella nebulifera*, the ordinary trophic individual divides twice, forming four small individuals, which become detached from one another and swim about independently. Sooner or later each of these small organisms attaches itself to one side of an ordinary stalked individual. In it the micronucleus divides three times and produces eight nuclei, of which seven degenerate and the remaining one divides once more. In the stalked individual the micronucleus divides twice, forming four nuclei, of which three degenerate, the other dividing into two. During these changes the cytoplasm of the two conjugants fuses completely. The wandering nucleus of the smaller conjugant unites with the stationary nucleus of the larger conjugant, the other nuclei degenerating. The single nucleus thus produced divides several times to form a number of nuclei, from some of which macronuclei are differentiated. Later the organism undergoes division.

Meiotic Division

In the foregoing paragraphs, references have been made to the divisions which the nuclei undergo prior to fusion. In all Metazoa, during the development of the gametes, the gametocyte nuclei undergo a reduction division, or **meiosis,** by which the number of chromosomes is halved; that is, each fully formed gamete possesses one-half the number of chromosomes typical to the species. The zygote stage restores the number.

In the Protozoa, meiotic division takes place presumably prior to or during sexual reproduction, but the process is understood only in a few species. Among the ciliates in which conjugation is common, meiosis seems to take place in the second micronuclear division, although in a few forms, for example, *Oxytricha fallax*, according to Gregory, the actual reduction takes place during the first division. Prandtl (1906) was the first to note the reduction in number of chromosomes in the Protozoa. In *Didinium nasutum*, he observed sixteen chromosomes in each of the daughter nuclei during the first division, but only eight in the second division. Since then, the fact that the reduction is accomplished at the time of the second micronuclear division has been confirmed in *Chilodon uncinatus* (four to two chromosomes) by Enriques in 1908 and by MacDougall in 1925; in *Carchesium polypinum* (sixteen to eight; Popoff, 1908); *Uroleptus mobilis* (eight to four; Calkins, 1919). In various species of Paramecium and other ciliates, the number of chromosomes is so large, possibly more than one hundred, that it has been impossible to observe the stage of actual reduction.

In *Monocystis rostrata*, a parasite of the earthworm, Muslow noted that the nuclei of the two gregarines which encyst together, multiply by a mitosis in which eight chromosomes are constantly present, but in the last division of gametic differentiation each daughter cell receives four chromosomes. In another species of Monocystis of the same host, Calkins and Bowling found that the normal number of chromosomes is ten, and that it is halved in the last gametic division. It will be seen from these that the zygote will contain the normal number of chromosomes.

On the other hand, in the coccidian, *Aggregata eberthi* (Dobell, 1925; Bělař, 1926), and in the gregarine, *Diplocystis schneideri* (Jameson, 1920), there is no reduction in the number of chromosomes during the gamete-formation and, therefore, the resulting zygote contains twice the typical number of chromosomes. The first zygotic nuclear division was found to be meiotic, thus restoring the number of chromosomes in each nucleus.

Paedogamy

In a few forms, it has been observed that the organism divides into two uninucleate individuals, and that the two bodies fuse completely into one after a reduction division of the nuclei. This process has been named **paedogamy.** Perhaps the classical example is that which was found by Hertwig (1898) in *Actinosphaerium eichhorni.* The organism encysts within a capsule, and the body divides into numerous uninucleate secondary cysts. The protoplasm of each of the latter divides into two cells and remains within a common cyst-wall. Their nuclei divide twice, and all the division products in each cell degenerate except one. Nuclear and cytoplasmic union between the two occurs, and a zygote is thus formed.

Autogamy

In some instances, the nucleus or nuclei divide once or twice without any division of the cytoplasm. The nuclei then fuse in pairs with one another after throwing off a certain portion of the chromatin material. This has been called **autogamy.** Undoubtedly several cases of so-called autogamy were due to misinterpretation, but in some Microsporidia, such a process has been recognized by several investigators (Fig. 136). In Myxosporidia the spore possesses a binucleate sporoplasm. Most observers agree that, prior to germination of the sporoplasm, the two nuclei undergo fusion (Fig. 28).

Endomixis

By pedigree culture methods, Woodruff and Erdmann have found that *Paramecium aurelia* undergoes, at an interval of thirty days, a complete nuclear reorganization without cell fusion. The macronucleus breaks up into a number of fragments, which become completely absorbed by the cytoplasm later. Each of the two micronuclei divides twice, some of the products forming a new macronucleus and others forming two new micronuclei. This nuclear reorganization which takes place periodically was termed **endomixis** by the above-mentioned authors. The process has further been found to occur in *Paramecium caudatum*, in which the micronucleus divides three times. Here four of the division products form new macronuclei, two degenerate, and two persist as new micronuclei. Endomixis has been found in several other ciliates.

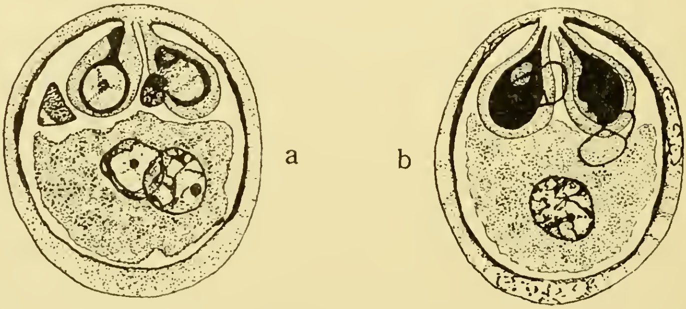


Fig. 28 Stained spores of *Myxosoma catostomi*, showing two nuclei in the sporoplasm (a), which later fuse into one (b). ×2600.

As to the significance of the fertilization and endomixis, the generally accepted theory is that these processes probably restore the "vitality" of the individual in which they occur.

References

Bělař, K. 1926 Der Formwechsel der Protistenkerne. Eine vergleichend-morphologische Studie. Ergebnisse und Fortschritte der Zoologie. Vol. 6.

Calkins, G. N. 1919 *Uroleptus mobilis.* 1. History of the nuclei during division and conjugation. Jour. Exper. Zool., Vol. 27.

———. 1926 The biology of the Protozoa. Philadelphia.

Calkins, G. N. and S. W. Cull. 1907 The conjugation of *Paramecium caudatum.* Arch. f. Protistenk., Vol. 10.

Doflein, F. and E. Reichenow. 1929 Die Lehrbuch der Protozoenkunde. Jena.

Erdmann, Rhoda and L. L. Woodruff. 1916 Periodic reorganization process in *Paramecium caudatum.* Jour. Exper. Zool., Vol. 20.

Gregory, L. H. 1923 The conjugation of *Oxytricha fallax.* Jour. Morph., Vol. 37.

Kudo, R. 1924 A biologic and taxonomic study of the Microsporidia. Illinois Biological Monogr., Vol. 9.

MacDougall, M. S. 1925 Cytological observation on gymnostomous ciliates, with a description of the maturation phenomena in diploid and tetraploid forms of *Chilodon uncinatus.* Quart. Jour. Micr. Sci., Vol. 69.

Woodruff, L. L. and Rhoda Erdmann. 1914 A normal periodic reorganization process without cell fusion in Paramecium. Jour. Exper. Zool., Vol. 17.

CHAPTER IV

OUTLINE OF THE CLASSIFICATION

THE SYSTEM of classification adopted here was formulated largely by Bütschli and has been modified from time to time by other protozoologists. In this system the Protozoa are divided into two subphyla: Plasmodroma and Ciliophora.

The Plasmodroma include three classes: (1) the Mastigophora, which have flagella; (2) the Sarcodina, which form pseudopodia; and (3) the Sporozoa, which possess no locomotor cell-organs. The Ciliophora include two classes: (1) the Ciliata, which have cilia throughout their life-cycle; and (2) the Suctoria, which show cilia only in the immature stage. In the Plasmodroma the nuclei are of a single type, but in the Ciliophora there are two types of nuclei. A synopsis of all classes will be given here for the convenience of the reader.

PHYLUM PROTOZOA

CHAPTER V

SUBPHYLUM 1 **PLASMODROMA** DOFLEIN

CLASS 1 **MASTIGOPHORA** DIESING

The class Mastigophora includes those Protozoa which possess one or more **flagella.** Aside from this common characteristic, the members of this class make a very heterogeneous assemblage. Since it includes a large number of chlorophyll-bearing organisms, it seems to stand in the way of a sharp distinction between the Protozoa and the Protophyta. Many of its members have been, and still are, classified with the Protophyta by botanists.

In the majority of the Mastigophora, each individual possesses one to four flagella during the entire life-cycle except in the encysted or palmella stage. In some forms there occur six or eight flagella, and in Hypermastigida an enormous number of flagella are usually found. The **palmella** stage (Fig. 29) is common among the Phytomastigina and, unlike the encysted stage, is capable not only of metabolic activity and growth but also of reproduction. Thus these forms show undoubtedly a close relationship to the algae.

All four types of nutrition, carried on separately or in combination, are to be found among the members of the Mastigophora. In holophytic forms, the chlorophyll is contained in the **chromatophores,** which are of various forms among different species (Fig. 15) and vary in color, being green, blue-green, yellow, brown, reddish-brown, red, etc. The difference in color is mainly due to the pigments which envelop the chlorophyll. Many forms adapt their mode of nutrition to changed environmental conditions, for instance, from holophytic to saprozoic in absence of sunlight. Holozoic, saprozoic and holophytic nutrition seem to be combined in Ochromonas. The chromatophore frequently contains a refractile granule or body, the **pyrenoid** (Fig. 15), which becomes the center of the formation of the paramylum body. Besides the latter, reserve food materials consisting of oil and carbohydrates are occasionally found.

In the less complicated forms, the body is naked except for a slight cortical differentiation of the ectoplasm to delimit the body surface. Such forms are capable of pseudopodial formation. In others there occurs a thin expansible pellicle secreted by the ectoplasm, which covers the body surface closely. These forms are often plastic and change their form in a peculiar fashion (Fig. 6). In still others the body is constant, being encased in a shell, test, lorica, or plate, which is composed of chitin, pseudochitin, or cellulose. Not infrequently a gelatinous secretion envelops the body. In one group, Choanoflagellidae, there is a collar-like structure located at the anterior end surrounding the flagellum.

The great majority of the Mastigophora possess a single nucleus, and only a few are multinucleated. The nucleus is usually of vesicular type with a conspicuous endosome. Contractile vacuoles are always present in the forms inhabiting fresh water. In the simple forms the contents of the vacuoles are discharged directly through the body surface to the exterior; in others there are several contractile vacuoles arranged around a reservoir, which opens to the exterior through the so-called cytopharynx. In the Dinoflagellida, there are apparently no contractile vacuoles, but non-contractile **pusules,** which seem to have hydrostatic function, are present in the cytoplasm. In forms with chromatophores, there occurs usually a reddish or brownish, rounded or elongated body, the **stigma,** which is situated near the base of the flagellum. It seems to be the center of phototropic activity of the organism which possesses it. A number of Mastigophora are capable of forming pseudopodia of various types which serve for food-capturing and locomotion.

Asexual reproduction of the Mastigophora is, as a rule, by longitudinal fission, but in some forms multiple fission also occurs under certain circumstances, and in others budding may take place. Colony-formation, due to incomplete separation of the daughter individuals, is widely found among the group. Sexual reproduction has been noted in a number of species. The development varies among different groups and will be briefly taken up for individual orders.

The class Mastigophora includes free-living as well as parasitic forms. Its members are found in fresh and salt waters of much wider range than are other groups, because of their holophytic nutrition. Many are free-swimming, others creep over the surface of submerged objects, and still others are sessile. Together with the algae, the Mastigophora compose a major portion of plankton life, which is the basis for the existence of all higher forms of aquatic animals. The parasitic forms are ectoparasitic or endoparasitic. The latter live either in the digestive tract or in the circulatory system of the host. Trypanosoma, a representative genus of the latter type, includes important disease-causing parasites of man and of domestic animals

According to Doflein, the Mastigophora are divided into two subclasses: Phytomastigina and Zoomastigina.

SUBCLASS I **PHYTOMASTIGINA** DOFLEIN

Most of the Phytomastigina possess chromatophores, and their usual method of nutrition is therefore holophytic, though a few are mixotrophic. The majority are conspicuously colored. Some that lack chromatophores are included in this group, since their morphology and development resemble closely those of typical Phytomastigina. According to Calkins, the subclass is divided into six orders, as follows:

With cellulose shell composed of plates; two flagella, one of which is
transverse . . . . Order 3 Dinoflagellida
Without cellulose shell composed of plates; no transverse flagellum
Chromatophores yellow or brown; contractile vacuoles simple
Cytopharynx absent; body not flattened . . . . . . Order 1 Chrysomonadida
Cytopharynx present; body flattened . . . . Order 2 Cryptomonadida
Chromatophores green; contractile vacuoles simple or complex
Without cytopharynx; vacuole simple . . . . Order 4 Phytomonadida
With cytopharynx; vacuole complex
Metabolic products paramylum . . . . Order 5 Euglenoidida
Metabolic products oil . . . . Order 6 Chloromonadida

ORDER I **CHRYSOMONADIDA** STEIN

Most of the Chrysomonadida are minute. They show various body organizations. Chromatophores are yellow to brown (rarely green or bluish) and usually discoid, though sometimes reticulated. The products of metabolism are refractile bodies, known collectively as **leucosin** (probably carbohydrates), fats and oils. Starches have never been found in them. The flagella, usually one or two in number, are planted at or near the anterior end of the body, with a stigma near the insertion point, as a rule, when there is but one flagellum.

Many Chrysomonadida are able to form pseudopodia for obtaining food materials, which vary among different species. Nutrition, though chiefly holophytic, is often holozoic or saprozoic also. Contractile vacuoles are invariably found in fresh-

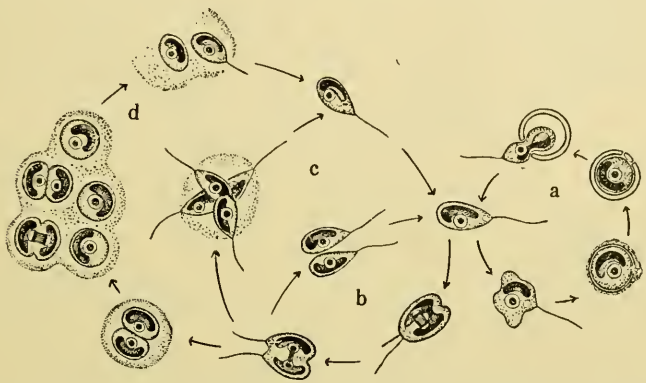


Fig. 29 Diagram showing the development of Chromulina. × about 200. (After Kühn, modified). a, encystment; b, fission; c, colony formation; d, palmella formation.

water forms. They are ordinarily of simple structure, although a few of them have rather complicated systems.

Under conditions not fully understood, the Chrysomonadida transform themselves into a rounded stage known as the palmella phase and undertake metabolic activities as well as multiplication (Fig. 29). Asexual reproduction is usually by longitudinal division during either the motile or the palmella stage. Incomplete separation of the daughter individuals followed by repeated fission, results in numerous colonial forms of all three types mentioned elsewhere (p. 51). Some resemble higher algae very closely. Sexual reproduction is entirely unknown in this group. Encystment occurs commonly among the chrysomonads. In this the flagellum is lost and a silicious wall is secreted around the cyst. There is usually an opening with a plug.

This group is divided into the following three suborders:

Motile stage dominant . . . . Suborder 1 Euchrysomonadina
Palmella stage dominant
  Sarcodina-like; flagellate stage unknown . . . . . . Suborder 2 Rhizochrysidina
  Palmella phase dominant . . . . Suborder 3 Chrysocapsina

Suborder 1 **Euchrysomonadina** Pascher

With one anterior flagellum . . . . Family 1 Chromulinidae
With two equal flagella . . . . Family 2 Isochrysidae
With two unequal flagella . . . . Family 3 Ochromonadidae
With calcareous discs and rods . . . . Family 4 Coccolithophoridae
With simple skeleton . . . . Family 5 Silicoflagellidae

Family 1 **Chromulinidae** Senn

Minute forms, naked or with sculptured shell; with a single flagellum; often with rhizopodia; a few colonial. Free-swimming or attached. Some fifteen genera.

Genus **Chrysapsis** Pascher. Chromatophores diffused or in a network. With stigma; amoeboid locomotion.

Chrysapsis sagene Pascher (Fig. 30, *a*). Body about 10 microns long; flagellum about 30 microns long. Fresh water.

Genus **Chromulina** Cienkowski. Body minute, ovoid. With one or two chromatophores. A single flagellum. Cysts possess a plug. Several species in clean fresh water. The presence of a large number of organisms sometimes gives a golden-brown color to the surface of the water.

Chromulina pascheri Hofeneder (Fig. 30, *b–d*). Body diameter about 15 to 20 microns.

Genus **Chrysococcus** Klebs. Shell spheroidal or ovoidal, smooth or sculptured and often brown-colored. Through an opening a flagellum protrudes. One or two chromatophores. One of the daughter individuals formed by binary fission leaves the parent shell and forms a new one.

Chrysococcus ornatus Pascher (Fig. 30, *e*). In fresh water. About 15 microns long.

Genus **Mallomonas** Perty. Body elongated; with silicious scales and often spines. Two chromatophores, rod-shaped. Several species.

Mallomonas ploesslii Perty (Fig. 30, *f*). Body about 25 to 30 microns long. Fresh water.

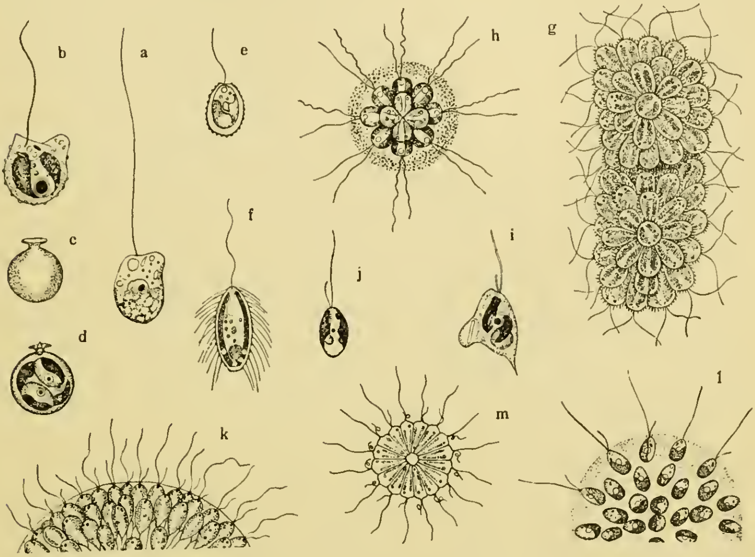


Fig. 30
a. *Chrysapsis sagene.* ×750 (After Pascher).
b–d. *Chromulina pascheri.* ×500 (After Hofeneder).
b, an individual from a colony; c, d, cysts.
e. *Chrysococcus ornatus.* ×450 (After Pascher).
f. *Mallomonas ploesslii.* ×400 (After Klebs).
g. *Synura uvella.* ×380 (After Stein).
h. *Syncrypta volvox.* ×325 (After Stein).
i. *Ochromonas mutabilis.* ×500 (After Senn).
j. *O. ludibunda.* ×400 (After Pascher).
k. *Uroglena volvox.* ×325 (After Stein, modified).
l. *Uroglenopsis americana.* ×350 (After Pascher).
m. *Cyclonexis annularis.* ×390 (After Stokes).

Family 2 **Isochrysidae** Pascher

Solitary or colonial chrysomonads with two equal flagella; with or without a pellicle (when present, often sculptured); some possess a stalk. Several genera.

Genus **Synura** Ehrenberg. Spherical colony composed of two to fifty ovoid individuals arranged radially. Body usually covered by short bristles. Two chromatophores lateral; no stigma. Asexual reproduction of individuals is by longitudinal division; that of a colony by bipartition. Cysts are spherical.

Synura uvella Ehrenberg (Fig. 30, *g*). Fresh water. If present in large numbers, the organism is said to be responsible for an odor of the water resembling that of ripe cucumber (Moore).

Genus **Syncrypta** Ehrenberg. Spherical colonies; individuals with two lateral chromatophores, are embedded in a gelatinous mass. Cysts unknown.

Syncrypta volvox Ehrenberg (Fig. 30, *h*). In standing water.

Family 3 **Ochromonadidae** Pascher

With two unequal flagella. The body has no pellicle and is therefore changeable. Contractile vacuoles are simple; with or without delicate test. Solitary or colonial. Free-swimming or attached.

Genus **Ochromonas** Wysotzki. Solitary or colonial. Body surface is delicate; posterior end is often drawn out for attachment. One or two chromatophores; usually with a stigma. Encystment.

Ochromonas mutabilis Klebs (Fig. 30, *i*). About 15 microns in diameter.

Ochromonas ludibunda Pascher (Fig. 30, *j*). Body about 15 microns long.

Genus **Uroglena** Ehrenberg. Spherical or ovoidal colonies, composed of ovoid or ellipsoidal individuals arranged along the periphery of a spherical gelatinous mass. All individuals are connected with one another by gelatinous processes running inward and meeting in a point. With a stigma and a plate-like chromatophore. Asexual reproduction of individuals by longitudinal fission; that of a colony by bipartition. Spherical cysts with spinous projections, and a long tubular process.

Uroglena volvox Ehrenberg (Fig. 30, *k*). In standing water.

Genus **Uroglenopsis** Lemmermann. Similar to Uroglena, but individuals without inner connecting processes.

Uroglenopsis americana (Calkins) (Fig. 30, *l*). When present abundantly in a water reservoir, the organism gives an offensive odor to the water (Calkins).

Genus **Cyclonexis** Stokes. Wheel-like colonial forms composed of ten to twenty wedge-shaped individuals. Young colonies are funnel-shaped. With two lateral chromatophores; no stigma; reproduction and encystment unknown.

Cyclonexis annularis Stokes (Fig. 30, *m*). Colony about 25 to 30 microns in diameter. In marshy water with Sphagnum.

Genus **Dinobryon** Ehrenberg. Solitary or colonial. Individuals with vase-like, hyaline, but sometimes, yellowish cellulose test which is drawn out at its base. The delicate body is elongated and attached to the base of the test with its attenuated posterior tip. One or two lateral chromatophores; usually with a stigma. Asexual reproduction by binary fission; one of the daughter individuals leaving the test as a swarmer, to form a new one. In colonial forms the daughter individuals remain attached to the inner margin of the opening of the parent tests and there secrete new tests. Encystment common; the spherical cysts possess a short process.

Dinobryon sertularia Ehrenberg (Fig. 31, *a*). Fresh water.

Genus **Hyalobryon** Lauterborn. Solitary or colonial. Individual body structure is similar to that of Dinobryon. The test in some cases, is tubular, and those of young individuals are attached to the exterior of the parent tests.

Hyalobryon ramosum Lauterborn (Fig. 31, *b*). Fresh water.

Genus **Stylopyxis** Balachonzeff. Solitary. The body is located at the bottom of a delicate stalked test with a wide aperture. Two lateral chromatophores.

Family 4 **Coccolithophoridae** Lohmann

The members of this family, with a few exceptions, occur in salt water only. With perforate (tremalith) or imperforate (discolith) discs, composed of calcium carbonate. One or two flagella; two yellowish chromatophores; a single nucleus; oil drops and leucosin. Nutrition holophytic. Examples:

Pontosphaera haeckeli Lohmann (Fig. 31, *c*).

Discosphaera tubifer Murray and Blackman (Fig. 31, *d*).

Family 5 **Silicoflagellidae** Borgert

Exclusively marine planktons. With silicious skeleton which envelops the body. Example: *Distephanus speculum* (Müller) (Fig. 31, *e*).

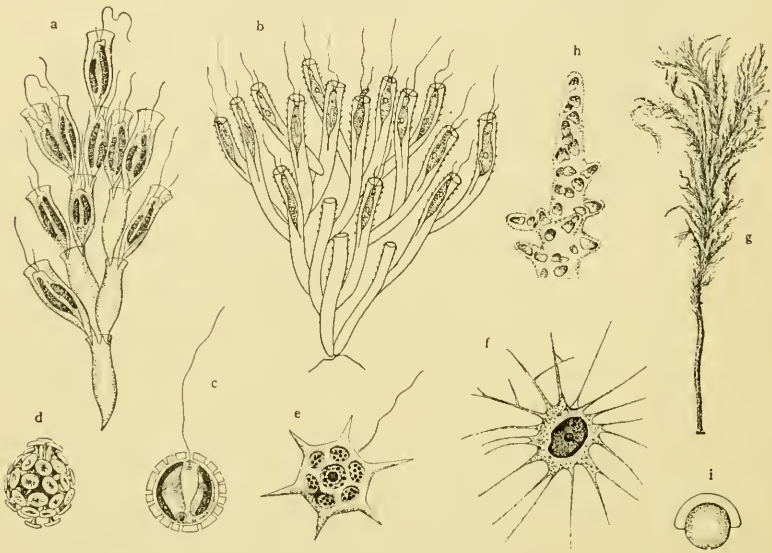


Fig. 31 a. *Dinobryon sertularia.* ×500 (After Scherffel and Senn).
b. *Hyalobryon ramosum.* ×400 (After Lauterborn).
c. *Pontosphaera haeckeli.* ×800 (After Kühn).
d. *Discosphaera tubifer.* ×500 (After Kühn).
e. *Distephanus speculum.* ×400 (After Kühn).
f. *Rhizochrysis scherffeli.* ×500 (After Doflein).
g–i. *Hydrurus foetidus.* g, an entire colony (after Berthold); h, a portion (×250 after Klebs); i, cyst (×600 after Klebs).

Suborder 2 **Rhizochrysidina** Pascher

No flagellate stage is known to occur. The organism possesses pseudopodia. Highly provisional group, based wholly upon the absence of flagella. Naked or with test; various forms. In some species chromatophores are entirely lacking, so that the organisms resemble some members of the Sarcodina. Several genera.

Genus **Rhizochrysis** Pascher. Body naked and amoeboid; with one or two chromatophores.

Rhizochrysis scherffeli Pascher (Fig. 31, *f*).

Suborder 3 **Chrysocapsina** Pascher

Palmella stage is prominent. Flagellate forms are transient. Colonial; individuals are enclosed in a gelatinous mass. One or two flagella, one chromatophore, and a contractile vacuole are typically present in each individual. One group of relatively minute forms and the other of large organisms. Among the latter, *Hydrurus foetidus* Kirchner (Figs. 15, *d–f;* 31, *g–i*) is conspicuous in having a large palmella stage, which may be cylindrical or dendritic, and which may grow from one to thirty centimeters long. Individuals are arranged loosely in the gelatinous matrix. Apical growth resembles much higher algae. Multiplication of individuals results in formation of pyramidal forms with a flagellum, a chromatophore, and a leucosin mass. The encysted stage may show a wing-like rim.

References

Calkins, G. N. 1926 The biology of the Protozoa. Philadelphia.

Doflein, F. and E. Reichenow. 1929 Lehrbuch der Protozoenkunde. Jena.

Kühn, A. 1921 Morphologie der Tiere in Bildern. I. H.; I Teil. Berlin.

Stokes, A. C. 1888 A preliminary contribution toward a history of the freshwater Infusoria of the United States. Jour. Trenton Nat. Hist. Soc., Vol. 1.

Geitler, L. 1926 Zur Morphologie und Entwickelungsgeschichte der Pyrenoide. Arch f. Protistenk., Vol. 56.

Lohmann, H. 1913 Ueber Coccolithophoriden. Verh. Deutsch. Zool. Ges., Bremen.

Pascher, A. 1913 Chrysomonadinae. Süsswasserflora Deutschlands, etc. Jena.

West, G. S. and F. E. Fritsch. 1927 A treatise on the British freshwater algae. Cambridge.

CHAPTER VI

ORDER 2 **CRYPTOMONADIDA** STEIN

THE CRYPTOMONADIDA differ from the Chrysomonadida in having a constant body form. Pseudopodia are very rarely formed, as the body surface is covered by a pellicle. The majority show dorso-ventral differentiation, with an oblique longitudinal furrow. One or two unequal flagella arise from the furrow or from the cytopharynx. In case two flagella are present, both may be directed anteriorly or one posteriorly. These organisms are free-swimming or creeping.

One or two chromatophores are usually present. They are discoid or band-form, and may be green, bluish green, blue, yellow, brown, reddish brown, or red. The nature of the coloring matter is not well understood, but it is said to be similar to that which is found in the Dinoflagellida and diatoms. One or more spherical pyrenoids which are enclosed within an envelope of amyloid substance are present. Nutrition is mostly holophytic; a few saprozoic or holozoic. Assimilation products are amyloid substances; fat and oil are produced in holozoic forms which feed upon bacteria and small Protozoa. The stigma is usually associated with the insertion point of the flagella. Contractile vacuoles, one or several, are simple and are situated near the cytopharynx. A single vesicular nucleus is ordinarily located near the middle of the body.

Asexual reproduction, by longitudinal fission, takes place in either the active or the non-motile stage. Sexual reproduction is unknown. Some members form palmella stages and others gelatinous aggregates. In the suborder Phaeocapsina, the palmella stage is permanent. Cysts are spherical, and the cyst wall is composed of cellulose. The Cryptomonadida abound in sea water, living also often as symbionts in marine organisms. A comparatively few forms are found in fresh water. According to Pascher, they are divided into two suborders:

Motile flagellate forms predominant.........Suborder 1 Eucryptomonadina
Palmella stage permanent.......................Suborder 2 Phaeocapsina

Suborder 1 **Eucryptomonadina** Pascher

Anterior end truncate; two anterior flagella; with an oblique furrow near anterior end . . . . Family 1 Cryptomonadidae

Reniform; with two lateral flagella; furrow equatorial . . . . Family 2 Nephroselmidae

Family 1 **Cryptomonadidae** Stein

Genus **Cryptomonas** Ehrenberg. Body elliptical with a firm pellicle. Anterior end truncate. Longitudinal furrow large, extending to the middle of the body, through which two equally long flagella arise. Two lateral chromatophores vary in color from green to blue green, brown, or rarely red. Holophytic; paramylum bodies. Fresh and salt waters.

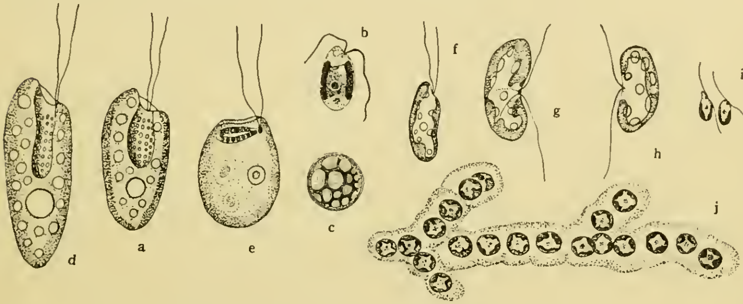


Fig. 32 a. *Cryptomonas ovata.* ×500 (After Doflein, modified).
b, c. *Chrysidella schaudinni.* ×1000 (After Winter).
d. *Chilomonas paramecium.* ×500 (After Doflein, modified).
e. *Cyathomonas truncata.* ×500 (After Doflein, modified).
f. *Cryptochrysis commuta.* ×500 (After Pascher).
g. *Protochrysis phaeophycearum.* ×600 (After Pascher).
h. *Nephroselmis olivacea.* ×500 (After Pascher).
i, j. *Phaeothamnion confervicolum.* ×450 (After Kühn).

Cryptomonas ovata Ehrenberg (Fig. 32, *a*). Length about 30 to 40 microns. Widely distributed among vegetation in fresh water.

Genus **Chrysidella** Pascher. Somewhat similar to Cryptomonas, but much smaller. Chromatophores much shorter. Those occurring in Foraminifera or Radiolaria as symbionts are known as Zooxanthellae. Several species.

Chrysidella schaudinni (Winter) (Fig. 32, *b*, *c*). Body less than 10 microns long. In the foraminiferan, *Peneroplis pertusus*.

Genus **Chilomonas** Ehrenberg. Similar to Cryptomonas in general body form and structure, but colorless because of the absence of chromatophores. With numerous assimilation products, amyloid bodies. Saprozoic.

Chilomonas paramecium Ehrenberg (Fig. 32, *d*). Length 30 to 50 microns. Very common in stagnant water and also in hay infusion. Widely distributed.

Genus **Cyathomonas** Fromentel. Body small, somewhat oval, much flattened. Anterior end obliquely truncate. With two equal or subequal anterior flagella. Colorless. The nucleus central; contractile vacuole usually anterior. A row of refractile granules close and parallel to the anterior margin of the body. Asexual reproduction by longitudinal fission. In stagnant water and infusion.

Cyathomonas truncata Ehrenberg (Fig. 32, *e*). Length about 20 microns. Often in infusion.

Genus **Cryptochrysis** Pascher. Furrow indistinct. Chromatophore brownish or olive-green. Some lose flagella and may assume amoeboid form. Two equal flagella.

Cryptochrysis commutata Pascher (Fig. 32, *f*). About 20 microns long. Fresh water.

Family 2 **Nephroselmidae** Pascher

Body reniform; with lateral equatorial furrow. Two flagella arising from the furrow, one directed anteriorly and the other posteriorly. Several genera.

Genus **Protochrysis** Pascher. Body with a distinct furrow, but without cytopharynx. A stigma at the base of the flagella. One or two chromatophores, brownish yellow. Pyrenoid central; two contractile vacuoles. Fission seems to take place during the resting stage.

Protochrysis phaeophycearum Pascher (Fig. 32, *g*). Body about 17 to 20 microns long.

Genus **Nephroselmis** Stein. Furrow indistinct; no stigma; cytopharynx distinct. Chromatophores discoid, brownish green in color. A central pyrenoid; with reddish globules.

Nephroselmis olivacea Stein (Fig. 32, *h*). 20 to 25 microns long.

Suborder 2 **Phaeocapsina** Pascher

Palmella stage predominant. These organisms are perhaps the border-line forms between brown algae and Cryptomonadida. Example: *Phaeothamnion confervicolum* Lagerheim (Fig. 32, *i*, *j*) which is less than 10 microns long.

References

Pascher, A. 1913 Cryptomonadinae. Süsswasserflora Deutschlands, etc. H. 2.

West, G. S. and F. E. Fritsch. 1927 A treatise on the British freshwater algae. Cambridge.

CHAPTER VII

ORDER 3 **DINOFLAGELLIDA** BÜTSCHLI

THE DINOFLAGELLIDA form one of the most distinct groups of the Mastigophora, inhabiting mostly marine water, and to a lesser extent fresh water. The modern tendency is to hold this group as an order of the Phytomastigina. In the general appearance, the arrangement of the two flagella, the characteristic furrows, and possession of brown chromatophores, the Dinoflagellida are closely related to the Cryptomonadida.

The body is covered by an envelope composed of cellulose. It may be simple smooth membrane, or it may be composed of two valves or of numerous plates, which are variously sculptured and possess manifold projections. Differences in the position and course of the furrow and in the projections of the envelope produce numerous asymmetrical forms. The furrows, or grooves, are a transverse **annulus** and a longitudinal **sulcus.** The annulus is a girdle around the middle or toward one end of the body. It may be a complete or incomplete ring or some-

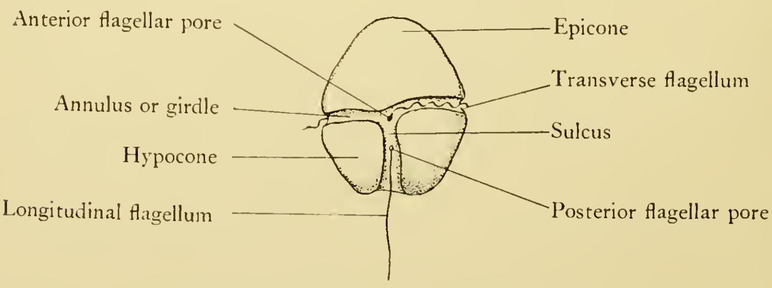


Fig. 33 Diagram of typical naked dinoflagellate. (After Lebour).

times spiral. While the majority show a single transverse furrow, a few may possess several. The part of the shell anterior to the annulus is called the **epitheca** and that posterior to the annulus the **hypotheca.** In case the envelope is not developed, the terms **epicone** and **hypocone** are used (Fig. 33). The sulcus may run from end to end or from one end to the annulus. The two flagella arise typically from the annulus, one being transverse and the other longitudinal.

The **transverse flagellum** which is often band-form, encircles the body and undergoes undulating movements, which in former years were looked upon as ciliary movements (hence the discarded name Cilioflagellata). In the suborder Adinida, this flagellum vibrates freely in a circle near the anterior end. The **longitudinal flagellum** often projects beyond the body and vibrates. Combination of the movements of these flagella produces whirling movements characteristic of the organisms.

The majority of Dinoflagellida possess a single somewhat massive nucleus with achromatic network, evenly scattered chromatin, and usually several endosomes. There are two kinds of vacuoles. One is often surrounded by a ring of smaller vacuoles and the other is large and opens to the exterior by a canal. The latter is known as the **pusule,** and its function is supposed to be hydrostatic. In many forms a stigma is present, and in some it is provided with an amylaceous lens and a dark pigment-ball. The majority of planktonic forms possess a large number of small chromatophores which are usually brownish or often slightly greenish and are located in the periphery of the body. Bottom-dwelling and parasitic forms are often colorless, because of absence of chromatophores. A few contain haematochrome. The method of nutrition is holophytic, holozoic, saprozoic, or mixotrophic. In holophytic forms, starch and fats are widely distributed.

Asexual reproduction is by binary or multiple fission in either the active or the resting stage. The mode of division differs among different groups. Encystment is of common occurrence. In some forms the cyst wall is formed within the test. The cysts remain alive for many years. In one instance, Ceratium cysts were found to retain their vitality after six and one-half years. Conjugation and copulation have been reported in certain forms, but definite knowledge on sexual reproduction awaits further investigation.

The Dinoflagellida are abundant in the plankton of the sea and play an important part in the economy of marine life as a whole. A number of parasitic forms are also known. Their hosts include various diatoms, copepods and several pelagic animals. The group is divided into three suborders as follows:

Naked or with bivalve shell; without annulus or sulcus. .Suborder 1 Adinida
Naked or with test; annulus and sulcus present at some stage........
Suborder 2 Dinifera
Naked without annulus or sulcus; without transverse flagellum........
Suborder 3 Cystoflagellata

Suborder 1 **Adinida** Bergh

Test bivalve; without any groove; with yellow chromatophores. Two flagella arise from the anterior end; one directed anteriorly, the other vibrates in a circle. Fresh and salt waters. Several genera.

Genus **Exuviaella** Cienkowski. Subspherical or oval. No anterior projection, except two flagella. Two lateral chromatophores, large brown, each with a pyrenoid and an amylum body. Nucleus posterior. Marine. Several species.

Exuviaella marina Cienkowski (Fig. 34, *a*, *b*). About 80 microns long.

Genus **Prorocentrum** Ehrenberg. Elongated oval; anterior end is bluntly pointed, with a spinous projection at the end. Chromatophores small, yellowish brown. Marine.

Prorocentrum micans Ehrenberg (Fig. 34, *c*). About 50 microns long. The cause of "red water."

Suborder 2 **Dinifera** Bergh

Typical Dinoflagellida with one to many transverse annuli and a sulcus. There are two flagella, one of which undergoes a typical undulating movement, while the other is usually directed posteriorly. According to Kofoid and Swezy, this suborder is divided into two tribes.

Body covered by a thick shell......................Tribe 1 Peridinioidae
Body naked or covered by a thin shell............Tribe 2 Gymnodinioidae

Tribe 1 **Peridinioidae** Kofoid and Swezy

The shell is composed of epitheca, girdle, and hypotheca, which may be divided into numerous plates. Body form various.

With annulus and sulcus
  Shell composed of plates; but no suture..........Family 1 Peridiniidae
  Breast plate divided by sagittal suture ....Family 2 Dinophysidae
Without annulus or sulcus.......................Family 3 Phytodiniidae

Family 1 **Peridiniidae** Bergh

The shell is composed of numerous plates. The annulus is usually at the equator and covered by a plate known as the **cingulum.** The plates which are variously sculptured and finely perforated vary in shape and number among different species.

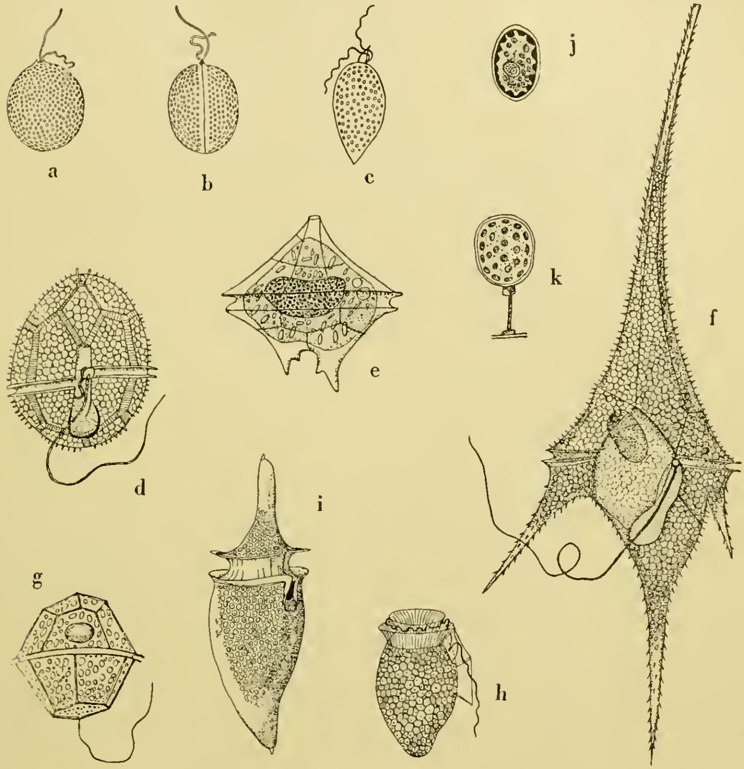


Fig. 34 a, b. *Exuviaella marina.* ×250 (After Schütt).
c. *Prorocentrum micans.* ×250 (After Schütt).
d. *Peridinium tabulatm.* ×500 (After Stein).
e. *P. divergens.* ×500 (After Calkins).
f. *Ceratium hirundinella.* ×400 (After Stein).
g. *Goniodoma acuminatum.* ×325 (After Stein).
h. *Dinophysis acuta.* ×430 (After Schütt).
i. *Oxyphysis oxytoxoides.* ×580 (After Kofoid).
j. *Phytodinium simplex.* ×250 (After Klebs).
k. *Stylodinium globosum.* ×225 (After Doflein).

In many species, some of the plates are drawn out into various processes, varying greatly in different seasons and localities even among one and the same species. These processes seem to retard the descending movement of the organisms from the upper to the lower level in the ocean when the flagellar activity ceases. The chromatophores are in the form of numerous small platelets and yellow or green in color. In some deep-sea forms, chromatophores do not occur. Chain formation by multiplication through fission occurs in some forms. Surface and pelagic forms inhabiting fresh and salt waters. Several genera.

Genus **Peridinium** Ehrenberg. Subspherical to ovoid; end-view reniform. Annulus slightly spiral with projecting rims. Often hypotheca with short horns and epitheca drawn out. Colorless, green or brown; stigma usually present. Cysts spherical. Salt or fresh water. Numerous species.

Peridinium tabulatum Claparède and Lachmann (Fig. 34, *d*). Fresh water form. Diameter about 45 microns.

Peridinium divergens (Ehrenberg) (Fig. 34, *e*). Salt water. Color yellow. Diameter about 45 microns.

Genus **Ceratium** Schrank. Body somewhat compressed; with one anterior and one to four posterior horn-like processes. Often large. Chromatophores are yellow, brown or greenish; color variation is conspicuous even among the one and the same species. Fission is said to take place at night and in the early morning. Numerous species. Specific identification is difficult due to a great variation. Fresh or salt water.

Ceratium hirundinella Müller (Fig. 34, *f*). Spinous projections on the shell. Seasonal and geographical variations. Chain-formation frequent. Length 150 to 250 microns and breadth 40 to 80 microns. Fresh water.

Genus **Goniodoma** Stein. Body polyhedral with a deep annulus. Epitheca and hypotheca slightly unequal in size, composed or regularly arranged armored plates. Chromatophores small brown platelets. Marine.

Goniodoma acuminatum (Ehrenberg) (Fig. 34, *g*). About 50 microns long.

Family 2 **Dinophysidae** Stein and Bergh

The epitheca is flattened and smaller than the hypotheca.

The annulus possesses elevated rims. Marine. Several genera.

Genus **Dinophysis** Ehrenberg. Body compressed. Chromatophores yellow. Marine.

Dinophysis acuta Ehrenberg (Fig. 34, *h*). Length about 45 microns. Widely distributed.

Genus **Amphisolenia** Stein. Epitheca is very small and composed of two plates; the large hypotheca, composed also of two elongated plates. Chromatophore unknown. In warm sea water.

Amphisolenia clavipes Kofoid.

Genus **Oxyphysis** Kofoid. Epitheca well developed; sulcus short; sulcal lists feebly developed. Annulus impressed. Pelagic in the sea.

Oxyphysis oxytoxoides Kofoid (Fig. 34, *i*).

Family 3 **Phytodiniidae** Klebs

Without grooves or flagella. Chromatophores yellow-brown. A very ill-defined group containing no definite characters of the order. Several genera in fresh or salt water.

Genus **Phytodinium** Klebs. Body spherical or ellipsoidal; chromatophores discoidal.

Phytodinium simplex Klebs (Fig. 34, *j*). In fresh water.

Genus **Stylodinium** Klebs. Body ovoidal with a stalk.

Stylodinium globosum Klebs (Fig. 34, *k*). About 40 microns long. Fresh water.

Tribe 2 **Gymnodinioidae** Poche

Naked or covered by a single piece cellulose membrane with the longitudinal and transverse furrows, and two flagella. Chromatophores which are mostly abundantly present are yellow or greenish platelets or bands. Stigma is sometimes present. Asexual reproduction in the active phase is binary fission, while that in the encysted condition is either binary or multiple division. Nutrition is holophytic, holozoic, saprozoic, or parasitic. The majority are deep-sea forms; a few coastal or fresh water forms also occur.

This tribe is divided into the following families:

With a cellulose membrane........................Family 1 Glenodiniidae
Without shell

Furrows rudimentary . . . . Family 2 Pronoctilucidae
Annulus and sulcus distinct
  Solitary
    With ocellus . . . . Family 3 Pouchetiidae
    Without ocellus
      With tentacles . . . . Family 4 Noctilucidae
      Without tentacles
        Free-living . . . . Family 5 Gymnodiniidae
        Parasitic . . . . Family 6 Blastodiniidae
  Permanently colonial . . . . Family 7 Polykrikidae

Family 1 **Glenodiniidae** Lebour

Shell composed of epitheca, annulus, and hypotheca; not divided into plates nor marked by sutures. Chiefly freshwater forms. One genus.

Genus **Glenodinium** Ehrenberg. Body spherical; ellipsoidal or reniform in end-view; several discoidal yellow to brown chromatophores. Horseshoe- or rod-shaped stigma.

Glenodinium uliginosum Schilling (Fig. 35, *a*). 36 to 43 microns long. Fresh water.

Family 2 **Pronoctilucidae** Lebour

(=Protodiniferidae Kofoid and Swezy)

Genus **Pronoctiluca** Fabre-Domergue. Body with an anterior tentacular process and sulcus; annulus poorly marked. Marine.

Pronoctiluca tentaculatum (Kofoid and Swezy) (Fig. 35, *b*). About 54 microns long. Marine.

Genus **Oxyrrhis** Dujardin. Body oval, asymmetrical posteriorly. Girdle incomplete. Marine.

Oxyrrhis marina Dujardin (Fig. 35, *c*). Body 22 to 32 microns long.

Family 3 **Pouchetiidae** Kofoid and Swezy

Ocellus consists of lens and melanosome (pigment mass). Sulcus and annulus somewhat twisted. Pusules usually present. Pelagic. Several genera.

Genus **Pouchetia** Schütt. Nucleus anterior to ocellus. Cytoplasm is colored. Holozoic. Cyst frequent. Pelagic.

Pouchetia fusus Schütt (Fig. 35, *d*). About 100 microns long.

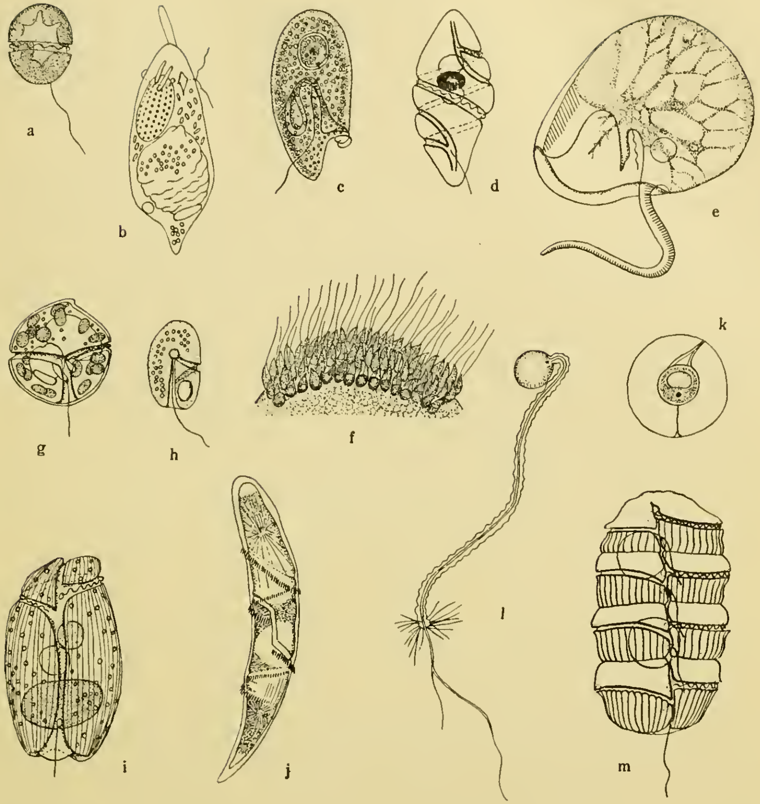


Fig. 35 a. *Glenodinium uliginosum.* ×250 (After West).
b. *Pronoctiluca tentaculatum.* ×550 (After Kofoid and Swezy).
c. *Oxyrrhis marina.* ×625 (After Senn).
d. *Pouchetia fusus.* ×250 (After Schütt from Kofoid and Swezy).
e, f. *Noctiluca scintillans.* e, profile (×60 after Allman from Kofoid and Swezy); f, exogenous budding (×100 after Robin).
g. *Gymnodinium agile.* ×550 (After Kofoid and Swezy).
h. *Hemidinium nasutum.* ×500 (After Stein).
i. *Amphidinium scissum.* ×660 (After Kofoid and Swezy).
j. *Blastodinium spinulosum.* ×180 (After Chatton).
k. *Chytriodinium parasiticum* in a copepod egg. (After Dogiel).
l. *Apodinium mycetoides.* ×475 (After Chatton).
m. *Polykrikos kofoidi.* ×250 (After Kofoid).

Family 4 **Noctilucidae** Kent

The somewhat contractile tentacle arises from the sulcal area and extends posteriorly. Formerly this group had been included in the Cystoflagellata. Studies by recent investigators, particularly Kofoid, show their affinities with the present suborder. Holozoic. Marine.

Genus **Noctiluca** Suriray. Body spherical, bilaterally symmetrical. Peristome marks the median line of the body. A cytostome at the bottom of peristome. With a distinct tentacle. The cytoplasm is much vacuolated, and cytoplasmic strands connect the central mass with the periphery. Colorless or blue-green, sometimes tinged with yellow coloration in the center. Swarmers are formed by budding, and each possesses one flagellum, girdle, and tentacle. Widely distributed in salt water. One species.

Noctiluca scintillans (Macartney) (= *N. miliaris* Suriray) (Fig. 35, *e, f*). Usually 500 to 1000 microns in diameter, with the extremes of 200 microns and 2mm.

Family 5 **Gymnodiniidae** Kofoid

Naked form with simple but distinct furrows. Several genera in fresh or marine water

Genus **Gymnodinium** Stein. Ordinarily naked, subcircular; numerous discoid chromatophores vari-colored (yellow to deep brown, green, or blue) or sometimes absent. Stigma occasionally present. Longitudinal fission in active form; cyst with a mucilaginous or firm envelope. Marine, brackish, or fresh water.

Gymnodinium agile Kofoid and Swezy (Fig. 35, *g*). About 28 microns long. In sandy beaches.

Genus **Hemidinium** Stein. Body oval; girdle about half a turn.

Hemidinium nasutum Stein (Fig. 35, *h*). Oval, assymetrical. Sulcus on hypocone. Chromatophores yellow or brown. Nucleus posterior. Transverse fission. 24 to 28 microns long. Fresh or brackish water.

Genus **Amphidinium** Claparède and Lachmann. Variable form; epicone small, girdle near the anterior end; sulcus straight on hypocone or also on part of epicone. With or without chromatophores Mainly holophytic, some holozoic Coastal or fresh water. Numerous species.

Amphidinium scissum Kofoid and Swezy (Fig. 35, *i*). Length 50 to 60 microns. In sandy shore.

Family 6 **Blastodiniidae** Kofoid and Swezy

All parasitic in or on plants and animals. Numerous genera.

Genus **Blastodinium** Chatton. Parasitic in the alimentary canal of Copepoda. Spindle-shaped, binucleated. The envelope which is not of cellulose nature often with two spirally arranged bristles. Spiral furrows. Chromatophores are often in yellowish brown network.

Blastodinium spinulosum Chatton (Fig. 35, *j*). In copepods of the genera Paracalanus and Clausocalanus.

Genus **Chytriodinium** Chatton. Parasitic in eggs of plankton copepods. Young individuals grow at the expense of host's egg and when fully formed, the body divides into numerous parts, each producing four swarmers.

Chytriodinium parasiticum (Dogiel) (Fig. 35, *k*). In copepod egg.

Genus **Oodinium** Chatton. Ovoid or spherical body with a short stalk. Ectoparasitic on Salpa, Annelida, Siphonophora, etc.

Genus **Apodinium** Chatton. With a much longer filiform stalk and with two nuclei (Fig. 35, *l*). Ectoparasitic.

Genus **Haplozoon** Dogiel. Parasitic in the intestine of polychaetes. *Haplozoon clymenellae* (Calkins) in *Clymenella torquata.*

Family 7 **Polykrikidae** Kofoid and Swezy

Two, four, or eight individuals permanently jointed. Each individual has a structure similar to Gymnodinium, the sulcus however extending the entire length. Color greenish to pink. Nuclei about one-half the number of individuals. Holozoic.

Genus **Polykrikos** Bütschli. With the above-mentioned characters

Polykrikos kofoidi (Chatton) (Fig. 35, *m*). Body greenish grey to rose in color. Composed of two, four, eight, or sixteen individuals. The cytoplasm contains nematocysts. Each nematocyst possesses presumably a hollow thread, and is discharged under suitable stimulation. A binucleate colony composed of four individuals measures about 110 microns long. Marine.

Suborder 3 **Cystoflagellata** Haeckel

Since Noctiluca which has been for many years placed in this suborder, is removed, according to Kofoid, into the second suborder, the Cystoflagellata become a highly ill-defined group. It includes two peculiar marine forms: *Leptodiscus medusoides*

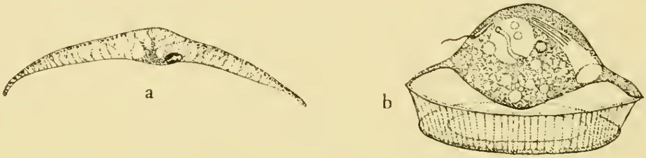


Fig. 36 a. *Leptodiscus medusoides*, profile. ×50 (After Hertwig).
b. *Craspedotella pileolus*. ×110 (After Kofoid).

Hertwig (Fig. 36, *a*), and *Craspedotella pileolus* Kofoid (Fig. 36, *b*), both of which are medusoid in general body form.

References

Chatton, E. 1920 Les Péridiniens parasites; morphologie, reproduction, ethologie. Arch. Zool. Exper., T. 59.

Kofoid, C. A. 1906 On the significance of the asymmetry of the Dinoflagellata. University of California Publ. Zool., Vol. 3.

———. 1920 A new morphological interpretation of Noctiluca and its bearing on the status of Cystoflagellata. Ibid., Vol. 19.

Kofoid, C. A. and Olive Swezy. 1921 The free-living unarmored dinoflagellata. Mem. Uni. California, Vol. 5.

Lebour, Marie V. 1925 The dinoflagellates of northern seas. London.

Pratje, A. 1921 *Noctiluca miliaris* Sur. Arch. f. Protistenk., Vol., 42.

Schilling, A. 1913 Dinoflagellatae (Peridineae). Süsswasserflora Deutschlands. etc. H. 3.

CHAPTER VIII

ORDER 4 **PHYTOMONADIDA** BLOCHMANN

THE PHYTOMONADIDA are small, more or less rounded, green flagellates with a close resemblance to the algae. All of them have a definite body form, and most of them are surrounded by a cellulose membrane, which is thick in some and thin in others. There is a definite opening in the membrane at the anterior end, through which one or two (or seldom four or more) flagella protrude. The majority possess numerous grass-green chromatophores, each of which contains one or more pyrenoids. The method of nutrition is mostly holophytic or mixotrophic; some colorless forms are, however, saprozoic. The metabolic products are usually amyloid substances. Some Phytomonadida are stained red, owing to the presence of haematochrome, or carotin. The contractile vacuoles may be located in the anterior part or scattered throughout the body. The nucleus is ordinarily centrally located. The nuclear division seems to be mitotic, and chromosomes have been definitely noted in several species.

Asexual reproduction is by longitudinal fission, and the daughter individuals remain within the parent membrane for some time. Sexual reproduction seems to occur widely. Isogamy or anisogamy takes place with various gradations. Colony formation also occurs, especially in the family Volvocidae. Encystment and formation of the palmella stage are common among many forms.

The Phytomonadida are divided into five families:

Without cellulose membrane; four or more flagella..................
Family 1 Polyblepharidae
With cellulose membrane
  Membrane a single piece
    With chromatophores
      Two or four flagella; solitary.........Family 2 Chlamydomonadidae
      Two flagella; colonial.........................Family 3 Volvocidae
    Without chromatophores.......................Family 4 Polytomidae
  Membrane composed of two valves................Family 5 Phacotidae

Family 1 **Polyblepharidae** Dangeard

Flagella are four or more in number. Lacking a cellulose membrane, the body form changes to a certain extent. Found mostly in salt water. Common genera are as follows:

Genus **Pyramimonas** Schmarda (=Pyramidomonas Stein). Small pyramidal or heart-shaped body; with bluntly drawn-out posterior end. There are usually four ridges in the anterior region. Four flagella; green chromatophores cup-shaped; with or without stigma; with a large pyrenoid in the posterior part. Contractile vacuoles in the anterior portion. Fresh water.

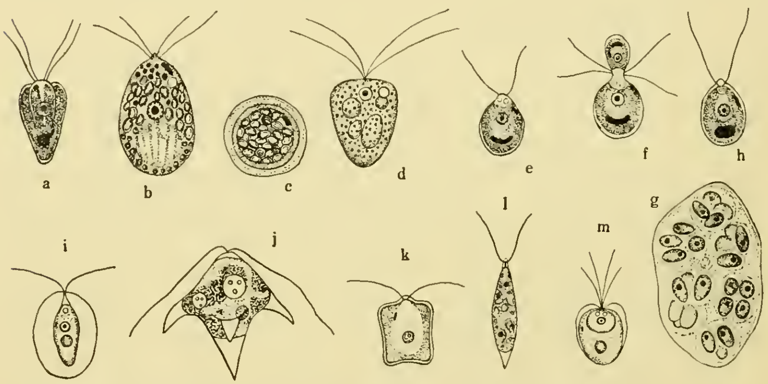


Fig. 37 a. *Pyramimonas tetrarhynchus*. ×300 (After Dill).
b, c. *Polytomella agilis*. ×750 (After Doflein).
d. *Collodictyon triciliatum*. ×300 (After Carter).
e–g. *Chlamydomonas monadina*. ×350 (After Goroschankin).
f, copulation; g, palmella phase.
h. *C. angulosa*. ×350 (After Dill).
i. *Haematococcus lacustris*. ×325 (After Stein).
j. *Brachiomonas submarina*. ×720 (After West).
k. *Lobomonas pentagonia*. ×830 (After Hazen).
l. *Chlorogonium euchlorum*. ×320 (After Jacobsen).
m. *Carteria cordiformis*. ×325 (After Stein).

Pyramimonas tetrarhynchus Schmarda (Fig. 37, *a*). Up to 40 microns in length.

Genus **Polytomella** Aragão. Body colorless, rounded with a small papilla at the anterior end, where four equally long flagella arise. Starch; with or without stigma. Encystment.

Polytomella agilis Aragão (Fig. 37, *b*, *c*). With stigma and numerous starch grains. Fresh water.

Genus **Collodictyon** Carter. Colorless. With pseudopodia. Holozoic.

Collodictyon triciliatum Carter (Fig. 37, *d*). About 35 microns long. Fresh water.

Genus **Medusochloris** Pascher. With four flagella; medusoid in form and movement. *Medusochloris phiale* Pascher.

Family 2 **Chlamydomonadidae** Bütschli

Solitary; spheroid, oval, or ellipsoid in form; with a cellulose membrane. Two or rarely four flagella. Chromatophores, stigma, and pyrenoids are usually present.

Genus **Chlamydomonas** Ehrenberg. Spherical, ovoid or elongated; sometimes flattened. Two flagella. The membrane is often thickened at the anterior end. Usually a large chromatophore, containing one or more pyrenoids. Stigma. A single nucleus. Contractile vacuoles two in number at the anterior end. Asexual reproduction and palmella formation are known. Sexual reproduction is isogamy. Enormous number of species.

Chlamydomonas monadina Stein (Fig. 37, *e-g*). Body about 20 microns long. Fresh water. Landacre noted that the organisms obstructed the sand filters used in connection with a septic tank, together with the diatom Navicula.

Chlamydomonas angulosa Dill (Fig. 37, *h*). Body about 15 to 20 microns. Fresh water.

Genus **Haematococcus** Agardh (=Sphaerella Sommerfeldt). Spheroidal or ovoid with a gelatinous envelope. Chromatophores peripheral and reticulate, with two to eight scattered pyrenoids. Several contractile vacuoles. Haematochrome is frequently abundant both in motile and in encysted stages. Asexual reproduction in motile form; sexual reproduction is isogamy.

Haematococcus lacustris (Girod) (Fig. 37, *i*). Body small, 8 to 30 microns long. Brick red; cysts are similarly colored. The cause of "red snow" or "red rain."

Genus **Brachiomonas** Bohlin. Lobate; with horn-like processes, all directed posteriorly; no contractile vacuoles. Ill-defined chromatophores parietal; with pyrenoids. Sexual and asexual reproduction.

Brachiomonas submarina Bohlin (Fig. 37, *j*). Body 15 to 24 microns long. Fresh water.

Genus **Lobomonas** Dangeard. Ovoid or angular with a thick wall and a number of processes. Chromatophores cup-shaped; one pyrenoid. Asexual and sexual reproduction.

Lobomonas pentagonia Hazen (Fig. 37, *k*). About 20 microns long. In fresh or brackish water.

Genus **Chlorogonium** Ehrenberg. Fusiform. Membrane thin and adheres closely to the protoplasmic body. Plate-like chromatophores usually present, sometimes ill-contoured. Four pyrenoids. Numerous scattered contractile vacuoles. A stigma; a central nucleus. Asexual reproduction by two successive transverse fissions during motile phase. Anisogamy reported.

Chlorogonium euchlorum Ehrenberg (Fig. 37, *l*). Length up to 50 microns. In stagnant water.

Genus **Carteria** Diesing. With the characteristics of Chlamydomonas, but with four flagella. Fresh water.

Carteria cordiformis (Carter) (Fig. 37, *m*). Body somewhat heart-shaped, length 10 to 20 microns.

Family 3 Volvocidae Ehrenberg

An interesting group of colonial flagellates. The individual is similar on the whole to that of Chlamydomonadidae, with two equally long flagella (four in Spondylomorum), green chromatophores, pyrenoids, stigma, and contractile vacuoles. The body is covered by a cellulose membrane and not plastic. The colony or **coenobium** is discoid or spherical. Exclusively freshwater inhabitants.

Genus **Gonium** Müller. Four or sixteen individuals arranged in one plane. Each cell ovoid or slightly polygonal, possesses two flagella which are arranged in the plane of the coenobium, and may or may not be covered by a gelatinous envelope. Protoplasmic connections among individuals occur frequently. Asexual reproduction through simultaneous divisions of the component cells. Sexual reproduction is isogamy and the zygotes are reddish in color.

Gonium sociale (Dujardin) (Fig. 38, *a*, *b*). Four individuals, 10 to 20 microns long, form a colony. In open water of ponds and lakes.

Gonium pectorale Müller (Fig. 38, *c*). Sixteen individuals form a colony; four individuals in the center; twelve peripheral. Individuals 7 to 11 microns long. In stagnant water of ponds and ditches.

Genus **Platydorina** Kofoid. Cells arranged in a slightly twisted plane. Flagella directed alternately to both sides.

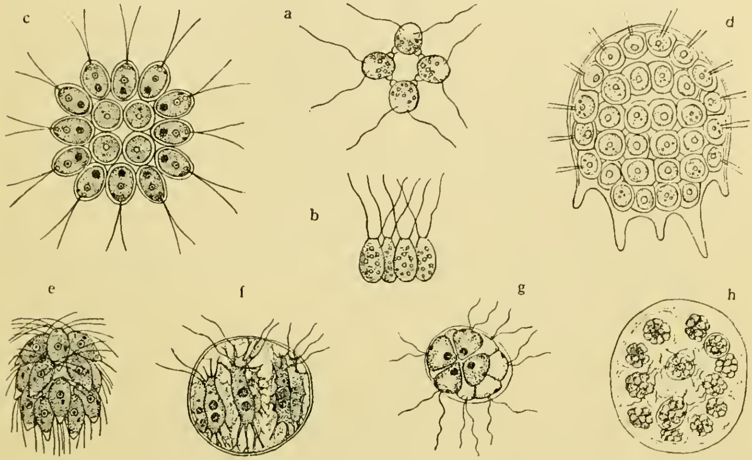


Fig. 38 a, b. *Gonium sociale.* ×320 (After Fritsch).
c. *G. pectorale.* ×240 (After Stein).
d. *Platydorina caudata.* × about 210 (After Kofoid).
e. *Spondylomorum quaternarium.* ×250 (After Stein).
f. *Stephanosphaera pluvialis.* ×190 (After Hieronymus).
g, h. *Pandorina morum.* ×200 (After Pringsheim).
h, a stage in asexual reproduction.

Platydorina caudata Kofoid (Fig. 38, *d*). Found in rivers and lakes. About 150 microns long by 130 microns wide.

Genus **Spondylomorum** Ehrenberg. Individuals similar to Carteria, but colonial. Sixteen individuals all directed anteriorly and arranged in four transverse rings. Asexual reproduction by simultaneous divisions of the component cells. Sexual reproduction unknown. Fresh water.

Spondylomorum quaternarium Ehrenberg (Fig. 38, *e*). About 45 microns long. In fresh water and soil.

Genus **Stephanosphaera** Cohn. Spherical colony, with eight individuals arranged in a ring. Flagella upon one face only. Individuals are pyriform with several processes. Asexual reproduction and isogamy. Fresh water.

Stephanosphaera pluvialis Cohn (Fig. 38, *f*). Diameter 30 to 60 microns. Fresh water.

Genus **Pandorina** Bory. Spherical or subspherical colony of usually sixteen (sometimes eight or thirty-two) biflagellate individuals which are closely packed within a gelatinous, but firm and thick matrix. Individuals are often angular. With stigma and chromatophores. Asexual reproduction through simultaneous division of each of the individuals. Anisogamy is preceded by division of each cell into 16 to 32 gametes. The zygotes are colored and covered by a smooth wall.

Pandorina morum (Müller) (Fig. 38, *g*, *h*). Individuals 8 to 15 microns long. Colony 20 to 40 microns in diameter. Common in ponds and ditches.

Genus **Eudorina** Ehrenberg. Spherical or ellipsoidal colony of usually 32 or sometimes 16 spherical cells. The cells are widely separated from one another and arranged along the periphery. Four at each pole and three groups of eight in between. Each cell is similar to that of Chlamydomonas. Asexual reproduction is similar to that of Pandorina. Isogamy. Macrogametes green spherical bodies, 32 to 64 in number; microgametes are numerous and occur in bundles. The reddish zygote possesses a smooth wall.

Eudorina elegans Ehrenberg (Fig. 39, *a*). In ponds, ditches and lakes.

Genus **Pleodorina** Shaw. Somewhat similar to Eudorina, being composed of 32, 64 or 128 ovoid or spherical cells. The cells are of two types: small somatic and large generative, and are located within a gelatinous matrix.

Pleodorina illinoisensis Kofoid (Fig. 39, *b*). Thirty-two cells: 4 vegetative and 28 reproductive individuals. They are arranged in five circles: 4 in each polar circle, 8 at the equator and 8 on either side of the equator. Four small vegetative cells are at the anterior pole. Colony 100 to 140 microns long by 84 to 102 microns wide.

Pleodorina californica Shaw. 64 or 128 cells, of which from one-half to two-thirds are reproductive cells.

Genus **Volvox** Linné. Often large spherical or subspherical colonies, consisting of a large number of cells which are differentiated into somatic and reproductive cells. The former are numerous and embedded in the gelatinous matrix of colony. The somatic cell contains a chromatophore, one or more pyrenoids, a stigma and several contractile vacuoles. In some there

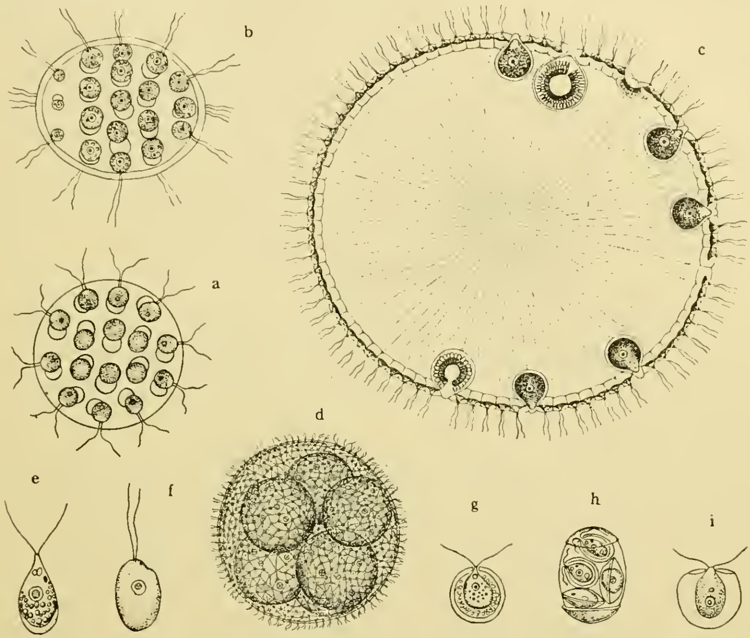


Fig. 39 a. *Eudorina elegans.* ×235 (After Goebel).
b. *Pleodorina illinoisensis.* ×150 (After Kofoid).
c. *Volvox globator.* × about 150 (After Janet).
d. *V. aureus.* ×80 (After Klein).
e. *Polytoma uvella* ×250 (After Francé).
f. *Parapolytoma satura* ×600 (After Jameson).
g, h. *Phacotus lenticularis.* ×325 (After Stein).
i. *Pteromonas angulosa.* ×500 (After West).

are protoplasmic connections between two neighboring somatic cells, in others such connections apparently do not exist. The generative cells are few and large. Both mono- and bi-sexual reproductions occur. The monosexual gametes are usually fewer and larger in size than the bisexual gametes, and each produces a young colony by repeated division. Bisexual reproduction is anisogamy. The zygotes are usually brownish red in color and their outer coverings may be smooth or spinous.

Volvox globator Leeuwenhoek (Fig. 39, *c*). Monoecious. About 700 microns in diameter. Common in European waters.

Volvox perglobator Powers. Dioecious. Diameter up to 1 mm. Common in American waters.

Volvox aureus Ehrenberg (Figs. 25; 39, *d*). Dioecious. Cytoplasmic threads are relatively thin. Diameter 200 to 800 microns.

Volvox spermatosphara Powers. Monoecious. Without any cytoplasmic connections between the cells. Diameter up to 600 microns.

Volvox tertius Meyer. Dioecious. Without cytoplasmic connections in mature state.

Family 4 **Polytomidae** Poche

These are colorless saprozoic Phytomonadida. Reserve amyloid material may occur. With two flagella located at the anterior end. Body form resembles in general way that of Chlamydomonas.

Genus **Polytoma** Ehrenberg. Body ovoid; colorless. Stigma if present red or pale-colored. Saprozoic, but numerous starch bodies are present in the posterior half of the body. Asexual reproduction in the motile stage. Sexual reproduction is isogamy. Zygotes are spherical, with a smooth wall. In infusion or stagnant water.

Polytoma uvella Ehrenberg (Fig. 39, *e*). Body oval to pyriform. Stigma may be absent. Widely distributed in water containing decaying organic substances.

Genus **Parapolytoma** Jameson. Anterior margin obliquely truncated, resembling a cryptomonad, but colorless. Stigma and starch absent. Division into four individuals within the envelope occurs.

Parapolytoma satura Jameson (Fig. 39, *f*). In fresh water. About 15 microns long.

Family 5 **Phacotidae** Poche

The thick shell is typically composed of two valves. Two flagella protrude from the anterior end. Stigma and chromatophores are present. Asexual reproduction takes place within the shell; the valves may become separated from each other owing to an increase in the gelatinous contents.

Genus **Phacotus** Perty. The valves are distinct. Body form circular in front view and lenticular in profile. The protoplasmic body does not fill the dark-colored shell completely. The flagella protrude through a foramina. Asexual reproduction into 2 to 8 individuals.

Phacotus lenticularis (Ehrenberg) (Fig. 39, *g*, *h*). In stagnant water. Body about 10 to 15 microns in diameter.

Genus **Pteromonas** Seligo. The body is broadly winged in the plane of the junction of the two valves. Protoplasmic body fills the shell. The chromatophore is cup-shaped and contains 1 to 6 pyrenoids. Asexual reproduction into 2 to 4 individuals. Sexual reproduction by isogamy. Zygotes are usually brown colored.

Pteromonas angulosa (Carter) (Fig. 39, *i*). With a rounded wing and four protoplasmic projections in profile. About 16 microns in diameter. Fresh water.

Genus **Coccomonas** Stein. The envelope is somewhat rectangular and shows a single opening at the anterior end for the flagella. Inner wall distinct. The protoplasm does not fill the space formed by the envelope. Asexual reproduction into four individuals.

Coccomonas orbicularis Stein. In ditches and ponds.

References

Crow, W. B. 1918 The classification of some colonial chlamydomonads. New Phytologist, Vol. 17.

Dangeard, P. 1900 Observations sur la structure et le développement du *Pandorina morum*. Le Botaniste, T. 7.

Entz, G. Jr. 1913 Cytologische Beobachtungen an *Polytoma uvella*. Verh. Deutsch. Zool. Ges. Ver., 23.

Janet, C. 1912, 1922, 1923 Le Volvox. I, II and III Memoires. Paris.

Kofoid, C. A. 1900 Plankton studies. Nos. 2 and 3. Ann. Mag. Nat. Hist., Ser. 7, Vol. 6.

Mast, S. O. 1928 Structure and function of the eye-spot in unicellular and colonial organisms. Arch. f. Protistenk., Vol. 60.

Pascher, A. 1927 Volvocales—Phytomonodinae. Süsswasserflora Deutschlands, etc., H. 4.

CHAPTER IX

ORDER 5 **EUGLENOIDIDA** BLOCHMANN

The Euglenoidida include many of the large flagellates of common occurrence. Some are plastic, but others have a definite body form with a well-developed, striated or variously sculptured pellicle. The body is usually elongated. At the anterior end, there is an opening through which a flagellum protrudes. In holophytic forms the so-called cytostome and the cytopharynx, if present, are apparently not concerned with food-taking, but seem to give a passage-way for the flagellum and also to excrete the waste fluid matters which become collected in the contractile vacuoles located around the reservoir.

In holozoic forms, a well-developed cytostome and cytopharynx are present. The contractile vacuoles form a complex structure and are highly characteristic of the group. There are several minute contractile vacuoles arranged around a reservoir which receives their contents, and discharges through the so-called cytopharynx. Ordinarily there is only one flagellum, but two or three are present in a few forms. Chromatophores are present only in Euglenidae and absent in the other two families. They are green and of various shapes, such as spheroidal, band-form, cup-form, discoid, or stellate. They usually contain pyrenoids. Some forms may contain haematochrome. A small but conspicuous stigma is invariably present near the anterior end of the body in chromatophore-bearing forms.

Reserve food material is the **paramylum,** the presence of which depends naturally on the metabolic condition of the organism. The paramylum body assumes diverse forms in different species, but is constant in each species, and this facilitates identification to a certain extent. Nutrition is holophytic in chromatophore-possessing forms, which, however, may be saprozoic, depending on the organic substances present in the water. The holozoic forms feed upon bacteria, algae and smaller Protozoa.

The nucleus, as a rule, is large and distinct and contains almost always a large endosome. Asexual reproduction is by longitudinal fission; sexual reproduction has been observed in a few species. Encystment is wide-spread. Most members of the group inhabit fresh water, but some live in brackish or salt water, and a few are parasitic in animals.

Following Calkins, the order is here divided into three families:

With chromatophores and stigma....................Family 1 Euglenidae
Without chromatophores or stigma
  With one flagellum............................Family 2 Astasiidae
  With two flagella.........................Family 3 Heteronemidae

Family 1 **Euglenidae** Stein

Body plastic ("euglenoid"), but, as a rule, more or less spindle-shaped during movement. The majority possess a single flagellum (with the exception of Eutreptia and Euglenamorpha) which arises in an opening at the anterior end. Green (sometimes red) chromatophores and stigma occur, though in some cases absent. Metabolic products are oil and paramylum. Asexual reproduction by longitudinal fission in either the active or the resting stage. Mostly freshwater inhabitants, but some marine.

Genus **Euglena** Ehrenberg. Body short or elongated spindle, cylindrical, or band-form. The pellicle is marked in some forms by longitudinal or spiral striations. In forms in which the pellicle is not well developed, the body is highly plastic. Actively moving individuals are ordinarily spindle-shaped, while those remaining in one place may show considerable changes of form. Some species are regularly spirally twisted. Stigma is usually located near the anterior end. Chromatophores are numerous and discoidal, bandform, or stellate. Pyrenoids are sometimes present; they may or may not be surrounded by amyloid sheath. Metabolic products are paramylum bodies which may be two in number, one being located on either side of the nucleus, and rod-like to ovoid in shape; numerous and small ovoidal; or discoidal and scattered throughout. The contractile vacuoles are very small and arranged around the reservoir located near the anterior end.

Asexual reproduction is by longitudinal fission; sexual reproduction has been reported in *Euglena sanguinea*. Encystment common. The members of this genus are common in stagnant water, especially where algae occur. When present in large numbers, the active organisms may form a green film on the surface of water and resting or encysted stages may produce conspicuous green spots on the bottom of the pond or pool. Numerous species in fresh water.

Euglena pisciformis Klebs (Fig. 40, *a*). Body about 25 to 30 microns long by 7 to 10 microns broad. Spindle in form, with bluntly pointed anterior and sharply attenuated posterior end. Highly active. Paramylum indistinct; chromatophores small and discoidal. Flagellum is fairly long. Common.

Euglena viridis Ehrenberg (Figs. 6; 40, *b*). Body 50 to 120 microns in length. Anterior end rounded, posterior end pointed. Spindle-shaped during motion; highly plastic when stationary. Pellicle smooth and obliquely striated. Chromatophores are more or less band-form and arranged in a stellate form. Nutrition is holophytic, but the organism is also able to carry on saprozoic nutrition, during which period the chromatophores are said to degenerate. Solitary and common.

Euglena acus Ehrenberg (Fig. 40, *c*). Body 100 to 200 microns long; narrow spindle-form; posterior end sharply pointed. Spiral striation on the pellicle is very delicate. Paramylum bodies are short rod-form. Nucleus central; stigma distinct; flagellum short. Movement sluggish. Solitary.

Euglena spirogyra Ehrenberg (Fig. 40, *d*). Body 150 to 260 microns long. With spirally arranged striations, consisting of small knobs on the pellicle. Two ovoidal paramylum bodies, one on either side of the nucleus which is located in the approximate center of the body. Movement sluggish. Flagellum short; stigma prominent. Solitary among algae.

Euglena oxyuris Schmarda (Fig. 40, *e*). Almost always spirally twisted; pellicle with spirally arranged striations. Two paramylum bodies are ovoid and conspicuously observable on either side of the nucleus. Body large, 250 to 400 microns long. Solitary.

Euglena sanguinea Ehrenberg (Fig. 40, *f*). Body about 55 to 120 microns long. With haematochrome. Often found in

Fig. 40 a. *Euglena pisciformis.* ×200 (After Klebs).
b. *E. viridis.* ×325 (After Doflein, modified).
c. *E. acus.* ×325 (After Stein).
d. *E. spirogyra.* ×325 (After Stein).
e. *E. oxyuris.* ×325 (After Stein).
f. *E. sanguinea.* ×100 (After Klebs).
g. *E. deses.* ×325 (After Stein).
h. *E. gracilis.* ×200 (After Klebs).
i. *Phacus pleuronectes.* ×325 (After Stein).
j. *P. longicaudus.* ×325 (After Stein)
k. *P. pyrum.* ×325 (After Stein).
l. *P. triqueter.* ×325 (After Stein).

crust on the surface or on the half-dry bed of a pool. It is considered, by some investigators, as a variety of *E. viridis*.

Euglena deses Ehrenberg (Fig. 40, *g*). Body about 100 to 150 microns in length. Elongated, highly plastic; stigma distinct at the anterior end which is sometimes attenuated. Nucleus central; chromatophores hemi-lenticular; numerous small paramylum bodies scattered. Flagellum short.

Euglena gracilis Klebs (Fig. 40, *h*). Body about 40 to 45 microns long. Cylindrical to elongated oval; flagellum less than the body length; chromatophores numerous and discoid; nucleus central.

Genus **Phacus** Nitzsch. Body greatly flattened; asymmetrical; body-form constant. Pellicle often with prominent longitudinal or oblique striations. Body structure is similar to that of Euglena. A single flagellum and a stigma. The nucleus is usually located near the posterior extremity. A short cytopharynx; green chromatophores, rounded discoid; paramylum body very conspicuous. Numerous species in fresh water, occur with Euglena.

Phacus pleuronectes (Ehrenberg) (Fig. 40, *i*). Short posterior elongation is slightly curved. A prominent fold on the convex side, extending to the middle of the body; longitudinally striated. One or more circular paramylum bodies. Colorless forms sometimes appear. Body up to 75 microns in length.

Phacus longicaudus (Dujardin) (Fig. 40, *j*). Body about 85 to 100 microns long. Usually twisted with a long caudal prolongation. Stigma prominent. A large discoidal paramylum body in the center of the body. Pellicle longitudinally striated.

Phacus pyrum (Ehrenberg) (Fig. 40, *k*). Length about 40 microns. Pyriform with a straight caudal prolongation. Pellicle with oblique striations.

Phacus triqueter (Ehrenberg) (Fig. 40, *l*). Body about 40 to 45 microns long. Ovate; with a longitudinal ridge; caudal prolongation is acuminate. Oblique striation distinct.

Genus **Lepocinclis** Perty. Body more or less ovo-cylindrical; rigid with a usually spirally striated pellicle. Often with a short posterior spinous projection; stigma sometimes present. Numerous discoidal chromatophores marginal; paramylum bodies usually large and ring-shaped, laterally disposed.

Pyrenoids absent. Longitudinal fission. Occur with Euglena and Phacus. Several species are known.

Lepocinclis ovum (Ehrenberg) (Fig. 41, *a*). About 20 to 40 microns long.

Genus **Trachelomonas** Ehrenberg. With a simple test which often possesses numerous spinous projections. Sometimes yellowish to dark brown in color. A single flagellum protrudes from the anterior aperture, the rim of which is frequently thickened to form a collar. Chromatophores are either two curved plates or numerous discs. Paramylum bodies, if present, are in the form of small grains. Stigma and pyrenoids are often present. Multiplication by longitudinal fission; one daughter individual retains the test and the flagellum, while the other escapes through the flagellar aperture, forms a new flagellum and secretes a test. Cysts common. Among algae. Specific differentiation is based upon the test. Numerous species.

Trachelomonas hispida (Perty) (Fig. 41, *b*). Ellipsoidal; about 35 microns long. Test with numerous minute spines. Aperture with or without a short neck. Brownish in color.

Trachelomonas cylindrica Ehrenberg (Fig. 41, *c*). About 25 microns long. Test elongate, without spines.

Trachelomonas armata Ehrenberg (Fig. 41, *d*). Body about 40 microns long. Subspherical; test surface finely punctate and brown in color. Numerous short spines surround the aperture; often with long spines along the posterior margin.

Genus **Cryptoglena** Ehrenberg. Body rigid, flattened. Two lateral band-form chromatophores; a single flagellum; nucleus posterior. Among algae.

Cryptoglena pigra Ehrenberg (Fig. 41, *e*). Body ovoid, pointed posteriorly. Flagellum short; stigma prominent. About 12 microns long.

Genus **Ascoglena** Stein. Encased in a flexible colorless to brown test which is attached with its base to foreign object. Solitary and without stalk. Body ovoidal, plastic; attached to the test with its posterior end. A single flagellum protrudes from the aperture end of the test. A stigma; numerous chromatophores discoid; with or without pyrenoids. Reproduction as in Trachelomonas. Cysts unknown.

Ascoglena vaginicola Stein (Fig. 41, *f*). Test about 50 microns high. Continental Europe.

Genus **Colacium** Ehrenberg. Stalked individuals form

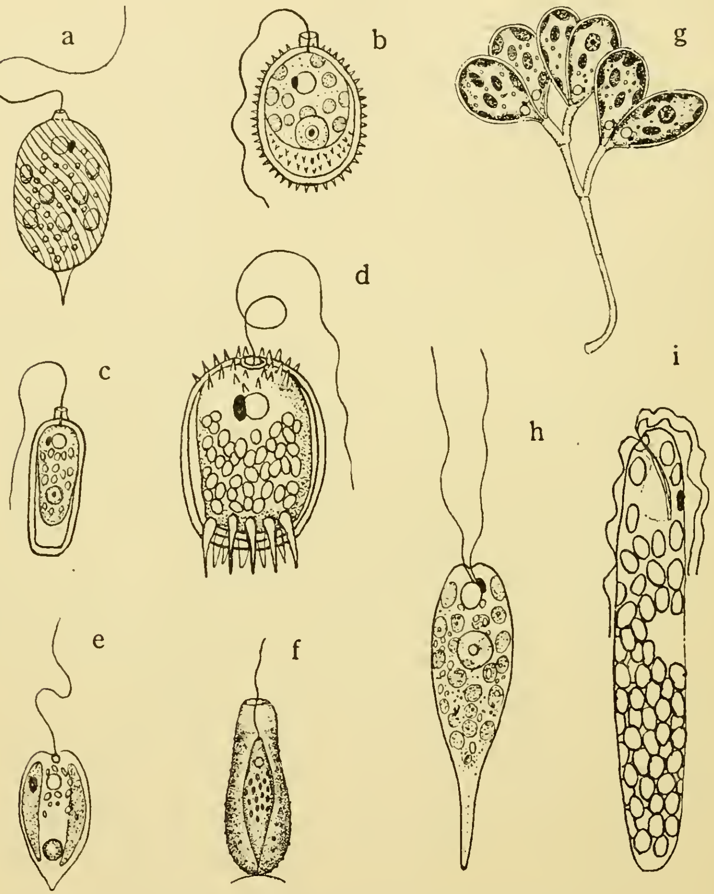


Fig. 41 a. *Lepocinclis ovum*. ×650 (After Stein).
b. *Trachelomonas hispida*. ×650 (After Stein).
c. *T. cylindrica*. ×650 (After Stein).
d. *T. armata*. ×650 (After Stein).
e. *Cryptoglena pigra*. ×650 (After Stein).
f. *Ascoglena vaginicola*. ×580 (After Stein).
g. *Colacium vesiculosum*. ×580 (After Stein).
h. *Eutreptia viridis*. ×400 (After Klebs).
i. *Euglenamorpha hegneri*. ×1100 (After Wenrich).

colony; frequently attached to plankton organisms, particularly copepods, rotifers, etc. Stalk is mucilaginous; individual cells pyriform, ellipsoidal or cylindrical. Without flagellum. Discoidal chromatophores numerous; with pyrenoids. Multiplication by longitudinal fission; also by swarmers, possessing a single flagellum and a stigma. Several species.

Colacium vesiculosum Ehrenberg (Fig. 41, *g*). Attached to freshwater copepods. Colony of 2 to 8 individuals; also solitary. Body about 30 microns long.

Genus **Eutreptia** Perty. With two flagella at the anterior end; pellicle distinctly striated. Body plastic; spindle-shaped during movement. Stigma; numerous discoid chromatophores; pyrenoids absent; paramylum bodies spherical or subcylindrical. Multiplication as in Euglena. Cyst with a thick stratified wall.

Eutreptia viridis Perty (Fig. 41, *h*). About 90 microns long. Fresh or salt water.

Genus **Euglenamorpha** Wenrich. Body form and structure similar to those of Euglena, but with three flagella and inhabiting the intestine of frog tadpoles. One species.

Euglenamorpha hegneri Wenrich (Fig. 41, *i*). Body 40 to 50 microns long.

Family 2 **Astasiidae** Bütschli

Similar to Euglenidae in body form and general structure, but without chromatophores. A single flagellum is present. Body is usually plastic, although it assumes an elongated form. There is a cytopharynx and cytostome, the former being associated with the reservoir of the contractile vacuoles. Stigma is absent, except in *Astasia ocellata*. The flagellum is usually straight and its free end vibrates in a characteristic manner. Asexual reproduction by longitudinal fission.

Genus **Astasia** Dujardin. Body metabolic, although usually elongate; stigma absent except in one species. Fresh or salt water.

Astasia margaritifera Schmarda (Fig. 42, *a*). Body spindleform when in motion. Pellicle indistinctly spirally marked. Numerous paramylum bodies small. Body about 60 microns long.

Genus **Urceolus** Mereschkowsky (=Phialonema Stein).

Body colorless, flask-shaped; a funnel-like neck; posterior region stout. A single flagellum protrudes from the funnel and reaches inward the posterior third of the body. Salt or fresh water.

Urceolus cyclostomus (Stein) (Fig. 42, *b*). Body about 50 microns long. Fresh water.

Genus **Peranema** Dujardin. Body oblong, with a broad, rounded or truncate posterior end during locomotion; highly changeable when stationary. The delicate pellicle shows a fine striation. The long flagellum tapers toward the free end and vibrates. Nucleus central; several contractile vacuoles. Saprozoic. In stagnant water; often in hay infusion.

Peranema trichophorum (Ehrenberg) (Fig. 42, *c*). Body 60 to 70 microns long. In stagnant water, infusion, etc. Common.

Genus **Petalomonas** Stein. Colorless body constant in form; pellicle often with longitudinal keels on one side. A single flagellum. Holozoic or saprozoic. Cytostome at the anterior end; cytopharynx fairly deep. Fresh water.

Petalomonas ervilia Stein (Fig. 42, *d*). Body about 45 microns long.

Genus **Menoidium** Perty. Body curved in a crescent or S-form. With a definite pellicle and a single flagellum.

Menoidium incurvum (Fresenius) (Fig. 42, *e*). About 15 to 25 microns long. Fresh water.

Genus **Scytomonas** Stein. Body oval or pyriform, with a delicate pellicle; a single flagellum. A contractile vacuole with a reservoir. Holozoic on bacteria. Longitudinal fission in motile stage. Coprozoic.

Scytomonas pusilla Stein (Fig. 42, *f*). About 15 microns long.

Genus **Copromonas** Dobell. Body elongated ovoid, with a single flagellum. A small cytostome at the anterior end. Holozoic on bacteria. Copulation is followed by an encystment (p. 52). Coprozoic in fecal matters of frog, toad, and man. Several authors hold that this genus is probably identical with Scytomonas which was indistinctly described by Stein.

Copromonas subtilis Dobell (Fig. 24, *a*). Body 7 to 20 microns long.

Family 3 **Heteronemidae** Calkins

Colorless body may be plastic or rigid with a variously marked pellicle. Flagella two in number, one directed anteriorly and the other usually posteriorly. Contractile vacuoles and reservoir. Stigma usually absent. Paramylum bodies are, as a rule, also present. Free-swimming or creeping.

Genus **Heteronema** Dujardin. Body plastic, rounded or elongated. Two flagella arise from the anterior end, one directed forward and the other trailing. The cytostome near the base of the flagella. Holozoic.

Fig. 42 a. *Astasia margaritifera.* ×410 (After Senn).
b. *Urceolus cyclostomus.* ×325 (After Stein).
c. *Peranema trichophorum.* ×400.
d. *Petalomonas ervilia.* ×325 (After Stein).
e. *Menoidium incurvum.* ×1050 (After Hall).
f. *Scytomonas pusilla.* ×325 (After Stein).
g. *Heteronema acus.* ×325 (After Stein).
h. *Distigma proteus.* ×325 (After Stein).
i. *Entosiphon sulcatum.* ×325 (After Stein).
j. *Anisonema acinus.* ×300 (After Klebs).
k. *A. truncatum.* ×325 (After Stein).
l. *A. emarginata.* ×400 (After Stokes.)
m. *Notosolenus apocamptus.* ×900 (After Stokes).
n. *N. sinuatus.* ×450 (After Stokes).

Heteronema acus (Ehrenberg) (Fig. 42, *g*). Extended body tapers towards both ends. Anterior flagellum as long as the body, the trailing one about one-half. Contractile vacuole near the anterior end; nucleus central. About 30 to 80 microns long. Fresh water and soil.

Genus **Distigma** Ehrenberg. Plastic; elongated when extended. Body surface without any marking. Two flagella unequal in length, directed forward. Cytostome and cytopharynx located at the anterior end. Endoplasm transparent. Holozoic. Fresh water; especially stagnant water, infusion, etc.

Distigma proteus (Stein) (Fig. 42, *h*). Longer flagellum about as long as the body, the other about one-half. Nucleus central; contractile vacuole anterior. When extended, about 100 microns long.

Genus **Entosiphon** Stein. Body more or less rigid; oval, flattened. Flagella arise from a cytostome at the anterior end. One flagellum trailing. The protrusible cytopharynx is a long conical tubule almost reaching the posterior end. The nucleus central and toward one side.

Entosiphon sulcatum (Dujardin) (Fig. 42, *i*). Body about 20 microns long. Fresh water and infusion.

Genus **Anisonema** Dujardin. Body as a rule oval, more or less flattened and asymmetrical. A slit-like ventral furrow. The flagellum arises from the anterior end. Cytopharynx long; contractile vacuole anterior; nucleus posterior. Fresh water.

Anisonema acinus Dujardin (Fig. 42, *j*). Body about 55 microns long.

Anisonema truncatum Stein (Fig. 42, *k*). Body about 40 to 45 microns long.

Anisonema emarginata Stokes (Fig. 42, *l*). Body about 15 microns long.

Genus **Notosolenus** Stokes. Free-swimming; rigid; oval. Ventral surface convex, dorsal surface with a broad longitudinal groove. Two flagella arise from the anterior end; one long, directed anteriorly and vibratile; the other shorter and trailing. Colorless.

Notosolenus apocamptus Stokes (Fig. 42, *m*). Body up to 10 microns in length.

Notosolenus sinuatus Stokes (Fig. 42, *n*). Body about 20 microns long. Both in standing water.

ORDER 6 **CHLOROMONADIDA** KLEBS

The Phytomastigina placed in this order are of rare occurrence and consequently not well known. The majority possess small discoidal grass-green chromatophores which on addition of an acid become blue-green. The metabolic products are fatty oil. Starch or allied carbohydrates are absent. Stigma is also not present.

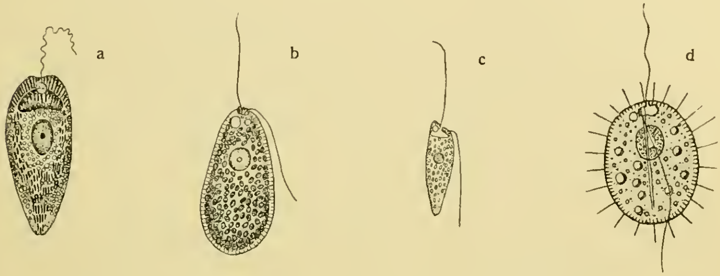


Fig. 43 a. *Gonyostomum semen.* ×325 (After Stein).
b. *Vacuolaria virescens.* ×275 (After Senn).
c. *Trentonia flagellata.* ×200 (After Stokes).
d. *Thaumatomastix setifera.* ×500 (After Lauterborn).

Genus **Gonyostomum** Diesing. With grass-green chromatophores. There are highly refractile trichocyst-like structures in the cytoplasm.

Gonyostomum semen Diesing (Fig. 43, *a*). Sluggish animal. Body about 45 to 60 microns long. In marshy water among decaying vegetation.

Genus **Vacuolaria** Cienkowski. Body grass-green, without trichocyst-like structures. Anterior end narrow. With two flagella. Cysts with a gelatinous envelope.

Vacuolaria virescens Cienkowski (Fig. 43, *b*). Body about 75 to 100 microns long. Fresh water.

Genus **Trentonia** Stokes. Bi-flagellate as in the last genus, but anterior margin is slightly bilobed.

Trentonia flagellata Stokes (Fig. 43, *c*). Slow-moving organism. Encystment is followed by binary fission. Body about 60 microns long. Fresh water.

Genus **Thaumatomastix** Lauterborn. Body colorless; pseudopodia formed. Two flagella; one extended anteriorly, the other trailing. Holozoic. Perhaps a transitional form between the Mastigophora and the Sarcodina.

Thaumatomastix setifera Lauterborn (Fig. 43, *d*). Body about 30 to 35 microns long.

References

Dangeard, P. 1901 Recherches sur les Eugléniens. Le Botaniste. P. 97.

Dobell, C. 1908 The structure and life-history of *Copromonas subtilis* nov. gen. et nov. spec.: A contribution to our knowledge of the Flagellata. Quart. Jour. Micr. Sci., (2) Vol. 52.

Lemmermann, E. 1913 Eugleninae. Süsswasserfl. Deutschlands, etc. H. 2.

Pascher, A. 1913 Chloromonadinae. Ibid. H. 2.

Wenrich, D. H. 1924 Studies on *Euglenamorpha hegneri* n.g., n.sp., a euglenoid flagellate found in tadpoles. Biol. Bull., Vol. 47.

West, G. S. and F. E. Fritsch. 1927 A treatise on the British freshwater algae. Cambridge.

CHAPTER X

SUBCLASS 2 **ZOOMASTIGINA** DOFLEIN

THE ZOOMASTIGINA lack both chromatophores and paramylum bodies. The body organization varies greatly from a simple to a very complex type. The majority possess a single nucleus which is, as a rule, vesicular in structure. In numerous forms a **parabasal body** is present (p. 23). Myonemes are present in several parasitic forms. Nutrition is holozoic, saprozoic, or parasitic. Asexual reproduction is by longitudinal fission; sexual reproduction is unknown. Encystment occurs widely. The Zoomastigina are free-living or parasitic in various animals.

According to Calkins, they are divided into four orders:

With pseudopodia besides flagella.................Order 1 Pantostomatida
Without pseudopodia, but with flagella
  With one or two flagella.......................Order 2 Protomonadida
  With two to eight flagella.....................Order 3 Polymastigida
  With more than eight flagella................Order 4 Hypermastigida

ORDER 1 **PANTOSTOMATIDA** SENN

The group contains those Zoomastigina which possess both pseudopodia and flagella. Flagella vary in number from one to several. Pseudopodia vary also greatly in form and in number.

The order is subdivided into two families as follows:

With numerous flagella.........................Family 1 Holomastigidae
With one to three, rarely four, flagella............Family 2 Rhizomastigidae

Family 1 **Holomastigidae** Senn

Genus **Multicilia** Cienkowski. Body spheroidal, but amoeboid. Flagella numerous, being 40 to 50 in number, long and evenly distributed. One or more nuclei. Holozoic. Food is obtained by means of pseudopodia. Contractile vacuoles are numerous. Multiplication by fission. Diameter of body less than 50 microns. Fresh or salt water.

Multicilia marina Cienkowski (Fig. 44, *a*). With a single nucleus. About 20 to 30 microns in diameter. Marine.

Multicilia lacustris Lauterborn (Fig. 44, *b*). Multinucleate. Body diameter 30 to 40 microns. Fresh water.

Multicilia palustris Penard. Fresh water.

Family 2 **Rhizomastigidae** Bütschli

The members of this family possess one to three, rarely four flagella and also axopodia or lobopodia. Thus they combine the chief characteristics of the Mastigophora and Sarcodina. Because of the constant presence of the flagella, they are ordinarily considered as belonging to the Mastigophora. There is a single nucleus. The flagellum arises from a basal granule which is often connected with the nucleus by a rhizoplast. Asexual reproduction is binary fission which takes place both in trophic and encysted stages. Sexual reproduction has been reported in one species. Method of nutrition is either holozoic or parasitic. Free-living and a few parasitic forms.

Genus **Mastigamoeba** Schulze. Monomastigote, uninucleate, with finger-like pseudopodia. Flagellum long and arises from the nucleus. Fresh water and soil.

Mastigamoeba aspera Schulze (Fig. 44, *c*). Large form. 150 microns in diameter.

Genus **Mastigina** Frenzel. With a single flagellum which arises from the nucleus located at one end. Body surface is tough, being frequently covered by ciliary projections, and shows a little tendency toward pseudopodial formation. Rolling movement. Fresh water, soil, or parasitic.

Mastigina setosa Goldschmidt (Fig. 44, *d*). Body length up to 140 microns.

Mastigina hylae Frenzel (Fig. 44, *e*). In the large intestine of many species of frog. Body about 100 microns long.

Genus **Mastigella** Frenzel. With a flagellum which is not connected with the nucleus. Pseudopodia numerous, digitate. Body-form changes actively and constantly. Contractile vacuole.

Mastigella vitrea Goldschmidt (Fig. 44, *f*). 150 microns long. Sexual reproduction has been reported to occur by Goldschmidt.

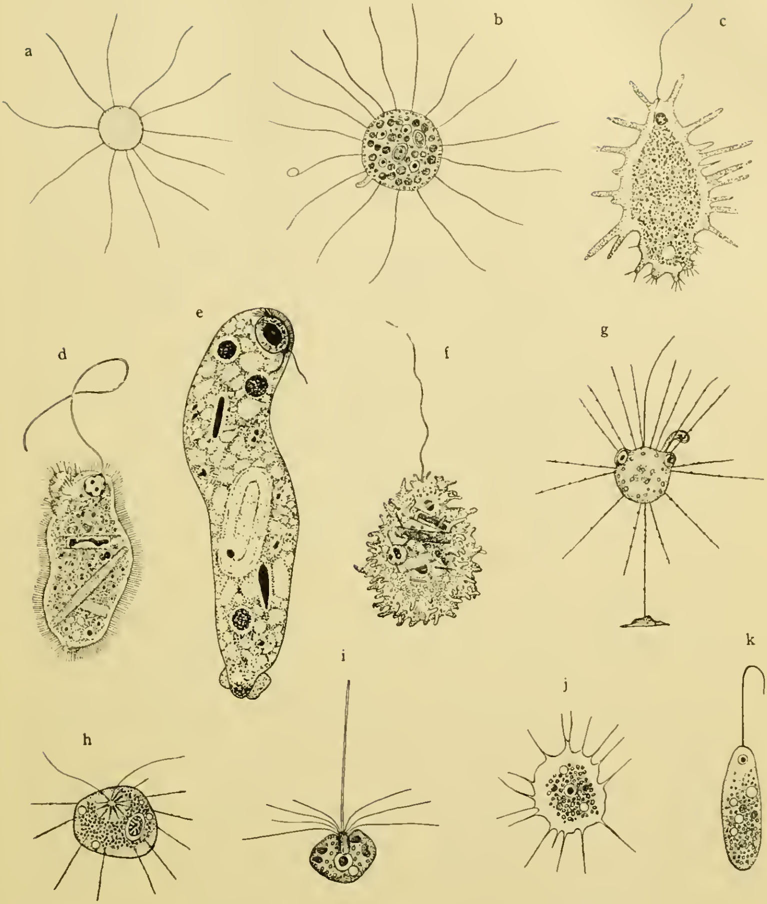


Fig. 44 a. *Multicilia marina.* ×300 (After Cienkowski).
b. *M. lacustris.* ×300 (After Lauberborn)
c. *Mastigamoeba aspera.* ×150 (After Schulze)
d. *Mastigina setosa.* ×275 (After Goldschmidt).
e. *M. hylae.* ×515 (After Becker).
f. *Mastigella vitreo.* ×275 (After Goldschmidt)
g. *Actinomonas mirabilis.* ×850 (After Griessmann from Doflein).
h. *Dimorpha mutans.* ×700 (After Blochmann).
i. *Pteridomonas pulex.* ×400 (After Penard).
j, k. *Ciliophrys infusionum.* ×400 (After Bütschli).

Genus **Actinomonas** Kent. Body generally spheroidal, with a single flagellum and radiating axopodia or filopodia. Ordinarily attached with a cytoplasmic process to foreign object, but undergoes free-swimming movement by withdrawing it. A single nucleus central; several contractile vacuoles. Holozoic.

Actinomonas mirabilis Kent (Fig. 44, *g*). Diameter about 10 microns; flagellum 20 microns long. Fresh water.

Genus **Dimorpha** Gruber. Ovoid or subspherical; with two flagella and radiating axopodia, all arising from an eccentric granule. The nucleus is also eccentric. Pseudopodia are sometimes withdrawn. In fresh water.

Dimorpha mutans Gruber (Fig. 44, *h*). Diameter up to 15 microns.

Genus **Pteridomonas** Penard. Body small, heart-shaped, usually attached with a long cytoplasmic process. From the opposite pole, there arises a single flagellum, around which occurs a ring of extremely fine filopodia or flagella. The nucleus central; a contractile vacuole. Holozoic. Fresh water.

Pteridomonas pulex Penard (Fig. 44, *i*). About 20 microns wide.

Genus **Ciliophrys** Cienkowski. Body spherical with extremely fine radiating filopodia, giving the appearance of a heliozoan, with perhaps a single flagellum which is difficult to distinguish from the numerous filopodia, but which becomes conspicuous when the pseudopodia are withdrawn. Fresh or salt water.

Ciliophrys infusionum Cienkowski (Fig. 44, *j,k*). Flagellated stage 25 to 30 microns long. Fresh water infusion.

Ciliophrys marina Caullery. Diameter about 10 microns. Salt water.

References

Becker, E. R. 1925 The morphology of *Mastigina hylae* (Frenzel) from the intestine of the tadpole. Jour. Paras., Vol. 11.

Lemmermann, E. 1914 Pantostomatineae. Süsswasserflora Deutschlands, etc. H. 1.

CHAPTER XI

ORDER 2 **PROTOMONADIDA** BLOCHMANN

THIS ORDER contains small Zoomastigina with one, two, or sometimes three flagella. The body is in many cases plastic, having no definite pellicle, and in some cases it is amoeboid. The method of nutrition is holozoic, saprozoic, or parasitic. The order includes a heterogeneous lot of Protozoa, mostly parasitic, whose affinities to one another are very incompletely known. Reproduction is, as a rule, by longitudinal fission, although budding or multiple fission has also been known to occur. Sexual reproduction, though reported in some forms, has not been confirmed.

In dividing the Protomonadida into ten families, Calkins' scheme has been chiefly followed:

With one flagellum
  Protoplasmic collar present
    Collar entirely enclosed in jelly . . . . Family 1 Phalansteriidae
    Collar not enclosed in jelly
      Without any lorica . . . . Family 2 Choanoflagellidae
      With lorica . . . . Family 3 Bicosoecidae
  Protoplasmic collar absent . . . . Family 4 Trypanosomatidae
With two flagella
  Undulating membrane present; parasitic . . . . Family 5 Cryptobiidae
  Undulating membrane absent
    Flagella of equal length . . . . Family 6 Amphimonadidae
    Flagella of unequal length
      One primary flagellum, the other secondary . . . . . Family 7 Monadidae
      One primary flagellum, the other trailing . . . . Family 8 Bodonidae
With three flagella; one primary, two trailing . . . . Family 9 Trimastigidae
With four flagella; two long, two short . . . . Family 10 Costiidae

Family 1 **Phalansteriidae** Kent

Genus **Phalansterium** Cienkowski. Body small and ovoid; with a flagellum and a narrow collar. Numerous individuals are embedded in gelatinous substance which assumes a dendritic form. The flagella protrude. Fresh water.

Phalansterium digitatum Stein (Fig. 45, *a*). The body about 17 microns long.

Family 2 **Choanoflagellidae** Stein

Small flagellates, sometimes with the second flagellum which serves for fixation of the body. A delicate collar surrounds the flagellum. Ordinarily sedentary forms. If temporarily freed, the organisms swim with the flagellum directed backward. Often colonial. Free-living in fresh water. Holozoic on bacteria or saprozoic.

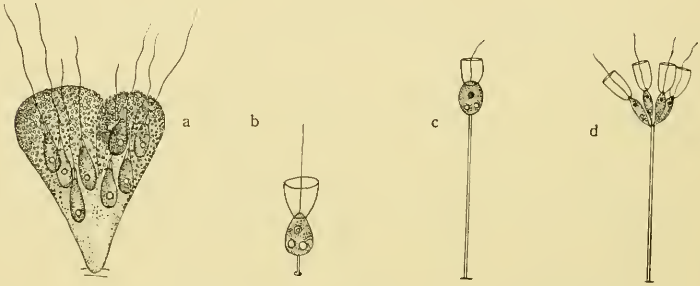


Fig. 45 a. *Phalansterium digitatum.* ×400 (After Stein).
b. *Monosiga ovata.* ×600 (After Kent).
c. *M. robusta.* ×575 (After Stokes).
d. *Codosiga utriculus.* ×1000 (After Stokes).

Genus **Monosiga** Kent. Solitary; with a cytoplasmic collar. Apparently without a shell. With or without stalk. Attached to fresh or salt water vegetation. Several species.

Monosiga ovata Kent (Fig. 45, *b*). About 10 to 15 microns long. Salt water.

Monosiga robusta Stokes (Fig. 45, *c*). About 13 microns long. Fresh water.

Genus **Codonosiga** Kent. Similar to Monosiga, but individuals are in a cluster-form at the end of a stalk which may have branches. Fresh water.

Codonosiga utriculus Stokes (Fig. 45, *d*). Attached to fresh water plants. Body about 11 microns in length.

Some of the other genera of the family are:

Genus **Desmarella** Kent. Band-form colonies; simple or branched.

Genus **Proterospongia** Kent. Stalkless individuals embedded irregularly in a jelly mass, with the collars protruding.

Genus **Sphaeroeca** Lauterborn. Similar to the last genus, but individuals with stalks and radiating.

Genus **Salpingoeca** Clark. With a vase-like lorica to which the stalked or stalkless organism is attached.

Family 3 **Bicosoecidae** Poche

Small monomastigote forms. With test. Solitary or colonial. Collar rudimentary or developed. Holozoic. Fresh water.

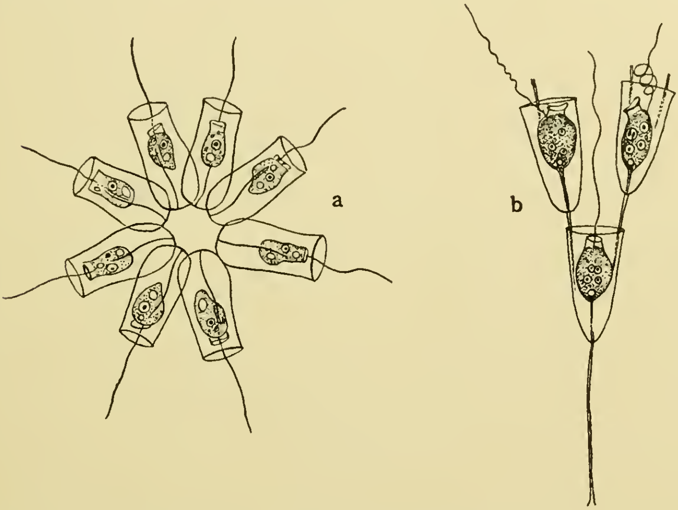


Fig. 46 a. *Bicosoeca socialis.* ×555 (After Lauterborn).
b. Part of a colony of *Poteriodendron petiolatum.* ×435 (After Stein).

Genus **Bicosoeca** James-Clark. Test vase-like; body small, ovoid with rudimentary collar, a flagellum extending through it. The protoplasmic body is anchored to the base by a cytoplasmic process (flagellum?). A nucleus and a contractile vacuole attached or free-swimming.

Bicosoeca socialis Lauterborn (Fig. 46, *a*). Free-swimming in fresh water. Lorica 23 microns by 12 microns; body about 10 microns long.

Genus **Poteriodendron** Stein. Colonial; test is vase-shaped and possesses a prolonged stalk.

Poteriodendron petiolatum (Ehrenberg) (Fig. 46, *b*). Test about 30 to 50 microns high. Fresh water.

Family 4 **Trypanosomatidae** Doflein

Body characteristically leaf-like, although changeable to a certain extent. A single nucleus and a blepharoplast. A single flagellum arises from a basal granule which may be independent from, or united with, the blepharoplast (Figs. 5 and 47). The

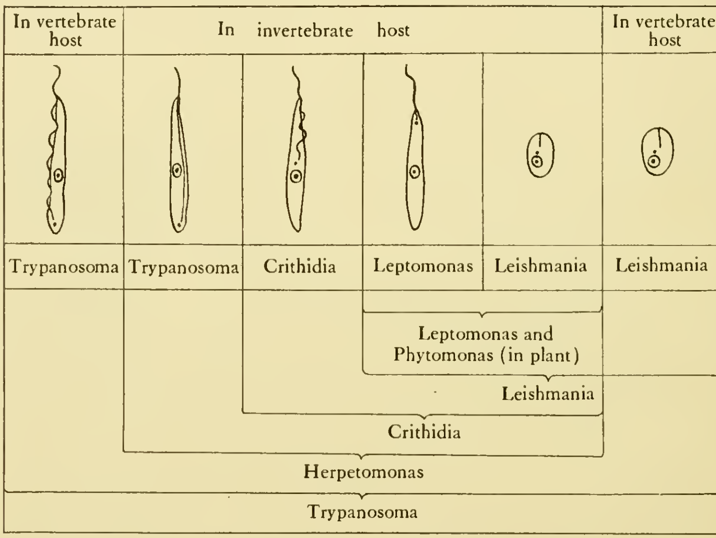


Fig. 47 Diagrams showing the structural differences among the genera of Trypanosomatidae. (After Wenyon).

basal portion of the flagellum forms the outer boundary of the undulating membrane which extends along the side of the body. Exclusively parasitic. This family contains a number of parasites which are responsible for serious diseases of man and domestic animals in various parts of the world.

Genus **Trypanosoma** Gruby. Parasitic in the circulatory system of vertebrates. The body is leaf-like, pointed at the flagellate end, and bluntly rounded, or rarely pointed, at the other. Polymorphism which seems to be due to differences in development, is common. The nucleus is located centrally.

Near the bluntly rounded end, there is a blepharoplast and usually a basal granule from which the flagellum arises and runs toward the other end, marking the outer margin of the undulating membrane. In most cases the flagellum extends

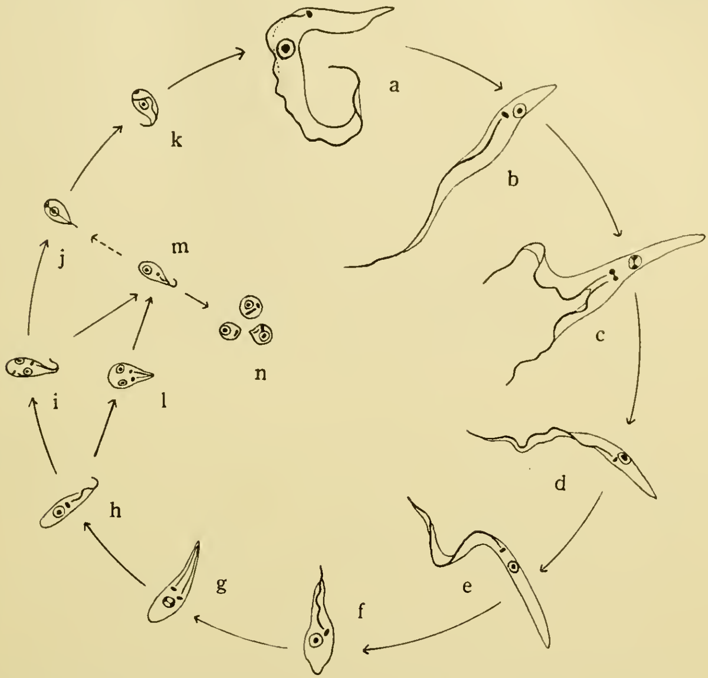


Fig. 48 The life cycle of *Trypanosoma melophagium* in the blood of sheep and in *Melophagus ovinus*. (After Hoare).

a, trypanosome as ingested by Melophagus with the sheep's blood; b–e, crithidia formation through division; f–h, large transitional crithidia in the hind-gut which by division are transformed into smaller forms; i–k, formation of metacyclic trypanosomes; l–m, formation of pyriform crithidia; n, leishmania forms.

freely beyond the body. Myonemes are common. Asexual reproduction is binary or rarely multiple fission. The organism is carried from host to host by blood-sucking invertebrates and undergoes definite changes in the alimentary canal of the latter (Fig. 48). Sexual reproduction is not known. A number of forms are pathogenic to their hosts and the diseased condition is termed **trypanosomiasis** in general.

A. Trypanosoma in Man

Trypanosoma gambiense Dutton (Fig. 49, *a*). Parasitic in the blood and lymph of man in certain regions of Africa; transmitted by the tsetse fly, *Glossina palpalis*. Reservoir hosts are domestic and wild animals. Body 15 to 30 microns long. Mature forms are slender and long, and shows a long flagellum; individuals formed by longitudinal fission are short and broad with no projecting flagellum. Half-grown forms are intermediate in size and structure. The organism is responsible for the "sleeping sickness" of man in Africa.

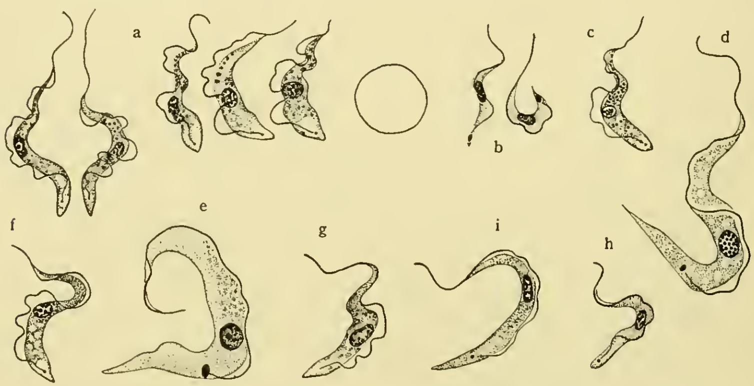


Fig. 49 Mammalian trypanosomes as seen in stained smears. ×1000. (After various authors).

a, five individuals of *Trypanosoma gambiense* and an erythrocyte of man; b, *T. cruzi;* c, *T. brucei;* d, *T. theileri;* e, *T. melophagium;* f, *T. evansi;* g, *T. equinum;* h, *T. equiperdum;* i, *T. lewisi.*

Trypanosoma cruzi (Chagas) (=*Schizotrypanum cruzi* Chagas) (Fig. 49, *b*). Parasitic in children in South America (Brazil, Peru, Venezuela, etc.). The trypanosome is a small curved form, measuring about 20 microns in total length. With a centrally located nucleus. A large blepharoplast is located close to the sharply pointed non-flagellate end. Multiplication takes place in the cells of nearly every organ of the host body. Upon entering a host cell, the trypanosome loses its flagellum and undulating membrane, and assumes a leishmania form which measures 2 to 5 microns in diameter. This form undergoes repeated binary fission, and a large number of daughter individuals are produced. They develop sooner or later into trypanosomes which, upon rupture of the host cell, become liberated into the blood stream. This trypanosome is transmitted by the reduviid bug, *Triatoma megista* and allied species. The diseased condition is known as "Chagas' disease."

B. Trypanosoma in Domestic Animals

Trypanosoma brucei Plimmer and Bradford (Fig. 49, *c*). Polymorphic. Body varies from 15 to 30 microns in length (average 20 microns). Transmitted by various species of tsetse flies, Glossina. The trypanosome is the most virulent of all. It causes the fatal disease known as "nagana" among mules, donkeys, horses, camels, cattle, swine, dogs, etc., which terminates in death of the host animal in from two weeks to a few months. Wild animals are equally susceptible. The disease occurs, of course, only in the region in Africa where the tsetse flies live.

Trypanosoma theileri Laveran (Fig. 49, *d*). Non-pathogenic large trypanosome which occurs in the blood of cattle. Cosmopolitan. The extremities of the body are sharply pointed; length 60 to 70 microns. Myonemes are well developed.

Trypanosoma americanum Crawley. This trypanosome was noted in American cattle and is probably identical with *T. theileri*. It is transmitted from cattle to cattle by tabanid flies.

Trypanosoma melophagium (Flu) (Fig. 49, *e*). Non-pathogenic trypanosome of the sheep. 50 to 60 microns long with attenuated ends. The development of the organism in *Melophagus ovinus* is illustrated in Fig. 48.

Trypanosoma evansi (Steel) (Fig. 49, *f*). In horses, mules, donkeys, cattle, dogs, camels, elephants, etc. The infection in horses seems to be usually fatal and known under the name of "surra." The trypanosome measures about 25 microns long and is monomorphic. Transmitted by tabanid flies. Widely distributed.

Trypanosoma equinum Vages (Fig. 49, *g*). In horses in South America, causing an acute disease known as "mal de Caderas." Other domestic animals do not suffer as much as do the horses. Length 20 to 25 microns. The trypanosome is peculiar in that it does not show any blepharoplast by ordinary staining.

Trypanosoma equiperdum Doflein (Fig. 49, *h*). In horses and donkeys. The cause of a chronic disease known as "dourine." Widely distributed. Length 25 to 30 microns. No intermediate host; transmission takes place directly from host to host during sexual act.

C. Trypanosoma in Other Mammals

Trypanosoma lewisi (Kent) (Fig. 49, *i*). In the blood of various species of the rat, Rattus. Cosmopolitan. Under ordinary conditions, the trypanosome is not pathogenic to the host. The organism which measures about 25 microns long, is very active. It is slender and possesses a long flagellum. Transmission by the flea, *Ceratophyllus fasciatus*, in the digestive tract of which the parasite undergoes asexual reproduction. When the infected fleas are eaten by a rat, the latter becomes the victim of a new infection.

Trypanosoma duttoni Thiroux. In the species of the mouse, Mus. Similar to *T. lewisi*, but rats are not susceptible, hence considered as a distinct species. Transmission by fleas.

Trypanosoma peromysci Watson. Similar to *T. lewisi*. In Canadian deer mice, *Peromyscus maniculatus* and others.

Trypanosoma nabiasi Railliet. Similar to *T. lewisi*. In rabbits, *Lepus domesticus* and *L. cuniculus*.

D. Trypanosoma in Birds and Reptiles

Trypanosoma paddae Laveran and Mesnil. In Java sparrow, *Munia oryzivora*.

Trypanosoma noctuae (Schaudinn). In the little owl, *Athene noctua*.

Several other species are known.

Crocodiles, snakes, and turtles are hosts for Trypanosoma. Transmission by blood-sucking arthropods or leeches.

E. Trypanosoma in Amphibians

Trypanosoma rotatorium (Meyer) (Fig. 50, *a*). In tadpoles and adults of various species of the frog. Between a slender form with a long projecting flagellum measuring about 35 microns long and a very broad one without free portion of the flagellum, various intermediate forms are to be noted in a single host. The blood vessels of internal organs, such as kidneys, contain more individuals than the peripheral vessels. A centrally located nucleus and a small blepharoplast. Undulating membrane is highly developed. Myonemes prominent. Multiplication by longitudinal fission. The leech, *Hemiclepsis marginata*, has been found to be the transmitter in some localities.

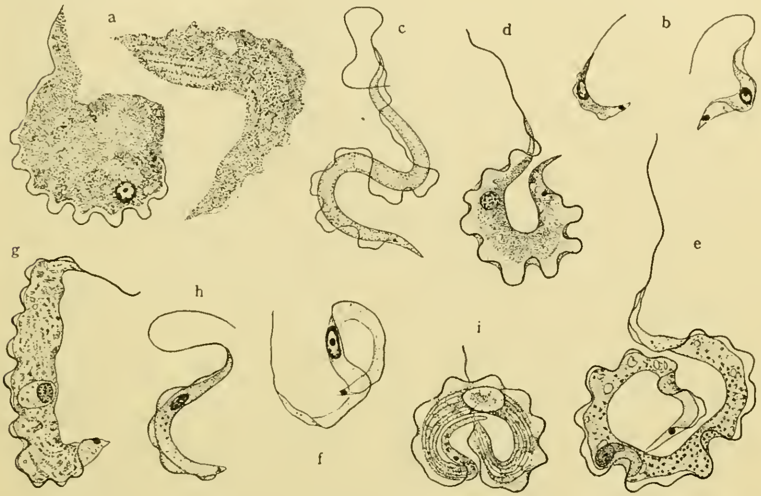


Fig. 50 a. *Trypanosoma rotatorium.* ×750.
b. *T. inopinatum.* ×1175.
c. *T. diemyctyli.* ×800 (After Hegner).
d. *T. giganteum.* ×500 (After Neumann).
e. *T. granulosum.* ×1000 (After Minchin).
f. *T. remaki.* ×1650 (After Kudo).
g. *T. percae.* ×1000 (After Minchin).
h. *T. danilewskyi.* ×1000 (After Laveran and Mesnil).
i. *T. rajae.* ×1600 (After Kudo).

Trypanosoma inopinatum Sergent and Sergent (Fig. 50, *b*). In the blood of various frogs. The trypanosome is almost always slender in form and measures 12 to 20 microns in length. Larger forms 30 to 35 microns, are also noted. In both forms, blepharoplast is comparatively large. Leeches transmit the organism from host to host.

Numerous species of Trypanosoma have been reported from the frog, but specific identification is indistinct. It is better and safer to hold that they belong to one of the two species mentioned above, until their development and transmission become known.

Trypanosoma diemyctyli Tobey (Fig. 50, *c*). In the blood of the newt, *Diemyctylus viridescens*. A comparatively large form. Body slender and measures about 50 microns long by 2 to 5 microns broad, the flagellum 20 to 25 microns long. Undulating membrane is well developed.

F. Trypanosoma in Fish

Both fresh and salt water fish are hosts to different species of trypanosomes. What effects these parasites exercise upon the host fish are not understood. Ordinarily only a few individuals are found in a host fish.

Trypanosoma granulosum Laveran and Mesnil (Fig. 50, *e*). In the eel, *Anguilla vulgaris*. Total length 70 to 80 microns.

Trypanosoma giganteum Neumann (Fig. 50, *d*). In *Raja oxyrhynchus*. Total length 125 to 130 microns.

Trypanosoma remaki Laveran and Mesnil (Fig. 50, *f*). In *Lucius lucius*, *L. reticulatus* and probably other species. Dimorphic. Total length 24 to 33 microns.

Trypanosoma percae Brumpt (Fig. 50, *g*). In *Perca fluviatilis*. Total length 45 to 50 microns.

Trypanosoma danilewskyi Laveran and Mesnil (Fig. 50, *h*). In the carp and goldfish. Widely distributed. About 40 microns long.

Trypanosoma rajae Laveran and Mesnil (Fig. 50, *i*). In various species of Raja. Length 30 to 35 microns.

Genus **Crithidia** Léger. Parasitic in arthropods and other invertebrates. The blepharoplast is located between the centrally located nucleus and the end from which the flagellum projects (Fig. 47). The undulating membrane is thus not so well developed as in Trypanosoma. The organism may lose the flagellum and form a leptomonas or rounded leishmania stage which leaves the host intestine with fecal matter and becomes the source of infection in other host animals.

Crithidia euryophthalmi McCulloch (Fig. 51, *a-c*). In the gut of the bug, *Euryophthalmus convivus* which feeds on *Lupinus* *arboreus* in the sand dunes on California coast. Multiple division and endogenous budding characterize this species.

Crithidia gerridis Patton (Fig. 51, *d*). In the gut of several species of water bugs belonging to the genera Gerris and Microvelia. Total length 22 to 45 microns.

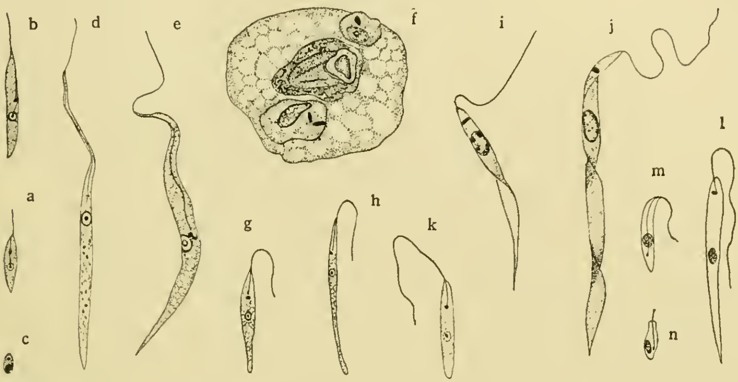


Fig. 51 a–c. *Crithidia euryophthalmi.* ×875 (After McCulloch). a, b, from the mid-gut; c, from the rectum.
d. *C. gerridis.* ×1070 (After Becker).
e, f. *C. hyalommae.* ×1000 (After O'Farrell).
g, h. *Leptomonas ctenocephali.* ×1000 (After Wenyon).
i, j. *Phytomonas elmassiani.* ×1500 (After Holmes). i, from milkweed, *Asclepias* sp.; j, from the gut of a suspected transmitter, the bug, *Oncopeltus fasciatus.*
k. *Herpetomonas muscarum.* ×1070 (After Becker).
l–n. Various phases of *H. drosophilae.* ×1000 (After Chatton and Léger).

Crithidia hyalommae O'Farrell (Fig. 51, *e, f*). In the body cavity of the tick (*Hyalomma aegyptium*) of the cattle in Egypt. The flagellate through its invasion of ova is said to be capable of infecting the offspring while it is still in the body of the parent tick.

Genus **Leptomonas** Kent. Exclusively parasitic in invertebrates. The blepharoplast is very close to the end beyond which the flagellum projects, and therefore there is no undulating membrane (Fig. 47). Non-flagellate phase resembles Leishmania.

Leptomonas ctenocephali Fantham (Fig. 51, *g, h*). In the hindgut of the dog flea, *Ctenocephalus canis*. Widely distributed.

Genus **Phytomonas** Donovan. Morphologically similar to Leptomonas (Fig. 47), but it occurs in both plants and invertebrates. In the latex of the plants belonging to the families: Euphorbiaceae, Asclepiadaceae, Apocynaceae, Sapotaceae and Utricaceae. Transmitted by hemipterous insects. The organism is often found in enormous numbers in localized areas in the host plant. The infection spreads from part to part. The infected latex is a clear fluid, owing to the absence of starch grains and other particles, and this results in the degeneration of the infected part of the plant. Several species.

Phytomonas davidi (Lafront). Body about 15 to 20 microns long by about 1.5 microns broad. The posterior portion of the body is often twisted two or three times. Multiplication by longitudinal fission. Widely distributed. In various species of Euphorbia.

Phytomonas elmassiani (Migone) (Fig. 51, *i, j*). In various species of milkweeds. Length 9 to 20 microns. Suspected transmitter, *Oncopeltus fasciatus*, according to Holmes. In South and North America.

Genus **Herpetomonas** Kent. Ill-defined genus (Fig. 47). Exclusively invertebrate parasites. Trypanosoma, Crithidia, Leptomonas and Leishmania forms occur during development. Several species.

Herpetomonas muscarum (Leidy) (= *H. muscae-domesticae* (Burnett)) (Fig. 51, *k*). In the gut of flies, belonging to the genera Musca, Calliphora, Sarcophaga, Lucilia, Phormia, etc.

Herpetomonas drosophilae (Chatton and Alilaire) (Fig. 51, *l–n*). In the intestine of *Drosophila confusa*.

Genus **Leishmania** Ross. All parasitic in vertebrate and invertebrate hosts, the latter not having been actually demonstrated, but suspected. Non-flagellate and flagellate forms occur (Fig. 47). Body very minute. In the vertebrate host the organism is not flagellated. Body spherical or ovoid, with a definite pellicle. With an eccentric nucleus and a blepharoplast. The body measures from 2 to 5 microns in diameter. The organism attacks endothelial cells of blood capillaries and mucosae; the spleen becomes highly enlarged. The transmitting agent is believed to be blood-sucking arthropods. In culture, the organism develops into leptomonad forms. This genus includes three "species" occurring in man, all of which are practically indistinguishable morphologically from one another, and, two of which are considered as identical.

Leishmania donovani (Laveran and Mesnil) (= *L. infantum* Nicolle) (Fig. 52, *a–f*). The organism attacks the endothelium and macrophage of man, causing the disease known as "kala azar." It occurs in India, China, west to southern Russia, and shores of the Mediterranean Sea.

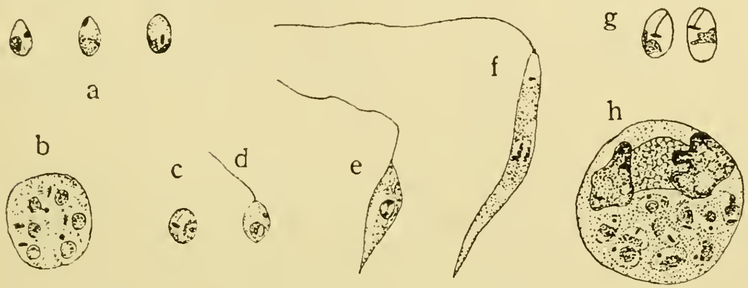


Fig. 52 a–f. *Leishmania donovani*. ×2000. (After Wenyon; Thomson and Robertson). a, three individuals from lymph smear of a kala azar patient; b, from a spleen smear; c–f, cultural forms.
g, h. *L. tropica*. ×2000 (After Wenyon; Thomson and Robertson). g, from an Oriental sore; n, the parasites in a polymorphonuclear cell from a sore.

Leishmania tropica (Wright) (Fig. 52, *g*, *h*). The organism infects the skin of the exposed part and rarely the mucous lining of the mouth, pharynx and nose of man. The resulting disease is usually called "Oriental sore." Distribution is similar to the above-mentioned species.

Leishmania brasiliensis Vianna. The organism occurs in South and Central America. Some authors consider this species as identical with *L. tropica*. Although morphologically identical, these species show specific serum reactions.

Genus **Oikomonas** Kent. A monoflagellate rounded organism, living in stagnant water, soil and exposed fecal matter. Uninucleate. Encystment common.

Oikomonas termo (Ehrenberg) (Fig. 53, *a*, *b*). About 4 to 5 microns long. Stagnant water and soil.

Genus **Histomonas** Tyzzer. Parasitic in domestic fowls. Body amoeboid with usually one flagellum which is connected with a blepharoplast.

Histomonas meleagris (Smith) (Fig. 53, *c*). Length 12 to 15 microns. Supposed to be the cause of the "black-head" of turkeys and chicken.

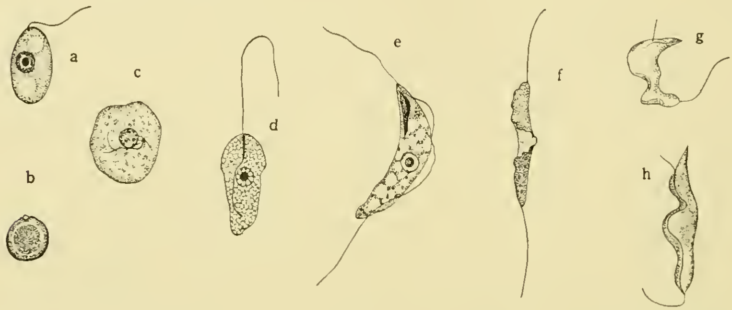


Fig. 53 a, b. *Oikomonas termo*. a, a stained trophozoite (×1000 after Martin); b, living cyst (×1250 after Sandon).
c. *Histomonas meleagris*. ×700 (After Tyzzer).
d. *Rhizomastix gracilis*. ×1000 (After Mackinnon).
e. *Cryptobia helicis*. ×1900 (After Bělař).
f. *C. borreli*. ×650 (After Mavor).
g, h. *C. cyprini*. ×665 (After Plehn).

Genus **Rhizomastix** Alexeieff. Body rounded with a central nucleus. A blepharoplast is located between the nucleus and the posterior end of the body. A long fiber runs from it to the anterior end and continues into the flagellum. In the spherical cyst, the nucelus undergoes division.

Rhizomastix gracilis Alexeieff (Fig. 53, *d*). Body about 13 microns long, flagellum 20 microns long. In the intestine of axolotles and tipulid larvae.

Family 5 **Cryptobiidae** Poche

Biflagellate trypanosome-like Protomonadida. One flagellum free, the other marks the outer margin of an undulating membrane. Blepharoplast is an elongated rod-like structure, often referred to as the parabasal body. All parasitic.

Genus **Cryptobia** Leidy (=Trypanoplasma Laveran and Mesnil). Parasitic in the reproductive organs of molluscs and other invertebrates and in blood and intestines of fish.

Cryptobia helicis Leidy (Fig. 53, *e*). In the reproductive organs of various species of Helix of America and Europe. Length 6 to 20 microns. Asexual reproduction through binary fission is known.

Cryptobia borreli (Laveran and Mesnil) (Fig. 53, *f*). In the blood of various freshwater fish such as Catostomus, Cyprinus, etc. Body 20 to 25 microns long.

Cryptobia cyprini (Plehn) (Fig. 53, *g*, *h*). In the blood of carp and goldfish. Comparatively rare. Body 10 to 30 microns long.

Cryptobia grobbeni (Keysselitz). In the gastrovascular cavity of Siphonophora. Size about 65 microns by 4 microns.

Family 6 **Amphimonadidae** Kent

Body naked or with a gelatinous envelope. With two equally long anterior flagella. Often colonial. Free-swimming or attached. One or two contractile vacuoles. Mainly fresh water.

Genus **Amphimonas** Dujardin. Small oval or rounded amoeboid form. Flagella at anterior end. Free-swimming or attached by an elongated stalk-like posterior process. Fresh or salt water.

Amphimonas globosa Kent (Fig. 54, *a*). Diameter of body about 23 microns. Fresh water.

Genus **Spongomonas** Stein. Individuals in granulated gelatinous masses. Colony reaches often several centimeters in height. In motile stage pointed pseudopodia are produced. Fresh water.

Spongomonas uvella Stein (Fig. 54, *b*). Body about 21 microns long. Colony about 50 microns high. Fresh water.

Genus **Cladomonas** Stein. Individuals are embedded in dichotomous dendritic gelatinous tubes which are united laterally. Fresh water.

Cladomonas fruticulosa Stein (Fig. 54, *c*). Body about 8 microns long. The whole colony reaches 85 microns in height.

Genus **Rhipidodendron** Stein. Similar to Cladomonas, but the tubes are fused lengthwise. Fresh water.

Rhipidodendron splendidum Stein (Fig. 54, *d*, *e*). Body about 13 microns long. Fully grown colony 350 microns high.

Genus **Spiromonas** Perty. Body elongated; without gelatinous covering and spirally twisted; two flagella from the anterior end. Solitary in fresh water.

Spiromonas augusta (Dujardin) (Fig. 54, *f*). Body about 10 microns long. Stagnant water.

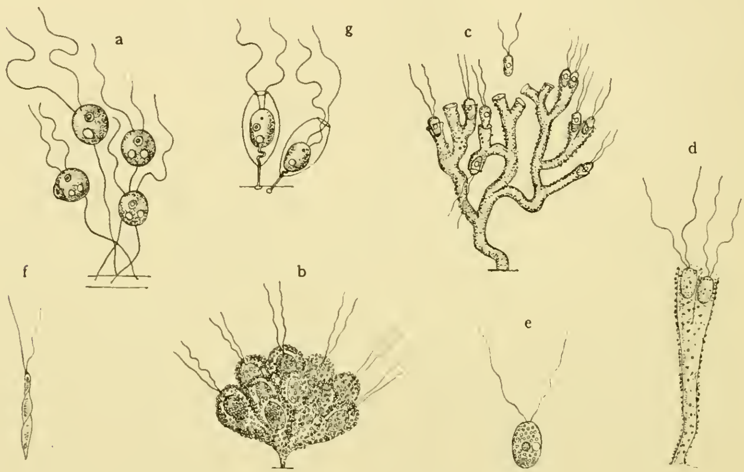


Fig. 54 a. *Amphimonas globosa.* ×400 (After Kent).
b. *Spongomonas uvella.* ×325 (After Stein).
c. *Cladomonas fruticulosa.* ×325 (After Stein).
d, e. *Rhipidodendron splendidum.* (After Stein). d, a young colony (×325); e, a free-swimming individual (×575).
f. *Spiromonas augusta.* ×750 (After Kent).
g. *Diplomita socialis.* ×750 (After Kent).

Genus **Diplomita** Kent. With transparent lorica; body attached to the bottom of the lorica by a retractile filamentous process. A rudimentary stigma (?). Fresh water.

Diplomita socialis Kent (Fig. 54, *g*). Pond water. Pale brown or yellow. Lorica 15 microns long.

Family 7 **Monadidae** Stein

Two flagella unequal in length: one primary and the other secondary. Motile or attached. One or two contractile vacuoles. Colony formation frequent. Free-living.

Genus **Monas** Ehrenberg. Known for a long time, but still very incompletely. Body not longer than 20 microns, plastic and actively motile ("dancing movement"). It attaches itself often to foreign objects.

Monas vulgaris (Cienkowski) (Fig. 55, *a*). Oval; with a single nucleus. About 15 microns long. In stagnant water and infusion.

Fig. 55 a. *Monas vulgaris.* ×750 (After Doflein).
b. *Stokesiella dissimilis.* ×375 (After Stokes).
c. *S. leptostoma.* ×630 (After Stokes).
d. A young colony of *Dendromonas virgaria.* ×500 (After Stein).
e. *Cephalothamnium cyclopum.* ×325 (After Stein).
f, g. *Anthophysa vegetans.* (After Stein). f, a colony (×170); g, a single individual (×575).
h. *Physomonas socialis.* ×500 (After Kent).

Genus **Stokesiella** Lemmermann. Body is attached by a fine cytoplasmic thread to a delicate and stalked vase-like test. Fresh water.

Stokesiella dissimilis (Stokes) (Fig. 55, *b*). Fresh water. Solitary. Lorica about 28 microns long.

Stokesiella leptostoma (Stokes) (Fig. 55, *c*). Fresh water. Often in groups. Lorica about 16 microns long.

Genus **Dendromonas** Stein. Colonial. Individuals without lorica, located at the end of the branched stalks. Fresh water.

Dendromonas virgaria (Weisse) (Fig. 55, *d*). Pond water. Body about 8 microns long; height of colony 200 microns.

Genus **Cephalothamnium** Stein. Colonial without test, but individuals are clustered at the end of a stalk which is colorless and rigid. Fresh water.

Cephalothamnium cyclopum Stein (Fig. 55, *e*). Body about 10 microns long. Attached to the body of Cyclops.

Genus **Anthophysa** Bory. Colonial forms, somewhat similar to Cephalothamnium. Stalks yellow or brownish and usually bent. Detached individuals are amoeboid with pointed pseudopodia.

Anthophysa vegetans (Müller) (Fig. 55, *f, g*). Common in stagnant water and infusion. Body about 5 or 6 microns long.

Genus **Physomonas** Kent. Solitary. Usually attached by a filiform flexible pedicel; anterior end obliquely truncate. No cytostome. Fresh or salt water. Some authors place this genus with Monas.

Physomonas socialis Kent (Fig. 55, *h*). Fresh water among decaying vegetation. Body 5 to 10 microns long.

Family 8 **Bodonidae** Bütschli

With two flagella; one is directed anteriorly and the other posteriorly and trailing. Flagella arise from the anterior end which is drawn out to a varying degree. One or several contractile vacuoles. Nutrition is holozoic or parasitic. Asexual reproduction is by binary fission.

Genus **Bodo** Ehrenberg (=Prowazekia Hartmann and Chagas). Small Protomonadida; ovoid, but plastic. Cytostome anterior; a single nucleus central or anterior. Flagella are connected with two blepharoplasts, near which is found a rounded parabasal body. Encystment common. Very common in stagnant water and infusion. Also frequently coprozoic.

Bodo caudatus (Dujardin) (Fig. 56, *a–i*). Body about 10 to 20 microns long.

Bodo edax Klebs (Fig. 56, *j, k*). About 10 to 15 microns long.

Genus **Rhynchomonas** Klebs. Similar to Bodo, but there is an anterior extension of the body, in which one of the flagella is embedded, while the other flagellum trails. A single nucleus. Minute forms.

Rhynchomonas nasuta (Stokes) (Fig. 56, *l*, *m*). In fresh water and also coprozoic.

Genus **Prowazekella** Alexeieff. Elongated pyriform. Two flagella from the anterior end; one is directed anteriorly, and the other posteriorly. A single nucleus anterior. The encysted

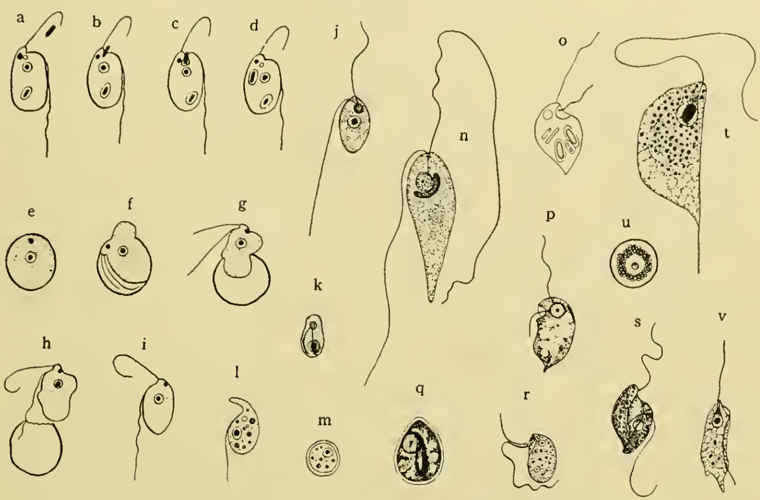


Fig. 56 a–i. *Bodo caudatus.* ×750 (After Sinton). a–d, feeding on a Bacillus; e–i, excystation in culture.
j, k. *B. edax.* ×700 (After Kühn).
l, m. *Rhynchomonas nasuta.* ×900 (After Parisi).
n. *Prowazekella lacertae.* ×1250 (After Kühn).
o–q. *Embadomonas intestinalis.* ×1900 (After Jepps).
r. *Phyllomitus undulans.* ×500 (After Stein).
s. *Colponema loxodes.* ×325 (After Stein).
t, u. *Cercomonas longicauda.* ×1000 (After Wenyon).
v. *C. crassicauda.* ×1000 (After Dobell).

stage is remarkable in that it is capable of increasing in size to a marked degree. Exclusively parasitic; in the intestine of various species of the lizard.

Prowazekella lacertae (Grassi) (Fig. 56, *n*). In the intestine of lizards belonging to the genera Lacerta, Tarentola, etc.

Genus **Embadomonas** Mackinnon. Body small, ovoid or pyriform. In the intestine of mammals and insects. Cytostome comparatively large. Nucleus anterior. Cysts are pyriform or ovoidal.

Embadomonas intestinalis (Wenyon and O'Connor) (Fig. 56, *o–q*). In man.

Embadomonas agilis Mackinnon. In the gut of trichopteran and tipulid larvae.

Genus **Phyllomitus** Stein. Body oval, cytostome large and conspicuous, with two unequal flagella which are united by a membrane. Fresh water and coprozoic.

Phyllomitus undulans Stein (Fig. 56, *r*). Body small 5 to 21 microns long.

Genus **Colponema** Stein. Body small, less than 30 microns long. Constant in form; ventral furrow conspicuous and widens at the anterior end. One flagellum arises from the anterior end and the other from the middle of body. One or two contractile vacuoles. Fresh water.

Colponema loxodes Stein (Fig. 56, *s*). Body up to 30 microns long.

Genus **Cercomonas** Dujardin. Biflagellate, both flagella arising from the anterior end of body. One directed anteriorly and the other runs backward over the body surface, becoming a trailing flagellum. Nucleus pyriform in shape and connected with the basal granules of the flagella. Spherical cysts uninucleate. Fresh water and coprozoic.

Cercomonas longicauda Dujardin (Fig. 56, *t, u*). Body pyriform and 5 to 20 microns long. Multiplication by binary fission. Fresh water. Often coprozoic.

Cercomonas crassicauda Dujardin (Fig. 56, *v*). Body about 10 to 14 microns long. Habitat similar to the last mentioned species.

Family 9 Trimastigidae Senn

Incompletely known forms with three flagella, of which one is directed anteriorly and the other two posteriorly. Body bilaterally symmetrical. No cytostome. Other structures unknown. Free-living in fresh water.

Genus **Trimastix** Kent. Ovate or pyriform. Contractile vacuole conspicuous.

Trimastix marina Kent (Fig. 57, *a*). About 18 microns long. Marine.

Genus **Dallingeria** Kent. Small; with drawn-out anterior end.

Dallingeria drysdali Kent (Fig. 57, *b*). Small fresh water form. Body length is less than 6 microns.

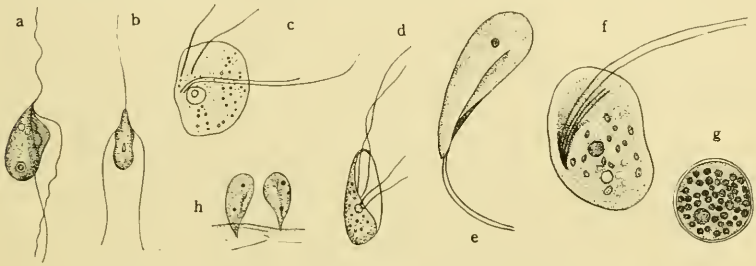


Fig. 57 a. *Trimastix marina.* ×625 (After Kent).
b. *Dallingeria drysdali.* ×1000 (After Kent).
c–h. *Costia necatrix.* c, d, (×600 after Weltner); e, f, (×1050 after Moroff); g, cyst (×1050 after Moroff); h, two individuals attached to the host fish integument (×375).

Family 10 **Costiidae**

With four flagella; two equally long and the other two equally short.

Genus **Costia** Leclerq. Body oval in front view; pyriform in profile. Along one side, there is a funnel-like depression, from the bottom of which the flagella arise. Ectoparasitic on fish.

Costia necatrix (Henneguy) (Fig. 57, *c–h*). Body 10 to 20 microns long by 5 to 10 microns broad. A single compact nucleus central; a contractile vacuole. Asexual reproduction is by longitudinal fission. Spherical uninucleate cysts measure 7 to 10 microns. When present in large numbers, the skin of fish appears to be covered with a whitish coat, and it is thought that the organisms are responsible for the death of young fish.

References

Christophers, S. R., H. E. Shortt and P. J. Barraud. 1926 The morphology and life-cycle of the parasite of Indian kala azar in culture. Indian Med. Res. Mem.

Hoare, C. A. 1923 An experimental study of the sheep-trypanosome (*T. melophagium* Flu, 1908), and its transmission by the sheep-ked (*Melophagus ovinus* L.). Parasit., Vol. 15.

Holmes, F. O. 1925 The relation of *Herpetomonas elmassiani* (Migone) to its plant and insect hosts. Biol. Bull., Vol. 49.

Laveran, A. and F. Mesnil. 1912 Trypanosomes et Trypanosomiases. Second edition. Paris.

Lemmermann, E. 1914 Protomastiginae. Süsswasserfl. Deutschlands, etc., H. 1.

Minchin, E. A. and J. D. Thomson. 1915 The rat trypanosome, *Trypanosoma lewisi*, in its relation to the rat flea, *Ceratophyllus fasciatus*. Quart. Jour. Micr. Sci., Vol. 60.

Nelson, R. 1922 The occurrence of Protozoa in plants affected with mosaic and related diseases. Michigan Agr. Coll. Bot. Stat., Tech. Bull., No. 58.

Wenyon, C. M. 1926 Protozoology. Vol. 1. London.

CHAPTER XII

ORDER 3 **POLYMASTIGIDA** BLOCHMANN

THE ZOOMASTIGINA grouped here possess three to eight flagella and, generally speaking, are minute forms with varied characters and structures. The majority inhabit the digestive tract of animals. Many possess a cytostome. One to many nuclei occur. The body is usually covered by a thin pellicle and, therefore, is somewhat plastic, although each species shows a more or less typical form. The cytoplasm does not show any special cortical differentiation. In many, there is an axial structure known as the **axostyle** or **axial filament** (p. 39). **Parabasal body** is invariably present and shows various forms. Contractile vacuole is generally absent. Nutrition is holozoic, saprozoic, or parasitic.

Asexual reproduction is by longitudinal fission, sometimes multiple. Encystment is common, and the cyst is responsible for infection of new hosts through the mouth. Sexual reproduction has not been definitely established. Some of the Polymastigida have recently been studied rather extensively by numerous investigators, but it is, as Calkins set forth clearly, impossible to place them in definite genetically related groups. Calkins' scheme is adopted in subdividing them into the following three tribes:

With one cytostome and kinetic element .... Tribe 1 Monozoa
With two cytostomes and kinetic elements .... Tribe 2 Diplozoa
With numerous nuclei and kinetic elements .... Tribe 3 Polyzoa

Tribe 1 **Monozoa** Calkins

Without cytostome and undulating membrane
  Without axostyle .... Group 1
  With axostyle .... Group 2
With cytostome
  Without undulating membrane; with axostyle .... Group 3
  With undulating membrane
    Without axostyle .... Group 4
    With axostyle .... Group 5

Group 1

Genus **Enteromonas** da Fonseca. Body globular. Two anterior flagella and one trailing flagellum.

Enteromonas hominis da Fonseca (Fig. 58, *a*). Body small, 5 to 6 microns in diameter. In human feces.

Genus **Tricercomonas** Wenyon and O'Connor. Body similar to that of Cercomonas, but with three anterior flagella and a posterior flagellum. Parasitic. Oblong cyst with four nuclei when mature.

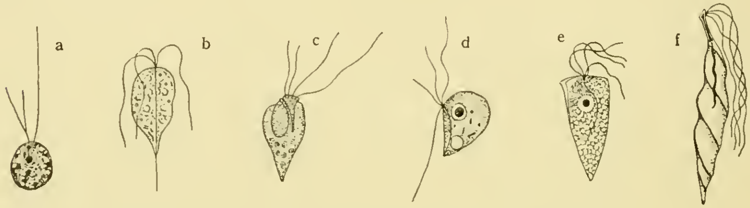


Fig. 58 a. *Enteromonas hominis.* ×1000 (After da Fonseca).
b. *Tricercomonas intestinalis.* ×1300 (After Wenyon and O'Connor).
c. *Tetramitus rostratus.* ×500 (After Klebs).
d. *T. pyriformis.* ×500 (After Klebs).
e. *Copromastix prowazeki.* ×800 (After Aragão).
f. *Streblomastix strix.* ×800 (After Kidder).

Tricercomonas intestinalis Wenyon and O'Connor (Fig. 58, *b*) In human intestine. Body 4 to 8 microns long. Rare, but widely distributed.

Genus **Tetramitus** Perty. Body ellipsoidal or pyriform. Four anterior flagella, unequal in length, one may be a trailing flagellum. Cystome distinct. Contractile vacuole. Holozoic. Fresh or salt water.

Tetramitus rostratus Perty (Fig. 58, *c*). Form variable; about 25 to 28 microns long. In stagnant water.

Tetramitus pyriformis Klebs (Fig. 58, *d*). About 18 microns long. In infusion.

Genus **Copromastix** Aragão. Four anterior flagella equally long. Body triangular or pyramidal. Coprozoic.

Copromastix prowazeki Aragão (Fig. 58, *e*). In human and rat feces. About 16 to 18 microns long.

Genus **Streblomastix** Kofoid and Swezy. Body elongated;

anterior flagella four in number. Nucleus an elongated spindle. With spirally arranged myonemes. Parasitic.

Streblomastix strix Kofoid and Swezy (Fig. 58, *f*). In the intestine of the termite, *Termopsis augusticollis*.

Group 2

Genus **Devescovina** Foà. Body oblong, axostyle is rigid and ends at the posterior end of the body. Three anterior flagella and one long trailing flagellum. Parabasal body wounds around the axostyle. Parasitic.

Devescovina lemniscata Kirby (Fig. 59, *a*). In the intestine of the termite, *Cryptotermis hermsi*. About 20 to 30 microns long.

Genus **Paradevescovina** Kirby. Minute; structure similar to that of Devescovina. The parabasal body is a curved rod

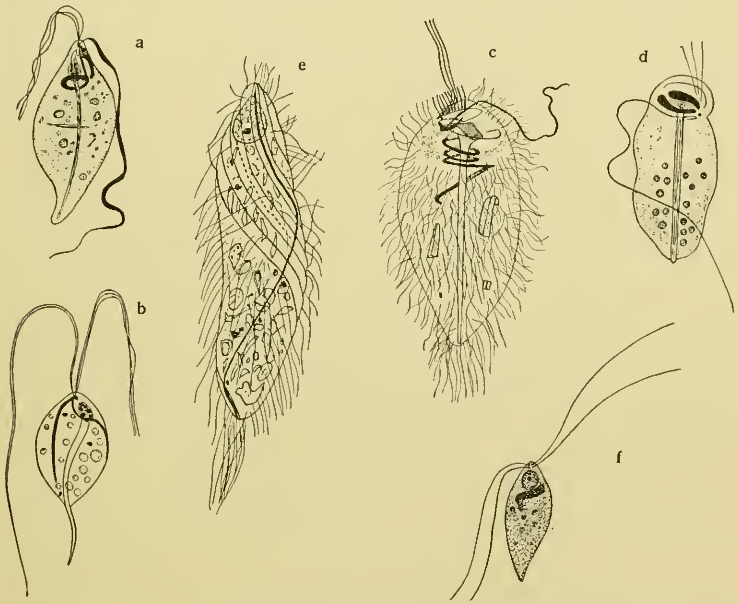


Fig. 59 a. *Devescovina lemniscata.* ×750 (After Kirby).
b. *Paradevescovina nana.* ×1250 (After Kirby).
c. *Metadevescovina debilis.* ×850 (After Light).
d. *Foaina gracilis.* ×900 (After Janicki).
e. *Dinenympha fimbriata.* ×625 (After Kirby).
f. *Monocercomonas bufonis.* ×1250 (After Alexeieff).

stretched between the blepharoplast and a point on the side of body. With a stout axostyle.

Paradevescovina nana Kirby (Fig. 59, *b*). In the termite, *Kalotermes hermsi*. Body length 10 to 15 microns.

Genus **Metadevescovina** Light. Body spindle to elongated oval in form; circular in cross-section. Body surface smooth, but often with attached bacteria. Nucleus anterior. Axostyle not protruding beyond the posterior end of body. The parabasal body is a spiral rod around the axostyle. Three sets of flagella. A single primary flagellum, three long secondary flagella and several tertiary flagella, all of which emerge from the region anterior to the nucleus. Feeding on bits of wood.

Metadevescovina debilis Light (Fig. 59, *c*). In the intestine of the termite, *Kalotermes hubbardi*. Body 35 to 40 microns long.

Genus **Foaina** Janicki. Body ellipsoidal; rigid axostyle protrudes a little. Flagella similar to those of Devescovina in number and appearance. Blepharoplast is somewhat back of the anterior tip. Parabasal body is composed of two curved rods.

Foaina gracilis Janicki (Fig. 59, *d*). In the gut of termites. Body about 25 to 30 microns long.

Genus **Dinenympha** Leidy. Four to eight posterior flagella arranged in spiral form. Axostyle free at the posterior end.

Dinenympha fimbriata Kirby (Fig. 59, *e*). In the intestine of the termite, *Reticulotermes hesperus*. Body 60 to 70 microns long.

Genus **Pyrsonympha** Leidy. Body ovoid; plastic. Axostyle is divided into two parts at its posterior margin and the whole vibrates in life. 4 to 8 posterior flagella. Several species in termites.

Pyrsonympha vertens Leidy. In *Termes flavipes*.

Genus **Monocercomonas** Grassi. Body small. Four flagella inserted in pairs in two places. Two flagella directed anteriorly, and two posteriorly. Axostyle filamentous.

Monocercomonas bufonis Dobell (Fig. 59, *f*). In frogs and toads. Body small, about 13 microns long.

Group 3

Genus **Eutrichomastix** Kofoid and Swezy (=Trichomastix Blochmann). Body pyriform; anterior end rounded. Cytostome and nucleus anterior. Three flagella of equal length arise from the anterior end, the fourth trailing. Axostyle projects beyond the posterior end of body. All parasitic.

Eutrichomastix serpentis (Dobell) (Fig. 60, *a*). In the large intestine of several species of the snake belonging to the genera: Pituophis, Eutaenia and Python. Body about 10 to 25 microns long.

Genus **Retortamonas** Grassi. Similar to Eutrichomastix in possessing four flagella, one of which trails. Cytostome (?). Axostyle indistinguishable; but a deeply staining axial filament is noted in numerous specimens, although some lack it entirely. Parasitic in the intestine of various insects.

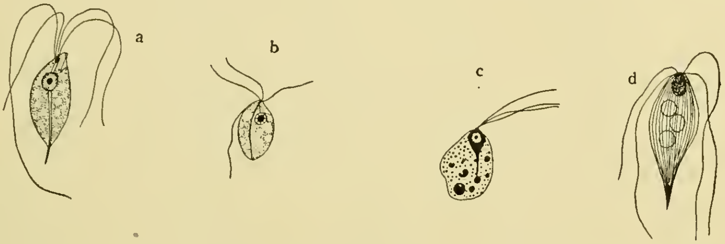


Fig. 60 a. *Eutrichomastix serpentis.* ×1085 (After Kofoid and Swezy).
b. *Retortamonas orthopterorum.* ×1850 (After Bělař).
c. *Protrichomonas legeri.* ×750 (After Alexeieff).
d. *Polymastix melolonthae.* ×400 (After Hamburger).

Retortamonas orthopterorum (Parisi) (Fig. 60, *b*). In cockroaches. Body very minute, 3 to 6 microns long.

Genus **Hexamastix** Alexeieff. Body similar to Eutrichomastix, but there are six flagella, of which one trails. Axostyle conspicuous and parabasal body prominent.

Hexamastix batrachorum Alexeieff. In amphibians.

Genus **Protrichomonas** Alexeieff. Three anterior flagella of equal length, arising from a blepharoplast located at the anterior tip. Parasitic.

Protrichomonas legeri Alexeieff (Fig. 60, *c*). In the oesophagus of the marine fish, *Box boops*.

Genus **Polymastix** Bütschli. Body pyriform. Four flagella arise from two blepharoplasts located at the anterior end. Cytostome and axostyle inconspicuous, but present. Ectoplasm is covered by longitudinally placed ridges. Parasitic in insects.

Polymastix melolonthae (Grassi) (Fig. 60, *d*). In the gut of the larvae of the cockchafer.

Group 4

Genus **Chilomastix** Alexeieff. Body pyriform, with a large cytostomal cleft at the anterior end. Nucleus anterior. Three anteriorly directed flagella and fourth flagellum undulates within the cleft. Cysts are common. In the intestine of vertebrates.

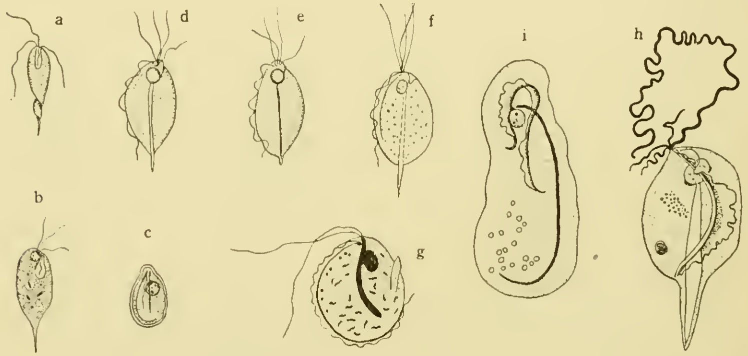


Fig. 61 a–c. *Chilomastix mesnili*. ×800. a, living individual; b, a stained specimen; c, a stained cyst.
d. *Trichomonas hominis*. ×800.
e. *T. elongata*. ×800.
f. *T. vaginalis*. ×650 (After Wenyon).
g. *Ditrichomonas termitis*. ×470 (After Cutler).
h. *Giantomonas herculea*. ×400 (After Dogiel).
i. *Myxomonas polymorpha*. ×300 (After Dogiel).

Chilomastix mesnili (Wenyon) (Fig. 61, *a–c*). In the human intestine; held to be a commensal, although often found in abundance in diarrhoeic stools. Length 10 to 15 microns long. Cysts measure 5 to 10 microns in length.

Group 5

Genus **Trichomonas** Donné. Body pyriform. Anterior flagella 3 or 4 in number; another flagellum runs along the outer margin of the undulating membrane, on the base of which there is an axoneme. The axostyle projects beyond the posterior end of body. Cysts have been noted in forms inhabiting animal intestines, but not in the species occurring in man. All parasitic in the intestine.

Trichomonas hominis (Davaine) (Fig. 61, *d*). In the human gut. 5 to 18 microns long.

Trichomonas elongata Steinberg (= *T. buccalis* Goodey and Wellings) (Fig. 61, *e*). In the human mouth; about 10 to 20 microns long.

Trichomonas vaginalis Donné (Fig. 61, *f*). In the human vagina. Body 10 to 25 microns long.

Genus **Ditrichomonas** Cutler. Similar to Trichomonas, but with two anterior flagella. Parasitic.

Ditrichomonas termitis Cutler (Fig. 61, *g*). In the gut of the termite, *Archotermopsis wroughtoni*.

Genus **Giantomonas** Dogiel. Somewhat similar to Trichomonas, but much larger. Three short flagella and a very long flagellum. Axostyle is large and the undulating membrane is well developed. Parasitic.

Giantomonas herculea Dogiel (Fig. 61, *h*). In the intestine of the termite, *Hodotermes mossambicus*. Body 60 to 75 microns long by 30 to 35 microns broad.

Genus **Myxomonas** Dogiel. Body highly amoeboid, without any flagella, but with an undulating membrane and a primitive axostyle. It is considered as a Trichomonas which lost its flagella and which became amoeboid. Parasitic.

Myxomonas polymorpha Dogiel (Fig. 61, *i*). In the intestine of the termite, *Hodotermes mossambicus*. Reaches 100 microns in length.

Tribe 2 **Diplozoa** Calkins

Genus **Hexamitus** Dujardin. Body small, more or less pyriform. Two nuclei near the anterior end. Six anterior and two posterior flagella. Cytostome indistinct. Encystment. Free-living. Several species.

Hexamitus inflatus Dujardin (Fig. 62, *a*). 15 to 25 microns long. Stagnant water and infusion.

Genus **Octomitus** Prowazek. Similar to Hexamitus, but parasitic. Body plastic; no cytostome; nutrition parasitic.

Octomitus intestinalis (Dujardin) (Fig. 62, *b*, *c*). About 10 to 16 microns long. In the intestine of the frog, also in midgut of *Trutta fario* and in the rectum of *Motella tricirrata* and *M. mustela* in European waters. Moore noted a similar form in young salmon and trout in North America, and named it *Octomitus salmonis*.

Octomitus periplanetae Bělař. In the gut of the cockroach.

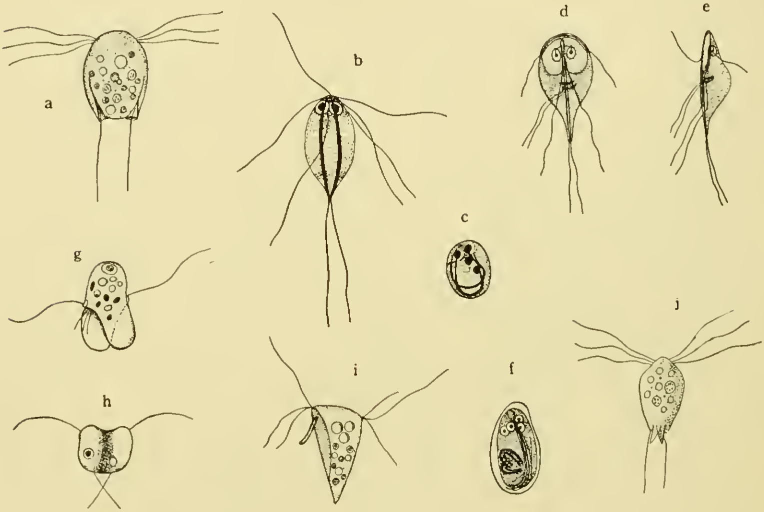


Fig. 62 a. *Hexamitus inflatus*. ×520 (After Klebs).
b, c. *Octomitus intestinalis*. ×1200 (After Alexeieff).
d–f. *Giardia intestinalis*. ×800 (After Kofoid and Swezy). d, front view; e, profile; f, cyst.
g. *Trepomonas agilis*. ×800 (After Klebs).
h. *Gyromonas ambulans*. ×400 (After Seligo).
i. *Trigonomonas compressa*, feeding on a Bacillus. ×370 (After Klebs).
j. *Urophagus rostratus*. ×600 (After Klebs).

Genus **Giardia** Künstler (=Lamblia Blanchard). Pyriform; bilaterally symmetrical. In profile, dorsal side convex; the ventral side possesses a single sucking disc at the anterior region. Eight flagella: four from the margin of the sucking disc;

two from the middle and two from the posterior end of body. Parasites in the intestine of various vertebrates. Several species.

Giardia intestinalis (Lambl) (Fig. 62, *d–f*). Body 12 to 18 microns long by 6 microns broad. Commensal in the human intestine.

Genus **Trepomonas** Dujardin. Body flattened and more or less rounded. Two cytostomal grooves on the posterior half, one on each side. Eight flagella (one long and three short flagella on each side) arise from the anterior margin of the groove. At the anterior end there occurs a horseshoe-like structure, in which two nuclei are located. Marine, parasitic, or coprozoic.

Trepomonas agilis Dujardin (Fig. 62, *g*). About 15 microns long. In infusion made from the sea water and once coprozoic(?).

Genus **Gyromonas** Seligo. Body small, constant, flattened; slightly spirally coiled. Four flagella from the anterior end. Cytostome not observed. Fresh water.

Gyromonas ambulans Seligo (Fig. 62, *h*). About 15 microns long.

Genus **Trigonomonas** Klebs. Body pyriform, but plastic. Cytostome on either side, from the anterior margin of which arise three flagella. Flagella are six in all. The two nuclei are situated near the anterior end. Rotation movement. Holozoic. Fresh water.

Trigonomonas compressa Klebs (Fig. 62, *i*). Length about 35 microns. Fresh water.

Genus **Urophagus** Klebs. Body somewhat resembles that of Hexamitus, but differs from the latter by the presence of a single cytostome, located at the posterior end of the body, where two short processes occur. Holozoic.

Urophagus rostratus Klebs (Fig. 62, *j*). About 20 microns long. Free-living.

Tribe 3 **Polyzoa** Calkins

This group includes those Polymatigida which inhabit the intestine of various species of termites, probably as symbionts. The majority are multinucleate. Each nucleus gives rise to a basal body (from which flagella extend), a parabasal body, and an axial filament. Janicki called this complex a **karyomasti-**

gont. In some forms the nucleus is not in the complex and this is called **akaryomastigont.**

Genus **Oxymonas** Janicki. Perhaps the most primitive of the group. A single nucleus and two groups of flagella. With an axostyle.

Fig. 63 a. *Oxymonas projector.* ×945 (After Kofoid and Swezy).
b. *Proboscidiella multinucleata.* ×435 (After Kofoid and Swezy).
c. *Calonympha grassii.* ×900 (After Janicki).
d. *Coronympha clevelandi.* ×1000 (After Kirby).

Oxymonas projector Kofoid and Swezy (Fig. 63, *a*). In the termite, *Kalotermes perparvum.*

Genus **Proboscidiella** Kofoid and Swezy. One to many nuclei, each with a karyomastigont. A single extensile and retractile proboscis. Binary fission. In the intestine of termites.

Proboscidiella multinucleata Kofoid and Swezy (Fig. 63, *b*). In the intestine of the termite, *Planocryptotermes nocens*.

Genus **Calonympha** Foà. Body rounded and quite large. Numerous long flagella arise from the anterior region, and numerous nuclei are arranged near the insertion points of the flagella. Thus numerous karyomastigonts occur. In some forms akaryomastigonts are present. Axial filaments form a bundle.

Calonympha grassii Foà (Fig. 63, *c*). In the termite, *Cryptotermis grassii*.

Genus **Stephanonympha** Janicki. Oval, but plastic. Pellicle sculptured with foreign bodies. Numerous nuclei are spirally arranged around the anterior end, each forming a karyomastigont.

Stephanonympha nelumbium Kirby. Size 45 microns by 27 microns. In the termite, *Cryptotermes hermsi*.

Genus **Snyderella** Kirby. Numerous nuclei scattered in the cytoplasm. Akaryomastigonts are close together and extend through the greater part of the peripheral region of the cytoplasm. The axial filaments are collected into a bundle.

Snyderella tabogae Kirby. In the termite, *Kalotermes longicollis*.

Genus **Coronympha** Kirby. Body pyriform with 16 nuclei which are arranged in a single circle in the anterior region of the body. Each nucleus is the center of a karyomastigont. Parasitic.

Coronympha clevelandi Kirby (Fig. 63, *d*). In the intestine of *Kalotermes clevelandi*.

References

Dobell, C. and F. W. O'Connor. 1921 The intestinal Protozoa of man. London.

Grassé, P. P. 1926 Contribution à l'étude des Flagellés parasites. Arch. zool. expér., T. 65.

Kofoid, C. A. and Olive Swezy. 1915 Mitosis and multiple fission in trichomonad flagellates. Proc. Amer. Acad. Arts and Sci., Vol. 51.

———. 1920 On the morphology and mitosis of *Chilomastix mesnili* (Wenyon), a common flagellate of the human intestine. University of California Publ. in Zool., Vol. 20.

———. 1922 Mitosis and fission in the active and encysted phases of *Giardia enterica* etc. Ibid., Vol. 20.

Wenyon, C. M. 1926 Protozoology. Vol. 1. London.

CHAPTER XIII

ORDER 4 **HYPERMASTIGIDA** GRASSI

ALL THE members of this order are inhabitants of the alimentary canal of the termite and other insects. The body organization is of extreme complexity, although there is only a single nucleus. Flagella are numerous and have their origin in blepharoplasts, located at the anterior region of the body. In some species, it has been established by Cleveland that there exists a true symbiotic relationship between the host insects and the protozoans (p. 6). Method of nutrition is either holozoic or parasitic. No cystostome has been detected. Bits of wood, starch grains, and other food materials, are taken in by means of pseudopodia.

Asexual reproduction is by longitudinal fission; multiple division has also been noted in some species under certain conditions. Sexual reproduction has so far not been observed. Encystment occurs only in Lophomonadidae. Because of the peculiarity and complexity of their structures and also of their common occurrence in termites, the Hypermastigida have in recent years been frequently studied.

This order is divided into the following eight families:

Body without segmented appearance
  Flagella arranged in spiral rows..............Family 1 Holomastigotidae
  Flagella not placed in spiral rows
    Flagella in one or more tufts
      One anterior tuft of flagella
        Flagella directed anteriorly............Family 2 Lophomonadidae
        Some directed posteriorly......................Family 3 Joenidae
      Two anterior tufts of flagella.............Family 4 Hoplonymphidae
      Four anterior tufts of flagella..............Family 5 Staurojoenidae
      Several anterior tufts (loriculae)...............Family 6 Kofoidiidae
    Flagella not in tufts.......................Family 7 Trichonymphidae
Body with segmented appearance...............Family 8 Cyclonymphidae

Family 1 **Holomastigotidae** Janicki

Flagella are arranged in spiral rows. A part of the posterior region may be free from flagella. The "anterior body" surrounds, or occurs near, the nucleus. Asexual reproduction by longitudinal division. Inhabitants in the intestine of termite.

Genus **Holomastigotes** Grassi. Body small and spindle-shaped. Few spiral rows reach from the anterior to the posterior end. The nucleus is located near the anterior end and is surrounded by a mass of dense cytoplasm. Nutrition by absorption of fluid material. Several species.

Holomastigotes elongatum Grassi (Fig. 64, *a*). In the intestine of termites. Widely distributed. Several subspecies.

Genus **Holomastigotoides** Grassi. Body large and spindle-shaped. Spiral rows of flagella as in the last genus, but more numerous (12 to 40 in number). A mass of dense cytoplasm surrounds the nucleus. Nucleus ovoid. Four species.

Holomastigotoides hartmanni Koidzumi (Fig. 64, *b*). Body 50 to 140 microns long. In *Coptotermes formosanus*.

Genus **Spirotrichonympha** Grassi. Body moderately large; elongated pyriform. The flagella are more deeply embedded in the cytoplasm in the anterior region of the body. The mass of dense cytoplasm is conical in form and its base indistinct. Spherical nucleus.

Spirotrichonympha leidyi Koidzumi (Fig. 64, *c*). In the termite, *Coptotermes formosanus*.

Genus **Spirotrichonymphella** Grassi. Body small and without spiral ridges. Posterior flagella longer. Not wood-feeding.

Spirotrichonymphella pudibunda Grassi. In an Australian termite, *Porotermes adamsoni*.

Genus **Microspirotrichonympha** Koidzumi. Body small, surface not ridged. Spiral rows of flagella only on the anterior half. Between the nucleus and the anterior extremity, there is a tubular structure. A mass of dense cytoplasm surrounds the nucleus. Axial rod may or may not occur.

Microspirotrichonympha porteri Koidzumi (Fig. 64, *d*). In the termite, *Leucotermes flaviceps*.

Family 2 **Lophomonadidae** Grassi

Numerous flagella arise from the anterior end in a tuft. Each flagellum originates in a blepharoplast from which extends inward an axial filament. A single nucleus is located near the anterior end and surrounded by a funnel-shaped space formed by the axial filaments. No cytostome. Parabasal body. Nutrition holozoic or parasitic. Asexual reproduction by binary or multiple fission. Encystment common. Sexual reproduction unknown. Parasites of cockroaches and termites.

Genus **Lophomonas** Stein. Body rounded or elongated.

Fig. 64 a. *Holomastigotes elongatum.* ×700 (After Koidzumi).
b. *Holomastigotoides hartmanni.* ×250 (After Koidzumi).
c. *Spirotrichonympha leidyi.* ×400 (After Koidzumi).
d. *Microspirotrichonympha porteri.* ×250 (After Koidzumi).
e–i. *Lophomonas blattarum.* (After Kudo). e, f, living trophozoites (×320); g, a stained specimen (×1150); h, highly spread individual containing the dividing nucleus (×1150); i, cyst (×1150).
j-l. *L. striata.* (After Kudo). j, a living trophozoite (×320); k a dividing form; l, a cyst (×1150).

Small. A single vesicular nucleus near the anterior end. Parasitic in the colon of the cockroach. Cysts common.

Lophomonas blattarum Stein (Figs. 2; 64, *e–i*). Body small, pyriform, but plastic. Axostyle may project beyond the posterior margin of the body. Active swimming movements. Holozoic in the colon of the cockroach. Binary or multiple fission. Body length 25 to 30 microns. Widely distributed.

Lophomonas striata Bütschli (Fig. 64, *j-l*). Body elongated spindle in form. Body surface with obliquely arranged needle-like structures which some investigators believe to be Protophyta (to which Grassé gave the name, *Fusiformis lophomonadis*). Axostyle is short, never protruding. Movement sluggish. Cyst spherical with the needle-like structures. In the same habitat as the last species.

Genus **Eulophomonas** Grassi. Similar to Lophomonas, but the flagella vary from 5 to 15 or a little more in number.

Eulophomonas calotermitis Grassi. In the termite, *Kalotermes flavicollis.*

Family 3 **Joenidae** Grassi

The flagella are confined mostly to the anterior end, but some of them are directed posteriorly. A conspicuous axostyle is always present. Parasites of termites.

Genus **Joenia** Grassi. Body ellipsoidal. Anterior portion is capable of forming pseudopodia. Flagellar tufts are in part directed anteriorly. Body surface is covered by numerous immobile short filamentous processes, which some authors hold to be symbiotic bacteria. The spherical nucleus at the anterior end; posterior to the nucleus, there is a conspicuous axostyle composed of numerous axial filaments. A parabasal apparatus surrounds it. Bits of wood used as food.

Joenia annectens Grassi (Fig. 65, *a*). In the termite, *Kalotermes flavicollis.*

Genus **Joenina** Grassi. The structure is more complicated than that of Joenia. Flagella are inserted at the anterior end in a semi-circle. Parabasal bodies are two elongated curved rods. Feeding on wood fragments.

Joenina pulchella Grassi. In the termite, *Porotermes adamsoni.*

Genus **Parajoenia** Janicki. Body oval and medium large.

Long flagella are arranged at the anterior end in two semicircular areas. There is a trailing flagellum. The posterior half of the body is covered by ciliary structure (symbiotic bacteria?). Nucleus large. Conspicuous axostyle runs backward from the nucleus. Two curved parabasal bodies.

Parajoenia grassii Janicki (Fig. 65, *b*). In the termite *Kalotermes castaneus*.

Genus **Joenopsis** Cutler. Body oval and large. There is a horseshoe-shaped pillar at the anterior end. Flagella arise from

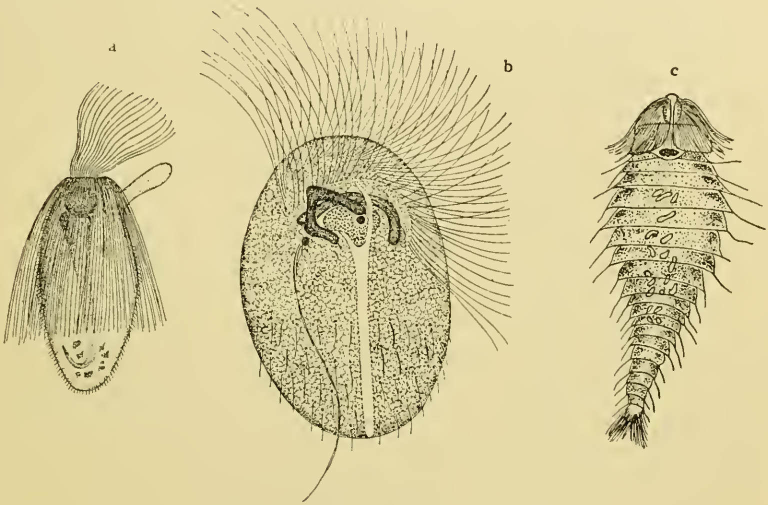


Fig. 65 a. *Joenia annectens*. (After Grassi and Foà).
b. *Parajoenia grassii*. ×940 (After Janicki).
c. *Cyclonympha strobila*. ×285 (After Dogiel).

the structure; some directed anteriorly, others posteriorly. Parabasal bodies long rods. A strong axostyle. Feeding on bits of wood.

Joenopsis polytricha Cutler. In the termite, *Archotermopsis wroughtoni*.

Genus **Microjoenia** Grassi. Body small, pyriform; anterior end flattened. The flagella are arranged in longitudinal rows. Axostyle. Parabasal body simple.

Microjoenia axostylis Cutler. In the termite, *Archotermopsis wroughtoni*.

Genus **Mesojoenia** Grassi. Body large. Flagellar tuft is spread over a wide area. Distinct axostyle, bent at the posterior end. Parabasal bodies two in number.

Mesojoenia decipiens Grassi. In the termite, *Kalotermes.*

Family 4 **Hoplonymphidae** Light

Two flagellar tufts; each arises from a plate near the anterior end of the slender body which is protected by a highly developed pellicular armor.

Genus **Hoplonympha** Light. Body slender fusiform, covered with thick, rigid pellicular armor. Each tuft of flagella arises from a plate connected with blepharoplasts at the anterior end. Nucleus near the anterior extremity, more or less triangular in form.

Hoplonympha natator Light (Fig. 66, *a*, *b*). In the intestine of the termite, *Kalotermes simplicicornis.*

Family 5 **Staurojoeniidae** Grassi

Four flagellar tufts arise from the anterior end.

Genus **Staurojoenia** Grassi. Body pyriform. Spherical nucleus central. Four flagellar tufts from the anterior end. Ingest wood fragments.

Staurojoenia assimilis Kirby (Fig. 66, *c*). In the intestine of the termite, *Kalotermes minor.*

Family 6 **Kofoidiidae** Light

Flagellar tufts are composed of several loriculae (permanently fused bundles). No axostyle, no parabasal body.

Genus **Kofoidia** Light. Body spherical. Between the oval nucleus and the bases of the flagellar tufts, there occurs a chromatic collar. Wood fragments as food.

Kofoidia loriculata Light (Fig. 66, *d*, *e*). In the termite, *Kalotermes simplicicornis.*

Family 7 **Trichonymphidae** Kent

The body is divisible into two regions: anterior and posterior. The surface of the anterior portion is differentiated into one or two thick ectoplasmic layers, densely traversed by numerous flagella. There is an "axial core" or "head organ" at the anterior tip. No cytostome. A single nucleus. Flagella numerous and long. They are arranged in longitudinal rows in the anterior third. Multiplication by simple longitudinal fission. Parasites of termites.

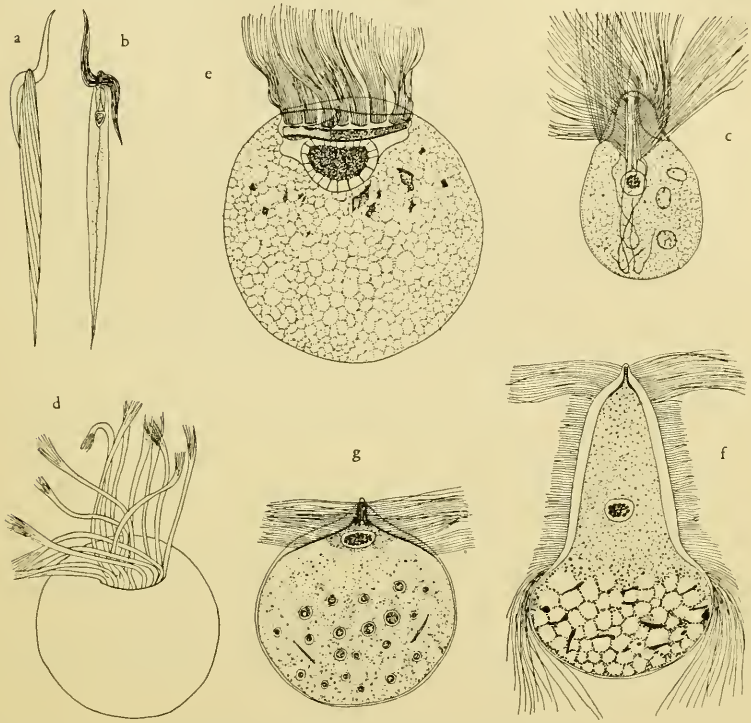


Fig. 66 a, b. *Hoplonympha natator.* ×450 (After Light).
c. *Staurojoenia assimilis.* ×200 (After Kirby).
d, e. *Kofoidia loriculata.* (After Light). d, from life (×175); e, a stained specimen (×300).
f. *Trichonympha campanula.* ×150 (After Kofoid and Swezy).
g. *Leidyopsis sphaerica.* ×150 (After Kofoid and Swezy).

Genus **Trichonympha** Leidy. Anterior portion consists of the nipple and the bell, both of which are composed of two layers. A distinct axial core. Nucleus central. Flagella located in longitudinal rows on the bell. Several species.

Trichonympha campanula Kofoid and Swezy (Figs. 12; 66, *f*). In the intestine of the termite, *Termopsis augusticollis.*

Genus **Pseudotrichonympha** Grassi. Two parts in the anterior end as in Trichonympha. The head organ with a spherical body at its tip and is surrounded by a single layer of ectoplasm; the bell is covered by two layers of ectoplasm. The nucleus lies freely. Body covered by spiral rows of short flagella.

Pseudotrichonympha grassii Koidzumi. In the termite, *Coptotermes formosanus.*

Genus **Gymnonympha** Dobell. Body oval or pyriform, but plastic. A spherical body at the anterior end, around the base of which is a ring of flagella. Flagella about half as long as the body. Posterior one-third shows longitudinally striated pellicle. Nucleus near the anterior end.

Gymnonympha zeylanica Dobell. In the termite, *Kalotermes militaris.*

Genus **Leidyopsis** Kofoid and Swezy. Ectoplasmic differentiation only in the anterior third, the remaining part is covered by a thin .pellicle. The axial core bears a hemispherical tip. Nucleus anterior. Long flagella arise from the anterior third of the body. Very similar to Gymnonympha.

Leidyopsis sphaerica Kofoid and Swezy (Fig. 66, *g*). In the termite, *Termopsis augusticollis.*

Genus **Leidyonella** Frenzel. Body large Anterior end is pointed. Flagella as long as the body. Pellicle with longitudinal striation.

Leidyonella cordubensis Frenzel. In an Argentine termite, *Eutermes inquilinus.*

Family 8 **Cyclonymphidae** Reichenow
(=Tetratonymphidae Koidzumi)

Body large and elongated. It is transversely ridged, and presents a metameric appearance. Each ridge with a single row of flagella. No cytostome. The anterior end is complex, containing a nucleus. Asexual reproduction by longitudinal fission.

Genus **Cyclonympha** Dogiel (=Tetratonympha Koidzumi). With the characters of the family.

Cyclonympha strobila Dogiel (=*Tetratonympha mirabilis* Koidzumi) (Fig. 65, *c*). In the termites of Japan. Body 110 to 170 microns long.

References

Cleveland, L. R. 1925 The effects of oxygenation and starvation on the symbiosis between the termite, Termopsis, and its intestinal flagellates. Biol. Bull., Vol. 48.

Dogiel, V. 1922 Untersuchungen an parasitischen Protozoen aus dem Darmkanal der Termiten. III. Trichonymphidae. Arch. Soc. Russe Protist., Vol. 1.

Janicki, C. v. 1910, 1915 Untersuchungen an parasitischen Flagellaten. I, II. Zeitschr. wiss. Zool., Vols. 95, 112.

Kofoid, C. A. and Olive Swezy. 1919, 1926 Studies on the parasites of termites. Univ. California Publ. Zool., Vols. 20, 28.

Koidzumi, M. 1921 Studies on the intestinal Protozoa found in the termites of Japan. Parasit., Vol. 13.

Kudo, R. 1926 Observations on *Lophomonas blattarum*, a flagellate inhabiting the colon of the cockroach, *Blatta orientalis*. Arch. f. Protistenk., Vol. 53.

CHAPTER XIV

CLASS 2 **SARCODINA** BÜTSCHLI

The members of this class do not possess any definite pellicle and, therefore, are capable of changing the body form and forming pseudopodia. The term "amoeboid" is often used to describe their appearance. The pseudopodia serve for both locomotion and food-capturing. The peripheral portion of the body shows no structural differentiation in Amoebaea, Proteomyxa, and Mycetozoa. Internal or external skeletal sturctures are variously developed in other orders. Thus in Testacea and Foraminifera, there is a well-developed test, or shell that usually has an aperture, through which the pseudopodia are extruded. In Heliozoa and Radiolaria, endoskeletons of various forms and materials are developed.

Unlike the Mastigophora or the Ciliata, the Sarcodina lack permanent cell-organs for capturing and ingesting the food matter, although some of them possess semi-permanent axopodia. The cytoplasm, as a rule, is differentiated into the ectoplasm and the endoplasm, but this differentiation is not constant. In Radiolaria, there is a perforated membranous "central capsule" between the ectoplasm and endoplasm. The endoplasm contains the nuclei, food vacuoles, various granules, and contractile vacuoles. The majority of the Sarcodina are uninucleate, but numerous species of Foraminifera and Mycetozoa are multinucleate. In one group (Paramoebidae), there is a peculiar "secondary nucleus."

The Sarcodina are typically holozoic, but in a few cases holophytic. The food consists of Protozoa, small Metazoa, and Protophyta, which present themselves conspicuously in the cytoplasm. One or more contractile vacuoles are invariably present in forms inhabiting fresh water, but absent, as a rule, in parasitic forms or in those which live in salt water The Sarcodina vary in size from a few microns up to several millimeters. Colonial Sarcodina, especially plasmodium-forming Mycetozoa, reach a considerable size.

Asexual reproduction is usually by binary (or rarely by multiple) fission, budding, or plasmotomy. Definite proof of sexual reproduction has been given in a comparatively small number. Encystment is common in the majority of both free-living and parasitic Sarcodina, but it is unknown in certain groups. The life-cycle has been worked out in a few forms. It seems to vary in different groups. The youngest stages are either amoeboid or flagellate, and on this account it is sometimes very difficult to distinguish the Sarcodina and the Mastigophora. In some forms the adult trophic stage may show an amoeboid or flagellate phase owing to differences in environmental conditions (p. 205). These points support strongly the view that both classes have descended from a common ancestor and have undergone evolutionary changes in two different directions.

The Sarcodina are divided into two subclasses, as follows:

With lobopodia, myxopodia, or filopodia . . . . Subclass 1 Rhizopoda
With axopodia (usually radiating) . . . . Subclass 2 Actinopoda

SUBCLASS 1 **RHIZOPODA** SIEBOLD

The term Rhizopoda is often used to designate the class but is used here for one of the subclasses. These Sarcodina possess pseudopodia which are not axopodia. The subclass is divided into five orders as follows:

Without test
  With radiating pseudopodia . . . . Order 1 Proteomyxa
  With rhizopodia; forming plasmodium . . . . Order 2 Mycetozoa
  With lobopodia . . . . Order 3 Amoebaea
With test
  Test single-chambered; chitinous . . . . Order 4 Testacea
  Test one to many chambers; calcareous . . . . Order 5 Foraminifera

ORDER 1 **PROTEOMYXA** LANKESTER

A number of incompletely known Rhizopoda are placed in this group. They possess few common characteristics. The pseudopodia are filopodia which often branch or anastomose with one another. In this respect the Proteomyxa show affinity to the Mycetozoa. Without any skeletons. Their life history is not well known. Flagellate swarmers and encysted stages occur commonly. The majority of the Proteomyxa lead parasitic life in fresh-water algae or green plants.

Three families and several genera are usually distinguished in this order.

Individuals often fused into pseudoplasmodium.....Family 1 Labyrinthulidae
Solitary and Heliozoa-like
  With flagellated swarmers........................Family 2 Zoosporidae
  Without flagellated swarmers...................Family 3 Vampyrellidae

Family 1 **Labyrinthulidae** Haeckel

The body is a small fusiform protoplasmic mass. Several individuals are grouped in a network of sparingly branched and anastomosing filopodia. Multiplication by fission. Under unfavorable conditions individuals encyst independently. Flagellated stage may or may not be present. Two genera.

Genus **Labyrinthula** Cienkowski. Minute forms feeding on various species of algae of both fresh and salt waters. Often brightly colored due to the chlorophyll bodies taken in as food.

Labyrinthula cienkowskii Zopf (Fig. 67, *a*). Attacks the fresh-water alga, Vaucheria.

Genus **Labyrinthomyxa** Duboscq. Body fusiform, amoeboid and flagellate phases variable in size. The flagellated stage penetrates through the host cell membrane.

Labyrinthomyxa sauvageaui Duboscq (Fig. 67, *b-e*). Fusiform bodies 7 to 11 microns long. Pseudoplasmodium formed. Amoeboid stage measures 2.5 to 14 microns; flagellate stage 7 to 18 microns long. Parasitic in *Laminaria lejolisii* at Roscoff, France.

Family 2 **Zoosporidae** Zopf-Delage

Body form irregular, but with radiating filopodia. The general appearance is somewhat like a heliozoan. Swarmers.

Genus **Pseudospora** Cienkowski. Body minute. Parasitic in algae and Mastigophora (including Volvocidae). The organism nourishes itself on the protoplasm of the host, grows, and multiplies into a number of smaller individuals by repeated division.

The latter are biflagellated, seek a new host, and transform themselves into amoeboid stages. Encystment common.

Pseudospora volvocis Cienkowski (Fig. 67, *f*, *g*). Parasitic in species of Volvox. Body diameter about 12 to 30 microns.

Pseudospora parasitica Cienkowski. Attacks Spirogyra and allied algae.

Pseudospora eudorini Roskin. Parasitic in *Eudorina elegans*.

Genus **Protomonas** Cienkowski. Body irregularly rounded with radiating filopodia. Food consists of starch grains. Division into biflagellate swarmers which become amoeboid and unite to form pseudoplasmodium. Fresh or salt water.

Protomonas amyli Cienkowski (Fig. 67, *h-j*). In fresh water.

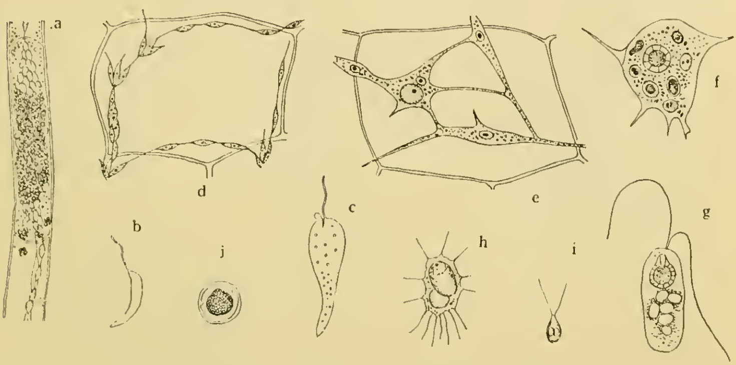


Fig. 67 a. *Labyrinthula cienkowskii.* × about 150 (After Doflein).
b–e. *Labyrinthomyxa sauvageaui.* (After Duboscq). b, c, small and large flagellated forms in life (×750); d, e, pseudoplasmodia formed by fusiform bodies and large amoebae (stained, ×375).
f, g. *Pseudospora volvocis.* ×500 (After Robertson).
h–j. *Protomonas amyli.* (After Zopf). h, amoeba; i, flagellate phase; j, cyst.

Family 3 **Vampyrellidae** Doflein

Filopodia radiate from all sides or formed from a limited area of the body. Flagellate swarmers absent. The organisms are able to bore through, by secreting probably a specific enzyme, the cellulose membrane of various algae and engulf the protoplasmic contents. The metabolic products of chlorophyll substance appear as carotin, a reddish substance, in the form of an irregular mass in the cytoplasm. The organism is as a rule multinucleate, but divides in the encysted stage into daughter individuals with one or many nuclei. The multinucleate cysts are often reddish, owing to the presence of the carotin.

Genus **Vampyrella** Cienkowski. The organism appears Heliozoa-like because of numerous filopodia which radiate. The cytoplasm is distinctly differentiated into the ectoplasm and endoplasm. The latter is vacuolated or granulated and often contains reddish carotin granules. Numerous vesicular nuclei and contractile vacuoles. Size varies from 50 to 700 microns. Multinucleate cysts may possess a stalk. Feed on the contents of algae in both fresh and salt waters. Several species.

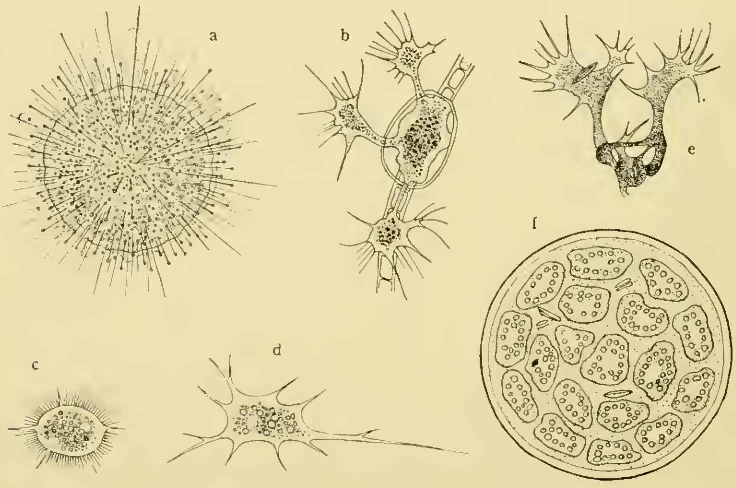


Fig. 68 a, b. *Vampyrella lateritia*. ×400. a, a rounded individual (after Leidy); b, young individuals budding out from a cyst (after Doflein).
c, d. *Nuclearia delicatula*. ×225 (After Cash).
e. *Arachnula impatiens*. ×500 (After Dobell).
f. *Chlamydomyxa montana*, encysted, with numerous secondary cysts. × about 400. (After Penard).

Vampyrella lateritia (Fresenius) (= *V. spirogyra* Cienkowski) (Fig. 68, *a*, *b*). Body spherical and orange-red in color except the hyaline ectoplasm. Feed on Spirogyra and other algae.

Genus **Nuclearia** Cienkowski. Body more or less rounded and colorless. The filopodia branching, but not anastomosing, may be confined to only a limited part of the body. Sometimes with a gelatinous envelope. There are one to many nuclei. The cyst is covered by a double envelope. Free-living.

Nuclearia simplex Cienkowski. Uninucleate.

Nuclearia delicatula Cienkowski (Fig. 68, *c*, *d*). Multinucleate; often bacteria adhering to the gelatinous envelope.

Genus **Arachnula** Cienkowski. Body irregularly chain-form with filopodia extending from the ends of the branches. Numerous nuclei and contractile vacuoles. Feed on diatoms and other microorganisms.

Arachnula impatiens Cienkowski (Fig. 68, *e*).

Genus **Chlamydomyxa** Archer. The naked body which measures up to 300 microns in diameter, is differentiated into the ectoplasm and endoplasm. The latter is often green-colored due to the presence of green spherules, and contains numerous vesicular nuclei and one or two contractile vacuoles. Secretion of a capsule round the body is followed by multiplication of the body into numerous secondary cysts. Cyst wall is cellulose. In Sphagnum swamp.

Chlamydomyxa montana Lankester (Fig. 68, *f*). Diameter 20 to 300 microns.

Genus **Rhizoplasma** Verworn. The body is spherical or sausage-shaped with anastomosing filopodia. The whole is orange-red in color. It contains a few nuclei and is said to measure from 5 to 10 millimeters. Found in Red Sea. *Rhizoplasma kaiseri* Verworn.

Genus **Dictomyxa** Monticelli. Similar to the above, but pseudopodia are said to be colorless; also found in salt water.

References

Calkins, G. N. 1926 The biology of the Protozoa. Philadelphia.

Doflein, F. and E. Reichenow. 1929 Lehrbuch der Protozoenkunde. Jena.

Kühn, A. 1926 Morphologie der Tiere in Bildern. H. 2; 2 T. Rhizopoden.

Cash, J. 1905 The British freshwater Rhizopoda and Heliozoa. Vol. 1. London.

Dobell, C. 1913 Observations on the life-history of Cienkowsky's Arachnula. Arch. f. Protistenk., Vol. 31.

Duboscq, O. 1921 *Labyrinthomyxa sauvageaui* n.g., n.sp., Protéomyxée parasite de *Laminaria lejolisii* Sauvageau. C. R. Soc. Biol., Vol. 84.

Leidy, J. 1879 Freshwater Rhizopods of North America. Report U. S. Geol. Survey, Vol. 12.

Roskin, G. 1927 Zur Kenntnis der Gettung Pseudospora Cienkowsky. Arch. f. Protistenk., Vol. 59.

Zopf, W. 1887 Handbuch der Botanik (A. Schenk), Vol. 3.

CHAPTER XV

ORDER 2 **MYCETOZOA** DE BARY

THE MYCETOZOA were formerly considered to be closely related to fungi, being known as Myxomycetes or Myxogasteres (the "slime molds"). Through extended studies of their life-histories, de Bary showed that they are more closely related to the Protozoa than to the Protophyta, although they stand undoubtedly on the border line between these two groups of organisms. The Mycetozoa occur on dead wood or decaying vegetable matter of various kinds.

The most conspicuous part of a mycetozoan is its **plasmodium** which is formed by the cytoplasmic fusion of several **myxamoebae** (amoebulae) without nuclear fusion, thus producing a large multinucleate protoplasmic body (Fig. 69, *a*). The greater part of the cytoplasm is granulated, although there is a thin layer of hyaline and homogeneous cytoplasm surrounding the whole body. The numerous vesicular nuclei are distributed throughout the granular cytoplasm. Many small contractile vacuoles are present in the peripheral portion of the plasmodium. The nuclei increase in number by multiplication as the body grows. The nuclear division seems to be amitotic during the growth period of the plasmodium, but is mitotic prior to the spore-formation. The granulation of the cytoplasm is due to the presence of enormous numbers of granules, which in Calcarinea are made up of carbonate of lime. The plasmodium is usually colorless, but sometimes yellow, green, or reddish. This coloration is due to numerous droplets of a fluid pigment scattered throughout the body.

The food varies in different species. The great majority feed on decaying vegetable matter, but some, such as Badhamia, devour living fungi. Thus the Mycetozoa are holozoic or saprozoic in their method of nutrition. The plasmodium is alkaline in reaction as a whole. Pepsin has been found in the plasmodium of Fuligo and is perhaps secreted into the food vacuoles, into which proteins are taken. The plasmodium of Badhamia is said to possess the power of dissolving the cellulose.

When exposed to unfavorable conditions, such as desiccation, the protoplasmic movement ceases gradually, foreign bodies

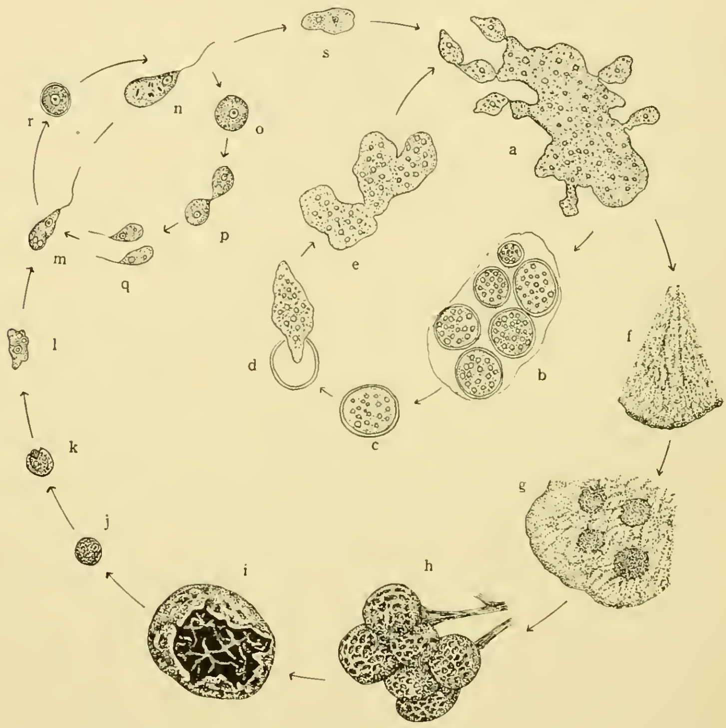


Fig. 69. Scheme of the life-cycle of an endosporous mycetozoan. Variously magnified. (Constructed after de Bary, Lister, and others).

a, plasmodium formation by fusion of numerous myxamoebae; b, c, sclerotium formation; d, e, germination of sclerotium and formation of plasmodium; f, portion of a plasmodium showing streaming protoplasmic thickenings; g, beginning of sporangium formation; h, six sporangia; i, sporangium opened, showing capillitium; j, a spore; k, germination of spore; l, myxamoeba; m, n, myxoflagellates; o–q, division of myxoflagellate; r, microcyst; s, myxamoeba.

are extruded, and the whole plasmodium becomes divided into numerous cysts, **sclerotia** of de Bary, each containing ten to twenty nuclei and being surrounded by a resistant wall (*b*).

These cysts may live as long as three years. Upon the return of favorable conditions, such as the addition of water to the preparation, the contents of the sclerotia germinate, fuse together, and thus again produce plasmodia (*c-e*).

When lack of food material occurs, the plasmodium undergoes changes and develops **sporangia.** The first indication of this process is the appearance of lobular masses of protoplasm in various parts of the body (*g*). These masses are at first connected with the streaming protoplasmic thickenings, but later become completely segregated into young sporangia. During the course of the formation of the sporangium, foreign bodies are thrown out of the body, and around each sporangium there is secreted a wall which, when mature, possesses a wrinkled appearance (*h*). The wall continues down to the substratum as a slender stalk of varying length, and in many genera the end of a stalk spreads into a network over the substratum, which forms the base for the stalk. This base is known as the **hypothallus.** With the external changes as outlined above, the interior of the sporangium becomes penetrated by an anastomosing network of flat bands which are continuous with the outer covering. This is called the **capillitium** (*i*).

Soon after the differentiation of these protective and supporting structures, the nuclei divide simultaneously by mitosis and the cytoplasm breaks up, directly or indirectly, into as many small bodies as there are nuclei. These uninucleate bodies are the **spores** which measure about 3 to 20 microns in diameter and which soon become covered by a more or less thick membrane (*j*), variously colored in different species. The membrane seems to be composed of cellulose.

The mature sporangium breaks open, sooner or later, and the spores are carried, and scattered, by the wind. When a spore falls into the water, its membrane ruptures, and the protoplasmic contents emerge as an amoebula (*k*, *l*). The amoebula possesses a single vesicular nucleus and contractile vacuoles, and undergoes a typical amoeboid movement. It assumes an elongated form and protrudes a flagellum from the nucleated end, thus forming a **myxoflagellate** (zoospore, swarmer) (*m*, *n*), which undergoes a peculiar dancing movement and is capable of forming short and pointed pseudopodia from the posterior end. It engulfs bacteria by means of its pseudopodia and grows in size. It multiplies by binary fission. In this process, the flagellum is withdrawn and the body becomes rounded. The nucleus undergoes a mitotic division, followed by a cytoplasmic constriction to form two daughter individuals (*o-q*). The multiplication seems to be repeated. The myxoflagellate may often become rounded and secrete a hyaline cyst-wall, thus forming the **microcyst** (*r*), which loses its flagellum permanently and transforms itself into a myxamoeba (*s*). The latter, through fusion with many others, produces the plasmodium described above. This is the general life-cycle of a typical endosporous mycetozoan.

In the genus Ceratiomyxa, the only genus of the exosporous form, in which spores are produced on the surface of **sporophores,** the development is briefly as follows: The plasmodium lives on or in decayed wood and presents a horn-like appearance (sporophore). The body is covered by a gelatinous hyaline substance, within which the protoplasmic movements may be noted. The protoplasm soon leaves the interior and accumulates at the surface of the mass; at first as a close-set reticulum, and then it becomes differentiated into a mosaic of polygonal cells, each containing a single nucleus. Each of these cells moves outward at right angles to the surface, still enveloped by the thin hyaline layer, which forms a stalk below it. These cells are the **spores,** which become ellipsoidal and are covered by a resistant membrane when mature. The spore is uninucleate at first, but soon becomes tetranucleate. When a spore reaches the water, the contents emerge as an amoebula which then divides three times, forming eight small bodies, each of which develops a flagellum and becomes a myxoflagellate. The remaining part of the development is presumably similar to that of the endosporous mycetozoan.

An enormous number of mycetozoan genera are known. The order is here divided into two suborders according to Lister. Further division into tribes, legions, sublegions, and families is given below, together with one or two genera for each family.

Spore develops into myxoflagellate; myxamoebae fuse completely and form the plasmodium....................Suborder 1 Euplasmodia

No flagellate stage; myxamoebae grouped prior to spore-formation, but do not fuse to form a true plasmodium.......Suborder 2 Sorophora

Suborder 1 **Euplasmodia** Lister

Spores develop within sporangia . . . . Tribe 1 Endosporeae
Spores violet or violet-brown . . . . Legion 1 Amaurosporales
Sporangia with lime . . . . Sublegion 1 Calcarinea
Lime in small granular form . . . . Family 1 Physaridae
Lime in crystalline form . . . . Family 2 Didymiidae
Sporangia without lime . . . . Sublegion 2 Amaurochaetinea
Sporangia stalked . . . . Family 1 Stemonitidae
Sporangia combined into aethalium . . . . Family 2 Amaurochaetidae
Spores variously colored, but never violet . . . . Legion 2 Lamprosporales
Capillitium absent or not forming a system of uniform threads . . . . Sublegion 1 Aneminea
Sporangium-wall membranous; with minute round granules . . . . Family 1 Cribrariidae
Sporangia solitary; sessile or stalked . . . . Family 2 Liceidae
Sporangium-wall membranous without granular deposits . . . . Family 3 Tubulinidae
Many sporangia more or less closely fused to form large bodies (aethalia); sporangium-wall incomplete and perforated . . . . Family 4 Reticulariidae
Sporangia forming aethalium . . . . Family 5 Lycogalidae
Capillitium a system of uniform threads . . . . Sublegion 2 Caloneminea
Capillitium threads with spiral or annular thickenings . . . . Family 1 Trichiidae
Capillitium combined into an elastic network with thickenings in forms of cogs, half-rings, spines, or warts . . . . Family 2 Arcyriidae
Capillitium abundant; sporangia normally sessile . . . . Family 3 Margaritidae
Spores develop on the surface of sporophores . . . . Tribe 2 Exosporeae
Spores white; borne singly on filiform stalk . . . . . . Family 1 Ceratiomyxidae

Family **Physaridae**

Genus **Badhamia** Berkeley (Fig. 70, *a*, *b*). Capillitium, a coarse network charged with lime throughout.

Genus **Fuligo** Haller (Fig. 70, *c*, *d*). Capillitium, a delicate network of threads with vesicular expansions filled with granules of lime.

Family **Didymiidae**

Genus **Didymium** Schrader (Fig. 70, *e*, *f*). Lime crystals stellate; distributed over the wall of sporangium.

Family **Stemonitidae**

Genus **Stemonitis** Gleditsch (Fig. 70, *g*, *h*). Sporangium-wall evanescent; capillitium arising from all parts of the columella to form a network.

Family **Amaurochaetidae**

Genus **Amaurochaete** Rostafinski (Fig. 71, *a*, *b*). With irregularly branching thread-like capillitium.

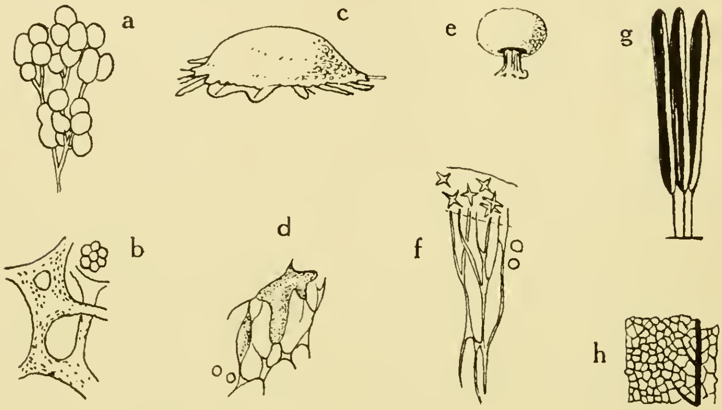


Fig. 70 a, b. *Badhamia utricularis* Berkeley. a, cluster of sporangia (×4); b, part of capillitium and spore-cluster (×140).
c, d. *Fuligo septica* Gmelin. c, a group of sporangia (×1/3); d, part of capillitium and two spores (×120).
e, f. *Didymium effusum* Link. e, sporangium (×12); f, portion of capillitium and wall of sporangium showing the crystals of calcium carbonate and two spores (×200).
g, h. *Stemonitis splendens* Rostafinski. g, three sporangia (×2); h, columella and capillitium (×42). (All after Lister.)

Family **Cribrariidae**

Genus **Cribraria** Persoon (Fig. 71, *c*). Sporangia stalked; wall is thickened and forms a delicate persistent network expanded at the nodes.

Family **Liceidae**

Genus **Orcadella** Wingate (Fig. 71, *d*). Sporangia stalked, furnished with a lid of thinner substance.

Family **Tubulinidae**

Genus **Tubulina** Persoon (Fig. 71, *e*). Sporangia without tubular extensions.

Family **Recticulariidae**

Genus **Reticularia** Bulliard (Fig. 71, *f*). Walls of convoluted sporangia incomplete, forming tubes and folds with numerous anastomosing threads.

Family **Lycogalidae**

Genus **Lycogala** Adanson (Fig. 71, *g*).

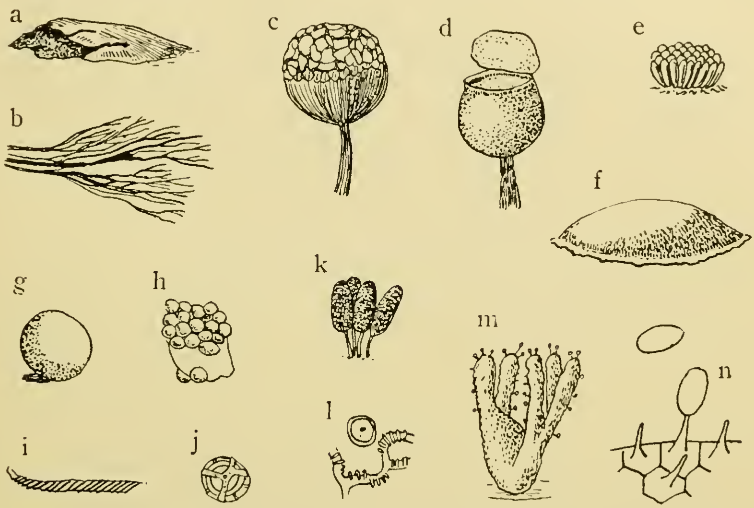


Fig. 71 a, b. *Amaurochaete fuliginosa* MacBride. a, group of sporangia (×1/2); b, capillitium (×10).
c. Sporangium of *Cribraria aurantiaca* Schrader, from which the spores have been dispersed. ×20.
d. *Orcadella operculata* Wingate. Sporangium with lid opened. ×80.
e. *Tubulina fragiformis* Persoon. Cluster of sporangia. ×3.
f. Aethalium of *Reticularia lycoperdon* Bull. Natural size.
g. Aethalium of *Lycogala miniatum* Persoon. Natural size.
h–j. *Trichia affinis* de Bary. h, group of sporangia (×2); i, elater (×250); j, spore (×400).
k, l. *Arcyria punicea* Persoon. k, four sporangia (×2); l, part of capillitium (×250) and a spore (×560).
m, n. *Ceratiomyxa fruticulosa* MacBride. m, sporophore (×40); n, part of mature sporophore, showing two spores (×480). (All after Lister.)

Family **Trichiidae**

Genus **Trichia** Haller (Fig. 71, *h–j*). Capillitium abundant, consisting of free elasters with spiral thickenings.

Family **Arcyriidae**

Genus **Arcyria** Wiggers (Fig. 71, *k*, *L*). Sporangia stalked; sporangium-wall evanescent above, persistent and membranous in the lower third.

Family **Margaritidae**

Genus **Margarita** Lister. Capillitium profuse, long, coiled hair-like.

Family **Ceratiomyxidae**

Genus **Ceratiomyxa** Schröter (Fig. 71, *m*, *n*).

Suborder 2 **Sorophora** Lister

Pseudo-plasmodium incomplete; myxamoeba a limax type................ Family 1 Guttuliniidae

Pseudo-plasmodium complete; myxamoeba with short pointed pseudopodia Family 2 Dictyosteliidae

Appendix

The Proteomyxa and the Mycetozoa as outlined above, are not distinctly defined groups. In reality, there are a number of forms which stand on the border line between them.

Phytomyxinae Schröter

These organisms which possess a large multinucleate amoeboid body, are parasitic in various plants and also in a few animals. They do not form any sporangium and their methods of spore-formation are simple.

Genus **Plasmodiophora** Woronin. Parasitic in the roots of cabbages and other Cruciferae. The organism produces knotty enlargements, sometimes known as "root-hernia," or "fingers and toes" (Fig. 72, *a*). The small spore (*b*) gives rise to a myxoflagellate (*c-e*) which penetrates into the host cell. The organism grows in size and the nucleus divides (*g*). Several myxamoebae fuse into a plasmodium, thus destroying the host cells. The nuclei undergo mitotic division. Finally the plasmodium divides into a large number of simple spores.

Plasmodiophora brassicae Woronin (Fig. 72). Parasitic in all species of Brassica.

Other genera are **Sorosphaera** Schröter, parasitic in Veronica; **Tetramyxa** Goebel, forming gall in Ruppia, etc.

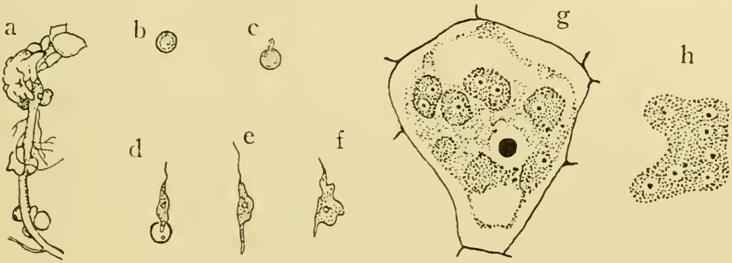


Fig. 72. *Plasmodiophora brassicae.*
a, root-hernia of cabbage; b, a spore (×620); c–e, stages in germination of spore (×620); f, myxamoeba (×620 after Woronin); g, a host cell with several young parasites (×400); h, an older parasite (×400 after Nawaschin).

References

de Bary. 1864 Die Mycetozoen. Second edition. Leipzig.

Jahn, E. 1901–1920 Myxomycetenstudien. I to X. Ber. Deutsch. Bot. Ges., Vols. 19, 20, 22–26, 29, 36, 37.

Jones, P. M. 1928 Morphology and cultural study of *Plasmodiophora brassicae.* Arch. f. Protistenk., Vol. 62.

Lister, A. 1924 A monograph on the Mycetozoa. Third edition. London.

MacBride, T. H. 1922 North American slime moulds. Second edition. New York.

CHAPTER XVI

ORDER 3 **FORAMINIFERA** d'ORBIGNY

THE FORAMINIFERA are comparatively large Protozoa, living almost exclusively in the sea. They were very abundant in geologic times and the fossil forms are important in applied geology (p. 12). The majority live on the ocean bottom, moving about sluggishly over the mud and ooze by means of their pseudopodia. Some are attached to various objects on the ocean floor, while others are pelagic in their habitat.

The cytoplasm of the Foraminifera is ordinarily not differentiated into ectoplasm and endoplasm. Contractile vacuoles are usually absent. The cytoplasm streams out through the apertures, and in perforated forms through the numerous pores, of the test, forming rhizopodia which are fine and often very long and which anastomose with one another to present a characteristic appearance. The streaming movements of the cytoplasm in the pseudopodia are quite striking; the granules move toward the end of a pseudopodium and stream back along its periphery. The body cytoplasm, is often loaded with brown granules which are apparently waste matter. In some forms such as *Peneroplis pertusus* (Fig. 76), these masses are extruded from the body from time to time, especially prior to the formation of a new chamber.

The **test** of the Foraminifera varies greatly in form and structure. When fresh, it may show various colorations—orange, pink, red or brown. The majority measure less than one millimeter, although larger forms may reach frequently five millimeters. The test may be silicious or calcareous. In some forms, various foreign materials, such as sand-grains, sponge spicules, etc., which are more or less abundantly found where these organisms live, are loosely or compactly cemented together by pseudochitinous or gelatinous substances. Certain forms show a specific tendency in the selection of foreign materials for the test. Silicious tests are comparatively rare, being found in some species of Miliolidae inhabiting either the brackish water of deep sea. Calcareous tests are sometimes imperforated, but even in such cases those of the young are always perforated. By far the majority of the Foraminifera possess perforated calcareous tests. The thickness varies considerably, as do also the

Fig. 73 Diagram showing the development of Foraminifera. (After Kühn). a–c, microspheric generation; d, uninucleate phase; e–g, megalspheric generation; h, isogametes; i–j, isogamy.

size and number of apertures, among different species. Frequently the perforations are very small in the young and later become large and coarse, while in others the reverse may be the case.

The form of the test varies greatly. In some there is only one chamber, composed of a central body and radiating arms which represent the material collected around the pseudopodia, as in Rhabdammina (Fig. 74, *a*), or of a tubular body alone, as in Hyperammina (Fig. 74, *d*). The many-chambered, or polythalmous, forms possess tests of various spirals. The first chamber is called the **proloculum.** It may be formed either by the union of two swarmers or by asexual reproduction (Fig. 73). The former is ordinarily small and known as the **microspheric** proloculum (*c*), while the latter, which is usually large, is called the **megalospheric** proloculum (*g*). To the proloculum are added many chambers which may be closely or loosely coiled or not coiled at all. These chambers are ordinarily undivided, but in

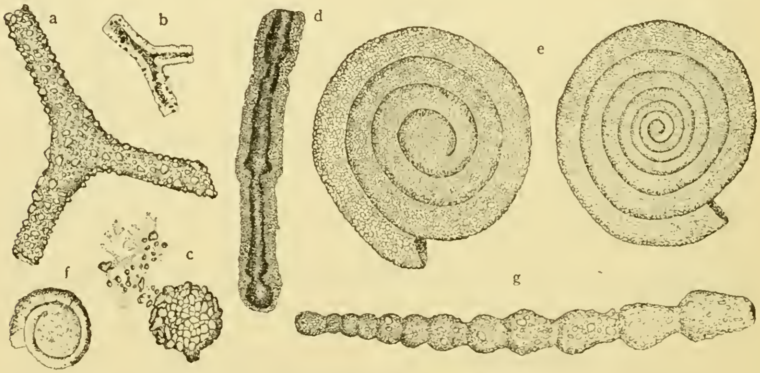


Fig. 74 a. *Rhabdammina abyssorum.* ×5 (After Kühn).
b. *Rhizammina algaeformis,* fragment of. ×14 (After Cushman).
c. *Saccammina sphaerica.* ×8 (After Rhumbler).
d. *Hyperammina subnodosa.* ×4 (After Brady).
e. *Ammodiscus incertus,* megalospheric and microspheric forms. ×20 (After Kühn).
f. *Silicina limitata.* ×13 (After Cushman).
g. *Reophax nodulosus.* ×3 (After Brady).

many higher forms they are divided into chamberlets. The chambers are delimited by the suture on the exterior of the test. The septa which divide the chambers are perforated by one or more foramina known as **stolon canals,** or passages, through which the living protoplasm extends throughout the chambers.

The last chamber has one or more apertures of variable size, through which the cytoplasm extends to the exterior as myxopodia.

The food of the Foraminifera consists mostly of diatoms and algae. Pelagic forms are known to capture other Protozoa and microcrustaceans.

All species of Foraminifera manifest a more or less distinct tendency toward a dimorphism: the smaller megalospheric form with a large proloculum and the larger microspheric form with a small proloculum (Fig. 73). The former is usually much more numerous than the latter. The microspheric form is multinucleate, in which the nuclei are scattered without apparent order, and vary in size proportionately with the size of the chambers. As the animal grows the nuclei increase in number. Around each of them a small island of cytoplasm becomes condensed (*c*). The uninucleate bodies thus formed leave the parent body, and each secretes around itself a test which is much larger than the proloculum of the parent individual (*d*, *e*). To this proloculum, new chambers are added one by one, as the animal grows (*f*) and at the same time the single nucleus shifts its position, so that the latter is almost always in the middle chamber. As the organism grows, endosomes appear in increasing numbers in the nucleus which multiplies finally into many nuclei (*g*). Each of these nuclei becomes the center of a **swarmer.** The swarmers leave the parent test and undergo fusion in pairs to produce zygotes (*h-j*). The zygote secretes a test around itself (*a*) and forms first a small proloculum, to which are added many chambers (*b*). This is the microspheric form. Thus here one sees an alternation of asexual and sexual generations. In some forms the microspheric generation appears to be unknown.

More than three hundred genera of extinct and living Foraminifera are now known. Cushman distinguished forty-five families. The present work follows Cushman in recognizing and differentiating forty-four families, and lists one genus as an example for each, but places the Allogromiidae in the order Testacea (p. 232).

Test entirely or in part arenaceous
  Test single-chambered or rarely an irregular group of similar chambers loosely attached

Test with a central chamber and two or more arms; fossil and recent . . . . Family 1 Astrorhizidae

Genus **Rhabdammina** Sars (Fig. 74, *a*)

Test without a central chamber, elongate, open at both ends; fossil and recent . . . . Family 2 Rhizamminidae

Genus **Rhizammina** Brady (Fig. 74, *b*)

Test a chamber or rarely series of similar chambers loosely attached, with normally a single opening; fossil and recent. . . . Family 3 Saccamminidae

Genus **Saccammina** Sars (Fig. 74, *c*)

Test two-chambered, a proloculum and long undivided tubular second chamber

Test with the second chamber, simple or branching, not coiled; mostly recent, fossils . . . . Family 4 Hyperamminidae

Genus **Hyperammina** (Fig. 74, *d*)

Test with the second chamber usually coiled at least in the young animal

Test of arenaceous material with much cement, usually yellowish or reddish brown; fossil and recent. . . . Family 5 Ammodiscidae

Genus **Ammodiscus** Reuss (Fig. 74, *e*)

Test of silicious material, second chamber partially divided; fossils only . . . . Family 6 Silicinidae

Genus **Silicina** Bornemann (Fig. 74, *f*)

Test typically many-chambered

Test with all chambers in a rectilinear series; fossil and recent . . . Family 7 Reophacidae

Genus **Reophax** Montfort (Fig. 74, *g*)

Test planispirally coiled at least in the young

Axis of coil short, many uncoiled forms; fossil and recent. . . . . . Family 8 Lituolidae

Genus **Lituola** Lamarck (Fig. 75, *a*)

Axis of coil usually long, all close-coiled

Interior not labyrinthic; fossil only. . . . . Family 9 Fusulinidae

Genus **Fusulina** Fisher (Fig. 75, *b*)

Interior labyrinthic; fossil only. . . . . Family 10 Loftusiidae

Genus **Loftusia** Brady

Test typically biserial at least in the young of the microspheric form; fossil and recent . . . . Family 11 Textulariidae

Genus **Textularia** Defrance (Fig. 75, *c*)

Test typically triserial at least in the young of the microspheric form

Aperture usually without a tooth, the test becoming simpler in higher forms; fossil and recent.........Family 12 Verneuilinidae

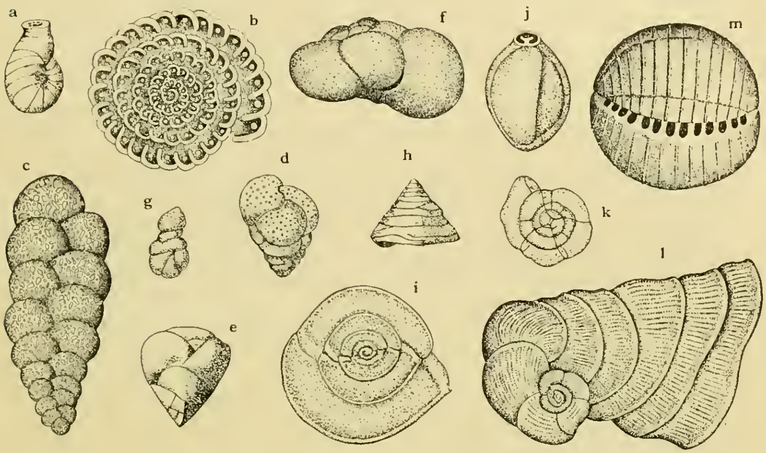


Fig. 75 a. *Lituola nautiloidea*. (After Cushman).
b. Section through a Fusulina. (After Carpenter).
c. *Textularia agglutinans*. ×90 (After Rhumbler).
d. *Verneuilina propinqua*. ×8 (After Brady).
e. *Valvulina triangularis*. (After d'Orbigny).
f. *Trochammina inflata*. ×32 (After Brady).
g. *Placopsilina cenomana*. (After Reuss).
h. *Tetrataxis palaeotrochus*. ×15 (After Brady).
i. *Spiroloculina limbata*. ×20 (After Brady).
j. *Triloculina trigonula*. ×15 (After Brady).
k. *Fischerina helix*. ×32 (After Heron-Allen and Earland).
l. *Vertebralina striata*. ×40 (After Kühn).
m. *Alveolinella mello*. ×35 (After Brady).

Genus **Verneuilina** d'Orbigny (Fig. 75, *d*)

Aperture typically with a tooth, the test becoming conical in higher forms; fossil and recent...........Family 13 Valvulinidae

Genus **Valvulina** d'Orbigny (Fig. 75, *e*)

Test with whole body labyrinthic, large, flattened, or cylindrical; recent...................................Family 14 Neusinidae

Genus **Neusina** Goës

Test trochoid at least while young

Mostly free and typically trochoid throughout; fossils and recent
Family 15 Trochamminidae

Genus **Trochammina** Parker and Jones (Fig. 75, *f*)

Attached; young trochoid, later stages variously formed; fossil and recent........................Family 16 Placopsilinidae

Genus **Placopsilina** d'Orbigny (Fig. 75, *g*)

Free; conical, mostly of large size; fossil only..Family 17 Orbitolinidae

Genus **Tetrataxis** Ehrenberg (Fig. 75, *h*)

Test coiled in varying planes, wall imperforate, with arenaceous portion only on the exterior; fossil and recent..............
Family 18 Miliolidae (in part)

Genus **Spiroloculina** d'Orbigny (Fig. 75, *i*)

Test calcareous, imperforate, porcellanous

Test with the chambers coiled in varying planes, at least in the young, aperture large, toothed; fossil and recent....................
Family 18 Miliolidae (in part)

Genus **Triloculina** d'Orbigny (Fig. 75, *j*)

Test trochoid; fossil and recent.................Family 19 Fischerinidae

Genus **Fischerina** Terquem (Fig. 75, *k*)

Test planispiral, at least in the young

The axis very short, chambers usually simple; fossil and recent..
Family 20 Ophthalmidiidae

Genus **Vertebralina** d'Orbigny (Fig. 75, *l*)

The axis short, test typically compressed and often discoid, chambers mostly with many chamberlets; fossil and recent.......
Family 21 Peneroplidae

Genus **Peneroplis** Montfort (Fig. 76)

The axis typically elongate, chamberlets developed; mainly fossil
Family 22 Alveolinellidae

Genus **Alveolinella** Douvillé (Fig. 75, *m*)

Test globular, apertures small, not toothed; recent only...........
Family 23 Keramosphaeridae

Genus **Keramosphaera** Brady

Test calcareous, perforate

Test vitreous with a glassy lustre, aperture typically radiate, not trochoid

Test planispirally coiled or becoming straight, or single chambered; fossil and recent....................Family 24 Lagenidae

Genus **Lagena** Walker and Jacob (Fig. 77, *a*)

Test biserial or elongate spiral; fossil and recent................ Family 25 Polymorphinidae

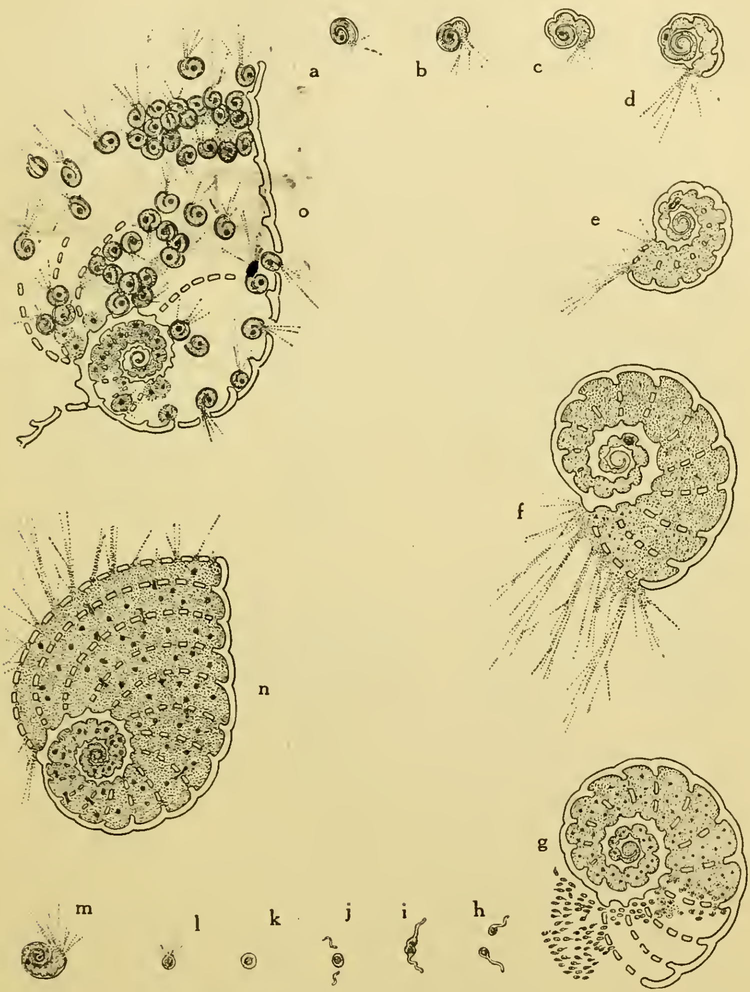


Fig. 76 Diagram showing the development of *Peneroplis pertusus*. (After Winter). a–f, megalospheric generation; g, gamete formation; h–k, isogamy; l–n, microspheric generation; o, multiple division.

Genus **Polymorphina** d'Orbigny

Test not vitreous, aperture not radiating
Test planispiral, occasionally trochoid, then usually with processes along the suture lines, septa single, no canal system; fossil and recent . . . . Family 26 Nonionidae

Genus **Elphidium** Montfort (Fig. 77, *b*)

Test planispiral, at least in the young, generally lenticular, septa double, canal system in higher forms; fossil and recent . . . . . .
Family 27 Camerinidae

Genus **Operculina** d'Orbigny (Fig. 77, *c*)

Test at least in the microspheric form generally biserial, aperture usually large, without teeth; fossil and recent . . . .
Family 28 Heterohelicidae

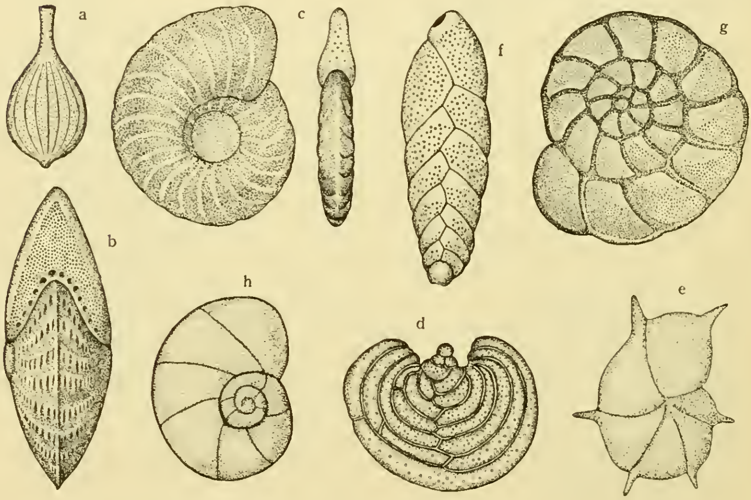


Fig. 77 a. *Lagena striata.* ×50 (After Rhumbler).
b. *Elphidium strigilata.* ×40 (After Kühn).
c. *Operculina ammonoides*, two views. ×50 (After Kühn).
d. *Pavonina flabelliformis.* ×30 (After Brady).
e *Hantkenina alabamensis.* ×40 (After Cushman).
f. *Bolivina punctata.* ×100 (After Kühn).
g. *Kotalia beccarii.* ×40 (After Kühn).
h. *Asterigerina carinata.* ×30 (after d'Orbigny from Cushman).

Genus **Pavonina** d'Orbigny (Fig. 77, *d*)

Test planispiral, bi- or tri-serial with elongate spines and lobed aperture; fossil and recent . . . . Family 29 Hantkeninidae

Genus **Hantkenina** Cushman (Fig. 77, *e*)

Test typically with an internal tube, elongate
  Aperture generally loop-shaped or cribrate; fossil or recent....
Family 30 Buliminidae

Genus **Bolivina** d'Orbigny (Fig. 77, *f*)

  Aperture narrow, curved, with an overhanging portion; mostly fossil and recent....................Family 31 Ellipsoidinidae

Genus **Ellipsoidina** Seguenza

Test trochoid, at least in the young of the microspheric form, usually coarsely perforate; when lenticular, with equatorial and lateral chambers
  Test trochoid throughout, simple; aperture ventral.
    No alternating supplementary chambers on ventral side; fossil and recent...........................Family 32 Rotaliidae

Genus **Rotalia** Lamarck (Fig. 77, *g*)

    Alternating supplementary chambers on ventral side; fossil and recent......................Family 33 Amphisteginidae

Genus **Asterigerina** d'Orbigny (Fig. 77, *h*)

  Test trochoid and aperture ventral at least in the young
    With supplementary material and large spines, independent of the chambers; fossil and recent....Family 34 Calcarinidae

Genus **Calcarina** d'Orbigny (Fig. 78, *a*)

    With later chambers in annular series or globose with multiple apertures, but not covering the earlier ones; fossil and recent...........................Family 35 Halkyardiidae

Genus **Halkyardia** Heron-Allen and Earland (Fig. 78, *b*)

    With later chambers somewhat biserial; aperture elongate in the axis of coil; fossil and recent.....Family 36 Cassidulinidae

Genus **Cassidulina** d'Orbigny (Fig. 78, *c*)

    With later chambers becoming involute, very few making up the exterior in the adult; aperture typically elongate, semi-circular; in a few species circular; fossil and recent
Family 37 Chilostomellidae

Genus **Allomorphina** Reuss (Fig. 78, *d*)

    With chambers mostly finely spinose and wall cancellated, adapted for pelagic life, globular forms with the last chamber completely involute; aperture umbilicate or along the sutures; fossil and recent...Family 38 Globigerinidae

Genus **Globigerina** d'Orbigny (Fig. 78, *e*)

Early chambers globigerine, later ones spreading and compressed; fossil and recent..........Family 39 Globorotaliidae

Genus **Globorotalia** Cushman

Test trochoid at least in the young, aperture peripheral or becoming dorsal

Mostly attached, dorsal side usually flattened; fossil and recent............................Family 40 Anomalinidae

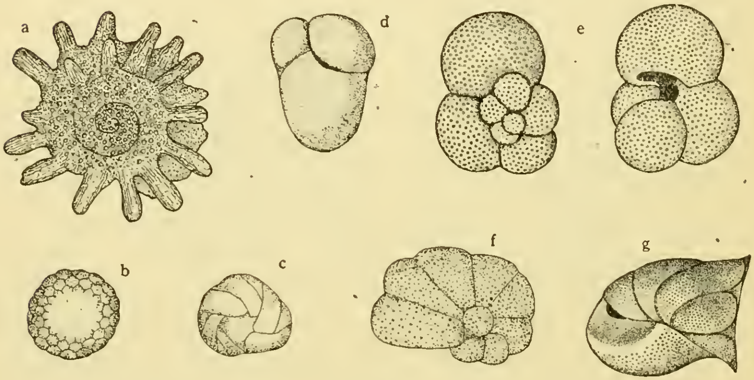


Fig. 78 a. *Calcarina defrancei.* ×23 (After Brady).
b. *Halkyardia radiata.* ×13 (After Cushman).
c. *Cassidulina laevigata.* ×25 (After Brady).
d. *Allomorphina trigona.* ×40 (After Brady).
e. *Globigerina bulloides.* ×30 (After Kühn).
f. *Anomalina punctulata.* (After d'Orbigny).
g. *Rupertia stabilis.* ×50 (After Brady).

Genus **Anomalina** d'Orbigny (Fig. 78, *f*)

Later chambers in annular series; fossil and recent..........
Family 41 Planorbulinidae

Genus **Planorbulina** d'Orbigny

Test trochoid in the very young, later growing upward

Later chambers in a loose spiral; fossil and recent........
Family 42 Rupertiidae

Genus **Rupertia** Wallich (Fig. 78, *g*)

Later chambers in masses or branching, highly colored; mostly recent and also fossil.........Family 43 Homotremidae

Genus **Homotrema** Hickson

Test trochoid in the very young of the microspheric form, chambers becoming annular later, with definite equatorial and lateral chambers, often with pillars; fossil only...........
Family 44 Orbitoididae

Genus **Orbitoides** d'Orbigny

References

Brady, B. H. 1884 Report on the Foraminifera dredged by H. M. S. Challenger, during the years 1873 to 1876. Rep. Voy. Challenger Zool., Vol. 9.

Cushman, J. A. 1928 Foraminifera: their classification and economic use. Sharon, Mass.

Rhumbler, L. 1904 Systematische Zusammenstellung der rezenten Reticulosa (Nuda u. Foraminifera). Arch. f. Protistenk., Vol. 3.

CHAPTER XVII

ORDER 4 AMOEBAEA EHRENBERG

THE AMOEBAEA show a very little cortical differentiation. There is no pellicle, test, or shell surrounding the body, although in some, such as *Amoeba verrucosa*, the surface seems to be much hardened. The cytoplasm is more or less distinctly differentiated into the ectoplasm and the endoplasm. The ectoplasm is hyaline and homogeneous, and appears tougher than the endoplasm. In the endoplasm, which is granulated or vacuolated, are found one or more nuclei, various food vacuoles, water vacuoles, crystals, and other bodies. In the fresh-water forms there is at least one distinctly visible contractile vacuole. The pseudopodia are lobopodia, and ordinarily both ectoplasm and endoplasm are found in them. They are formed by streaming or fountain movements of the cytoplasm. In some members of the order, the formation of pseudopodia is described as eruptive since the granules which are found in the endoplasm break through the border line between the ectoplasm and the endoplasm and suddenly flow into the pseudopodia.

The life-history is not completely known, even among such common forms as *Amoeba proteus*. Asexual reproduction is ordinarily binary fission, although occasionally multiple fission takes place. Encystment is common for both free-living and parasitic forms. Sexual reproduction, which has been reported for a few species, has not been confirmed.

The Amoebaea inhabit all sorts of fresh, brackish and salt waters. They are also found in most soil and on ground covered with decaying leaves. Many are inhabitants of the digestive tract of various animals, and some of them are pathogenic.

The taxonomic status of the group is highly uncertain and confusing, since their life-histories are mostly unknown and since numerous Protozoa other than the members of this group often possess amoeboid stages. Forms such as Pantostomatida, may rightly be considered as belonging to either the Sarcodina or the Mastigophora. In the present work they have been placed in the latter group (p. 129).

According to Calkins, four families are recognized here.

With amoeboid and flagellate stages.................. Family 1 Bistadiidae
Amoeboid stage only
  With one or more nuclei of one type
    Free-living.................................. Family 2 Amoebidae
    Parasitic.................................. Family 3 Endamoebidae
  With a cytoplasmic "secondary nucleus"......... Family 4 Paramoebidae

Family 1 **Bistadiidae** Doflein

The Amoebaea placed in this family possess both amoeboid and flagellate phases (diphasic). In the former, the organism undergoes amoeboid movement by means of lobopodia and in the latter the body is more or less elongated. Binary fission seems to take place during the amoeboid phase only. Thus the members are diphasic organisms, in which the amoeboid stage predominates over the flagellate. The amoeboid phase of this family is frequently called the "limax amoeba" which under cultural conditions may be changed into flagellated individuals, as for example, by the addition of water to the culture medium. Under natural circumstances, it is often exceedingly difficult by observing amoebae to determine whether they belong to this family or the family Amoebidae.

There is a good deal of confusion with regard to the various generic names created for the amoebae of the "limax" type. Calkins' definition and differentiation are followed here.

Genus **Naegleria** Alexeieff (=Vahlkampfia Chatton and Lalung-Bonnaire (in part); Wasielewskia Hartmann and Chagas). Minute forms. The flagellate phase possesses two flagella. The amoeboid phase is much similar to the genus Vahlkampfia (family Amoebidae, p. 206), with lobopodia. The cytoplasm is differentiated into the ectoplasm and endoplasm. The vesicular nucleus contains a large endosome. There is usually a conspicuous contractile vacuole. Food vacuoles contain bacteria. Fission takes place in the amoeboid stage only. Encystment is common; the cyst contains a single nucleus. Free-living in stagnant water and moist soil; often coprozoic.

Naegleria gruberi (Schardinger) (Fig. 79, *a-c*). Body about

10 to 50 microns in diameter; the cyst wall possesses several openings.

Naegleria bistadialis (Puschkarew) (Fig. 79, *d-f*). Similar in size, but the cyst wall smooth.

Genus **Trimastigamoeba** Whitmore. The flagellate stage bears three flagella of nearly equal length. The vesicular nucleus with a large endosome. The amoeboid stage is small,

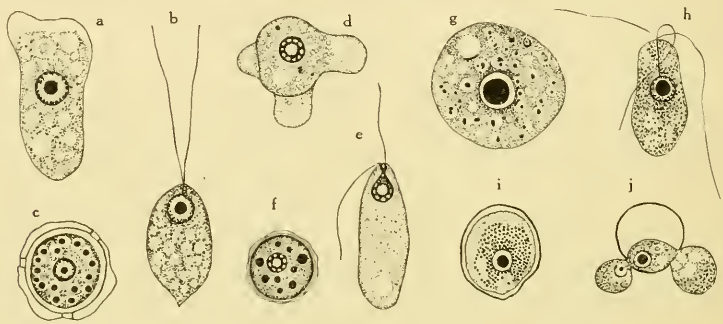


Fig. 79 a–c. Trophozoite, flagellate phase and cyst (all stained) of *Naegleria gruberi*. ×750 (After Alexeieff).
d–f. Similar stages of *N. bistadialis*. ×750 (After Kühn).
g–j. Trophozoite, flagellate phase, cyst and excystation of *Trimastigamoeba philippinensis*. ×950 (After Whitmore).

being less than 20 microns in diameter. Uninucleate cyst with smooth wall. Coprozoic. One species.

Trimastigamoeba philippinensis Whitmore (Fig. 79, *g-j*).

Family 2 **Amoebidae** Doflein

These amoebae do not show flagellated stage (monophasic). They are free-living in fresh or salt water, in damp soil, moss, etc. One, two, or many nuclei occur. Contractile vacuoles usually present in fresh-water forms. Multiplication by binary or multiple fission. Encystment is widely spread. The life-history is not well known.

Genus **Amoeba** Ehrenberg. Body large; often one millimeter in diameter. With short blunt lobopodia. As a rule, a single contractile vacuole, and typically one nucleus. Nuclear structure can be used for specific differentiation to a certain extent. Holozoic on Protophyta, Protozoa, Rotifera, and in a few cases even Nematoda. The endoplasm contains crystals which are enclosed in vacuoles and which possess form and size characteristic of various species (Schaeffer). These crystals seem to be composed of calcium phosphate and probably metabolic products. Numerous species.

Amoeba proteus (Pallas) (Fig. 80, *a-d*). A widely distributed large amoeba living in fresh water, reaching often 600 microns

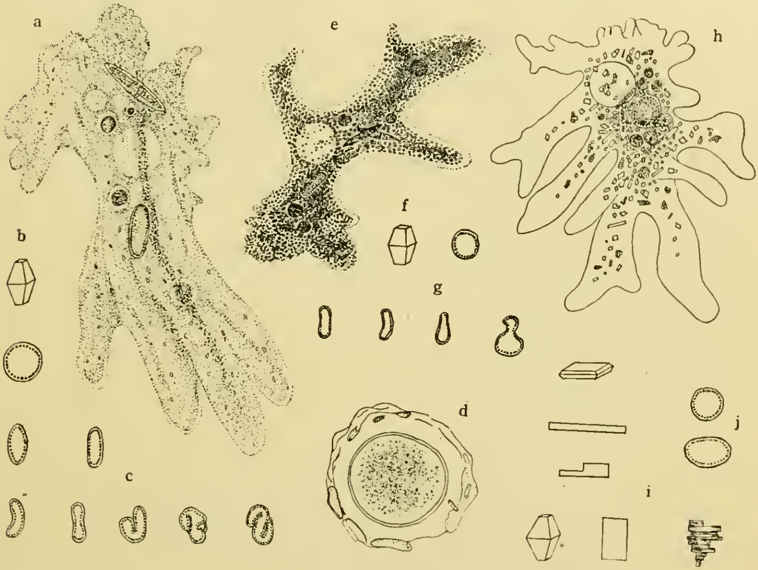


Fig. 80 a–d. *Amoeba proteus*. (After Schaeffer, except d). a, an active trophozoite (×100); b, typical form of crystal; c, eight nuclei in optical section; d, encysted form (after Doflein).
e–g. *Amoeba discoides*. (After Schaeffer). e, active trophozoite (×100); f, typical crystal; g, five nuclei in optical section.
h–j. *Amoeba dubia*. (After Schaeffer). h, active trophozoite (×100); i, various forms of crystals found in it; j, two nuclei in optical section.

or more in diameter. The amoeba creeps with a few large lobopodia, but floating individuals may possess a large number of short blunt lobopodia which show longitudinal ridges. The differentiation of the cytoplasm into two regions is usually distinct. One nucleus occurs in each individual and is characteristically discoidal. But various modifications in nuclear forms are equally characteristic of the species. Food vacuoles contain numerous organisms co-existing in the water. Crystals are elongated bipyramid and measure up to 4.5 microns in length (Schaeffer). The development is not well established. Asexual reproduction is usually binary fission, but under certain conditions division into four individuals is said to be of common occurrence (Doflein). Encystment is common. By using this amoeba Gruber found the now well-established fact that the nucleus and cytoplasm are dependent upon each other.

Amoeba discoides Schaeffer (Fig. 80, *e-g*). Body about 400 microns long during movement. A few blunt and smooth lobopodia. Endoplasm contains bipyramidal truncate crystals, about 2.5 microns in length. The nucleus is always discoidal in form, without infolded surface. Usually one contractile vacuole. In fresh water.

Amoeba dubia Schaeffer (Fig. 80, *h-j*). Body about 400 microns in diameter. Numerous pseudopodia flattened and with smooth surface. The nucleus circular in front view, oblong in profile. Crystals few in number, but large and of various shape. Contractile vacuole one or more. In fresh water.

Amoeba verrucosa Ehrenberg (Fig. 81, *a, b*). Body irregularly rounded with wart-like expansions. Body surface is usually wrinkled, as though invested with a membrane. The diameter varies from 50 to 200 microns. Pseudopodia short, broad, and blunt. Differentiation of the cytoplasm is fairly distinct. The nucleus is ovoidal. The contractile vacuole is solitary and large. Multiplication by binary fission. Fresh water among algae.

Genus **Pelomyxa** Greeff. A large sluggish amoeba which contains a few to numerous nuclei. The cytoplasmic differentiation is poor. Pseudopodia small in number and are short and broad; the animal undergoing a rolling movement. Besides the nuclei, diatoms, bacteria, water vacuoles and sand-grains, endoplasm usually contains refractile bodies which are thought to be either reserve food material similar to glycogen or metabolic products used by symbiotic bacteria. Contractile vacuole has not been noticed with certainty. Multiplication by binary fission. Gamete formation has been reported; it is presumed that uninucleate bodies undergo fusion to form zygotes which develop into multinucleate forms. Several species in fresh water.

Pelomyxa palustris Greef (Fig. 81, *c*). Inhabitants of stagnant water, creeping on the bottom in the mud. The amoeba is large, often measuring 2 mm. or more in diameter. Sluggish with one broad pseudopodium, by which the organism under-

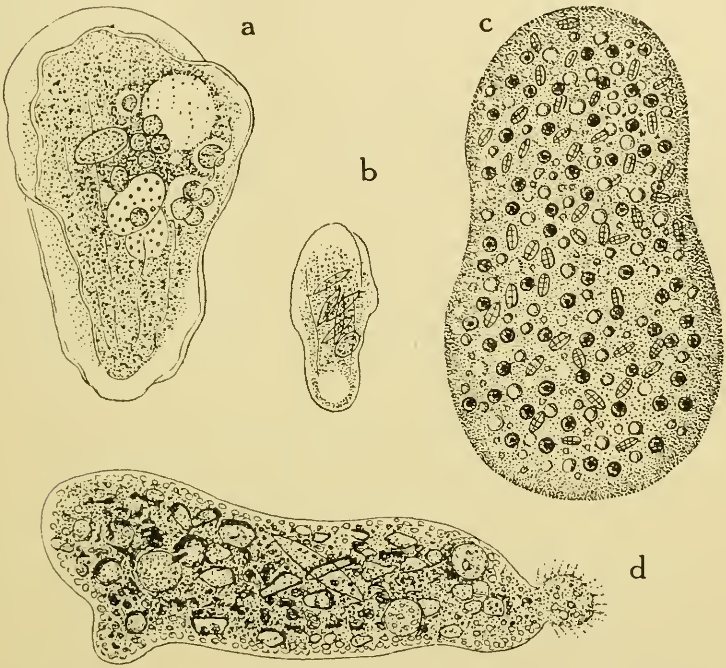


Fig. 81 a, b. Large and small individuals of *Amoeba verrucosa*. ×500 (After Leidy).
c. *Pelomyxa palustris*. ×80 (After Kühn).
d. *P. villosa*. ×250 (After Leidy).

goes rolling movement. The cytoplasm is not at all differentiated into two regions. Numerous vacuoles and vesicular nuclei present. The nuclei exceed one thousand in number. Various inclusions often color the body brown to black and make it appear opaque. Symbiotic bacteria, *Cladothrix pelomyxae* Veley, occur regularly. Some individuals extrude inclusions and encyst, becoming covered by two or three cyst walls. The contents multiply into several multinucleate bodies. Cosmopolitan.

Pelomyxa villosa (Leidy) (Fig. 81, *d*). Similar to the last species, but much smaller; 250 microns long. With numerous villi at the posterior extremity. In a similar habitat.

Genus **Vahlkampfia** Chatton and Lalung-Bonnaire. The characteristics are: The nucleus contains a large endosome and peripheral chromatin, and divides by "promitosis" (p. 45). The cyst is uninucleate. It is a small amoeba, exhibiting snail-like movement and possessing a perforated wall when encysted. Body small, not exceeding 50 microns when fully extended. Ordinarily one broad pseudopodium is formed in the direction of movement, although it cannot be made a basis for taxonomic consideration.

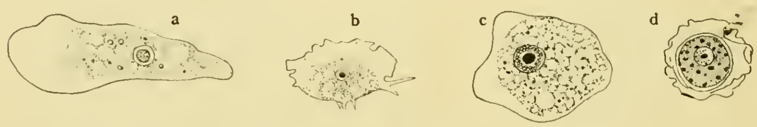


Fig. 82 a. *Vahlkampfia limax*. ×500.
b. *V. patuxent*. ×500 (After Hogue).
c, d. *Hartmannella hyalina*. ×700 (After Dobell).
c, trophozoite; d, cyst, both stained.

Vahlkampfia limax (Dujardin) (Fig. 82, *a*). Body 30 to 40 microns long. Fresh water; soil.

Vahlkampfia patuxent Hogue (Fig. 82, *b*). The amoeba was found in the alimentary canal of the oyster. Fairly uniform in size being about 20 microns long during the first few days of artificial cultivation, but later reaching as long as 140 microns in diameter. Ordinarily one large pseudopodium composed of the ectoplasm is seen, presenting a broad fan-shape. In culture, pseudopodium-formation is explosive. Holozoic on bacteria. No contractile vacuoles. Multiplication by fission or budding. Encystment rare; the cyst contains a single nucleus.

Genus **Hartmannella** Alexeieff. This genus includes small amoebae with the following nuclear characteristics. The nucleus is vesicular. A large endosome is located in the center and numerous chromatin granules are scattered along the periphery. At the time of division, the endosome disintegrates and chromosomes and spindle fibers appear. There are no so-called polar caps during division as are found in Vahlkampfia.

Hartmannella hyalina (Dangeard) (Fig. 82, *c*, *d*). Easily cultivated from old feces of man and animals and also from water. More or less rounded body measures less than 20 microns in diameter. A single nucleus and a contractile vacuole. Binary fission. The spherical cyst measures 10 to 15 microns in diameter, covered with a smooth inner and a much wrinkled outer wall.

Genus **Sappinia** Dangeard. With two closely associated nuclei.

Sappinia diploidea (Hartmann and Nägler). Coprozoic in the feces of widely different animals. The pseudopodia are short and broad, and few. The highly vacuolated endoplasm contains two nuclei, food vacuoles, and a contractile vacuole. A wrinkled surface is sometimes noticed. The nuclei divide simultaneously. During encystment, two individuals come together and secrete a common cyst wall. The two nuclei fuse so that each individual possesses a single nucleus; finally the cytoplasmic masses of the two individuals unite into one. Each nucleus gives off reduction bodies which degenerate. Two nuclei now come in contact without fusion, thus a binucleate cyst is formed. After leaving the cyst-wall, the binucleate amoeba grows and multiplies (Hartmann and Nägler).

Family 3 Endamoebidae Calkins

Endoparasitic amoebae with a wide zoological distribution. The trophozoite is comparatively small and live mostly within the lumen of the digestive tract of the host. Multiplication by binary fission.

Genus **Endamoeba** Leidy. The nucleus is spherical or oblong and possess a very thick membrane. In life, it is filled with numerous yellowish granules of uniform size along its peripheral portion. Upon staining, they disappear and in their places a fine chromatic network becomes noticeable. Several endosomes are to be seen along the inner margin of this network. The central portion is coarsely reticulated. The cytoplasm of actively moving individuals shows very prominent striations. Parasitic in invertebrates.

Endamoeba blattae (Bütschli) (Fig. 83). Cosmopolitan and often observed in the colon of several species of the cockroach. Its size varies from 10 to 150 microns in diameter. Rounded amoebae which form broad lobopodia, show a distinct differentiation of the cytoplasm. Elongated forms with a few pseudopodia, show the ectoplasm only at the ends of the pseudopodia. The endoplasm of actively motile individuals shows a marked striation, a condition not seen in other amoebae. No contractile vacuoles are noted, although fluid-filled vacuoles are seen in large numbers The food consists of mainly starch grains, yeast cells, bacteria, and Protozoa, all of which coexist

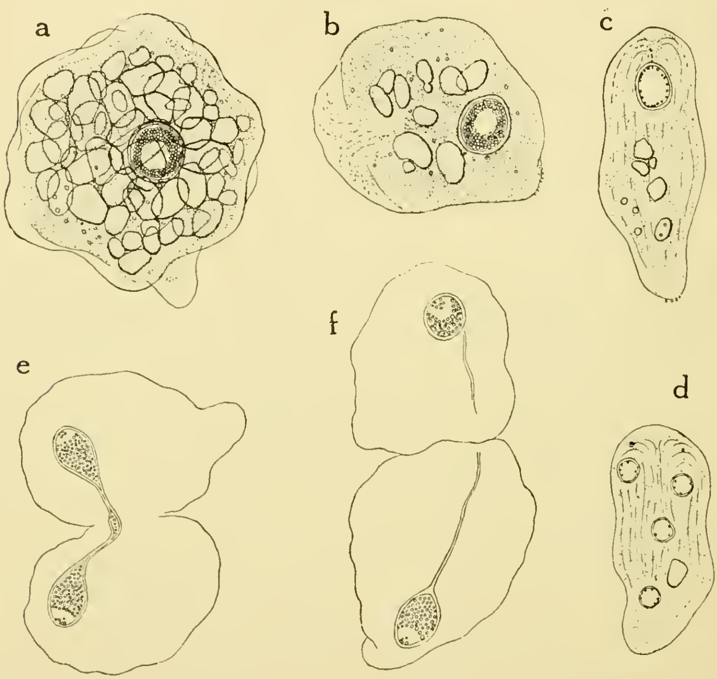


Fig. 83 *Endamoeba blattae*, as seen in life. ×400 (After Kudo). a, b, active trophozoites; c, d, precystic forms; e, a stage in binary fission; f, the same amoeba twenty minutes later.

in the host's colon. The amoeba shows preference toward the starch grain. Prior to encystment, the body diminishes in size. Cyst membrane is formed and the nucleus undergoes repeated division, so that cysts containing over sixty nuclei are often encountered. The further development is unknown. Mercier holds that when the multinucleate cysts gain entrance to the intestine of a host insect through its mouth, each of the cyst nuclei becomes the center of a gamete. When the cyst-membrane ruptures, the gametes are set free and anisogamy takes place, resulting in the formation of numerous zygotes which develop into the habitual amoebae. This observation has not been confirmed.

Fig. 84 Endamoebae of termites. (After Kirby).
a. *Endamoeba disparata.* ×665.
b. *E. majestas.* ×350.
c. *E. simulans.* ×350.
d. *E. sabulosa.* ×665.

Endamoeba thomsoni Lucas. Smaller amoebae occurring in the same habitat.

Endamoeba disparata Kirby (Fig. 84, *a*). In the intestine of the termite, *Microtermes hispaniolae.* Body 20 to 40 microns long. Active. The amoeba feeds on bits of wood.

Endamoeba majestas Kirby (Fig. 84, *b*). In the same habitat. Body 65 to 165 microns in diameter. Many short pseudopodia. Numerous food particles in the cytoplasm.

Endamoeba simulans Kirby (Fig. 84, *c*). In the intestine of the termite, *Microtermes panamaensis.* Body 50 to 150 microns in diameter.

Endamoeba sabulosa Kirby (Fig. 84, *d*). In the same habitat. Small, 19 to 35 microns in diameter.

Genus **Entamoeba** Casagrandi and Barbagallo. This genus was established by Casagrandi and Barbagallo who did not know the existence of the genus Endamoeba. The nucleus has the following characteristics: Vesicular; nuclear membrane is thin, but distinct. A comparatively small endosome is located in or near the center and there are varying numbers of peripheral chromatin granules free or attached to the nuclear wall. Numerous species in man, mammals, and invertebrates. A number of authors hold that there is not a sufficient difference between the genera Endamoeba and Entamoeba to justify their generic separation, and so combine them.

A. Entamoebae of man

Entamoeba histolytica Schaudinn (Fig. 85, *a-f*). The amoeba is small and measures 20 to 30 microns in diameter. Its cytoplasm is usually differentiated distinctly. Large lobopodia are often formed in an explosive manner, and are composed exclusively of ectoplasm. The endoplasm contains a single vesicular nucleus which appears in life as a ring and food vacuoles containing erythrocytes, tissue cells, leucocytes, etc., of the host in variable number. The typical nucleus shows upon staining the following parts: a nuclear membrane, peripheral chromatin granules, a centrally located small endosome rich in chromatin material surrounded by a clear ring and an indistinct achromatic network with a few scattered chromatin granules. This amoeba invades the tissues of the gut-wall and multiply by binary fission. Under certain circumstances not well understood, the active trophozoite extrudes its undigested food material and decreases in size, possibly by division also. Such a form is sluggish and shows frequently glycogen bodies and elongated refractile bodies which stain deeply with a nuclear stain (hence called the **chromatoid bodies**). This phase is known as the **precystic stage.** The cyst is formed when the precystic stage ceases to move and becomes surrounded by a definite cyst-membrane. The cyst measures 5 to 20 microns in diameter. At first it contains a single nucleus which divides later twice and tetranucleate cyst is formed. The glycogen and chromatoid bodies become absorbed, as the cyst grows older. The changes between the cyst and the young trophozoite are not known, although in recent years numerous investigators have been able to cultivate the amoeba *in vitro* and noted in some cases the excystation of the cyst contents as multinucleate amoebae.

This amoeba was first definitely recognized by Lösch in Russia in 1873. It is now known to have a wide geographical distribution. The incidence of infection among man depends mainly upon the sanitary conditions of the community, since the infection is carried from man to man through cysts. Craig estimates that ten per cent of the general population of the

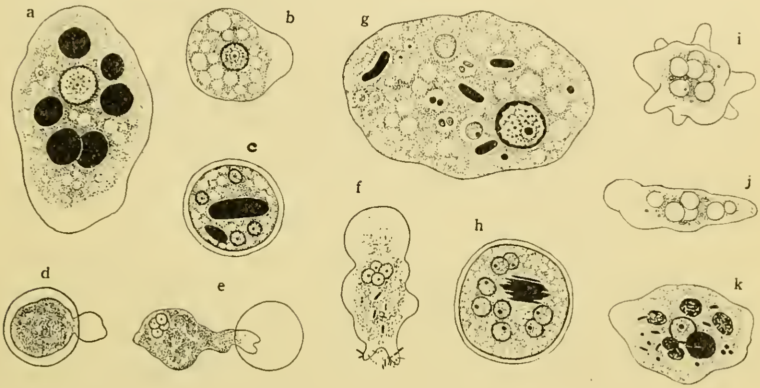


Fig. 85 Entamoebae of man.
a–f. *Entamoeba histolytica*. a, a stained trophozoite (×1000); b, stained precystic stage (×1000); c, a stained cyst (×1000); d–f, excystation in culture (×700 after Yorke and Adams).
g, h. *Entamoeba coli*. ×1000. g, stained trophozoite; h, stained cyst.
i–k. *E. gingivalis*. ×500. i, j, living trophozoites; k, stained trophozoite.

United States harbor this organism. An acute infection by *Entamoeba histolytica* is manifested clinically by dysentery. In chronic cases, the host may void a number of infective cysts without suffering himself. Such a man is known as a "carrier." The amoeba invades the liver also and causes in it various abscesses of a serious nature. Numerous varieties are known.

Entamoeba coli (Lösch) (Fig. 85, *g*, *h*). The amoeba varies from 15 to 40 microns in diameter. Its cytoplasm is indistinctly differentiated. Lobopodia are slowly formed and body movement is sluggish. The endoplasm shows several food vacuoles containing varying number of bacteria. The nucleus is observable in life. Compared with that of *E. histolytica*, the endosome is somewhat larger and located ordinarily eccentrically and the peripheral chromatin granules are more conspicuous in the present species. Multiplication by binary fission is known. The precystic stage is similar in appearance to that of the last species with the exception of the nuclear structure, and, therefore, the differentiation of the two species at this stage is, as a rule, impossible. The cyst resembles also that of *E. histolytica*, but the mature cyst contains normally eight nuclei and measures 10 to 30 microns in diameter. In young cysts there are glycogen bodies which are larger than those found in *E. histolytica*. The chromatoid bodies are splinter-like and often grouped. This amoeba seems to have been observed first by Lewis in 1870 in India. It is a commensal in the human intestine and widely distributed throughout the world.

Entamoeba gingivalis Gros (= *E. buccalis* Prowazek) (Fig. 85, *i-k*). The amoeba is a fairly active form. A few blunt pseudopodia are formed and retracted actively. It varies in size from 10 to 40 microns, the majority measuring 10 to 20 microns in diameter. The cytoplasm is ordinarily distinctly differentiated; the ectoplasm is very hyaline and the endoplasm granulated. A single nucleus, numerous food particles which consist of degenerating tissue or pus cells, leucocytes, bacteria, erythrocytes, etc., are found in the endoplasm. The nucleus resembles that of *E. histolytica*, but the location of the endosome is inconstant. The amoeba multiplies by binary fission. Cyst is unknown. The transmission of the amoeba from man to man is, therefore, considered direct.

This amoeba was the first endoparasitic amoeba discovered and observed by Gros in 1849 in the human tartar. As to the effect of the amoeba upon the host, some investigators believe that it is the probable cause of pyorrhoea alveolaris, but the majority of the investigators are inclined to think that it is a commensal of the human mouth.

B. Entamoebae of domestic animals

Almost all domestic animals harbor one or more amoebae in their digestive tracts and many of them resemble those occurring in man, although distinct specific names were given to them.

In horses

Entamoeba intestinalis Gedoelst. In colon and caecum.

Entamoeba equi Fantham. Found in feces; contained erythrocytes; cysts tetranucleate.

Entamoeba gingivalis var. *equi* Nieschulz. Found around the teeth.

In cattle

Entamoeba bovis Liebetanz. In stomach. Diameter 5 to 20 microns.

In sheep

Entamoeba ovis Swellengrebel. With uninucleate cyst.

In goats

Entamoeba caprae Fantham.

In swine

Entamoeba polecki (Prowazek). In the large intestine; 10 to 12 microns in diameter; the cyst with a single nucleus.

Entamoeba debliecki Nieschulz. Smaller form; 5 to 10 microns in diameter; the cyst with a single nucleus.

In dogs

Entamoeba venaticum Darling. In the large intestine. Similar to *E. histolytica*. As the dog is experimentally infected with the latter, this amoeba which was discovered from spontaneous amoebic dysentery cases of dogs, in one of which was noted abscesses of liver, is probably *E. histolytica*.

An Entamoeba from the mouth and indistinguishable from *Entamoeba gingivalis* of the human mouth.

In cats

Entamoeba histolytica Schaudinn. Cats are easily infected by *E. histolytica* and show typical symptoms. Spontaneous dysentery due to this human amoeba was also noted.

C. Entamoebae of other mammals

In rabbits

Entamoeba cuniculi Brug. This amoeba is said to resemble *E. coli* in both the trophic and encysted stages.

In guinea-pigs

Entamoeba cobaye Walker (= *E. caviae* Chatton). Similar to *E. coli*.

In rats and mice

Entamoeba muris (Grassi). The amoeba also resembles *E. coli*.

An Entamoeba resembling *E. histolytica* has been recognized often and is probably identical with the latter.

D. Entamoebae of birds

Entamoeba lagopodis Fantham. Tetranucleate cysts were found in the intestine of the grouse, *Lagopus scoticus*.

Entamoeba anatis Fantham. An amoeba with mono- or tetra-nucleate cysts were found in the intestine of a duck.

Entamoeba gallinarum Tyzzer. This amoeba occurs in the intestine of fowls. Cysts octonucleate.

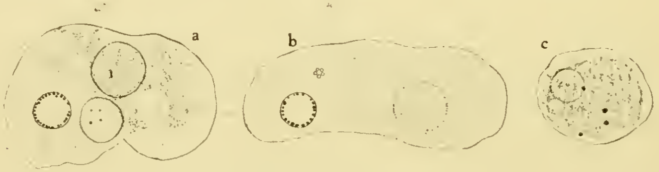


Fig. 86 *Entamoeba testudinis* from the large intestine of *Terrapene carolina*. ×665. a, b, living; c, stained trophozoites.

E. Entamoebae of reptiles

Entamoeba testudinis Hartmann (Fig. 86). In the intestine of turtles, *Testudo graeca*, *T. argentina* and *T. calcarata;* and also in *Terrapene carolina*.

Entamoeba barreti Taliaferro and Holmes. In the large intestine of the snapping turtle, *Chelydra serpentina*. It shows a close resemblance to the last species.

Entamoeba serpentis da Cunha and da Fonseca. In the intestine of the snake, *Drimobius bifossatus* of South America.

F. Entamoebae of amphibians

Entamoeba ranarum (Grassi) (Fig. 87, *a*, *b*). In the large intestine of various species of frogs. It somewhat resembles *E. histolytica*. Its size varies 10 to 50 microns in diameter. The cysts are usually tetranucleate, but some contain as many as 16 nuclei. Amoebic abscess of the liver was reported in a frog.

Entamoeba sp. Chatton. In the rectum of the newt, *Triton palmatus.*

Entamoeba sp. Alexeieff. In *Triton taeniatus.* These two forms resemble closely *E. ranarum.*

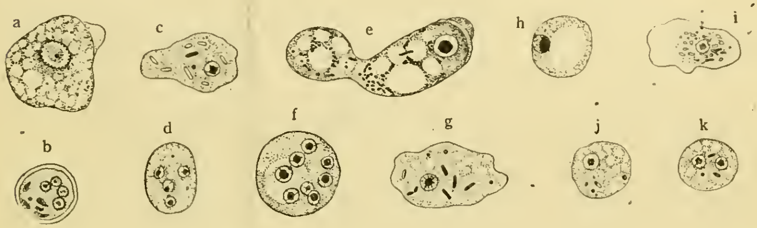


Fig. 87 a, b. Trophozoite and cyst of *Entamoeba ranarum.* ×650 (After Mercier and Mathis).
c, d. Trophozoite and cyst of *Endolimax nana.* ×1000.
e, f. Trophozoite and cyst of *E. ranarum.* ×500 (After Epstein and Ilovaisky).
g, h. Trophozoite and cyst of *Iodamoeba bütschli.* ×1000.
i–k. A living and two stained trophozoites of *Dientamoeba fragilis.* ×1100 (After Kudo).

G. Entamoebae of invertebrates

Entamoeba aulastomi Nöller. In the intestine of the horse leech, *Aulastomum gulo.* Trophozoites measure about 35 microns or larger. The cysts are ordinarily tetranucleate and measure 7 to 11 microns in diameter.

Entamoeba minchini Mackinnon. In the intestine of the tipulid larvae. Size 5 to 30 microns. Cysts contain nuclei up to ten in number.

Entamoeba mesnili Keilin. In the intestine of the larva of the dipterous insects, *Trichocera hiemalis* and *T. annulata.* Body 6 to 24 microns long and multinucleate. Plasmotomy. The cysts 8 to 11 microns in diameter, contain two or four nuclei.

Entamoeba apis Fantham and Porter. In *Apis mellifica.* Somewhat resembles *E. coli.*

Entamoeba belostomae Brug. In the intestine of *Belstoma* sp., a water bug.

Genus **Endolimax** Kuenen and Swellengrebel. Small parasitic amoeba. The genus is ill-defined. The nucleus possesses a definite membrane and there is a comparatively large irregularly shaped endosome which is composed of chromatin granules embedded in an achromatic ground mass. Several achromatic threads may be seen connecting the endosome with the membrane. One species occurs in the human intestine. Commensal.

Endolimax nana (Wenyon and O'Connor) (Fig. 87, *c*, *d*). Inhabitant of the large intestine of man. The amoeba is, as a rule, sluggish, although lobopodial formation may be quite active. It varies in diameter from 6 to 12 microns. The cytoplasm is fairly well differentiated into the ectoplasm and endoplasm. The latter contains a nucleus which is difficult to make out in life, and food vacuoles which contain bacteria. The cyst is usually ovoid, measures 8 to 10 microns in diameter, and contains when mature four nuclei. Widely distributed. It is considered as a commensal.

Endolimax gregariniformis (Tyzzer). In the caecum of the fowls. The small amoeba measures 4 to 12 microns in diameter. Nucleus vesicular with a large endosome. Rounded cysts are uninucleate.

Endolimax ranarum Epstein and Ilovaisky (Fig. 87, *e*, *f*). In the large intestine of frogs. Small amoeba of the Vahlkampfia type. The vesicular nucleus shows a large endosome, radiating achromatic strands, and small peripheral chromatin granules. The cyst measures up to 25 microns long and contains eight nuclei.

Endolimax blattae Lucas. In the colon of the cockroach.

Genus **Iodamoeba** Dobell. Small amoeba parasitic in the intestine of man and mammals. The vesicular nucleus possesses the following structure, if properly stained: A distinct membrane, a large endosome rich in chromatin, a layer of globules which surround the endosome and which do not stain deeply, and achromatic strands between the endosome and the membrane. The cysts are ordinarily uninucleate and contain a large glycogen vacuole which stains conspicuously with iodine.

Iodamoeba bütschli (Prowazek) (=*I. williamsi* Prowazek) (Fig. 87, *g*, *h*). Inhabitant of the large intestine of man. The sluggish trophozoites vary in size from 9 to 13 microns. The cytoplasm is ill-defined and contains bacteria which are taken in as food. The cysts are mostly of irregular shape and measure 6 to 15 microns in diameter. In the nucleus of the cyst, the large endosome comes in contact with the nuclear membrane at one point. A large iodinophilous vacuole.

Iodamoeba suis O'Connor. In the intestine of pig; widely distributed. Indistinguishable from the last species. It is considered by some that the pigs are probably reservoir hosts of this human parasite.

Genus **Dientamoeba** Jepps and Dobell. Small parasitic amoeba of the large intestine of man. The number of the binucleate trophozoites is often greater than that of the uninucleate forms. The nucleus has a delicate membrane. Its central endosome consists of several chromatin granules embedded in plasmosomic substances and is connected with the nuclear membrane by delicate achromatic strands. One species.

Dientamoeba fragilis Jepps and Dobell (Fig. 87, *i-k*). Commensal in the human intestine.

Genus **Schizamoeba** Davis. The nucleus of the trophozoite is vesicular and without any endosome, but with chromatin granules arranged along the nuclear wall. Each trophozoite possesses one to many nuclei. The cyst nuclei which are formed by the fragmentation of those of the trophozoite, possess a large rounded chromatic endosome connected at one side with the nuclear membrane by achromatic strands, in which are embedded chromatin granules. Parasitic in the stomach of salmonoid fish. One species.

Schizamoeba salmonis Davis (Fig. 88, *a*, *b*). The amoeba is sluggish and measures 10 to 25 microns in diameter. Multiplication by binary fission, the nuclear division being amitotic. The amoeba contains from one to several nuclei. The cysts are said to be usually more abundant than the trophozoites and their appearance seems to be correlated with the amount of available food. The cysts are spherical and measure 15 to 35 microns in diameter, being surrounded by a thin membrane.

The number of nuclei in each varies from three to a large number. During the encystment, the chromatin bodies of the trophozoite become collected in several masses which then disintegrate and each chromatin grain becomes the endosome of the newly formed nucleus. Sooner or later, the cyst contents divide into several (four to eleven) multinucleate bodies and the whole increases in size. Finally the cyst membrane disintegrates and the multinucleate bodies become set free. The

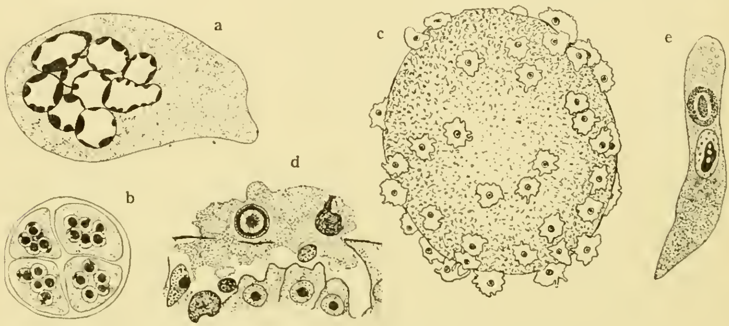


Fig. 88 a, b. *Schizamoeba salmonis.* ×800 (After Davis).
c, d. *Hydramoeba hydroxena.* (After Reynolds and Looper). c, a heavily attacked *Hydra oligactis* which lost its tentacles (×70); d, section of an infected hydra showing a trophozoite feeding on ectodermal cells (×350).
e. *Paramoeba pigmentifera* with its nucleus in the center. ×600. (After Janicki).

amoeba is said to occur in the mucous covering of the stomach of the salmonoid fish and the cysts occur in both stomach and intestine. Aside from the loss of certain amount of food available to the host fish, no pathogenic effect of the amoeba upon the host fish was noted by the discoverer.

Genus **Hydramoeba** Renolds and Looper. Ectoparasitic on Hydra. The nucleus has the following characteristics in stained condition: There is a large central endosome composed of a centrosome (?) and chromatin granules are embedded in an achromatic mass. Fine achromatic strands radiate from the endosome to the membrane. In the nuclear sap zone, there is a ring composed of numerous rod-shaped chromatin bodies arranged regularly. The cytoplasm contains one or more contractile vacuoles. This genus may be looked upon as a primitive parasitic amoeba.

Hydramoeba hydroxena (Entz) (Fig. 88, *c*, *d*). Parasitic in various species of Hydra. First found by Entz; Wermel found in Russia that 90 per cent of Hydra he studied were infected; Reynold and Looper made experimental studies and concluded that infected Hydra die on an average in 6.8 days and that the amoeba disappears in from 4 to 10 days if removed from a host Hydra. The body is more or less rounded with blunt lobopodia. Size 60 to 380 microns. The nucleus shows some twenty refractile peripheral granules in life. Contractile vacuoles are one to many. Food vacuoles contain the contents of the host cell such as pigments, nuclei, cnidoplasts, etc. It multiplies by binary fission. Encystment has not yet been observed.

Family 4 **Paramoebidae** Poche

The amoebae possess a nucleus and nucleus-like secondary cytoplasmic structure. These two cell-organs multiply by division simultaneously. Free-living or parasitic.

Genus **Paramoeba** Schaudinn. With the family characters.

Paramoeba pigmentifera (Grassi) (Fig. 88, *e*). Sluggish amoeba with an average length of 30 microns. The cytoplasm is distinctly differentiated. The secondary nucleus-like body is larger than the nucleus. Flagellate swarmers are said to occur. Parasitic in the coelom of Chaetognatha, such as *Sagitta claparedei*, *Spadella bipunctata*, *S. inflata, and S. serratodentata.*

References

A. Free-living forms

Cash, J. 1905 The British freshwater Rhizopoda and Heliozoa. Vol. 1.

Dellinger, O. P. 1906 Locomotion of amoebae and allied forms. Jour. Exper. Zool., Vol. 3.

Leidy, J. 1879 Freshwater Rhizopods of North America. Report U. S. Geol. Surv. Terr., Vol. 12.

Penard, E. 1902 Faune rhizopodique du Bassin du Léman. Geneva.

Schaffer, A. A. 1917 Notes on the specific and other characteristics of *Amoeba proteus* Pallas (Leidy), *A. discoides* spec. nov., and *A. dubia* spec. nov. Arch. f. Protistenk., Vol. 37.

———. 1926 The taxonomy of the amebas with descriptions of thirty-nine new marine and fresh-water species. Publ. Carnegie Inst. of Washington, No. 345.

TAYLOR, MONICA. 1924 *Amoeba proteus.* Quart. Jour. Mirc. Sci., Vol. 69.

WILSON, C. W. 1916 On the life-history of a soil amoeba. Uni. California Publ. Zool., Vol. 16.

B. Parasitic forms

BOECK, W. C. AND C. W. STILES. 1923 Studies on various intestinal parasites (especially amoebae) of man. U. S. Publ. Health Service, Hyg. Lab. Bulletin, No. 133.

CRAIG, C. F. 1926 A manual of parasitic Protozoa of man.

DOBELL, C. 1919 The amoebae living in man. London.

DOBELL, C. AND F. W. O'CONNOR. 1921 The intestinal Protozoa of man. London.

KIRBY, H. JR. 1927 Studies on some amoebae from the termite Microtermes, with notes on some other Protozoa from the Termitidae. Quart. Jour. Micr. Sci., Vol. 71.

KUDO, R. 1926 Observations on *Endamoeba blattae.* Amer. Jour. Hyg., Vol. 6.

NÖLLER, W. 1922 Die wichtigsten parasitischen Protozoen des Menschen und der Tiere. I Teil, Vol. 1. Berlin.

WENYON, C. M. 1926 Protozoology. Vol. 1. London.

CHAPTER XVIII

ORDER 5 **TESTACEA** SCHULTZE

THIS ORDER, which is also known as the Thecamoeba, comprises those amoeboid organisms which are covered by a single-chambered shell, or test, within which the body can be completely withdrawn. The test has usually a single aperture through which the cytoplasm is extruded as pseudopodia. The test varies somewhat in shape and structure. A chitinous or pseudochitinous membrane forms the basis of all tests. It may be thickened, as in Arcella, or composed of foreign bodies cemented together, as in Difflugia. In Euglypha silicious platelets are formed in the endoplasm and deposited on the membrane.

The cytoplasm is well differentiated into the ectoplasm and the endoplasm. The ectoplasm is conspicuously observable at the aperture of the shell where the pseudopodia are formed. The pseudopodia are slender and composed of ectoplasm only. Thus they are mainly filopodia. The endoplasm is, on the whole, granulated or vacuolated and contains food vacuoles, contractile vacuoles and nuclei. The number of nuclei present in a single individual varies from one to many. In some forms there are present regularly in the cytoplasm numerous deeply staining chromatin granules known as chromidia (p. 22).

Asexual reproduction is either by longitudinal fission, in forms with a soft shell, or by transverse division or budding. In some forms multiple division occurs. Sexual reproduction by amoeboid or flagellate gametes has been observed in a number of species. Encystment is known to occur in the majority of forms here grouped. The Testacea are mostly inhabitants of fresh water, but a few live in salt water. A number of species are semi-terrestrial, being found in moss or moist soil, especially peaty soil.

This group is divided into the following four families:

Test simple and membranous
  Pseudopodia filose or simply branched . . . . Family 1 Arcellidae
  Pseudopodia reticulate . . . . Family 2 Allogromiidae
Test with foreign bodies, plates or scales
  Chitinous test with foreign bodies . . . . Family 3 Difflugiidae
  Chitinous test with platelets or scales . . . . Family 4 Euglyphidae

Family 1 Arcellidae Schulze

The generic differentiation of the family is based mainly upon the form and structure of the test.

Genus **Arcella** Ehrenberg. Test transparent, chitinous, colorless to brown (when old), and densely punctated. In dorsal view it is circular, angular, or stellate; in profile plano-convex to hemispherical. Variously ornamented. Aperture circular, central, and inverted like a funnel. Occasionally spinous. The protoplasmic body does not fill the test and is connected with the latter by ectoplasmic strands. Pseudopodia few, digitate, blunt, simple or branched. Two nuclei, chromidia, and several contractile vacuoles. Fresh water. Numerous species.

Arcella vulgaris Ehrenberg (Figs. 4; 89, *a*). Height of test about one-half the diameter. Hemispherical. Dome evenly convex; aperture central and circular. Test colorless, yellow, or brown. The protoplasmic body conforms with the shape of the test, but does not fill the latter. Pseudopodia are lobose and hyaline. Two vesicular nuclei; numerous food vacuoles, chromidia, and contractile vacuoles conspicuously present. Diameter of test 50 to 150 microns. In the ooze of stagnant water and on submerged plants. Also in moist soil. Cosmopolitan.

Arcella dentata Ehrenberg (Fig. 89, *b*). Test in aperture view circular and dentate; in profile crown-like. Diameter more than twice the height. Aperture circular and large. Colorless to brown. The protoplasm as in *A. vulgaris*. Diameter of test 130 to 200 microns. In the ooze of fresh water ponds.

Arcella discoides Ehrenberg (Fig. 89, *c*). Test circular in aperture view; plano-convex in profile. Diameter is about three or four times the height. Test coloration and body structure similar to those of the last two species. Diameter of test 70 to 260 microns. In ponds and marshes.

Genus **Pyxidicula** Ehrenberg. Test patelliform; rigid, transparent, and punctate. Aperture is circular and almost the full diameter of the test. The cytoplasm is similar to that of Arcella, but the nucleus is usually one. Contractile vacuoles one or more. Fresh water.

Pyxidicula operculata (Agardh) (Fig. 89, *d*). Test smooth; colorless or brown. A single vesicular nucleus. Pseudopodia short, lobose or digitate. Diameter about 20 microns. On aquatic plants.

Genus **Pseudochlamys** Claparède and Lachmann. Test discoid, flexible when young. The body protoplasm contains a central nucleus and several contractile vacuoles.

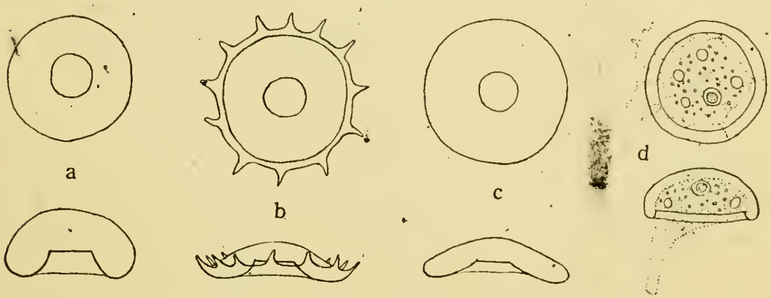


Fig. 89 a. *Arcella vulgaris*. ×200.
b. *A. dentata*. ×200.
c. *A. discoides*. ×200.
d. *Pyxidicula operculata*. ×800 (After Penard).

Pseudochlamys patella Claparède and Lachmann (Fig. 90, *a*). Young test flexible and hyaline, older ones rigid and brown. Young forms often rolled up like a scroll. A short finger-like pseudopodium is protruded between the folds. Diameter 40 to 45 microns. Freshwater plants, under moss, or in soil.

Genus **Difflugiella** Cash. Test ovoid, not compressed, flexible transparent membrane; colorless protoplasm filling up the test, usually with chlorophyllous food material. Median pseudopodia lobular or digitate with aciculate ends; lateral pseudopodia long, straight, and fine, tapering to a point. One species.

Difflugiella apiculata Cash (Fig. 90, *b*, *c*). Length about 40 microns. Among floating vegetation.

Genus **Cryptodifflugia** Penard. Minute test yellowish or brownish. Difflugia-like in general appearance, compressed; with or without foreign bodies. Pseudopodia long and acutely pointed.

Cryptodifflugia oviformis Penard (Fig. 90, *d*). Test ovoid, compressed; without foreign bodies. Crown hemispherical. Aperture truncate. The cytoplasm contains chlorophyllous food particles. Length about 15 to 20 microns. In marshy ground among Sphagnum.

Genus **Lesquereusia** Schlumberger. Test compressed, oval or globular in profile, narrowed at the neck which is bent; semi-spiral in appearance. With curved or comma-shaped rods or with sand-grains (in one species). The protoplasmic body does not fill the test. Pseudopodia long, blunt; simple or branched..

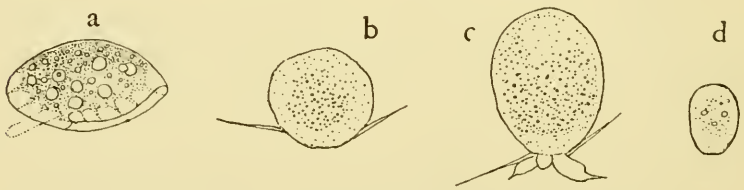


Fig. 90 a. *Pseudochlamys patella.* ×500.
b, c. *Difflugiella apiculata.* ×400.
d. *Cryptodifflugia oviformis.* ×480 (All after Cash).

Lesquereusia spiralis (Ehrenberg) (Fig. 91, *a*). Aperture circular; border distinct. The cytoplasm appears pale yellow. A single nucleus. About 120 microns long by 95 microns broad. In marsh.

Genus **Hyalosphenia** Stein. Test ovoid or pyriform; aperture convex; homogeneous and hyaline, mostly compressed. Crown uniformly arched. Protoplasm partly filling the test. Several blunt pseudopodia simple or digitate. Some ten species.

Hyalosphenia papilio Leidy (Fig. 91, *b*). Test yellowish; transparent or delicately punctated; in front view, pyriform or oblong. A minute pore on each side of crown and sometimes one also in the center. Aperture convex. In narrow lateral view, elongate pyriform, aperture a shallow notch. The protoplasm contains chlorophyllous particles and oil globules. Posteriorly located nucleus is indistinct. Pseudopodia digitate. Length 110 to 150 microns. In swamp among sphagnum.

Genus **Leptochlamys** West. Test ovoid, thin transparent chitinous membrane, circular in optical section. Aperture end slightly expanded from a very short neck. Circular aperture often oblique. Body fills the test and without vacuoles. Pseudopodium is single, short, broadly expanded and sometimes cordate. One species.

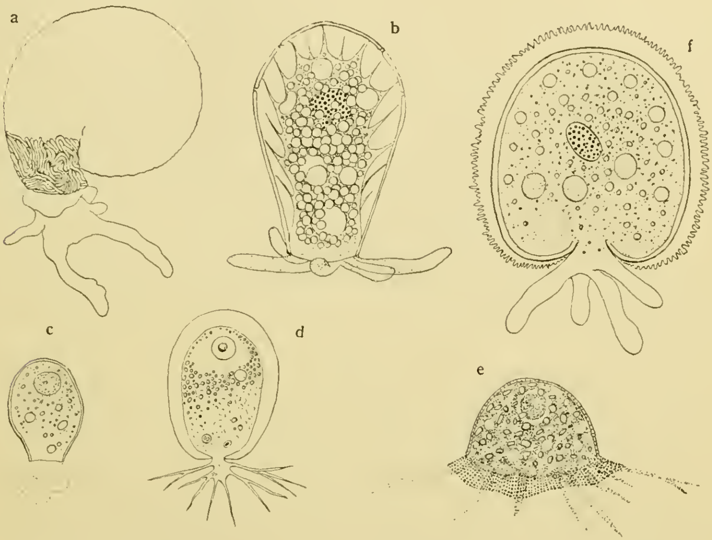


Fig. 91 a. *Lesquereusia spiralis.* ×200 (After West from Cash).
b. *Hyalosphenia papilio.* ×250 (After Leidy).
c. *Leptochlamys ampullacea.* ×250 (After West).
d. *Chlamydophrys stercorea.* ×500 (After Wenyon).
e. *Cochliopodium bilimbosum.* ×500 (After Leidy).
f. *Amphizonella violacea.* ×200 (After Greeff).

Leptochlamys ampullacea West (Fig. 91, *c*). A large nucleus posterior. Green or brown food particles. Length 45 to 55 microns. Among algae.

Genus **Chlamydophrys** Cienkowski. Rigid test circular in cross-section. Aperture often on the drawn-out neck. The protoplasm fills the test and contains a vesicular nucleus, with chromidia in the endoplasm. The zonal differentiation of the cytoplasm distinct. Refractile waste granules give the animal a characteristic appearance. The pseudopodia are variously branched. Free-living or coprozoic.

Chlamydophrys stercorea Cienkowski (Fig. 91, *d*). Coprozoic and in soil. Test 18 to 20 microns long by 12 to 15 microns broad. Mature cysts yellowish brown and measure 12 to 15 microns in diameter. The organism multiplies by budding from the aperture end.

Genus **Cochliopodium** Hertwig and Lesser. Minute test thin flexible, chitinous, capable of expansion and contraction, with or without extremely fine hair-like processes. Pseudopodia blunt or pointed, but not acicular. Several species.

Cochliopodium bilimbosum (Auerbach) (Fig. 91, *e*). Test hemispherical. Pseudopodia conical with pointed ends. Dimensions 24 to 56 microns. Among algae and in the ooze in ponds, springs, ditches and other freshwater bodies.

Genus **Amphizonella** Greeff. Test membranous with a double marginal contour. The inner membrane smooth and well-defined; the outer serrulate. Aperture inverted. A single nucleus. Pseudopodia blunt, digitate, and divergent.

Amphizonella violacea Greeff (Fig. 91, *f*). Test patelliform, violet-tinted; endoplasm with chlorophyllous corpuscles and grains. Movement sluggish. Average diameter 150 microns.

Genus **Zonomyxa** Nüsslin. Test rounded pyriform, flexible, chitinous, violet-colored. Endoplasm vacuolated, with chlorophyllous particles. Several nuclei. Pseudopodia simple, not digitate.

Zonomyxa violacea Nüsslin (Fig. 92, *a*). A single lobular pseudopodium with an accuminate end. Four nuclei. Diameter 140 to 160 microns. Actively motile forms 250 microns or more long. Among Sphagnum.

Genus **Microcorycia** Cockerell. Test discoidal or hemispherical, flexible, with a diaphanous continuation or fringe around the periphery, being folded together or completely closed; crown of test with circular and radial ridges. The body protoplasm does not fill the test; one or two nuclei; pseudopodia lobular or digitate. A few species.

Microcorycia flava (Greeff) (Fig. 92, *b*). Test yellowish brown. Crown with few small foreign bodies. Endoplasm with yellowish brown granules. Two nuclei close together; contractile vacuoles. Diameter 80 to 100 microns. In mosses.

Genus **Parmulina** Penard. Test ovoid, chitinoid with foreign bodies. Aperture capable of being closed, a single nucleus, one or more contractile vacuoles. A few species.

Parmulina cyathus Penard (Fig. 92, *c*). Small test flexible; ovoid in aperture view; hemi-circular in profile. Aperture a long narrow slit when the test is closed; circular or elliptical when opened. Length 40 to 55 microns. In mosses.

Fig. 92 a. *Zonomyxa violacea.* ×150 (After Penard).
b. *Microcorycia flava.* ×180 (After Wailes).
c. *Parmulina cyathus.* ×375 (After Penard).
d. *Capsellina timida.* ×200 (After Brown).
e. *Diplochlamys leidyi.* ×200 (After Wailes).

Genus **Capsellina** Penard. Test hyaline, ovoid, membranous; with or without a second outer covering. Aperture linear. A single nucleus; one or more contractile vacuoles; pseudopodia filose. Two species.

Capsellina timida Brown (Fig. 92, *d*). Small, oval; elliptical in cross-section. Endoplasm with numerous oil-like globules. A single filopodium. 35 microns long by 25 microns broad. In mosses.

Genus **Diplochlamys** Greeff. Test hemispherical or cup-shaped, flexible with a double envelope. Inner envelope a membranous sac with an elastic aperture, the outer envelope with loosely attached foreign bodies. Aperture large. Nuclei one to over one hundred in number. Pseudopodia few, short; digitate or pointed. Several species.

Diplochlamys leidyi Greeff (Fig. 92, *e*). Test dark grey; inner envelope projecting beyond the outer aperture. One to twenty nuclei. Diameter 80 to 100 microns. In mosses.

Family 2 **Allogromiidae** Cash and Wailes

This family is frequently included in the Foraminifera.

Genus **Allogromia** Rhumbler. Test a thin chitinoid membrane, rather rigid, smooth or slightly coated with extraneous matter; broadly ovoid or spherical; aperture terminal. One or more nuclei. Numerous contractile vacuoles. Pseudopodia are filopodia and numerous, being formed from a short peduncle, branching and anastomosing, with numerous motile granules. Several species in fresh or marine water.

Allogromia fluvialis (Dujardin). Test spherical or subspherical; smooth or sparsely covered with silicious particles. Cytoplasm yellowish, filling the test, with foreign particles; aperture not seen. A single large nucleus and numerous contractile vacuoles. Pseudopodia long, anastomosing, often enveloping the test. 50 to 250 microns long. On aquatic plants, moss, and soil.

Allogromia ovoidea Rhumbler (Fig. 93, *a*). In salt water.

Genus **Microgromia** Hertwig and Lesser. Test small, hyaline, spherical or pyriform, not compressed; terminal aperture circular. Pseudopodia long straight or branching, filose or anastomosing, arising from a peduncle. A single nucleus; one contractile vacuole. Solitary or colonial.

Microgromia socialis (Archer) (Fig. 93, *b*). The cytoplasm is bluish in color. A contractile vacuole near the aperture. Pseudopodia arise from a peduncle, attenuate, branching, anastomosing; often connecting numerous individuals into a more or less closely aggregated colony. Multiplication by fission of the body and also by the formation of zoospores. Diameter 25 to 35 microns. Among aquatic vegetation.

Genus **Lieberkühnia** Claparède and Lachmann. Test ovoidal or spherical, with or without attached foreign particles. Aperture usually single, lateral, or subterminal; flexible. One or more nuclei; numerous contractile vacuoles. Pseudopodia formed from a long peduncle located in the test, reticulate, often enveloping the test.

Lieberkühnia wagneri Claparède and Lachmann (Fig. 93, *c*). Test ovoid or subspherical, usually devoid of adherent particles. Aperture subterminal, oblique, flexible. Slightly yellowish protoplasm fills the test. Nucleus vesicular and numerous (80 to 150 in number); numerous contractile vacuoles. Pseudopodia long and anastomosing. Length 60 to 160 microns. On fresh-water or marine algae.

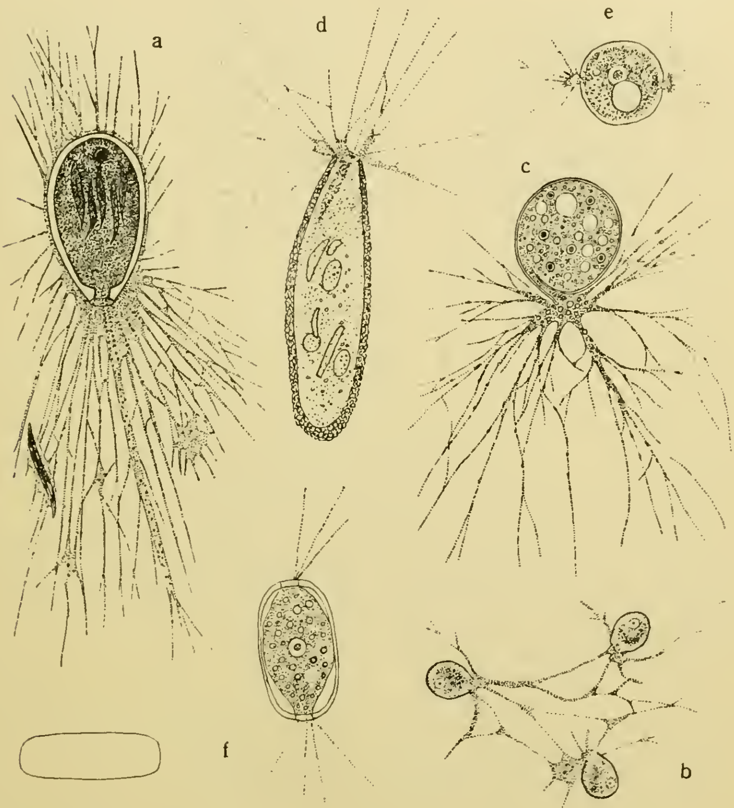


Fig. 93 a. *Allogromia ovoidea.* ×about 50 (After Schultze).
b. *Microgromia socialis.* ×165 (After Cash).
c. *Lieberkühnia wagneri.* ×140 (After Verworn).
d. *Rhynchogromia nigricans.* ×200 (After Cash and Wailes).
e. *Diplophrys archeri.* ×700 (After Hertwig and Lesser).
f. *Amphitrema flavum.* ×355 (After Cash and Wailes).

Genus **Rhynchogromia** Rhumbler. Test rigid or flexible, chitinous, and elongate, with foreign bodies. Aperture terminal or slightly oblique. Finely granulated cytoplasm fills the test. Nucleus one or more. One to several contractile vacuoles. Pseudopodia arise from a peduncle; numerous, branching or anastomosing; often enveloping the test.

Rhynchogromia nigricans (Penard) (Fig. 93, *d*). Test large; circular in cross-section. With a single nucleus. Length 220 to 400 microns. In submerged moss in ponds.

Genus **Diplophrys** Barker. Test thin, spherical; aperture two, located at opposite poles. Cytoplasm colorless; a single nucleus; several contractile vacuoles. Filopodia radiating. One species.

Diplophrys archeri Barker (Fig. 93, *e*). Invariably with one, two, or three colored oil droplets. Pseudopodia highly attenuated, radiating, straight or branched. Multiplication into two or four daughter individuals. Solitary or colonial. Diameter 8 to 20 microns. In submerged plants in fresh water.

Genus **Amphitrema** Archer. Test ovoid, symmetrical, compressed; composed of a transparent membrane, with or without adherent foreign bodies. Aperture two, located at opposite poles. The endoplasm contains Zoochlorellae. A central nucleus; one to several contractile vacuoles. Straight filopodia, sparsely branched, radiating. Several species.

Amphitrema flavum (Archer) (Fig. 93, *f*). Test chitinoid, brown, cylindrical with equally rounded ends in front view; elliptical in profile; ovoid with a small central oval aperture in end-view. Size about 45 to 80 microns long by 23 to 45 microns broad. In Sphagnum.

Genus **Lecythium** Hertwig and Lesser. Test thin, flexible, colorless. Aperture elastic and terminal. Colorless cytoplasm fills the test. A large nucleus located posteriorly. Numerous filopodia, long, branching, not anastomosing.

Lecythium hyalinum (Ehrenberg) (Fig. 94, *a*). Spheroidal. Aperture circular with a short flexible neck. A single contractile vacuole. Diameter 20 to 45 microns. In submerged vegetation.

Genus **Pseudodifflugia** Schlumberger. Test ovoid, usually rigid, with foreign bodies; circular or elliptical in cross-section. Aperture terminal. Granulated cytoplasm colorless or greyish.

A single nucleus, posterior; a single contractile vacuole. Filopodia long straight or branching, but not anastomosing. Several species.

Pseudodifflugia gracilis Schlumberger (Fig. 94, *b*). Test yellowish or brownish. Subspherical, with fine sand-grains; aperture without neck. About 30 to 55 microns long. In fresh water.

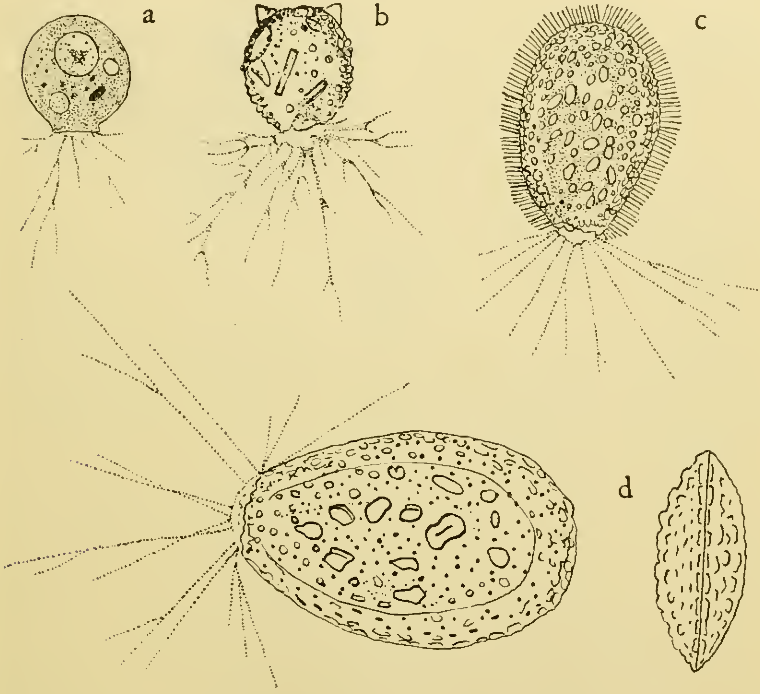


Fig. 94 a. *Lecythium hyalinum.* ×500 (After Cash and Wailes).
b. *Pseudodifflugia gracilis.* ×500 (After Cash).
c. *Diaphoropodon mobile.* ×400 (After Cash and Wailes).
d. *Clypeolina marginata.* ×500 (After Cash and Wailes).

Genus **Diaphoropodon** Archer. Test ovoid flexible, with minute foreign bodies and a thick covering of fine, hyaline hair-like projections ("cil"). Pseudopodia long, filose, branching, but not anastomosing.

Diaphoropodon mobile Archer (Fig. 94, *c*). Test brown;

aperture terminal, of various shape. Granulated cytoplasm does not fill the test. A single nucleus, large; one or two contractile vacuoles. Length 60 to 120 microns; projections 8 to 10 microns long. Among aquatic plants.

Genus **Clypeolina** Penard. Test ovoid, compressed, formed of a double envelope; the outer envelope is composed of two valves with scales and particles; the inner envelope a membranous sac. Filopodia long, often branched.

Clypeolina marginata Penard (Fig. 94, *d*). The outer test-valves yellow to dark brown; lenticular in cross-section. Aperture terminal, wide. The endoplasm contains numerous small globules. A single nucleus; a contractile vacuole. Length 80 to 150 microns. Among aquatic plants in ponds and marshes.

Family 3 **Difflugiidae** Taránek

Genus **Difflugia** Leclerc. Test variable in shape, but generally circular in cross-section; composed of cemented quartz-sand, diatoms and other foreign bodies. Aperture terminal. Often with Zoochlorellae. The cytoplasmic body almost fills the test. A single nucleus and numerous contractile vacuoles. Pseudopodia several, cylindrical, simple or branching; end rounded or pointed. Numerous species occur in fresh water, peat, woodland soil and meadows.

Difflugia oblonga Ehrenberg (= *D. pyriformis* Perty) (Fig. 95, *a*). Test pyriform, flask-shaped, or ovoid; neck variable in length. Fundus rounded with occasionally one to three conical processes. Aperture terminal, typically circular. Test composed of angular sand-grains and diatoms. The cytoplasm contains chlorophyllous bodies and is therefore bright green in color. Length 100 to 300 microns, width 50 to 100 microns. In the ooze of freshwater ponds, ditches and bogs. Also in moist soil. Several varieties.

Difflugia urceolata Carter (Fig. 95, *b*). A large ovoid, rotund test, with a short neck and a rim around the aperture. Length 200 to 230 microns, breadth 150 to 200 microns. In ditches, ponds, sphagnous swamps, etc.

Difflugia arcula Leidy (Fig. 95, *c*). Test hemispherical, base slightly concave, but not invaginated; aperture triangular, central, trilobed. Test yellowish with scattered sand-grains or diatoms. Diameter 100 to 140 microns. In sphagnous swamp, moss, and soil.

Difflugia lobostoma Leidy (Fig. 95, *d*). Test ovoid to subspherical. Aperture terminal; with 3 to 6 lobes. Test usually composed of sand-grains and rarely with diatoms. The endoplasm is colorless or greenish. Diameter 80 to 120 microns. In ponds, ditches, soil, and moss.

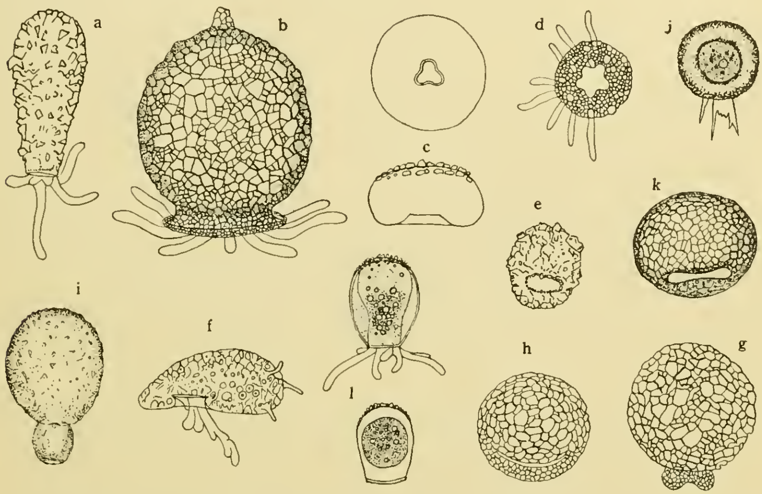


Fig. 95 a. *Difflugia oblonga.* ×100 (After Cash).
b. *D. urceolata.* ×100 (After Leidy).
c. *D. arcula.* ×125 (After Leidy).
d. *D. lobostoma.* ×100 (After Leidy).
e. *D. constricta.* ×150 (After Cash).
f. *Centropyxis aculeata.* ×150 (After Cash).
g. *Cucurbitella mespiliformis.* ×150 (After Wailes).
h. *Plagiopyxis callida.* ×150 (After Wailes).
i. *Pontigulasia vas.* ×150 (After Cash).
j. *Phryganella acropodia.* ×140 (After Cash).
k. *Bullinula indica.* ×100 (After Wailes).
l. *Heleopera petricola.* ×140 (After Cash).

Difflugia constricta (Ehrenberg) (Fig. 95, *e*). Test laterally ovoid, fundus more or less prolonged obliquely upward, rounded, and simple or provided with spines. Soil forms are spineless. Aperture antero-inferior, large, circular or oval and its edge inverted. Test composed of quartz sand-grains. Colorless to brown. The cytoplasm is colorless. Length 80 to 340 microns. In the ooze of ponds and in soil.

Genus **Centropyxis** Stein. Test circular, ovoid, or discoid. Aperture eccentric, circular or ovoidal, often with a lobate border. With or without spines. The cytoplasm is colorless; pseudopodia digitate.

Centropyxis aculeata Stein (Fig. 95, *f*). Test variable in contour and size; with 4 to 6 spines; opaque or semi-translucent; with fine sand-grains or diatom shells. Pseudopodia sometimes knotted or branching. When encysted, the protoplasm assumes a spherical form in the thicker part of the test; granulated, colorless or with green globules. Diameter 100 to 150 microns; aperture 50 to 60 microns.

Genus **Cucurbitella** Penard. Test ovoid with sand grains, not compressed; aperture terminal, circular, surrounded by a four-lobed annular collar. The cytoplasm is grey, granular, and contains symbionts, the Zoochlorellae. A single large nucleus; one to many contractile vacuoles; pseudopodia numerous, digitate.

Cucurbitella mespiliformis Penard (Fig. 95, *g*). Length 115 to 140 microns; diameter 80 to 105 microns. In the ooze or on vegetation in ponds and ditches.

Genus **Plagiopyxis** Penard. Test sub-circular in dorsal view; ovoid in profile; aperture linear or lunate. Cytoplasm grey, with a single nucleus and a contractile vacuole.

Plagiopyxis callida Penard (Fig. 95, *h*). Test grey, yellowish, or brown. A large vesicular nucleus; pseudopodia numerous, radiating, short, pointed or palmate. Diameter 55 to 135 microns.

Genus **Pontigulasia** Rhumbler. Test similar to that of Difflugia, but with a constriction of the neck and internal to it, a diaphragm made of the same substances as those of the test.

Pontigulasia vas (Leidy) (Fig. 95, *i*). Test rounded or ovoid, constriction deep and well-marked; with sand-grains and other material. Aperture terminal. Length 125 to 170 microns. Fresh water ponds.

Genus **Phryganella** Penard. Test spheroidal to ovoid, with sand-grains and minute diatom shells. Aperture terminal, rounded. Pseudopodia drawn out to a point. Fresh water bodies.

Phryganella acropodia (Hertwig and Lesser) (Fig. 95, *j*). Test circular in aperture view; hemispherical in profile. Yellowish or brownish, semi-transparent, and covered with sand-grains and scales. Aperture terminal. In aperture view, the sharply pointed pseudopodia radiating. Colorless endoplasm contains a single nucleus and a variable number of chlorophyllous bodies. Diameter 30 to 50 microns. In the sphagnous ooze of ponds and ditches.

Genus **Bullinula** Penard. Test ellipsoidal, flattened on one face, with silicious plates. On the flattened surface, ∞-shaped aperture. A single nucleus; pseudopodia digitate or spatulate, simple or branched.

Bullinula indica Penard (Fig. 95, *k*). Test dark brownish. Diameter 140 to 250 microns. In sphagnum and other mosses.

Genus **Heleopera** Leidy. Test variable in color; fundus hemi-spherical, almost always with sand-grains. Test surface covered with amorphous scales, often overlapping. Aperture truncate, narrow, elliptic, notched in narrow lateral view. A single nucleus; pseudopodia variable in number, thin, digitate or branching. Fresh water.

Heleopera petricola Leidy (Fig. 95, *l*). Test variable in size and color, strongly compressed; fundus rough with sand-grains of various size. Aperture linear or elliptic, its edge thin, convex in front view. A single nucleus posterior. Pseudopodia numerous, slender, branching. Length 80 to 100 microns. In sphagnum and boggy places.

Genus **Averintzia** Schouteden. Test similar to that of Heleopera, but small aperture elliptical. Test thickened around the aperture.

Averintzia cyclostoma (Penard). Test dark violet color, with sand-grains of different size; elliptical in cross-section. Pseudopodia unobserved. Length 135 to 180 microns. In sphagnum and other aquatic plants.

Family 4 **Euglyphidae** Wallich

Genus **Euglypha** Dujardin. Test hyaline, ovoid, composed of circular, oval, or scutiform silicious imbricated scales, arranged in longitudinal rows; aperture bordered with regularly arranged denticulate scales. Usually with spines. One or two nuclei large, placed centrally; contractile vacuoles. Filopodia, dichotomously branched. Numerous species.

Euglypha acanthophora (Ehrenberg) (=*E. alveolata* Dujardin) (Fig. 1). Test ovoid, or slightly elongate toward the aperture. 3 to 7 scales protruding around the circular aperture. Body-scales elliptical. The cytoplasm almost fills the test. Length 50 to 100 microns. In sphagnum and submerged plants.

Euglypha cristata Leidy (Fig. 96, *a*). Elongated test small, not compressed, with a long neck, fundus rounded with 3 to 8 spines.. Scales oval. Aperture circular and bordered by a single row of 5 or 6 denticulated scales. Cytoplasm colorless. A single posterior nucleus. Filopodia fine. Reserve scales are collected around the exterior of the aperture, unlike other forms in which they are kept within the cytoplasm. Length 30 to 70 microns; diameter 10 to 25 microns. In mosses.

Euglypha mucronata Leidy (Fig. 96, *b*). Test large, fundus conical, with one or two terminal spines. Aperture circular bordered by a single row of 6 to 8 denticulated scales. Length 100 to 150 microns; diameter 30 to 60 microns. In sphagnum.

Genus **Paulinella** Lauterborn. Test small ovoid, not compressed; with silicious plates in alternating transverse rows. Aperture terminal. The body cytoplasm does not fill the test completely. A single nucleus located posteriorly.

Paulinella chromatophora Lauterborn (Fig. 96, *c*). Scales arranged in 11 or 12 rows, five plates in each row. The cytoplasm with one or two curved chromatophores; no food particles. One contractile vacuole. Length 20 to 32 microns; diameter 14 to 23 microns. Among vegetation of fresh or brackish water.

Genus **Cyphoderia** Schlumberger. Test retort-shaped; colorless to yellow, made up of a thin chitinous membrane covered with discs or scales. Aperture terminal, oblique, circular. The cytoplasm does not fill the test completely. Nucleus large, posteriorly located. Pseudopodia few, long, filose, simple or branched.

Cyphoderia ampulla (Ehrenberg) (Fig. 96, *d*). Test usually yellow, translucent, composed of discs arranged in diagonal rows. Circular in cross-section. Aperture circular; oblique. Cytoplasm grey, contains many granules and food particles. A single nucleus; two contractile vacuoles. Pseudopodia long straight or curved filopodia. Length 60 to 200 microns; diameter 30 to 70 microns.

Genus **Campascus** Leidy. Test retort-shaped with curved neck, rounded triangular in cross-section. Aperture circular, oblique, with a thin transparent discoid collar.

Fig. 96 a. *Euglypha cristata.* ×250 (After Wailes).
b. *E. mucronata.* ×250 (After Wailes).
c. *Paulinella chromatophora.* ×750 (After Wailes).
d. *Cyphoderia ampulla.* ×150 (After Cash).
e. *Campuscus cornutus.* ×125 (After Leidy).
f. *Trinema enchelys.* ×250 (After Wailes).

Campascus cornutus Leidy (Fig. 96, *e*). Test pale-yellow, retort-shaped; with a covering of small sand particles; triangular in cross-section. A single nucleus and a contractile vacuole. Filopodia straight. Length 110 to 140 microns. In the ooze of mountain lakes.

Genus **Trinema** Dujardin. Test small, hyaline, ovoid, compressed anteriorly, with circular silicious plates. Aperture circular, oblique, invaginated. A single nucleus placed posteriorly. Filopodia not branched.

Trinema enchelys (Ehrenberg) (Fig. 96, *f*). One or two contractile vacuoles; pseudopodia attenuate, radiating and long. Length 30 to 100 microns, breadth 15 to 60 microns. In mosses and other vegetation.

Genus **Corythion** Taránek. Test small, hyaline, composed of small oval silicious plates; compressed; elliptical in optical cross-section. Aperture subterminal, ventral or oblique; circular or oval. Numerous filopodia.

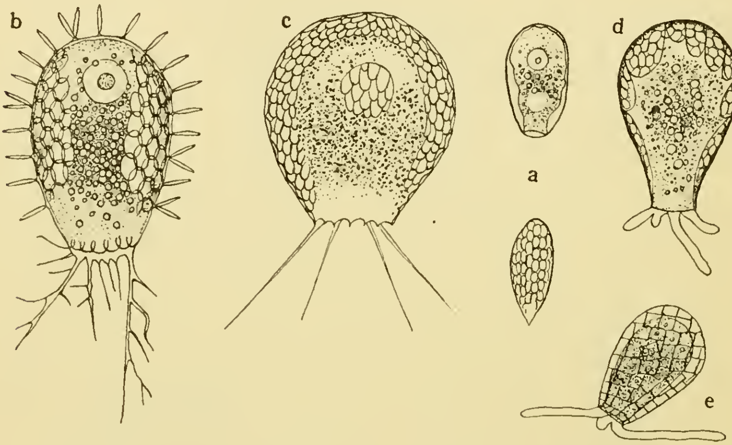


Fig. 97 a. *Corythion pulchellum.* ×350 (After Wailes).
b. *Placocista spinosa.* ×200 (After Wailes).
c. *Assulina seminulum.* ×400 (After Wailes).
d. *Nebela collaris.* ×200 (After Cash).
e. *Quadrula symmetrica.* ×200 (After Cash).

Corythion pulchellum Penard (Fig. 97, *a*). Aperture lenticular, cytoplasm colorless. Contractile vacuoles 2 to 3. 25 to 35 microns long by 15 to 20 microns broad. In mosses.

Genus **Placocista** Leidy. Test ovoid, hyaline, compressed; lenticular in optical cross-section, with oval or subcircular silicious scales. Aperture wide, linear, with flexible undulate borders. A large nucleus posterior. Often with Zoochlorellae. Pseudopodia filose, branching and numerous, generally arising from a protruded portion of the cytoplasm.

Placocista spinosa (Carter) (Fig. 97, *b*). Margin of the test with spines, either single or in pairs. Two contractile vacuoles; cytoplasm colorless, but occasionally with Zoochlorellae. Several filopodia, branching. Test 115 to 170 microns long by 70 to 100 microns wide. In sphagnum.

Genus **Assulina** Ehrenberg. Test brown or colorless, ovoid, compressed, with elliptical scales, arranged in diagonal rows. Aperture oval, terminal, bordered by a thin chitinous dentate membrane. A single nucleus is located posteriorly; contractile vacuoles. Several filopodia, divergent, sometimes branched.

Assulina seminulum (Ehrenberg) (Fig. 97, *c*). Protoplasm not completely filling up the test, with numerous food particles; one contractile vacuole. Pseudopodia few, straight, divergent, slender, seldom branched. Test 60 to 150 microns long by 50 to 75 microns broad. In mosses.

Genus **Nebela** Leidy. Test thin, ovate or pyriform; compressed, with circular or oval plates or discs of uniform or various size; highly irregular. The endoplasm with oil-globules; a single nucleus posterior. The protoplasm does not fill the test and is connected with the latter by numerous ectoplasmic strands at the fundus end. Pseudopodia blunt, rarely branched. Numerous species.

Nebela collaris (Ehrenberg) (Fig. 97, *d*). Test pyriform, fundus obtuse in profile, aperture without any notch. The endoplasm contains chlorophyllous food particles. Pseudopodia digitate, short, usually 3 to 6 in number. Test 130 microns long by 85 to 90 microns broad. In marshes among sphagnum.

Genus **Quadrula** Schulze. Test pyriform, hemi-spherical, or discoidal, consisting of a homogeneous chitinous film, with quadrangular silicious or calcareous plates, arranged generally in oblique series, not overlapping. A single nucleus. The body and pseudopodia similar to those of Difflugia. Fresh water.

Quadrula symmetrica (Wallich) (Fig. 97, *e*). Compressed, smaller plates near the aperture. The cytoplasm very clear, containing chlorophyllous granules. Three to five pseudopodia digitate. A single nucleus posterior. Test about 95 microns long by 60 to 70 microns broad. In sphagnum and other mosses.

References

Cash, J. 1905, 1909 The British freshwater Rhizopoda and Heliozoa. Vols. 1, 2.

Cash, J. and G. H. Wailes. 1915, 1918 The British freshwater Rhizopoda and Heliozoa. Vols. 3, 4.

Deflandre, G. 1928 Le genre Arcella Ehrenberg. Arch f. Protistenk., Vol. 64.

Goette, A. 1916 Ueber den Lebenscyclus von *Difflugia lobostoma*. Arch. f. Protistenk., Vol. 37.

Hegner, R. W. 1920 The relations between nuclear number, chromatin mass, cytoplasmic mass, and shell characteristics in four species of the genus Arcella. Jour. Exper. Zool., Vol. 30.

Jennings, H. S. 1916 Heredity, variation and the results of selection in the uniparental reproduction of *Difflugia corona*. Genetics. Vol. 1.

Leidy, J. 1879 Freshwater Rhizopods of North America. Rep. U. S. Geol. Survey. Vol. 12.

Penard, E. 1905 Les Sarcodinés des Grands Lacs. Geneva.

CHAPTER XIX

SUBCLASS 2 **ACTINOPODA** CALKINS

THE SARCODINA placed in this subclass possess axopodia and are divided into two orders: the Heliozoa and the Radiolaria.

ORDER 1 **HELIOZOA** HAECKEL

The Heliozoa are, as a rule, spherical in form with radiating axopodia. They are somewhat similar in appearance to the Radiolaria, but do not possess the central capsule of the latter. The body of a typical heliozoan, such as Actinophrys, is spherical when undisturbed and shows numerous radiating axopodia. The cytoplasm is differentiated, distinctly in Actinosphaerium, or indistinctly in other forms, into the coarsely vacuolated ectoplasm and the less transparent and highly vacuolated endoplasm, in which is located the nucleus.

The food of the Heliozoa consists of living Protozoa or Protophyta. Thus their mode of obtaining nourishment is holozoic. A large organism may sometimes be captured by a group of Heliozoa which gather around the prey. When an active ciliate or a small rotifer comes in contact with an axopodium, it seems to become suddenly paralyzed and, therefore, it has been suggested that the pseudopodia contain some poisonous substances. The axial filaments of the axopodia disappear and the pseudopodia become enlarged and surround the food completely. Then the food matter is carried into the main part of the body and is digested.

The ectoplasm contains several contractile vacuoles and numerous refractile granules which are scattered throughout. The endoplasm is denser and is usually devoid of granules. In the axopodium, the cytoplasm undergoes streaming movements. The hyaline and homogeneous axial filament runs straight through both the ectoplasm and the endoplasm, and terminates in a point just outside the nuclear membrane.

When the pseudopodium is withdrawn, its axial filament disappears completely. The latter sometimes disappears without the withdrawal of the pseudopodium itself.

In Acanthocystis the nucleus is eccentric (Fig. 100, *b*). There is, however, a **central granule,** or centroplast, in the center of the body from which radiate the axial filaments of the axopodia. In multinucleate Actinosphaerium, the axial filaments terminate at the periphery of the endoplasm. In Camptonema, an axial filament arises from each of the numerous nuclei (Fig. 98, *c*).

The skeletal structure of the Heliozoa varies among different species. The body may be naked, covered by a gelatinous mantle, or provided with a lattice-test with or without spicules. The spicules are variable in form and location and may be used for specific differentiation. In some forms there occur colored bodies bearing chromatophores, which are considered as holophytic Mastigophora living in the Heliozoa as symbionts.

The Heliozoa multiply by binary fission or budding. Incomplete division may result in the formation of colonies, as in Rhaphidiophrys. In Actinosphaerium, mitotic division of the nucleus has been observed by Hertwig, who described the appearance of some 150 chromosomes, conspicuous centrosomes, and spindle fibers. In Acanthocystis and Oxnerella (Fig. 19), the central granule behaves somewhat like the centrosome in a metazoan mitosis. Budding has been known in numerous species. In Acanthocystis the nucleus undergoes amitosis several times, thus forming several nuclei, one of which remains in place while the others migrate toward the body surface. Each peripheral nucleus becomes surrounded by a protruding cytoplasmic body which becomes covered by spicules and which is set free in the water as a bud. These small individuals are supposed to grow into larger forms, the central granule being produced from the nucleus during the growth. Formation of swarmers is known in a few genera. Sexual reproduction occurs in some forms (p. 57).

The Heliozoa live chiefly in fresh water, although some inhabit the sea. Only a few are attached forms. According to Hertwig and Lesser, the Heliozoa are here divided into four suborders:

Without skeleton; no jelly mantle. . . . . Suborder 1 Aphrothoraca
With gelatinous mantle; no silicious spicules. . . . . Suborder 2 Chlamydophora
With isolated or united spicules. . . . . Suborder 3 Chalarothoraca
Skeleton glubular, silicious with many apertures. . . Suborder 4 Desmothoraca

Suborder 1 **Aphrothoraca** Hertwig

Without envelope or skeleton in the active stage; envelope in encysted stage.

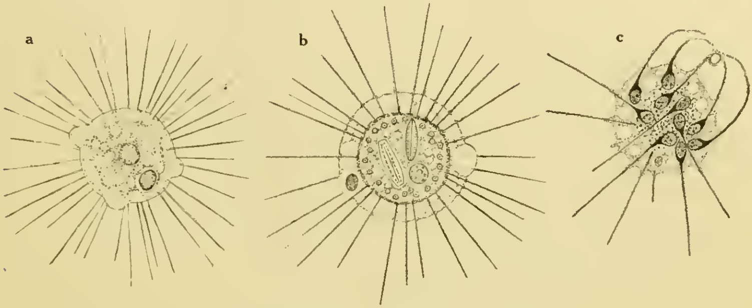


Fig. 98 a. *Actinophrys sol.* ×265.
b. *Actinosphaerium eichhorni.* ×30.
c. *Camptonema nutans.* ×230 (After Schaudinn).

Genus **Actinophrys** Ehrenberg. Spherical with a smooth membranous envelope; cytoplasm vacuolated, especially ectoplasm. With symbiotic Zoochlorellae. A central nucleus; one large contractile vacuole. Axopodia straight, numerous, axial filament arising from the surface of the nucleus. "Sun animalcules." Several species.

Actinophrys sol Ehrenberg (Fig. 98, *a*). Spherical. Ectoplasm contains numerous large vacuoles; endoplasm granulated with numerous small vacuoles. A large central nucleus. Solitary but may be colonial when young. Body diameter 40 to 50 microns. Among plants in still fresh water.

Genus **Actinosphaerium** Stein. Spherical. Ectoplasm consists almost entirely of large vacuoles in one or several layers; endoplasm with numerous small vacuoles. Numerous nuclei. Axial filaments of the pseudopodia end in the ectoplasm. Two species.

Actinosphaerium eichhorni Ehrenberg (Fig. 98, *b*). Numerous nuclei scattered in the peripheral portion of the endoplasm.

Two or more contractile vacuoles large. Axial filaments arise from a narrow zone of dense cytoplasm at the border line between endoplasm and ectoplasm. Body large, diameter 80 to 1000 microns. Among aquatic plants in freshwater ponds.

Genus **Camptonema** Schaudinn. Body spheroidal. Axial filaments of axopodia end in the nuclei which are about 50 in number. Contractile vacuoles (?) numerous and small in size. Marine.

Camptonema nutans Schaudinn (Fig. 98, *c*). About 150 microns in diameter.

Genus **Oxnerella** Dobell. Spherical. Cytoplasm indistinctly differentiated. Eccentric nucleus with a large endosome. Axial filaments take their origin in the central granule. No contractile vacuoles. Nuclear division is typical mitosis (Fig. 19).

Oxnerella maritima Dobell (Fig. 19). Small, diameter 10 to 22 microns. Solitary, floating or creeping. Salt water.

Suborder 2 **Chlamydophora** Archer

Body is covered by a gelatinous envelope containing no silicious scales.

Genus **Astrodisculus** Greeff. Spherical with gelatinous envelope, free from inclusions, sometimes absent. No demarcation between the two regions of the cytoplasm. Freshwater inhabitants. Four species.

Astrodisculus radians Greeff (Fig. 99, *a*). Outer surface of the investment often with adherent foreign bodies and bacteria. The cytoplasm is often loaded with green, yellow, or brown granules. A single nucleus eccentric; a contractile vacuole. Diameter of body 13 to 25 microns. In pools and ditches.

Genus **Actinolophus** Schulze. Body pyriform, enveloped in a gelatinous mantle. With a stalk which is apparently hollow. Axopodia long and numerous. An eccentric nucleus. Marine.

Actinolophus pedunculatus Schulze (Fig. 99, *b*). Diameter 30 microns. Stalk about 100 microns long. In marine water.

Genus **Heterophrys** Archer. Body spherical, mucilaginous envelope thick, with numerous radial, chitinoid spicules which project beyond its periphery; nucleus single, eccentric. Axial filaments of axopodia originate in a central granule. Four species.

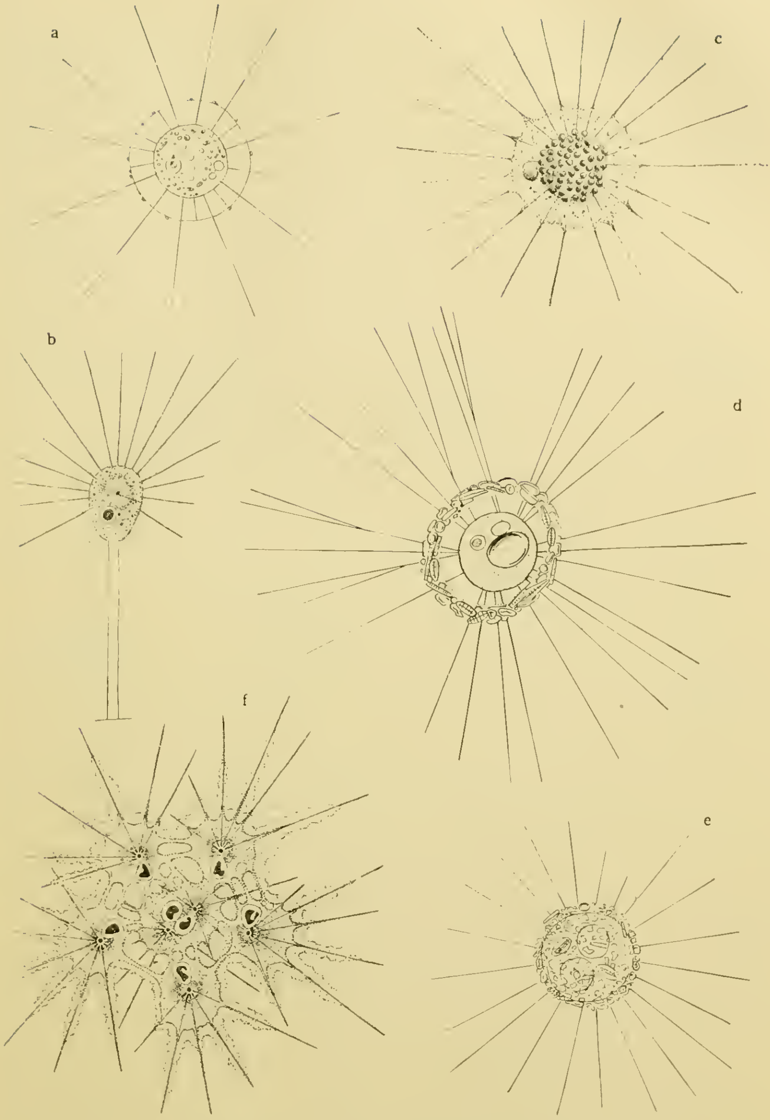


Fig. 99 a. *Astrodisculus radians.* ×600 (After Penard).
b. *Actinolophus pedunculatus.* ×400 (After Schultze).
c. *Heterophrys myriopoda.* ×250 (After Calkins).
d. *Elaeorhanis oculea.* ×300 (After Penard).
e. *Lithocolla globosa.* ×250 (After Penard).
f. *Sphaerastrum fockei.* ×300 (After Stubenrauch).

Heterophrys myriopoda Archer (Fig. 99, *c*). Endoplasm and nucleus eccentric; ectoplasm is loaded with spherical algae, living probably as symbionts. Contractile vacuoles indistinct. Diameter 50 to 80 microns. In pools and marshes, and also among marine algae.

Genus **Elaeorhanis** Greeff. Body spherical. Mucilaginous envelope with sand-grains and diatom frustules. The cytoplasm with a large oil globule; a single nucleus, eccentric; one or more contractile vacuoles; pseudopodia not granular. One species.

Elaeorhanis oculea (Archer) (Fig. 99, *d*). The cytoplasm bluish with a large yellow oil globule; without any food particles. No central granule. Pseudopodia rigid, but apparently without axial filament (?), sometimes forked. Young forms are colonial; solitary when old. Outer diameter 50 to 60 microns, body itself 25 to 30 microns. In lakes and pools.

Genus **Lithocolla** Schulze. Spherical body; outer envelope with usually one layer of sand-grains and diatom frustules. No oil globule. Nucelus eccentric. Two species.

Lithocolla globosa Schulze (Fig. 99, *e*). The ectoplasm is reddish in color with numerous small colored granules. Nucleus large; central granule is unknown. Diameter of envelope 35 to 50 microns. In lakes, ponds, and rivers; also in brackish water.

Genus **Sphaerastrum** Greeff. Body somewhat flattened. The greater part of the axopodia and the body are covered by a thick gelatinous mantle. A central granule and an eccentric nucleus.

Sphaerastrum fockei Greeff (Fig. 99, *f*). Diameter about 30 microns. Often colonial. In swamps.

Suborder 3 **Chalarothoraca** Hertwig and Lesser

Heliozoa with isolated or united spicules.

Genus **Pompholyxophrys** Archer. Spherical body; outer mucilaginous envelope with minute colorless spherical granules arranged in concentric layers. Nucleus single, eccentric; contractile vacuoles. Pseudopodia long, straight, acicular.

Pompholyxophrys punicea Archer (Fig. 100, *a*). The cytoplasm colorless or reddish, with usually many colored granules and green to brown food particles; nucleus large, eccentric.

Solitary, active. Diameter 25 to 35 microns. Outer envelope 5 to 10 microns larger. In pools.

Genus **Acanthocystis** Carter. Spherical without mucilaginous mantle, but with silicious scales arranged tangentially and radiating silicious spines with ends pointed or bifurcated. Nucleus and endoplasm eccentric. The central granule distinct. Several species.

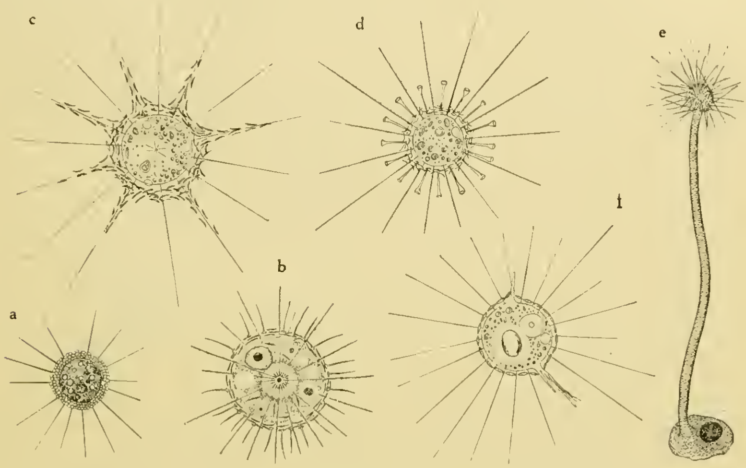


Fig. 100 a. *Pompholyxophrys punicea.* ×170 (After West).
b. *Acanthocystis aculeata.* ×200 (After Stern).
c. *Raphidiophrys pallida.* ×200 (After Penard).
d. *Raphidiocystis tubifera.* ×330 (After Penard).
e. *Wagnerella borealis.* ×50 (After Kühn).
f. *Pinaciophora fluviatilis.* ×165 (After Penard).

Acanthocystis aculeata Hertwig and Lesser (Fig. 100, *b*). Tangential scales stout and pointed, curved and nail-headed. The cytoplasm greyish; nucleus eccentric; a single contractile vacuole. Diameter 35 to 40 microns. Spines about one-third the diameter of body. In lakes, ponds, and pools.

Genus **Raphidiophrys** Archer. Spherical. Mucilaginous envelope with spindle-shaped or discoidal spicules which extend normally outwards along the pseudopodia. Nucleus and endoplasm eccentric. Solitary or colonial. Several species.

Raphidiophrys pallida Schulze (Fig. 100, *c*). Outer gelatinous envelope crowded with curved lenticular spicules, forming accumulations around the pseudopodia. Ectoplasm granulated; nucleus eccentric. Contractile vacuoles. Axial filaments arise from the central granule. Solitary. Diameter 50 to 60 microns. In vegetation in still water.

Genus **Raphidiocystis** Penard. Spicules unlike those occurring in the last genus. With radiating needle-like spicules.

Raphidiocystis tubifera Penard (Fig. 100, *d*). With characteristic spicules. Body diameter about 18 microns; envelope 25 microns. Fresh water.

Genus **Wagnerella** Mereschkowsky. Body spherical, supported by a cylindrical stalk with an enlarged base. Small silicious spicules. The nucleus is located in the base of the stalk. Reproduction through budding.

Wagnerella borealis Mereschkowsky (Fig. 100, *e*). Body up to 180 microns in diameter. Stalk often up to 1.1 mm. in length. In marine water.

Genus **Pinaciophora** Greeff. Spherical. Outer envelope is composed of imbricated circular discs, each being perforated with nineteen minute pores. Cytoplasm reddish. One species.

Pinaciophora fluviatilis Greeff (Fig. 100, *f*). Diameter 45 to 50 microns, but somewhat variable. In ponds.

Suborder 4 **Desmothoraca** Hertwig and Lesser

Homogeneous capsule, with or without perforation, often with a pedicel or stalk.

Genus **Clathrulina** Cienkowski. Envelope spherical, homogeneous, with numerous openings regularly arranged. With a stalk. Body protoplasm central, not filling the capsule. The single nucleus centrally located. Pseudopodia numerous, straight or forked, granular. A few species.

Clathrulina elegans Cienkowski (Fig. 101, *a*). Envelope colorless to brown, perforated by numerous comparatively large openings which are circular or polygonal. One or more contractile vacuoles. Nucleus central. Diameter 30 to 90 microns; openings 6 to 10 microns; stalk 120 to 350 microns long by 3 or 4 microns wide. Solitary or colonial. Among vegetation in ponds and pools.

Genus **Hedriocystis** Hertwig and Lesser. Envelope spherical, openings minute, surrounded by polyhedral facets or ridges. With stalk. Solitary or colonial. Thiee species.

Hedriocystis reticulata Penard (Fig. 101, *b*). Envelope colorless or pale yellow, proliferations regularly polygonal with raised borders. Stalk solid, straight; a single nucleus, located near the center; one contractile vacuole. Axopodia(?), each arising from a pore in the center of a facet. Solitary. Capsule about 25 microns in diameter; body about 12 microns in diameter; stalk about 70 microns long by 1 to 1.5 microns in width. In marshy pools.

Genus **Choanocystis** Penard. Spherical envelope with perforations which possess conical borders; the openings of the cones are provided with funnel-like extensions, the edges of which nearly touch one another.

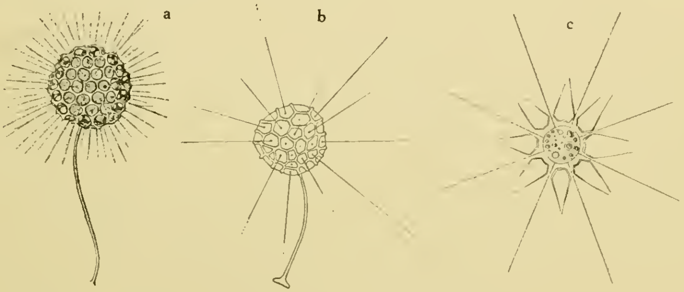


Fig. 101 a. *Clathrulina elegans.* ×165 (After Leidy).
b. *Hedriocystis reticulata.* ×330 (After Brown from Cash).
c. *Choanocystis lepidula.* ×460 (After Penard).

Choanocystis lepidula Penard (Fig. 101, *c*). Diameter 10 to 13 microns. In freshwater body.

References

Bělař, K. 1922, 1924 Untersuchungen an *Actinophrys sol* Ehrenberg. I, II. Arch. f. Protistenk., Vols. 46, 48.

Cash, J. and G. H. Wailes. 1921 The British freshwater Rhizopoda and Heliozoa. Vol. 5. London.

Kühn, A. 1926 Morphologie der Tiere in Bildern. 2 H., 2 T. Rhizopoden. Berlin.

Leidy, J. 1879 Freshwater Rhizopods of North America. Rep. U. S. Geol. Survey. Vol. 12.

Penard, E. 1904 Les Héliozoaires d'eau douce. Geneva.
1905 Les Sarcodinés des Grands Lacs. Geneva.

CHAPTER XX

ORDER 2 **RADIOLARIA** MÜLLER

The radiolaria are pelagic forms found abundantly in the sea. A very large number of species occur in various oceans. In fact a vast area of the ocean floor is covered with the ooze made up chiefly of radiolarian skeletons. They seem to have been equally abundant during former geologic ages, since rocks composed of their skeletons occur in various geological formations. Thus this group is the second group of Protozoa important to geologists.

The body is mostly spherical in form, although radially or bilaterally symmetrical forms are also encountered. The cytoplasm is divided into two distinct regions which are sharply delimited by a membranous structure known as the **central capsule.** This is a single or double perforated membrane of pseudochitinous or mucinoid nature. Although its thickness varies a great deal, the capsule is ordinarily very thin and only made visible after the use of reagents. Its shape varies according to the form of the organism. In spherical forms it is spherical, in discoidal or lenticular forms it is more or less ellipsoidal, while in a few cases it shows a number of protruding processes. The capsule is capable of extension as the animal grows and of dissolution at the time of multiplication. The cytoplasm on either side of the capsule communicates with the other side through pores, which may be large and few or small and numerous. The intracapsular portion of the body is the seat of reproduction and contains reserve food material, while the extracapsular portion is nutritive and hydrostatic in function. The intracapsular cytoplasm is granulated, often greatly vacuolated, and is stratified either radially or concentrically. It contains one or more nuclei, pigments, oil droplets, fat globules, and crystals. The nucleus is usually of vesicular type, but its form, size, and structure, vary among different species and also at different stages of development even in one and the same species.

A thin assimilative layer, or matrix, surrounds the central capsule. In Tripylea, waste material forms a brownish mass, known as the **phaeodium,** around the chief aperture (**astropyle**) of the capsule. Then there is a highly alveolated region, termed **calymma,** in which the alveoli are apparently filled with a mucilaginous secretion of the cytoplasm. Brandt showed that the vertical movement of some Radiolaria is due to the formation and expulsion of a fluid which consists of water saturated with carbon dioxide. Under ordinary weather and temperature conditions, the interchange between the alveoli and the exterior is gradual and there is a balance of loss and gain of the fluid, so that the organisms float on the surface of the sea. Under rough weather conditions or in extraordinary temperature, the pseudopodia are withdrawn, the alveoli burst, and the organisms descend into deeper water, where the alveoli are formed again.

The Radiolaria feed on microplankton such as copepods, diatoms, and other Protozoa. The food is taken in through the pseudopodia and passed down into the deeper region of the calymma where it is digested in a food vacuole. The Radiolaria can, however, live under experimental conditions without solid food if kept under light. This is ordinarily attributed to the action of the yellow corpuscles which are present in various parts of the body, although they are, as a rule, located in the calymma. In Actipylea they are found only in the intracapsular cytoplasm, and in Tripylea they are absent altogether. They are spherical bodies, about 15 microns in diameter, with a cellulose wall, two chromatophores, a pyrenoid, starch, and a single nucleus. They appear to multiply by fission. These bodies are considered as Zooxanthellae (p. 93). In the absence of organic food material, the Radiolaria use the products of the holophytic nutrition of these symbiotic organisms.

The axopodia arise either from the extracapsular cytoplasm or from the intracapsular portion and radiate in spherical forms in all directions, as in Heliozoa. In Actipylea, myonemes are present in certain pseudopodia and produce circular groups of short, rod-like bodies, clustered around each of the radial spines (Fig. 103, *c*). They connect the peripheral portion of the body with the pseudopodial covering of the spicule and possess a great contractile power, supposedly with hydrostatic function.

The skeletal structure of the Radiolaria varies considerably from simple to complex and has taxonomic value. The chemical nature of the skeleton is used in distinguishing the major subdivisions of the group. In the Actipylea it seems to be made up of strontium sulphate, while in the three other groups, Peripylea, Monopylea and Tripylea, it consists fundamentally of silicious substances. The skeleton of the Actipylea is sharply marked from that of others in form and structure. The majority of this group possess twenty rods arranged in a diverse way, and radiating from the center. The rod-shaped skeletons emerge from the body in most cases along five circles, which are comparable to the equatorial, the two tropical and the two circumpolar circles of the globe. This is known as **Müller's law**, since J. Müller first noticed the arrangement in 1858.

The life history of the Radiolaria is very incompletely known (Fig. 102). Binary or multiple fission or budding has been observed in some Peripylea, Actipylea, and Tripylea. Multiple division is known to occur in Thalassophysidae, in which it is the only known means of reproduction. The central capsule becomes very irregular in its outline and the nucleus breaks up into numerous chromatin globules. Finally the capsule and the intracapsular cytoplasm become transformed into numerous small bodies, each containing several nuclei. Further changes are unknown.

Formation of swarmers is known in some forms. In Thallassicolla, the central capsule becomes separated from the remaining part of the body and the nucleus divides into a number of small nuclei, around each of which condenses a small ovoidal mass of cytoplasm. These small bodies soon develop flagella. In the meantime the capsule descends to a depth of several hundred meters, where its wall bursts and the flagellate swarmers are liberated. Two kinds of swarmers, isoswarmers and anisoswarmers, are recognized. The former often contain a crystal and a few fat globules. Of the latter, the macroswarmers possess a nucleus and refringent spherules in the cytoplasm, while the microswarmers contain a granular nucleus. Some forms possess two flagella, one of which is coiled around the groove of the body, which makes them resemble certain Dinoflagellida. Further development is unknown; it is, however, supposed that the anisoswarmers are sexual and isoswarmers are asexual generations.

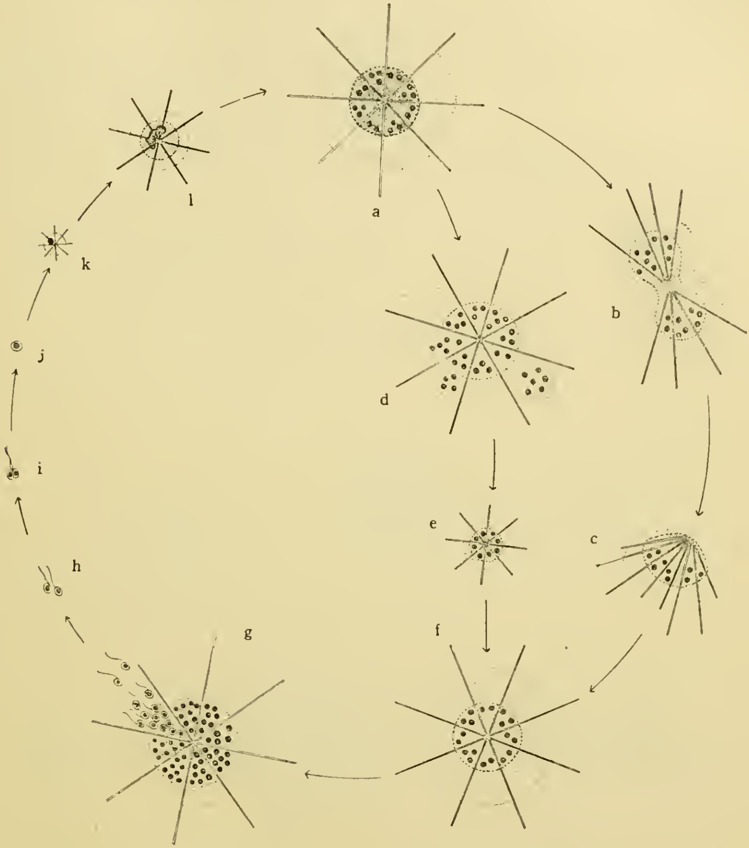


Fig. 102 The life-cycle of Actipylea. (After Kühn, modified).
a, grown individual; b, c, binary fission; d, e, budding process; f, adult individual similar to a; g, formation of swarmers; h–j, supposed, but not observed, gametogony of two swarmers producing a zygote; k, l, young individuals.

Enormous number of species of the Radiolaria are now known. An outline of the classification is given below, together with a few examples of the genera.

Skeleton composed of strontium sulphate.............Suborder 1 Actipylea
Skeleton not composed of strontium sulphate
The central capsule uniformly perforated; skeletons are either tangential to the capsule or radiating without reaching the intracapsular region ....Suborder 2 Peripylea
The central capsule not uniformly perforated
The capsule monaxonic which bears at one pole a perforated plate forming the base of an inward directed cone.....Suborder 3 Monopylea
The capsule with three openings (one astropyle and two parapyles) .... Suborder 4 Tripylea

Suborder 1 **Actipylea** Hertwig

Radial spines, 10 to 200, not arranged according to Müller's law........... Legion 1 Actinelida
Spines radiate from a common center. Haeckel considered these as the ancestral forms............................Family 1 Actineliidae

Genus **Actinelius** (Fig. 103, *a*)

With 10 to 16 diametral spines irregularly arranged..................... Family 2 Acanthociasmidae

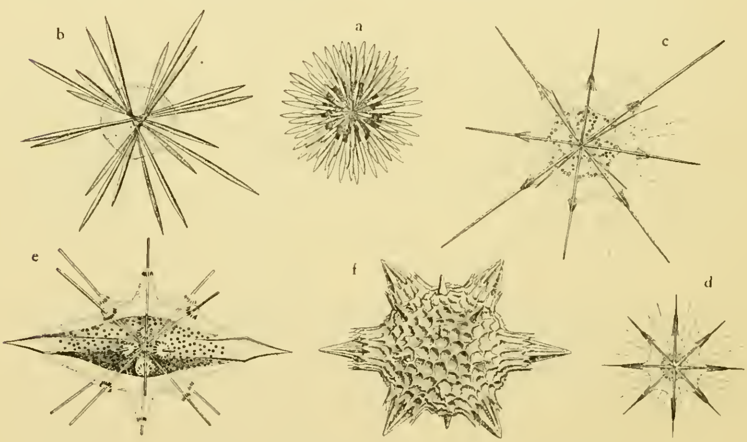


Fig. 103 a. *Actinelius primordialis.* ×24 (After Haeckel).
b. *Acanthociasma planum.* ×65 (After Mielck).
c. *Acanthometron elasticum.* (After Hertwig).
d. *Acanthonia tetracopa.* ×40 (After Schewiakoff).
e. *Amphilonche hydrometrica.* ×130 (After Haeckel).
f. *Hexaconus serratus.* ×100 (After Haeckel) (From Kühn).

Genus **Acanthociasma** (Fig. 103, *b*)

Radial spines few, arranged according to Müller's law; without tangential skeletons.................................Legion 2 Acanthometrida

Spines more or less uniform in size
Spicules circular in cross-section............Family 1 Acanthometridae

Genus **Acanthometron** (Fig. 103, *c*)

Spicules cruciform in cross-section............Family 2 Acanthoniidae

Genus **Acanthonia** (Fig. 103, *d*)

Two opposite spines much larger..............Family 3 Amphilonchidae

Genus **Amphilonche** (Fig. 103, *e*)

Radial spines few, arranged according to Müller's law; with tangential skeletons..................................Legion 3 Acanthophractida
20 radial spines of equal size; shell composed of small plates, each with one pore.................................Family 1 Sphaerocapsidae

Genus **Sphaerocapsa**

Two or six larger spines
Two enormously large conical sheathed spines...Family 2 Diploconidae

Genus **Diploconus**

Six large spines.............................Family 3 Hexalaspidae

Genus **Hexaconus** (Fig. 103, *f*)

Suborder 2 **Peripylea** Hertwig

Solitary; skeleton wanting or simple spicules; mostly spherical...Legion 1 Collodaria
The nucleus spherical with smooth membrane
With intracapsular vacuoles; with or without spicules...Family 1 Physematiidae

Genus **Lampoxanthium** (Fig. 104, *a*)

With extracapsular vacuoles; with or without spicules...Family 2 Thalassicollidae

Genus **Thalassicolla** (Fig. 104, *b*)

The nuclear wall not smooth
The nuclear wall branching out into pouches; structure similar to the last ....Family 3 Thalassophysidae

Genus **Thalassophysa**

The nuclear wall crenate
With a huge double spicule; large forms..Family 4 Thalassothamnidae

Genus **Thalassothamnus**

With a latticed skeleton with branched and thorny spines...Family 5 Orosphaeridae

Genus **Orosphaera**

Solitary; skeleton highly developed and complex; often concentric; small spherical....................................Legion 2 Sphaerellaria

Central capsule and skeleton spherical.............Family 1 Sphaeroidae

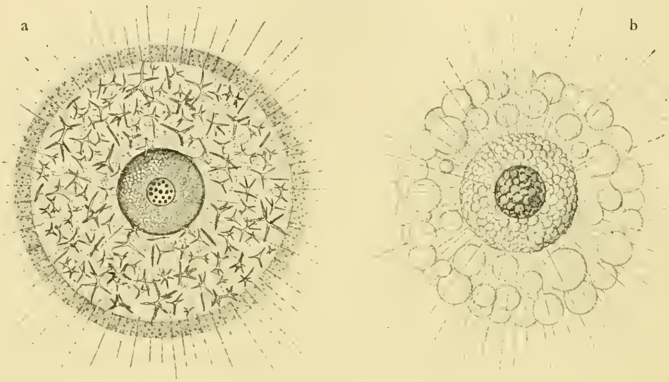


Fig. 104 a. *Lampoxanthium pandora.* ×20 (After Haeckel).
b. *Thalassicolla nucleata.* ×16 (After Huth) (From Kühn).

Genus **Hexacontium** (Fig. 105, *a*)

Central capsule and skeleton elliptical or cylindrical..Family 2 Prunoidae

Genus **Pipetta** (Fig. 105, *b*)

Central capsule and skeleton discoidal or lenticular....Family 3 Discoidae

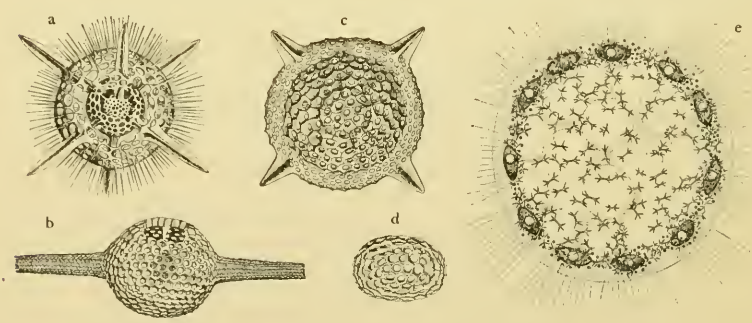


Fig. 105 a. *Hexacontium asteracanthion.* ×130.
b. *Pipetta tuba.* ×100.
c. *Staurocyclia phacostaurus.* ×130.
d. *Cenolarus primordialis.* ×100.
e. *Sphaerozoum ovodimare.* ×33 (All after Haeckel from Kühn).

Genus **Staurocyclia** (Fig. 105, *c*)

Similar to the above, but flattened . . . . Family 4 Larcoidae

Genus **Cenolarus** (Fig. 105, *d*)

Colonial; individuals with anastomosing extracapsular cytoplasm, embedded in a jelly mass . . . . Legion 3 Polycyttaria

Without latticed skeleton, but with silicious spicules arranged tangentially to the central capsule . . . . Family 1 Sphaerozoidae

Genus **Sphaerozoum** (Fig. 105, *e*)

The central capsule of each individual enclosed in a latticed skeleton . . . . Family 2 Collosphaeridae

Genus **Collosphaera**

Suborder 3 **Monopylea** Hertwig

Without any skeleton . . . . Legion 1 Nassoidea
Family 1 Nassoidae

Genus **Cystidium** (Fig. 106, *a*)

With skeleton

Without a complete latticed skeleton . . . . Legion 2 Plectellaria

Skeleton a basal tripod . . . . Family 1 Plectoidae

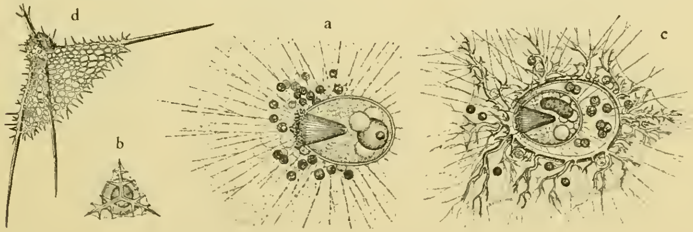


Fig. 106 a. *Cystidium princeps.* ×120.
b. *Triplagia primordialis.* ×25.
c. *Lithocircus magnificus.* ×100.
d. *Dictyophimus hertwigi.* ×83 (All after Haeckel from Kühn).

Genus **Triplagia** (Fig. 106, *b*)

Skeleton a simple or multiple sagittal ring . . . . Family 2 Stephoidae

Genus **Lithocircus** (Fig. 106, *c*)

With a complete latticed skeleton . . . . Legion 3 Cyrtellaria

Lattice skeleton single, without constriction . . . . Family 1 Cyrtoidae

Genus **Dictyophimus** (Fig. 106, *d*)

Lattice skeleton is multiple . . . . Family 2 Botryoidae

Genus **Phormobothrys**

Suborder 4 **Tripylea** Hertwig

Without skeleton; with isolated spicules. . . . . .Legion 1 Phaeocystina
Skeleton consists of radial hollow rods and fine tangential needles. . . . .
. . . . .Family 1 Aulacanthidae

Genus **Aulacantha** (Fig. 107, *a*)

With foreign skeleton covering body surface. . . . .Family 2 Caementellidae

Genus **Caementella** (Fig. 107, *b*)

With skeleton
One or two (concentric) usually spherical skeletons. .Legion 2 Phaeosphaeria
Outer lattice skeleton with triangular or areolar meshes. . . . .
. . . . .Family 1 Sagosphaeridae

Genus **Sagenoscene**

One lattice skeleton with hollow radial bars. .Family 2 Aulosphaeridae

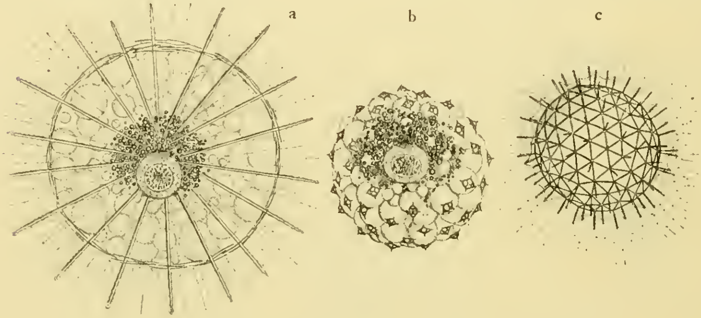


Fig. 107 a. *Aulacantha scolymantha.* ×33 (After Kühn).
b. *Caementella stapedia.* ×65 (After Haeckel).
c. *Aulosphaera labradoriensis.* ×9 (After Haecker) (From Kühn).

Genus **Aulosphaera** (Fig. 107, *c*).

Two concentric lattice skeletons connected by radial bars. . . . .
. . . . .Family 3 Cannosphaeridae

Genus **Cannosphaera**

One skeleton, simple, but variable in shape, bilaterally symmetrical. . . . . . .
. . . . .Legion 3 Phaeogromia
Skeleton with fine diatomaceous graining. . . . . .Family 1 Challengeridae

Genus **Challengeron** (Fig. 108, *a*)

Skeleton smooth or with small spines. . . . . .Family 2 Medusettidae

Genus **Medusetta** (Fig. 108, *b*)

One skeleton; spherical or polyhedral, with an opening (phylom) and with radiating spines . . . . Legion 4 Phaeocalpia

Skeleton spherical or polyhedral, with uniformly distributed large rounded pores . . . . Family 1 Castanellidae

Genus **Castanidium** (Fig. 108, *c*)

Skeleton similar to the last, but the base of each radial spine is surrounded by pores . . . . Family 2 Circoporidae

Genus **Circoporus** (Fig. 108, *d*)

Skeleton flask-shaped with one or two groups of spines . . . . Family 3 Tuscaroridae

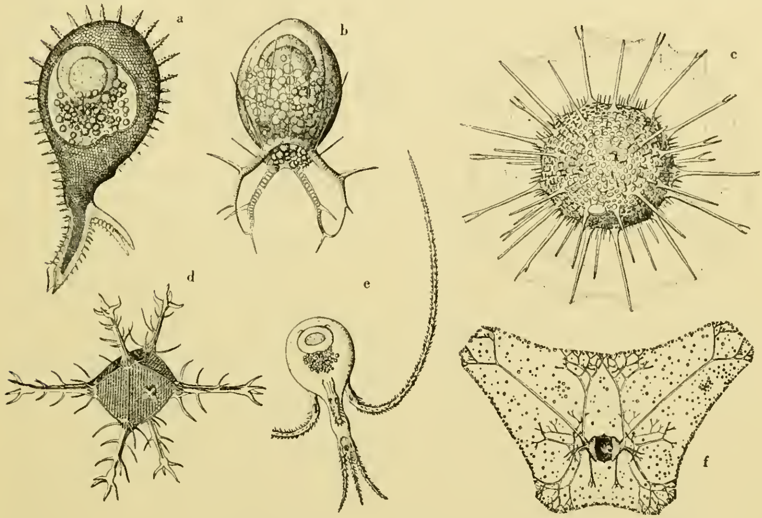


Fig. 108 a. *Challengeron wyvillei.* ×105 (After Haeckel).
b. *Medusetta ansata.* ×230 (After Borgert).
c. *Castanidium murrayi.* ×25 (After Haecker).
d. *Circoporus octahedrus.* ×65 (After Haeckel).
e. *Tuscarora murrayi.* ×7 (After Haeckel).
f. *Coelodendrum ramosissimum.* ×10 (After Haecker) (From Kühn).

Genus **Tuscarora** (Fig. 108, *e*)

Central portion of the skeleton consists of two valves . . . . Legion 5 Phaeoconchia

Valves thin, each with a conical process which divides into branched tubes . . . . Family 1 Coelodendridae

Genus **Coelodendrum** (Fig. 108, *f*)

References

BRANDT, K. 1905 Zur Systematikder koloniebildenden Radiolarien. Zool. Jahrb. Suppl., Vol. 8.

BORGERT, A. 1905–1913 Meherere Arbeiten über Familien der Tripyleen. Ergebnis. d. Planktonexpedition. Vol. 3.

HAECKEL, E. 1862–1887 Die Radiolarien. Eine Monographie. I, II. 1887 Report on the Radiolaria collected by H. M. S. Challenger. Challenger Rep. Zool., Vol. 18.

HAECKER, V. 1908 Tiefseeradiolarien. Wiss. Ergebn. Deutsch. Tiefsee-Exp. a. d. Dampfer "Valdivia." Vol. 14.

HERTWIG, R. 1879 Der Organismus der Radiolarien. Jena.

CHAPTER XXI

CLASS 3 **SPOROZOA** LEUCKART

ALL SPOROZOA are parasitic and produce **spores.** As a rule, they are incapable of movement, but some when immature move about by means of pseudopodia. They have no cilia or flagella. In the forms that are confined to one host, the spore usually possesses a resistant envelope to withstand unfavorable conditions. In those having two hosts, as in Plasmodium, the **sporozoite** does not have a definite membrane or wall.

The method of nutrition is by osmosis only. The food material absorbed from the host, may be dissolved cytoplasm, tissue fluid, body fluid, or dissolved food material in the digestive tract of the host.

Both asexual and sexual reproduction are known in numerous forms. Asexual reproduction is by binary or multiple fission, or by budding. The rate of division of the trophozoite is much greater than that of protozoans belonging to other classes, and this results in the formation of a large number of individuals. This multiplication is collectively known as the **schizogony** (or agamogony), and the products are **schizonts** (or agamonts, merozoites). The sexual reproduction is by isogamous or anisogamous copulation or autogamy. This reproduction marks the beginning of the **sporogony,** or spore-formation, and the initial stages are called gametocytes, or **sporonts.** In some groups sexual reproduction has not been clearly observed.

The Sporozoa are parasitic in animals of almost every phylum from Protozoa to Chordata. Numerous important parasites are, therefore, placed in this group. Schaudinn divided the Sporozoa into two groups, Telosporidia and Neosporidia, and this scheme has been followed by several students. Some recent authors consider these two groups as separate classes. This, however, does not seem to be wise, as the basis of distinction between them is entirely different from that used for distinguishing the other four classes: Sarcodina, Mastigophora, Ciliata, and Suctoria. For this reason, the Sporozoa are put together in a single class and divided into three subclasses as follows:

The spore with the polar filament which is typically coiled within a
polar capsule . . . . Subclass 2 Cnidosporidia
The spore without polar filament
The spore simple, with one sporozoite; incompletely known . . . .
. . . . Subclass 3 Acnidosporidia
Simple spore with one to several sporozoites or without resistant
envelope; asexual and sexual reproduction typically alternate . . .
. . . . Subclass 1 Telosporidia

SUBCLASS 1 TELOSPORIDIA SCHAUDINN

In this subclass of the Sporozoa the spores have neither polar capsule nor polar filament. Each spore contains one to several sporozoites and is formed at the end of the trophic life of the individual. In the forms which parasitize two hosts, there occur naked sporozoites instead of spores.

The infection of a new host begins with the entrance of mature spores through the mouth, or with the introduction of the sporozoites by blood-sucking invertebrates directly into the blood stream, of the host. The sporozoites enter specific host cells and there grow at the expense of the latter. In the Coccidia and the Haemosporidia, the trophozoite continues its intracellular existence, but in the Gregarinida it leaves the host cell and grows in an organ cavity of the host. Except Eugregarinina, the trophozoite of the Telosporidia undergoes schizogony and produces a large number of schizonts, or merozoites, which invade new host cells, thus spreading the infection within the host body. The schizonts sooner or later develop into gametocytes.

In the Coccidia and the Haemosporidia, anisogametocytes are often noted. Each macrogametocyte develops into a single macrogamete and each microgametocyte into several microgametes. Anisogamy results in the formation of a large number of zygotes. Each zygote develops into a spore which contains one to many sporozoites or into a number of naked sporozoites. In the Gregarinida two fully mature trophozoites (gametocytes) encyst together and the nucleus in each divides repeatedly to form numerous gametes. The gametes fuse in pairs with those produced in the other gametocyte within the common envelope. The zygotes develop into spores, each containing sporozoites of variable number. When these spores enter a new host, the changes outlined above are repeated. The Telosporidia are parasitic in vertebrates and higher invertebrates.

The subclass is divided into three orders, as follows:

Mature trophozoite intracellular and small
  Zygote non-motile; sporozoites within spore . . . . Order 1 Coccidia
  Zygote motile; sporozoites without envelope . . . . Order 2 Haemosporidia
Mature trophozoite extracellular, large; zygote non-motile; sporozoites in spore . . . . Order 3 Gregarinida

ORDER 1 COCCIDIA LEUCKART

The Coccidia show a wide zoological distribution, attacking the vertebrates and higher invertebrates alike. The majority are parasites of the epithelium of the digestive tract and its associated glands. Asexual reproduction is by schizogony and sexual reproduction by anisogamy in the majority of species. Both kinds of reproduction take place in one and the same host body, with the exception of such forms as Aggregata.

The Coccidia are ordinarily divided into two suborders:

Gametocytes similar in size; independent; each microgametocyte developing into numerous microgametes . . . . Suborder 1 Eimeridea
Gametocytes dissimilar; associated with each other during the latter part of trophic life; a few microgametes . . . . Suborder 2 Adeleidea

Suborder 1 Eimeridea Léger

These Coccidia are, as a rule, intracellular parasites of the epithelium of the digestive tract of the hosts. In many of them, there occurs an alternation of asexual (schizogonic) and sexual (sporogonic) generations. In some there is also alternation of hosts.

As an example of the life-cycle of a typical coccidian, that of *Eimeria schubergi*, a parasite of the intestine of the centipede, *Lithobius forficatus*, as worked out by Schaudinn, may be stated here briefly (Fig. 109). The infection begins when the oocysts of the coccidian gain entrance into the host through the mouth.

The **sporozoites** escape from the spores and make their way through the micropyle of the oocyst into the gut lumen (*p*). By active movement they reach the gut epithelium and enter the host cells (*a*). These **schizonts** grow into large rounded bodies. The nucleus multiplies in number. The newly formed nuclei move to the body surface, and each becomes surrounded

Fig. 109 Scheme of development of *Eimeria schubergi*. ×400 (After Schaudinn).

a, entrance of a sporozoite in the gut epithelium of host and growth of schizont; b, three stages in schizogony to form merozoites, which repeat schizogony or; c, become macro- and micro-gametocyte; d, e, formation of macrogamete; f–h, formation of microgametes; i, mature gametes; j, k, fertilization; l–n, stages in spore formation; o, oocyst containing four mature spores, each with two sporozoites; p, germination of spores.

by a small mass of cytoplasm, forming what is called a **merozoite.** When the host cells rupture, the merozoites are set free in the gut lumen, make their way into new host cells and repeat the process (*b*). Instead of growing into schizonts, some merozoites transform themselves into **macro-** or **micro-gametocytes** (*c*). Each macrogametocyte contains refractile bodies, and becomes mature **macrogamete,** after extruding part of its nuclear material (*d. e*). In the microgametocyte, the nucleus divides several times and each division-product assumes a compact appearance (*f-h*). The biflagellate comma-shaped **microgametes** thus produced, show activity when freed from the host cells (*i*). A microgamete and a macrogamete unite to form a **zygote** which secretes a distinct membrane around itself (*j*). The nucleus divides twice and produces four nuclei (*k–m*). This stage is known as the **oocyst.** Each of the four nuclei becomes the center of a **sporoblast** which secretes a membrane and transforms itself into a **spore** (*n*). Its nucleus, in the meantime, undergoes a division, so that two sporozoites become developed in the spore (*o*). Thus an oocyst of this species contains four spores and eight sporozoites. Oocysts in the fecal matter of the host become the sources of infection in new hosts.

In dividing the suborder into the following four families, Reichenow's scheme has been adopted:

Body cylindrical or vermiform; schizogony in motile stage ....
.... Family 1 Selenococcidiidae
Body not cylindrical nor vermiform
  Alternation of generations and of hosts .... Family 2 Aggregatidae
  No alternation of hosts
    Association of gametocytes begin early; numerous microgametes . .
    .... Family 3 Dobellidae
    Gametocytes independent .... Family 4 Eimeriidae

Family 1 Selenococcidiidae Léger and Duboscq

Genus **Selenococcidium** Léger and Duboscq. Parasitic in the intestine of the lobster in Europe. The single nucleus of the vermiform trophozoite divides three times, producing eight nuclei. The trophozoite becomes rounded after entering the cell of the gut-epithelium and divides into eight schizonts. This is apparently repeated. From these develop gametocytes. Numerous microgametes are formed from a microgametocyte. Copulation and sporogony unknown. Only one species.

Selenococcidium intermedium Léger and Duboscq (Fig. 110).

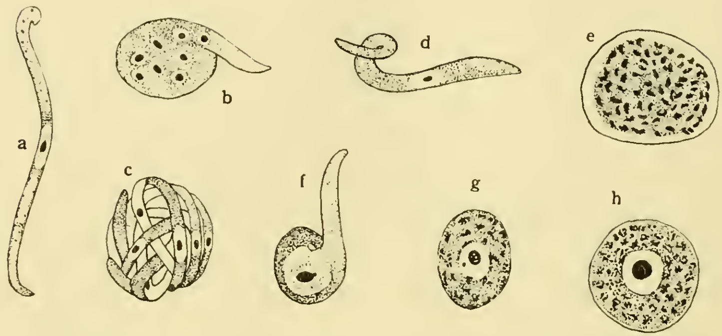


Fig. 110 *Selenococcidium intermedium.* ×550 (After Léger and Duboscq). a, a schizont in the host gut; b, c, schizogony; d, microgametocyte; e, microgametes; f, macrogametocyte; g, macrogamete; h, zygote or oocyst.

Family 2 **Aggregatidae** Reichenow

Genus **Aggregata** Frenzel. With alternation of generations and of hosts. The zygote forms numerous spores, each containing several sporozoites.

Aggregata eberthi (Labbé) (Fig. 111). Schizogony in the crab, *Portunus depurator*, and sporogony in the cephalopod, *Sepia officinalis*. The spore germinates in the digestive tract of the crab (*a*, *b*), and the sporozoites undergo growth and schizogony (during which six chromosomes are distinctly visible) in the peri-intestinal connective tissue cells (*c*, *d*). When the crab is eaten by a cuttlefish, the merozoites penetrate the gut wall (*e*) and there develop into micro- and macro-gametocytes, and further into gametes. Anisogamy results in zygote-formation (*g*). The nucleus of the zygote or oocyst shows 12 chromosomes which become divided into two groups of six at the first nuclear division (Dobell, Bělař) (*h*). Each of these two nuclei undergoes mitotic division repeatedly and produce numerous sporoblasts (*i*) and finally spores (*a*). Each spore contains three sporozoites and a residual mass. Several other species have been observed in the same groups of the hosts.

Genus **Caryotropha** Siedlecki. Oocysts develop numerous spores, each with many sporozoites.

Caryotropha mesnili Siedlecki. In the body cavity of the marine annelid, *Polymnia nebulosa.*

Genus **Angeiocystis** Brasil. Oocysts develop few spores, each containing about 30 sporozoites.

Fig. 111 Developmental stages of *Aggregata eberthi.* (After Dobell).
a. A fully mature spore with three sporozoites. ×665.
b. A spore germinating in the midgut of the crab. ×665.
c. A schizont in an epithelial cell of midgut of the same host. ×665.
d. Section of the midgut of the crab with four cysts containing merozoites. ×20.
e. A merozoite in a cell of caecal epithelium of Sepia. ×330.
f. A large cyst with microgametes. ×100.
g. Fertilization. ×330.
h. Reduction division in the zygote. ×330.
i. A stage in spore-formation. ×120.

Angeiocystis audoniniae Brasil. In the marine worm, *Audoninia tentaculata.*

Family 3 **Dobelliidae** Ikeda

Genus **Dobellia** Ikeda. The schizonts are differentiated sexually. Association of the two schizonts for gametogony begins early as in the Adeleidea, but numerous microgametes are produced, which condition is not found in the latter group. One species.

Dobellia binucleata Ikeda. In the gut of the sipunculoid *Petalostoma minutum.*

Family 4 **Eimeriidae** Léger

Genus **Eimeria** Schneider. The zygote develops four spores, each containing two sporozoites.

Eimeria schubergi (Schaudinn) (Fig. 109).

A. Eimeria in Mammals

Eimeria stiedae (Lindemann) (Fig. 112). In the biliary epithelium of the liver of rabbits, especially young ones. Heavy infection is believed to be the cause of the death of host animals, which may occur in an epidemic form. The oocyst measures about 20 to 40 microns long.

Eimeria zurnii (Rivolta). In the gut-epithelium of cattle. The oocyst is 13 to 28 microns long by 12 to 20 microns broad.

Eimeria faurei (Moussu and Marotel) (Fig. 113, *a*). In sheep and goat. The oocyst is ovoid and measures 20 to 40 microns long by 17 to 26 microns broad.

Eimeria debliecki Douwes (Fig. 113, *b*). In pigs. The ovoid oocysts vary greatly in size. Length 12 to 33 microns, breath 10 to 21 microns.

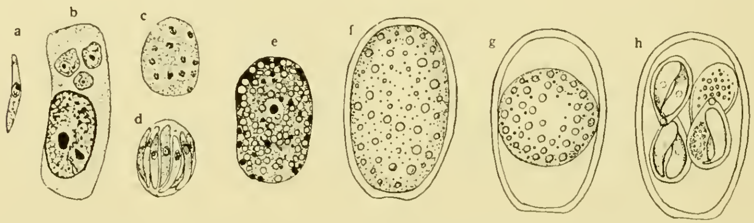


Fig. 112 *Eimeria stiedae.* a, schizont; b, an epithelial cell with three schizonts; c, d, schizogony; e, macrogametocyte (×950 all after Hartmann); f–h, development of oocyst (×625 after Wasielewski).

Eimeria canis Wenyon (Fig. 113, *c, d*). In dogs. The oocyst varies from 18 to 45 microns long by 11 to 28 microns broad.

Eimeria felina Nieschulz. In cats. The oocysts are colorless and measure 21 to 26 microns long by 13 to 17 microns wide.

Eimeria falciformis (Eimer) (Fig. 113, *e*). In mice. The oocysts are subspherical and measure 16 to 21 microns by 11 to 17 microns.

Eimeria nieschulzi Dieben. In rats. The oocyst measures 18 to 26 microns by 14 to 20 microns.

B. Eimeria in Birds

Eimeria tenella (Railliet and Lucet) (Fig. 113, *f*). In the caecum, large intestine, and lower small intestine of chicken.

The oocysts are ovoid and measure 20 to 26 microns by 17 to 23 microns. Tyzzer found this species in cases of acute coccidiosis.

Eimeria mitis Tyzzer (Fig. 113, *g*). In the upper portion of the small intestine of chicken. The oocysts are subspherical and measure about 16 microns in diameter.

Eimeria acervulina Tyzzer (Fig. 113, *h*). In the small intestine of chicken. The oocyst oval, measures 18 to 20 microns by 14 to 16 microns. Associated with a serious chronic coccidiosis (Tyzzer).

Eimeria maxima Tyzzer (Fig. 113, *i*). In the middle portion of the small intestine of chicken. The oocyst is oval and measures 22 to 43 microns by 17 to 30 microns.

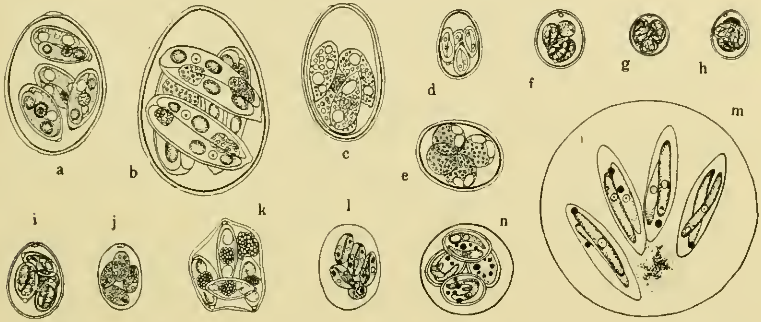


Fig. 113 a. *Eimeria faurei.* ×600 (After Wenyon).
b. *E. debliecki.* ×800 (After Wenyon).
c, d. *E. canis.* ×485 (After Wenyon).
e. *E. falciformis.* ×550 (After Wenyon).
f. *E. tenella.* ×450 (After Tyzzer).
g. *E. mitis.* ×325 (After Tyzzer).
h. *E. acervulina.* ×325 (After Tyzzer).
i. *E. maxima.* ×350 (After Tyzzer).
j. *E. ranarum.* ×500 (After Laveran and Mesnil).
k. *E. ranae.* ×500 (After Dobell).
l. *E. prevoti.* ×500 (After Laveran and Mesnil).
m. *E. sardinae.* ×450 (After Thomson and Robertson).
n. *E. clupearum.* ×450 (After Thomson and Robertson).

Eimeria meleagridis Tyzzer. In the caecum of the turkey. The oocyst is about 24 microns by 17 microns.

Eimeria meleagrimitis Tyzzer. In the lower portion of the small intestine of the turkey. The oocyst measures about 18 microns by 15 microns.

C. Eimeria in Amphibians

Eimeria ranarum (Labbé) (Fig. 113, *j*), *E. prevoti* (Laveran and Mesnil) (Fig. 113, *l*), and *E. ranae* Dobell (Fig. 113, *k*) have been found in the gut-epithelium of the frog.

Eimeria neglecta Nöller. In the gut of the tadpole.

D. Eimeria in Fish

Not infrequently fish are infected by species of Eimeria. When such fish are used for food, coccidian oocysts occurring in them, may appear in human feces and may be mistaken as human parasites.

Eimeria sardinae (Thélohan) (Fig. 113, *m*). In the testis of the sardine. Finding the oocysts which measure 30 to 50 microns in diameter in human stools, Dobell named it *Eimeria oxyspora*.

Eimeria clupearum (Thélohan) (Fig. 113, *n*). In the liver of herrings, mackerels, and sprats. The oocyst measures 18 to 33 microns in diameter. Dobell found some oocysts of this species in human feces and called it *Eimeria wenyoni*.

Genus **Jarrina** Léger and Hesse. The oocyst is ovoid; one end is rounded, the other drawn out into a short neck. With four spores, each with two sporozoites.

Jarrina paludosa Léger and Hesse. In the intestine of birds, *Fulica atra* and *Gallinula chloropus*. The oocyst measures 15 microns by 11 microns.

Genus **Isospora** Schneider. The oocyst produces two spores, each containing four sporozoites.

Isospora hominis (Railliet and Lucet) (= *I. belli* Wenyon) (Fig. 114, *a–c*). In the human intestine. The oocysts observed in the feces measure 25 to 33 microns long.

Isospora bigemina (Stiles) (Fig. 114, *d*). In cats and dogs. The oocyst measures 10 to 14 microns by 7 to 9 microns.

Isospora rivolta (Grassi) (Fig. 114, *e*). In cats and dogs. The oocyst measures 20 to 25 microns by 15 to 20 microns.

Isospora felis Wenyon (Fig. 114, *f*). In cats and dogs. The oocyst measures 39 to 48 microns by 26 to 37 microns.

Isospora lacazei (Labbé). Many passarine birds seem to be hosts to this coccidian. The oocyst measures 18 to 26 microns by 15 to 20 microns.

Isospora lieberkühni (Labbé) (Fig. 114, *g*). In the kidney of the frog. The oocyst measures about 40 microns long.

Genus **Cyclospora** Schneider. Development similar to that of Eimeria. The zygote develops into an oocyst with two spores, each possessing two sporozoites.

Fig. 114 a–c. *Isospora hominis.* ×700 (After Dobell).
d. *I. bigemina.* ×465 (After Wenyon).
e. *I. rivolta.* ×465 (After Wenyon).
f. *I. felis.* ×465 (After Wenyon).
g. *I. lieberkühni.* ×330 (After Laveran and Mesnil).

Cyclospora caryolytica Schaudinn (Fig. 115, *a*). In the gut-epithelium of the ground mole.

Genus **Caryospora** Léger. The zygote develops into an oocyst with a single spore containing eight sporozoites. Membrane thick and yellow in color.

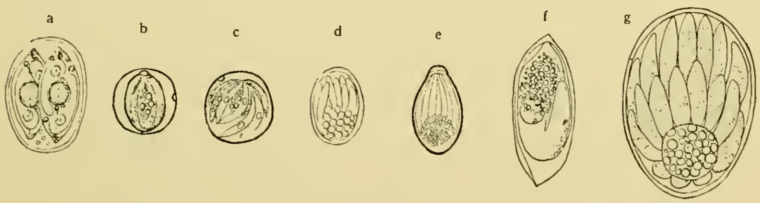


Fig. 115 a. *Cyclospora caryolytica.* ×1000 (After Schaudinn).
b, c. *Caryospora simplex.* ×600 (After Léger).
d. *Pfeifferinella ellipsoides.* ×1000 (After Wasielewski).
e. *P. impudica.* ×600 (After Léger and Hollande).
f. *Barrouxia ornata.* ×1000 (after Schneider).
g. *Lankesterella minima*, a mature cyst in an endothelial cell. ×750 (After Nöller).

Caryospora simplex Léger (Fig. 115, *b*, *c*). In the gut-epithelium of the viper, *Vipera aspis.*

Genus **Pfeifferinella** Wasielewski. The oocyst contains eight sporozoites; without any spore. The macrogamete forms a receiving tube for the microgamete.

Pfeifferinella ellipsoides Wasielewski (Fig. 115, *d*). In the liver of *Planorbis cornua*.

Pfeifferinella impudica Léger and Hollande (Fig. 115, *e*). In the liver of the land snail, *Limax marginatus*.

Genus **Barrouxia** Schneider. The zygote develops into an oocyst, in which numerous spores, each containing a single sporozoite, develop. The spore membrane may be uni- or bivalve and a caudal prolongation may occur in some species.

Barrouxia ornata Schneider (Fig. 115, *f*). In *Nepa cinerea*. The spherical oocyst measures 34 to 37 microns; the spores 20 microns by 10 microns.

Genus **Lankesterella** Labbé. Typically parasites of the endothelial cell of cold-blooded vertebrates. Development is not completely known.

Lankesterella minima (Chaussat) (Fig. 115, *g*). The frog acquires infection through the introduction of the sporozoites by the leech. The sporozoites make their way into the blood capillaries of various organs. There they apparently enter the endothelial cells. Schizogony produces numerous merozoites which bring about infection of many host cells. Ultimately macro- and micro-gametocytes are formed; anisogamy produces zygotes. The zygotes transform themselves into oocysts, in which a number of sporozoites develop. These sporozoites are set free upon disintegration of the oocyst wall in the plasma and enter the erythrocytes (Nöller).

Genus **Cryptosporidium** Tyzzer. Lumen-dwelling form. The oocyst contains four sporozoites. Exceedingly minute organisms.

Cryptosporidium muris Tyzzer. In the stomach lumen of the white mouse.

Cryptosporidium parvum Tyzzer. In the intestine of the mouse.

Suborder 2 **Adeleidea** Léger

The Adeleidea are on the whole similar to the Eimeridea in their habitat and development. But the schizonts develop into micro- and macro-gametocytes which become attached to each other in pairs during the course of the development into gametes (Fig. 116, *f*, *g*). Each microgametocyte produces a few microgametes (*h*). The zygote divides into numerous sporoblasts, each of which develops into a spore with two or four sporozoites (*i–j*).

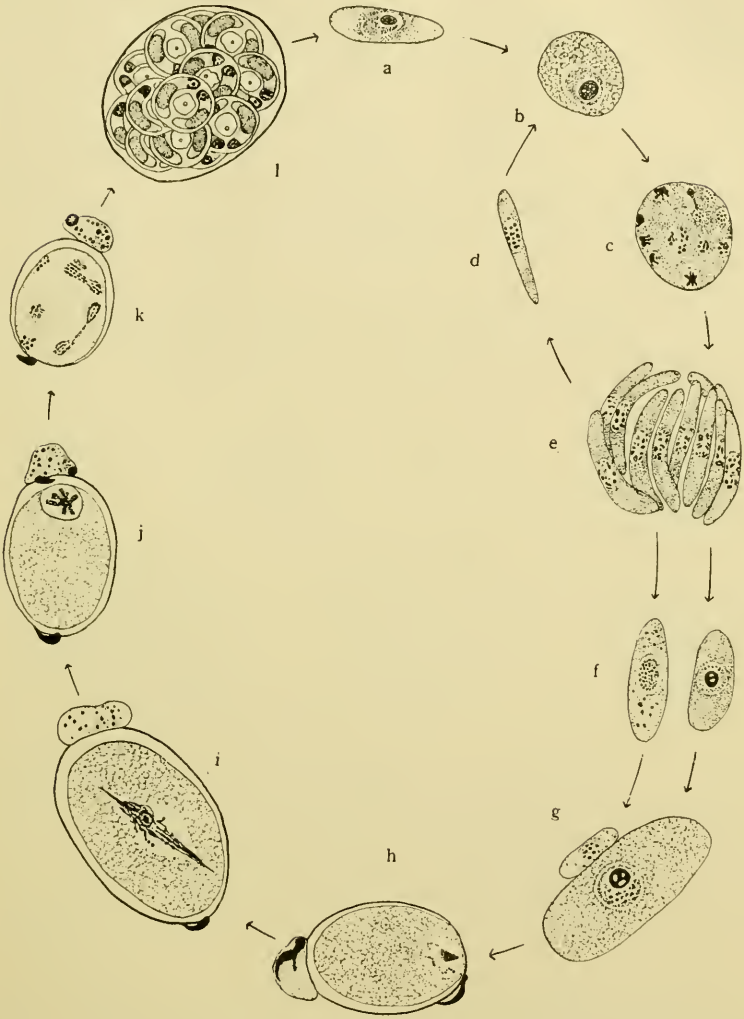


Fig. 116 Development of *Adelea ovata*. ×600 (After Schellack and Reichenow).

a, schizont which enters the gut epithelium of the host centipede; b–d, schizogony; e, larger forms of merozoites; f, microgametocyte (left) and macrogametocyte (right); g, association of gametocytes; h, i, fertilization; j, zygote; k, nuclear division of the zygote; l, mature oocyst with numerous spores.

The suborder is here divided into the following two families:

Parasitic in the epithelium of the digestive tract and its appended glands of chiefly invertebrates . . . . Family 1 Adeleidae
Parasitic in the cells of the circulatory system of vertebrates . . . . Family 2 Haemogregarinidae

Family 1 **Adeleidae** Léger

Genus **Adelea** Schneider. The zygote develops into a thinly walled oocyst which contains numerous flattened spores, each with two sporozoites. In arthropods.

Adelea ovata Schneider (Fig. 116). In the centipede, *Lithobius forficatus.*

Genus **Adelina** Hesse. The oocyst is thick-walled. The spore is spherical and comparatively small in number.

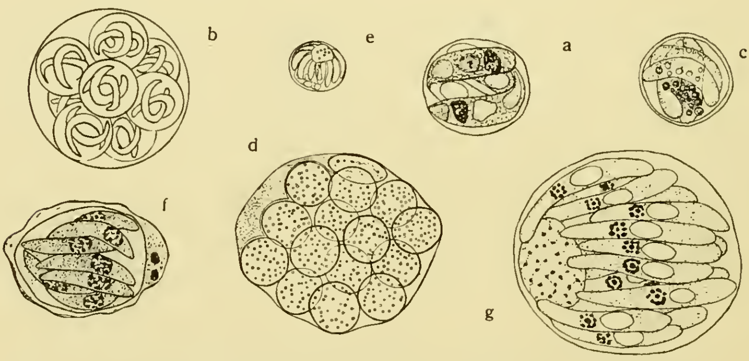


Fig. 117 a. A spore of *Adelina dimidiata.* ×1000 (After Schellack).
b. An oocyst of *A. octospora* with eight spores. ×1000 (After Hesse).
c. A spore of *Orcheobius herpobdellae.* ×550 (After Kunze).
d, e. *Klossiella muris.* ×280 (After Smith and Johnson). d, host's kidney cell with fourteen sporoblasts; e, a spore.
f. An oocyst of *Legerella hydropori.* ×1000 (After Vincent).
g. A spore of *Karyolysus lacertarum.* ×700 (After Reichenow).

Adelina dimidiata (Schneider) (Fig. 117, *a*). In the intestine of various species of myriapods belonging to the genus Scolopendra.

Adelina octospora Hesse (Fig. 117, *b*). The spherical oocyst contains eight spores. In the coelom of *Slavina appendiculata.*

Genus **Klossia** Schneider. The oocyst contains a large number of spherical spores, each with four sporozoites. Parasitic in the kidneys of the molluscs, Helix and Succinea.

Klossia helicina Schneider. Kidney parasite of various species of land-snails, belonging to the genera Helix, Succinea, and Vitrina.

Genus **Orcheobius** Schuberg and Kunze. Macrogametes vermiform. The spores are not so numerous, each with four sporozoites.

Orcheobius herpobdellae Schuberg and Kunze (Fig. 117, *c*). In the testis of the leech, *Herpobdella atomaria* (*Nephelis vulgaris*).

Genus **Klossiella** Smith and Johnson. The oocyst contains a number of spores, each with numerous sporozoites. A microgametocyte produces two microgametes. In the kidney of mammals.

Klossiella muris Smith and Johnson (Fig. 117, *d*, *e*). In the kidney of the mouse.

Genus **Legerella** Mesnil. The oocyst contains numerous sporozoites. Spores are entirely lacking. In arthropods.

Legerella hydropori Vincent (Fig. 117, *f*). In the epithelium of the Malpighian tubules of the water beetles, Hydroporus and Hyphydrus.

Family 2 **Haemogregarinidae** Léger

Genus **Haemogregarina** Danilewsky. The schizogony takes place in the blood cells of vertebrates. Merozoites develop into gametocytes. The changes which result in the formation of one macrogamete from each of the macrogametocytes and of two or four microgametes from each microgametocyte, take place in the leech or other blood-sucking invertebrates. Zygotes are produced. Development of sporozoites in the invertebrate hosts are illustrated in Fig. 118.

Haemogregarina stepanowi Danilewsky (Fig. 118). Schizogony in the turtle, *Emys orbicularis* and sexual reproduction in the leech, *Placobdella catenigera*. The sporozoites are introduced into the blood of the chelonian host by the leech (*a*). They enter the erythrocytes and grow (*d-g*). In the bone marrow, they undergo schizogony, each producing 12 to 24 merozoites (*h*). The schizogony is repeated (*i*). Some mero-

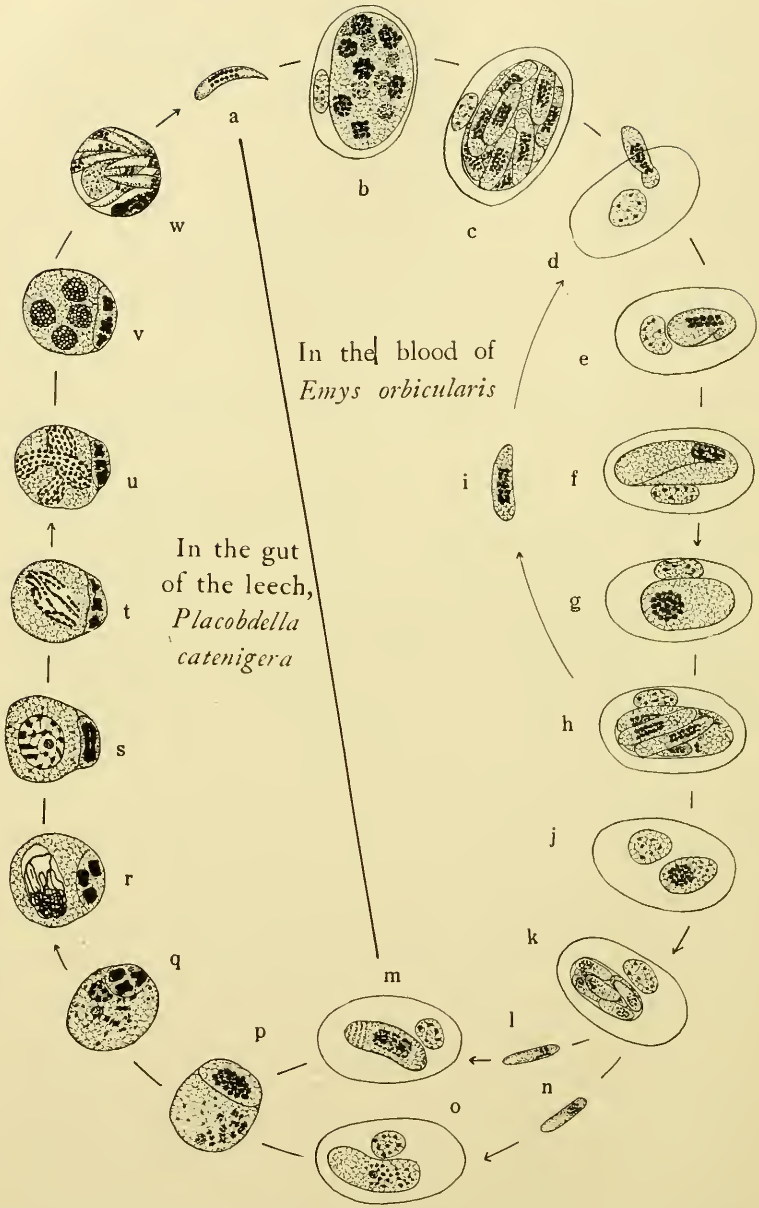


Fig. 118 Development of *Haemogregarina stepanowi*. ×1200 (After Reichenow).

a, sporozoite; b–i, schizogony, j–k, gametocyte formation; l, m, microgametocytes; n, o, macrogametocytes; p, q, association of gametocytes; r, fertilization; s–w, division of the zygote nucleus to form eight sporozoites.

zoites produce only six merozoites (*j*, *k*) which become the gametocytes (*l-o*). The gametogony takes place in the leech. Four microgametes are formed from each microgametocyte and become associated with a macrogametocyte in the gut of the leech (*p-r*). The zygote (*s*) nucleus divides three times, and eight sporozoites are formed (*t-w*).

Haemogregarina are commonly found in various frogs (Fig. 119, *a–e*) and in marine and fresh water fishes (Fig. 119, *f–j*).

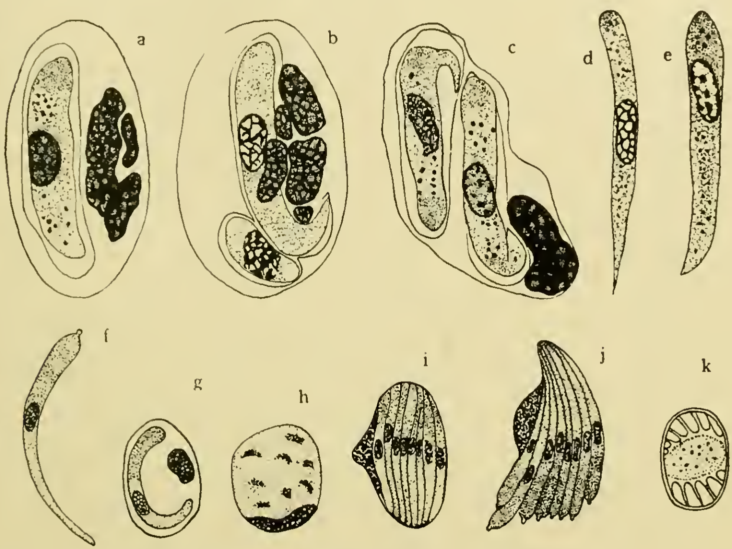


Fig. 119 a–e. Haemogregarina of frogs. ×1400 (After Kudo).
f–j. *Haemogregarina simondi* Laveran and Mesnil, from the blood of the sole, *Solea vulgaris*. ×1300 (After Laveran and Mesnil). f, extra corpuscular form; g–j, schizogonic stages in the erythrocyte.
k. A spore of *Hepatozoon muris*. ×415 (After Miller).

Genus **Hepatozoon** Miller. The schizogony occurs in the cells of the liver, spleen, and other organs of vertebrates. The merozoites enter erythrocytes or leucocytes and develop into gametocytes. In blood sucking arthropods (ticks, mites), the microgametes and macrogametes develop and unite in pairs. The zygotes become oocysts which increase in size and develop sporoblasts, spores and sporozoites.

Hepatozoon muris (Balfour) (Fig. 119, *k*). In various species of the rat, Rattus. Several specific names were proposed for the forms based upon the difference in host, locality, and effect upon the hosts, but they are so indistinctly defined that the specific separation is impossible.

The invertebrate host is the mite. The schizogony occurs in the liver of the rat. Young gametocytes invade the mononuclear leucocytes and appear as haemogregarines. When the blood is taken up by the mite, *Laelaps echidninus*, the two gametes unite to form a vermicular body which penetrates the gut-epithelium and reaches the peri-intestinal tissue and grows. Becoming surrounded by a cyst-membrane, the cyst contents break up into a number of sporoblasts and then into spores, each of which contains a number of sporozoites. When a rat devours the infected mites, it becomes infected.

Genus **Karyolysus** Labbé. The schizogony occurs in the endothelial cells of a vertebrate host (reptiles). Some merozoites which are in reality young gametocytes enter the erythrocytes where they remain without further changes. When a mite sucks the infected blood, gametogony and fertilization takes place, producing zygotes which develop in the epithelial cells and become the oocysts. In the latter a number of sporoblasts are formed and these are capable of vermicular movement and make their way into the ovum, where each transforms itself into a spore and develops a number of sporozoites.

Karyolysus lacertarum (Danilewsky) (Fig. 117, *g*). In the lizard, *Lacerta muralis*. Transmission by the mite, *Liponyssus saurarum*.

References

Calkins, G. N. 1926 The biology of the Protozoa. Philadelphia.

Doflein, F. and E. Reichenow. 1929 Lehrbuch der Protozoenkunde. Jena.

Labbé, A. 1899 Sporozoa. Das Tiereich. 5 L.

Wasielewski, V. 1896 Sporozoenkunde. Jena.

Wenyon, C. M. 1926 Protozoology. Vols. 1 and 2. London.

Andrews, J. M. 1926 Coccidiosis in mammals. Amer. Jour. Hyg., Vol. 6

Dobell, C. 1925 The life-history and chromosome cycle of *Aggregata eberthi.* Parasit., Vol. 17.
Miller, W. W. 1908 *Hepatozoön perniciosum.* U.S. Publ. Health Service, Hyg. Lab. Bull., No. 46.
Pérard, C. 1924, 1925 Recherches sur les coccidies et les coccidioses du lapin. Ann. Inst. Pasteur. Vols. 38, 39.
Reichenow, E. 1921 Die Coccidien. Prowazek-Nöller's Handbuch der pathog. Protozoen. Vol. 3.
Schaudinn, F. 1900 Untersuchungen über den Generationswechsel bei Coccidien. Zool. Jahrb. Abt. Morph.. Vol. 13.
Tyzzer, E. E. 1929 Coccidiosis in gallinaceous birds. Amer. Jour. Hyg., Vol. 10.
Wenyon, C. M. 1926 Protozoology. Vol. 2. London.

CHAPTER XXII

ORDER 2 **HAEMOSPORIDIA** DANILEWSKY

THE DEVELOPMENT of the Haemosporidia is, on the whole, similar to that of the Coccidia in that they undergo asexual reproduction, or schizogony, and also sexual reproduction, or sporozoite-formation; but the former takes place in the blood of vertebrates and the latter in the alimentary canal of some blood-sucking invertebrates. Thus one sees that the Haemosporidia do not pass any part of their development outside of a host body; hence, the sporozoites do not possess a resistant membrane.

The Haemosporidia are minute and usually intracellular parasites of erythrocytes. The malarial parasites of man are typical members of this order. The development of *Plasmodium vivax* is as follows (Fig. 120): Infected anopheline mosquitoes introduce the **sporozoites** (*a*), which invade the erythrocytes (*b*), grow, and undergo schizogony, forming a number of **merozoites** (*c–f*). The latter upon liberation from the host cells, attack other erythrocytes. Some of the merozoites become **macrogametocytes** (*g*) and others **microgametocytes** (*i*, *j*). No further changes ordinarily take place in the human body, but the schizogony is repeated. The protozoan produces melanin (or haemozoin) which is apparently the matabolic product of the organism at the expense of the haemoglobin. When the blood is taken into the stomach of a suitable species of anopheline mosquito, the gametocytes undergo development, forming **macrogametes** and **microgametes** (*h*, *k*). They unite in pairs (*l*) and thus **ookinetes** (zygotes) (*m*) are formed. The ookinetes penetrate the stomach wall and become lodged between the epithelium and the elastic membrane of the stomach (*n*). There they grow and the nuclei undergo rapid and repeated divisions, finally producing an enormous number of minute sporozoites (*o*, *p*). These sporozoites are set free through the rupture of the cyst wall in the body cavity, find their way into the salivary glands and wait for an opportunity of being inoculated into a new victim (*q*). The schizogony occurs regularly, and it is thought that the typical malarial fever is caused by some toxic substance which is liberated into the blood plasma when the merzoites become set free in the latter.

The Haemosporidia are divided into three families, as follows:

Schizogony in the peripheral blood of vertebrates...... Family 1 Plasmodiidae
Gametocytes in the peripheral blood corpuscles; schizogony elsewhere..
.... Family 2 Haemoproteidae
Minute parasites of erythrocytes; incompletely known.... Family 3 Babesiidae

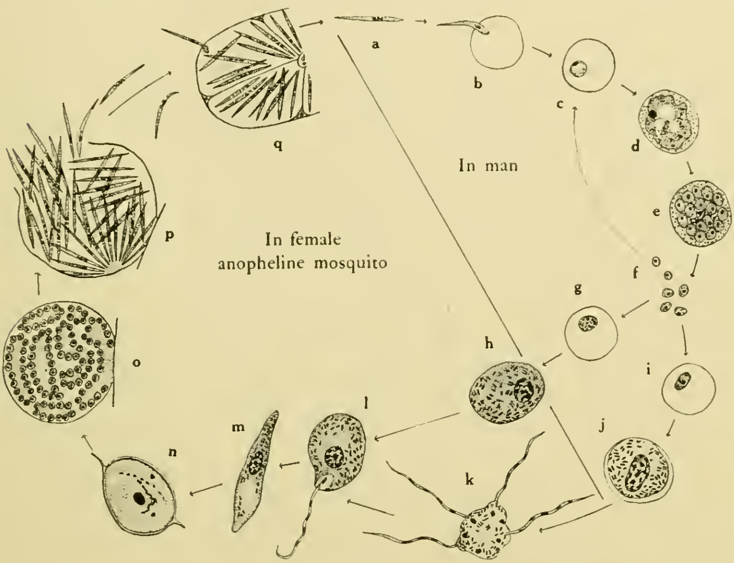


Fig. 120 Life-cycle of *Plasmodium vivax*. (Compiled after various authors).
a. Sporozoite entering human blood plasma.
b. Sporozoite entering erythrocyte.
c. Young schizont.
d–f. Schizogony.
g, h. Macrogametocytes.
i, j. Microgametocytes.
k. Microgametes formed in the stomach of the mosquito.
l. Union of gametes.
m. Zygote or ookinete, penetrating through gut wall.
n. Rounding up of an ookinete between the gut wall and the elastic membrane.
o. Oocyst in which sporozoites are being developed.
p. Mature oocyst ruptured and the sporozoites set free in the body fluid.
q. Sporozoites entering the salivary gland.

Family 1 **Plasmodiidae** Mesnil

Genus **Plasmodium** Marchiafava and Celli. This genus contains the important malarial organisms of man and birds. As stated above, the schizogony takes place in the erythrocyte of a vertebrate host and anisogamy and sporozoite-formation occur in the mosquitoes belonging to the genus Anopheles or Culex. Numerous species. Three species in man.

Plasmodium vivax (Grassi and Feletti) (Fig. 121, *a–g*). The parasite of the benign tertian malaria of man. Schizogony is

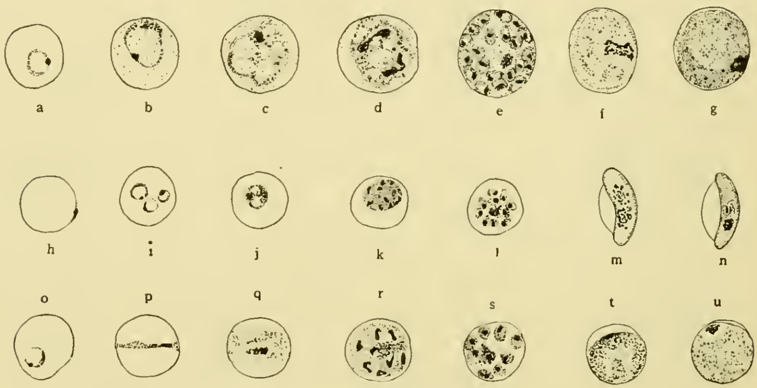


Fig. 121 a–g. *Plasmodium vivax.* ×1000.
h–n. *P. falciparum.* ×1000.
o–u. *P. malariae.* ×1000.
a–e, h–l, o–s, schizogony; f, m, t, microgametocytes; g, n, u, macrogametocytes).

completed in 48 hours. The infected erythrocyte becomes enlarged. As to its distinction with the other two species see below. Widely distributed over the temperate and tropical countries.

Plasmodium falciparum (Welch) (Fig. 121, *h–n*). The parasite of the malignant tertian, subtertian, or aestivo-autumnal malaria of man. Schizogony is completed in about 48 hours, but frequently irregular. The schizonts adhere to the capillary wall, to which the malignancy of the species is attributed. The gametocytes are crescentic; some authors therefore place this species in another genus, Laverania. Of more limited distribution in tropical and subtropical regions of the world.

Plasmodium malariae (Laveran) (Fig. 121, *o–u*). The parasite of the quartan malaria of man. Schizogony is completed in 72 hours. In tropical and subtropical countries.

Numerous species of female mosquitoes belonging to the genus Anopheles transmit these organisms. The malaria parasites are usually studied in stained blood films or smears and, therefore, the following comparison of the above-mentioned three species of Plamodium is based upon observations of stained specimens.

	P. vivax	*P. falciparum*	*P. malariae*
Completion of schizogony	48 hours	24 to 48 hours	72 hours
Diameter of ring forms	One-third to one-half of the host cell	One-sixth of the host cell	One-third to one-half of thehost cell
Size of infected cells	Greater than normal cells	Normal	Normal
Dots in infected cells	Schüffner's dots	Maurer's dots	Not seen
Grown schizonts	Round, large	Round, small	Elongate, medium
Pigment granules	Rod-shaped	Small, triangular	Large, irregular
Number of merozoites from a single schizont	15 to 24	8 to 10 or more	6 to 12
Arrangement of merozoites within host cell	Two rings or scattered	Two rings or scattered	One ring
Gametocytes	Rounded	Crescentic	Rounded

Plasmodium praecox (Grassi and Feletti) (Fig. 122, *a–d*). The organism is parasitic in birds, causing the so-called "bird malaria." Numerous birds such as lark, canary, sparrow, finch, barn-yard fowls, duck, pigeon, crow, owl, etc., are known to harbor the organism. The mosquito in which the sexual reproduction takes place belongs to the genus Culex. The life-history is similar to that of *Plasmodium vivax* outlined above.

Family 2 **Haemoproteidae** Doflein

The schizogony takes place in the endothelial cells of vertebrates. Certain merozoites penetrate into the circulating blood cells, in whic hthey develop into gametocytes. If the blood is taken up by a specific blood-sucking invertebrate host, the gametocytes develop into gametes which unite to form the zygotes that undergo changes similar to the processes stated above for the family Plasmodiidae.

Genus **Haemoproteus** Kruse. Young gametocytes enter erythrocytes. They produce pigment granules at the expense of the haemoglobin of the host cells. The fully formed gametocyte is halter-shaped and hence the name Halteridium (Labbé). Parasitic in birds and reptiles.

Haemoproteus columbae Celli and Sanfelice (Fig. 122, *e*, *f*). A parasite of the pigeon, *Columba livia*, and has been found to be widely distributed. The schizogony takes place in the endothelial cells of the capillaries of the pigeon's lungs and other organs. The sexual reproduction occurs in species of flies belonging to the genus Lynchia.

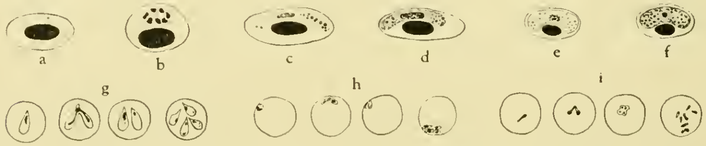


Fig. 122 a–d. *Plasmodium praecox.* ×800 (After Hartman). a, b, schizogony; c, microgametocyte; d, macrogametocyte.
e, f. Micro- and macro-gametocyte of *Haemoproteus columbae.* ×600. (After Aragão).
g. *Babesia bigemina.* ×1000 (After Nuttall and Graham-Smith).
h. *B. bovis.* ×1000 (After Nuttall).
i. *Theileria parva.* ×1000 (After Nuttall).

Genus **Leucocytozoon** Danilewsky. Blood-parasites of various birds. Certain cells in the peripheral blood are infected by forms which are interpreted as macro- and micro-gametocytes. No pigments are produced. The infected host cells appear to be young erythrocytes, in which haemoglobin has not yet developed and which has become spindle-shaped. Schizogony probably takes place in the endothelial cells of internal organs. Since their life-history is unknown, these organisms have been put in various places. Following the majority of recent authors, the genus is provisionally placed in this family. Several species.

Leucocytozoon ziemanni (Laveran). In the little owl, *Athene noctua.*

Family 3 **Babesiidae** Poche

The members of this family are minute and non-pigmented parasites of the erythrocytes of various mammals. They are transmitted from host to host by ticks. Numerous genera have been proposed.

Genus **Babesia** Starcovici. Body pear-shaped. Arranged in couples. Multiplication by binary fission.

Babesia bigemina (Smith and Kilborne) (Fig. 122, *g*). The organism of the "Texas fever" (or Red-water fever) of cattle. The very first demonstration that an arthropod plays an important rôle in the transmission of a protozoan parasite. The infected cattle contain in their erythrocytes oval or pyriform bodies, in which a compact nucleus and vacuolated cytoplasm are noted. The division is peculiar in that it appears as a budding process at the beginning. No other stages are known. The arthropod which transmits the organism is the tick belonging to the genus Margaropus. The tick remains fixed to one host during its entire growth period, but drops off to lay eggs. The infection is carried through the egg and embryo, and the young ticks which find a new host cattle are already infected. The Texas fever once caused a considerable amount of damage to the animal industry in the southern United States.

Babesia bovis Starcovici (Fig. 122, *h*). A much smaller form which occurs in European cattle.

Babesia are also known to occur in pigs, sheep, goats, horses, dogs, and other mammals.

Genus **Theileria** Bettencourt, França, and Borges. Unlike Babesia, Theileria do not multiply actively in the erythrocite. The schizogony takes plce in the endothelial cells of the capillaries of the spleen, liver, and other organs. The members are parasites of mammals.

Theileria parva (Theiler) (Fig. 122, *i*). The cause of a cattle fever in Africa, known as the "East Coast fever," which differs from the Texas fever. The organism is transmitted by cattle ticks.

Genus **Cytamoeba** Labbé. Small amoeboid, structureless organism occurring sometimes in amphibian erythrocytes.

Cytamoeba bacterifera Labbé. In frogs of Europe and America.

References

Aragão, H. 1908 Ueber die Entwicklungsgang und Uebertragung von *Haemoproteus columbae*. Arch. f. Protistenk., Vol. 12.

Hartman, E. 1927 Three species of bird malaria. Ibid., Vol. 60.

MacCallum, W. C. 1898 On the haematozoon infection of birds. Jour. Exper. Med., Vol. 3.

Ross, R. 1928 Studies on malaria. London.

Thomson, J. G. and A. Robertson. 1929 Protozoology London.

Wenyon, C. M. 1926 Protozoology. Vol. 2. London.

CHAPTER XXIII

ORDER 3 **GREGARINIDA** LANKESTER

The gregarinida are chiefly coelozoic parasites in invertebrates, especially arthropods and annelids. They obtain their nourishment from the host's organ-cavity through osmosis. The vast majority of the Gregarinida do not undergo schizogony, or asexual reproduction, and the increase in number is carried on solely by the sporogony following gametogony. In a small group, however, schizogony takes place as well as sexual reproduction and this is used as the basis for the division into two suborders, as follows:

No schizogony..............................Suborder 1 Eugregarinina
Schizogony takes place.....................Suborder 2 Schizogregarinaria

Suborder 1 **Eugregarinina** Doflein

This suborder includes the majority of the so-called gregarines which are common parasites of arthropods. When the spore gains entrance to a suitable host, it germinates and the sporozoites emerge and enter the epithelial cells of the digestive tract. There they grow large and protrude from the host cells to which they are now attached by various cell-organs of attachment. These trophozoites sooner or later become detached from the host cells and move about in the lumen of the gut. This stage is ordinarily most frequently encountered. It is usually vermiform and large. The body which is covered by a definite pellicle shows a clear differentiation into the ectoplasm and endoplasm. The former contains myonemes which enable the organism to undergo a gliding movement. In one group, Acephalina, the body is of a single compartment, but in another group, Cephalina, the body is divided into two compartments which are separated from each other by an ectoplasmic septum. The smaller anterior part is the **protomerite** and the larger posterior part, the **deutomerite,** contains a single nucleus. The protomerite may possess an attaching process with hooks or other structures at its anterior end; this is called the **epimerite.**

Each trophozoite increases in size, and finally two encyst together. These are gametocytes. Within the cyst membrane, the nucleus in each gametocyte undergoes repeated division, forming a large number of small nuclei which by a process of budding transform themselves into numerous gametes. The gametes may be isogamous or anisogamous. Each of the gametes produced in one gametocyte unites with one formed within the other, so that a large number of zygotes are produced. Each zygote becomes surrounded by a resistant membrane and its contents develop into the sporozoites which are usually

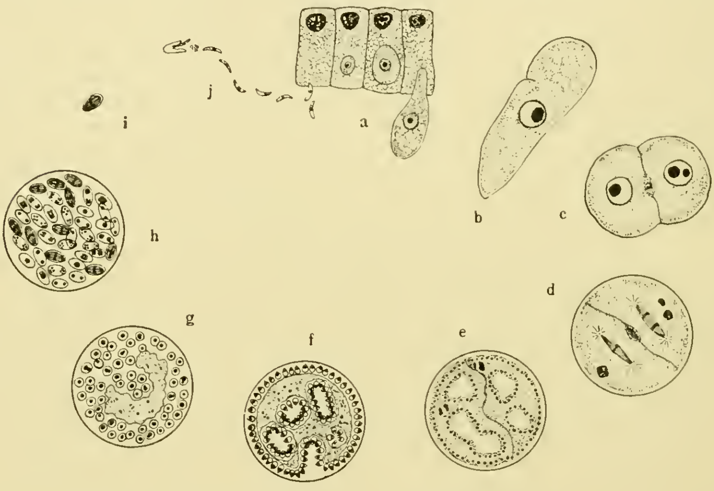


Fig. 123 The development of *Lankesteria culicis*. × about 500. (After Wenyon).
a. Entrance of sporozoites into the epithelial cell and growth stages of trophozoites.
b. Trophozoite free in the host gut lumen.
c. Association of grown trophozoites in pair.
d–f. Stages in gamete-formation.
g. Gametogony.
h. Development of spores from zygotes.
i. A spore.
j. Germination of spore in the host gut.

eight in number. These spores germinate when taken into the alimentary canal of a host animal and the liberated sporozoites undergo changes outlined above.

According to Wenyon, in a typical Eugregarinina, *Lankesteria culicis* (Fig. 123) of *Aedes aegypti*, the development in a new host begins when a larva of the mosquito ingests the spores. From each spore are liberated eight sporozoites (*j*), which enter the epithelial cells of the stomach and grow (*a*). These trophozoites leave the host cells later and become mingled with the food material present in the stomach lumen of the host (*b*). When the larva pupates, the trophozoites enter the Malpighian tubules, where they become associated in pairs and encyst (*c*). The two nuclei divide repeatedly and produce large numbers of gametes (*d-f*) which copulate in pairs (*g*). The zygotes thus formed develop into spores, each possessing eight sporozoites (*h*). Meanwhile the host pupa emerges as an adult mosquito, and the spores which become set free in the lumen of the tubules pass into the intestine, from which they are discharged into the water. Larvae swallow the spores and acquire infection.

Two legions are distinguished here:

Trophozoite single-chambered........................Legion 1 Acephalina
Trophozoite with more than one chamber.............Legion 2 Cephalina

Legion 1 **Acephalina** Kölliker

Genus **Monocystis** Stein. Body highly contractile and motile. A large residual mass of cytoplasm after sporulation. Spore fusiform, symmetrical, with eight sporozoites. Common and widely distributed parasites in the seminal vesicles of various species of Lumbricus and Pachydrilus and also in microcrustaceans. Numerous species. Several species frequently may occur in a host individual at the same time and, consequently, specific identification is a matter of great difficulty.

Monocystis rostrata Muslow (Fig. 124, *a-d*). In the seminal vesicle of *Lumbricus terrestris*.

Genus **Zygocystis** Stein. Pyriform trophozoites are paired in young as well as mature stages. The endoplasm is not vacuolated. The spore contains eight sporozoites. In Lumbricus and crustaceans.

Zygocystis cometa Stein. In the seminal vesicle and body cavity of *Lumbricus agricola*.

Genus **Pleurocystis** Hesse. Trophozoites elongated spindle-shape, attached to the host's cell in pairs. The spore contains eight sporozoites. One species.

Pleurocystis magna (Cuénot). In the seminal vesicle of *Lumbricus terrestris* and *L. herculeus.*

Genus **Pterospora** Racovitza and Labbé. Body pyriform, the narrow end is prolonged into four bifurcated processes. Solitary or associated with broad ends. Body capable of movement. Cysts spherical or oval. The spore possesses dissimilar extremities and its outer envelope (epispore) is drawn out into three lateral processes. Number of sporozoites eight (?).

Pterospora maldaneorum Racovitza and Labbé (Fig. 124, *e, f*). In the body cavity of the worm, *Liocephalus liopygus.*

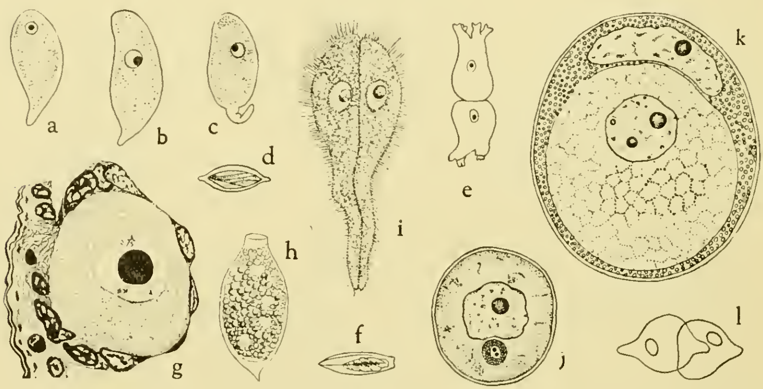


Fig. 124 a–d. *Monocystis rostrata.* (After Muslow). a–c, grown trophozoites (×45); d, a spore (×600).
e, f. *Pterospora maldaneorum.* (After Labbé). e, grown trophozoites (×30); f, a spore (×400).
g, h. *Lithocystis brachycercus.* ×1000 (After Pixell-Goodrich). g, a trophozoite attached to the coelomic side of the host gut; h, a spore from life.
i. Two trophozoites of *Urospora chiridotae* in association. ×150 (After Pixell-Goodrich).
j–l. *Gonospora minchini.* (After Goodrich and Pixell-Goodrich). j, a young sporozoite in host's egg (×250); k, fully grown trophozoite in egg (×250); l, free trophozoites in association (×60).

Genus **Cystobia** Mingazzini. Body large; form irregular. Fully grown trophozoite contains two nuclei, on account of the early union of two individuals. The spore is oval and its envelope is drawn out at one end in a bottle-neck fashion. Parasites of the blood vessel and coelom of Holothuria.

Cystobia irregularis (Minchin). In the blood vessel of *Holothuria nigra.*

Genus **Lithocystis** Giard. Body large; form ovoid or cylindrical. Body-surface with hair-like processes; endoplasm with crystals of calcium oxalate. The spore is ovoid, but its envelope with a long process; arranged radially. Number of sporozoites eight (?).

Lithocystis schneideri Giard. In the coelom of echinoderms.

Lithocystis brachycercus Pixell-Goodrich (Fig. 124, *g*, *h*). In the coelom of *Chiridota laevis.*

Genus **Urospora** Schneider. Body large; frequently in association. Cyst spherical. Each individual undergoes sporulation independently. The spore is oval and possesses a long filamentous process at one end. In the body cavity of Tubifex, Nemertinea, Sipunculus, Synapta, and Chiridota. Several species

Urospora saenuridis (Kölliker). In the seminal vesicle and general body cavity of *Tubifex tubifex*

Urospora chiridotae (Dogiel) (Fig. 124, *i*). In the blood vessel of *Chiridota laevis*

Genus **Gonospora** Schneider. Trophozoite large and polymorphic, oval, pyriform or vermiform. Cysts spherical. The ends of the spore are dissimilar. In the coelom of polychaetes. Several species.

Gonospora minchini Goodrich and Pixell-Goodrich (Fig. 124, *j-l*). In the coelom of *Arenicola ecaudata.* Young trophozoites invade and grow within the egg.

Genus **Lankesteria** Mingazzini. Body more or less spatulate and small. Cysts spherical. The spore is oval and flattened and contains eight sporozoites.

Lankesteria planariae (Mingazzini). In the gastro-vascular cavity of Planaria.

Lankesteria culicis (Ross) (Fig. 123). In the gut of *Aedes aegypti.*

Genus **Nematocystis** Hesse. Trophozoites are nematode-like.

Nematocystis magna (Schmidt). In *Lumbricus terrestris.*

Genus **Rhynchocystis** Hesse. Body ovoid or cylindrical, with a proboscis-like process at the anterior end.

Rhynchocystis pilosa (Cuénot). In *Lumbricus terrestris*, *L. rubellus*, and *L. castaneus*.

Genus **Allantocystis** Keilin. Body elongate pyriform. Association endwise without changing forms, hence the cyst is elongated. Spores asymmetrically fusiform. Number of sporozoites within a spore unknown.

Allantocystis dasyhelei Keilin (Fig. 125, *a-d*). Grown trophozoite 70 microns by 20 microns. Cyst 150 microns by 20 microns. The spore is 18 microns by 7 microns. In the space between the gut-epithelium and the peritrophic tube of larvae of *Dasyhelea obscura*, a ceratopognid insect of the elm and horse-chestnut trees.

Legion 2 **Cephalina** Delage

The body is divided into the protomerite and deutomerite by an ectoplasmic septum. An endwise association of two trophozoites (**syzygy**), is common. The anterior individual is called the **primite** and the posterior **satellite**. Parasites of the digestive tracts of invertebrates, especially arthropods. Some of the representatives are as follows:

Genus **Gregarina** Dufour. Trophozoites associative. The epimerite is small, globular or cylindrical. The spore is dolioform to cylindrical. The cyst opens by sporoducts. Many species.

Gregarina blattarum Siebold (Fig. 125, *e*). In the digestive tract of the cockroach.

Gregarina locustae Lankester (Fig. 125, *f*). In the intestine of the Carolina locust, *Dissosteria carolina*.

Gregarina oviceps Diesing (Fig. 125, *g*). In the intestine of the crickets, *Gryllus* spp.

Genus **Hirmocystis** Léger. Two to twelve or more trophozoites are associated in a line. The epimerite a small cylindrical papilla. The cyst opens by simple rupture. The spore is ovoidal.

Hirmocystis harpali Watson (Fig. 125, *h*). In the intestine of the beetle, *Harpalus pennsylvanicus erythropus*.

Genus **Leidyana** Watson. Solitary. Epimerite a simple globular sessile knob. The cyst possesses sporoducts. The spore dolioform.

Leidyana erratica (Crawley) (Fig. 125, *i*). In the intestine of the crickets, *Gryllus abbreviatus* and *G. pennsylvanicus*.

Genus **Stenophora** Labbé. Trophozoites solitary. Epimerite simple or absent. The cyst opens by simple rupture. The spore is ovoid and possesses an equatorial line. Parasites of myriapods

Stenophora cockerellae Ellis (Fig. 125, *j*). In the gut of *Orthomorpha coarctata*.

Genus **Acutispora** Crawley. Trophozoites solitary. Pseudocyst. The spore is biconical and possesses a thick blunt endosporic rod at each end. In centipedes.

Acutispora macrocephala Crawley (Fig. 125, *k*). In the gut of *Lithobius forficatus*.

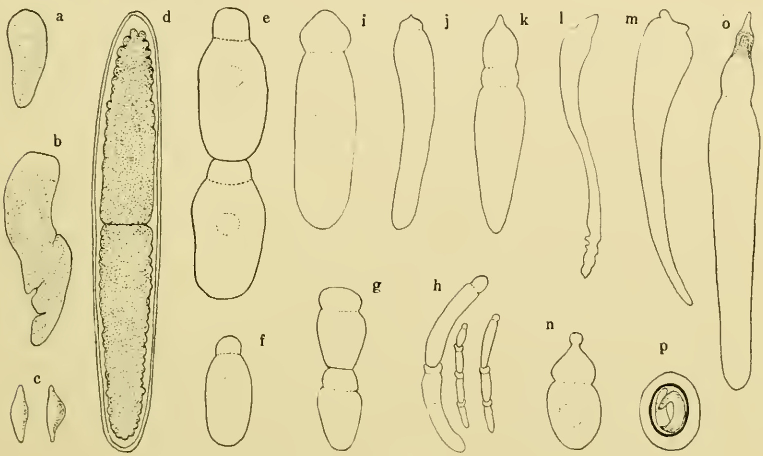


Fig. 125 a–d. *Allantocystis dasyhelei*. ×400 (After Keilin). a, b, trophozoites; c, two spores; d, cyst.
e. *Gregarina blattarum*. ×40.
f. *G. locustae*. ×50 (After Leidy).
g. *G. ovíceps*. ×25 (After Crawley).
h. *Hirmocystis harpali*. ×37 (After Watson).
i. *Leidyana erratica*. ×125 (After Watson).
j. *Stenophora cockerellae*. ×50 (After Ellis).
k. *Acutispora macrocephala*. ×50 (After Crawley).
l. *Asterophora philica*. ×50 (After Leidy).
m. *Amphoroides calverti*. ×100 (After Watson).
n. *Steinina rotunda*. ×100 (After Watson).
o. *Stylocephalus giganteus*. ×50 (After Ellis).
p. Spore of *Porospora portunidarum*. ×750 (After Léger and Duboscq).

Genus **Nina** Grebnecki. Protomerite formed of two long narrow horizontal lobes fused and upturned spirally at one end. Periphery shows many teeth, from which project long slender filaments. The spores are in chain form. In the intestine of myriapods.

Nina gracilis Grebnecki. In the gut of *Scolopendra cingulata.*

Genus **Asterophora** Léger. Epimerite a thick horizontal disc with a milled border and a stout style projecting from the center. The spore cylindro-biconical. In Neuroptera and Coleoptera.

Asterophora philica (Leidy) (Fig. 125, *l*). In the gut of the coleopteran, *Nyctobates pennsylvanica.*

Genus **Amphoroides** Labbé. Epimerite a globular sessile papilla. Protomerite cup-shaped. The spore is curved. In myriapods.

Amphoroides calverti (Crawley) (Fig. 125, *m*). In the gut of Callipus and Lysiopetalum.

Genus **Steinina** Léger and Duboscq. Solitary. Epimerite a short motile digitform process changing into a flattened structure. The spore is biconical. In Coleoptera.

Steinina rotunda Watson (Fig. 125, *n*). In the gut of *Amara augustata.*

Genus **Stylocephalus** Ellis. Solitary. Epimerite a dilated papilla at the end of a long process. The cyst covered with small papillae and indentations. The spore is hat-shaped. In various arthropods and molluscs.

Stylocephalus giganteus Ellis (Fig. 125, *o*). In the gut of coleopteran insects belonging to the genera Eleodes, Eusattus, and Asida.

Genus **Porospora** Schneider. The schizogony takes place in a crustacean and sporogony occurs in a molluscan host. The development is peculiar. The mature spore contains a single vermiform sporozoite which becomes attached to the gut-epithelium of the crab. It develops into a very long trophozoite. One, two, or sometimes three of them unite and encyst together. The nucleus divides repeatedly and finally a number of "gymnospores" are formed. Certain authors hold this change as asexual, or schizogonic, reproduction, and hence include the genus in the suborder Schizogregarinaria. When the parasites are passed in the feces of the host crab, the gymnospores enter the gill of a mollusc and there undergo copulation (Hatt). The zygotes develop into naked or encapsulated elongate vermiform bodies which, when taken into a host crustacean, develop into trophozoites. Several species.

Porospora portunidarum Frenzel (Fig. 125, *p*). The trophozoite is very large. In the crab, Portunus, and the mollusc, Cardium.

Genus **Dendrorhynchus** Klein. Body elongated. Epimerite a disc, surrounded by numerous ramified papillae. Cyst elliptical; spores spindle-shaped (?).

Dendrorhynchus systeni Keilin. Fully grown trophozoite 250 microns by 20 microns. The spore measures 19 microns by 7 microns. In the midgut of larvae of a dolichopodid fly, *Systenus* sp., found in the decomposed sap of the elm tree.

Suborder 2 **Schizogregarinaria** Léger

The Schizogregarines are intestinal parasites of arthropods, annelids, and tunicates. When the spore gains entrance to the digestive tract of a specific host through the mouth, it germinates and the sporozoites are set free (Fig. 126). These sporozoites develop into trophozoites either in the gut-lumen or within the host cells, and undergo schizogony (*c*), which may be binary or multiple fission or budding. The fully grown trophozoites become paired as in Eugregarinina and encyst, in which condition they undergo sexual reproduction followed by sporogony. Each individual which is now a gametocyte, produces gametes (*d-e*). Fusion of two gametes follows (*f*). The zygote develops into a spore containing one to eight sporozoites (*g*, *a*). Several genera.

Genus **Schizocytsis** Léger. Mature trophozoite multinucleate; ovoid or cylindrical with differentiated anterior end. Schizogony by multiple division. The trophozoites become associated, encyst, and produce a large (up to 30) number of spores, each of which contains eight sporozoites. In Diptera, Annelida, and Sipunculoida.

Schizocystis gregarinoides Léger (Fig. 126). In the gut of Ceratopogon larvae.

Genus **Ophryocystis** Schneider. Parasites of the Malpighian tubules of Coleoptera. Schizogony by binary fission or multiple division. The schizonts are conical and are attached to the surface of the host cells by pseudopodial processes. From a pair of trophozoites, a single spore is produced, in which eight sporozoites develop.

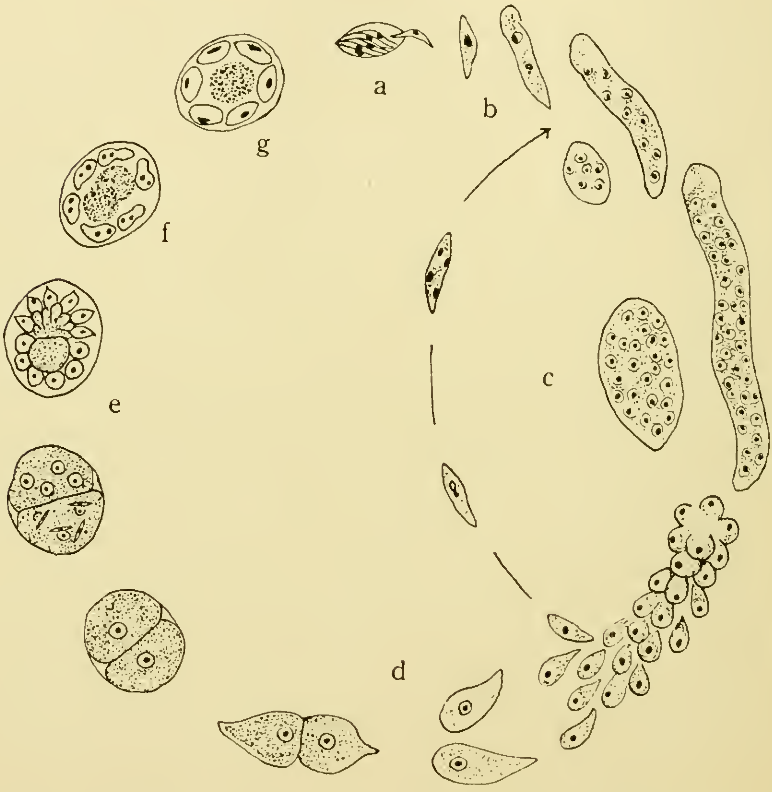


Fig. 126 Development of *Schizocystis gregarinoides*. ×1000 (After Léger)
a. Germinating spore.
b. Growth of schizonts.
c. Schizogony.
d. Two gametocytes and their association.
e. Stages in gamete formation.
f. Gametogony.
g. Cyst containing zygotes, each of which develops into a spore (a).

Ophryocystis mesnili Léger (Fig. 127, *a*). In the mealworm, *Tenebrio molitor*.

Genus **Lipotropha** Keilin. Schizogonic and sporogonic stages intracellular. The oocyst contains sixteen spores, each possessing eight sporozoites. In the fat body of Systenus larvae. One species.

Lipotropha macrospora Keilin (Fig. 127, *b*, *c*). The spore measures about 13.5 microns by 3 microns.

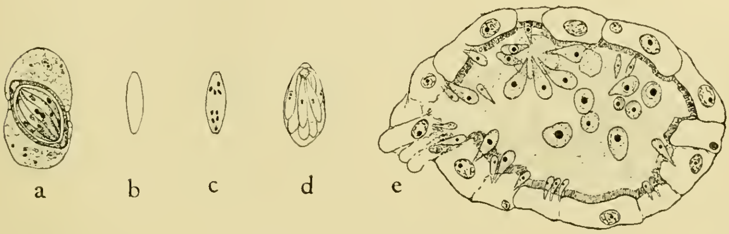


Fig. 127 a. A sporulating stage of *Ophryocystis mesnili*. ×1000. (After Léger).
b, c. Spores of *Lipotropha macrospora*. ×600 (After Keilin).
d, e. *Caulleryella pipientis*. (After Buschkiel). d, a spore (×900); e, section of gut of *Culex pipiens*, showing the trophozoites (×150).

Genus **Caulleryella** Keilin. Schizogony into 16 schizonts. Each gametocyte gives rise to 8 gametes, and hence 8 zygotes The spore contains 8 sporozoites. Parasitic in the intestine of dipterous larvae.

Caulleryella pipientis Buschkiel (Fig. 127, *d*, *e*). In the gut of *Culex pipiens*.

References

Doflein, F. and E. Reichenow. 1929 Lehrbuch der Protozoenkunde. Jena.

Hesse, E. 1909 Contribution à l'étude des Monocystidées des Oligochètes. Arch. Zool. Exper., T. 3.

Watson Kamm, Minnie. 1916, 1922 Studies on gregarines. I. II. Illinois Biological Monogr., Vols. 2 and 7.

CHAPTER XXIV

SUBCLASS 2 **CNIDOSPORIDIA** DOFLEIN

THE CHARACTER common to all Sporozoa belonging to this subclass is the presence of resistant **spores** which are of unique structure. Each spore possesses one to four **polar capsules** and one to many **sporoplasms.** The membrane which envelops these structures may be a single-piece or bi- or tri-valved. Within each of the polar capsules is coiled a **polar filament.**

In the orders Myxosporidia and Actinomyxidia, there appear several cells during the process of sporulation. These cells give rise to one to many sporoplasms, or generative cells, capsulogenous cells, and spore membrane. This condition is not observed in other groups of Protozoa. For this reason some writers recognize a close affinity between these two orders and the Mesozoa. The method of multiplication in the Cnidosporidia is schizogonic and sporogonic. The schizogony is binary or multiple fission, budding, or plasmotomy. The nuclear division varies from amitosis to mitosis. Isogamous, anisogamous, and autogamous reproduction have been reported in a number of forms. In many cases, the zygote is the sporont, in which one to many spores become differentiated.

No secondary or intermediate host has been found for any of the Cnidosporidia. They are exclusively parasites of the lower vertebrates and invertebrates. Since cnidosporidian infections occur frequently in epidemic forms among such economically important animals as the silkworm, honey bees, and commercial fishes, the organisms possess considerable practical significance.

The Cnidosporidia are here divided into four orders as follows:

The spore large; with bivalve membrane; one, two or four polar capsules visible *in vivo*............................Order 1 Myxosporidia

The spore large; with trivalve membrane; three distinctly visible polar capsules.................................Order 2 Actinomyxidia

The spore is small; with one-piece membrane; one (rarely two) polar filament; polar capsule, if present, invisible *in vivo* .... Order 3 Microsporidia
The spore small, barrel-shaped; a thick filament, coiled beneath the spore membrane; three sporoplasms .... Order 4 Helicosporidia

ORDER 1 MYXOSPORIDIA BÜTSCHLI

The Myxosporidia are characterized by the possession of a spore which shows the following structure: The **spore** is of various shape and dimension. It is covered by a bivalve chitinoid **spore membrane,** the two valves meeting in a **sutural plane** which is either twisted (in three genera) or more or less straight. The membrane may possess various markings or processes. The **polar capsule,** with its short coiled **filament,** varies in number from one to four. Except in the family Myxidiidae, in which one polar capsule is situated near each of the poles of the spore, the polar capsules are always grouped at one end which is designated as the anterior end of the spore. Below or between (in Myxidiidae) the polar capsules there is a **sporoplasm.** Ordinarily a young spore possesses two nuclei which fuse into one when the spore becomes mature. In Myxobolidae there is a glycogenous substance in a vacuole which stains mahogany red with iodine and which is known as the **iodinophilous** (iodophile) **vacuole.**

The Myxosporidia are almost exclusively parasites of lower vertebrates, especially fishes. Both fresh and salt water fishes have been found to harbor, or to be infected by, Myxosporidia in various regions of the world. A few occur in Amphibia and Reptilia, but no species has been found to occur in either birds or mammals. When a spore gains entrance into the digestive tract of a specific host fish, the **sporoplasm** leaves the spore as an amoebula which penetrates through the gut-epithelium and, after a period of multiplication, enters the tissues of certain organs, where it grows into a **schizont** at the expense of the host tissue cells, and the nucleus divides repeatedly. Some nuclei become surrounded by masses of cytoplasm and become the **sporonts** (Fig. 128). The sporonts grow and their nuclei divide several times, forming six to eighteen daughter nuclei, each with a small mass of cytoplasm. The number of the nuclei thus produced depends upon the structure of the mature spore, and also upon whether one or two spores are developed in a sporont. When the sporont develops into a single spore, it is called a monosporoblastic sporont. If two spores are formed within a sporont, which is usually the case, the sporont is called disporoblastic, or **pansporoblast.** The spore-formation begins usually in the central area of the large trophozoite, which continues to grow. The surrounding host tissue becomes degenerated or modified and forms an envelope which is often large enough to be visible to the naked eye. This is ordinarily referred to as a **myxosporidian cyst.** If the site of infection is near the body surface, the large cyst breaks and the mature spores become set free in the water. In case the infection is confined to internal

Fig. 128 Stages in spore-formation of *Myxosoma catostomi.* ×725 (After Kudo).

a, sporont; b–j, developmental stages of spores; k, l, two views of stained spores; m, n, o, front, end, and side views of preserved, unstained spores.

organs, the spores will not be set free while the host fish lives. Upon its death and distintegration of the body, however, the liberated spores become the sources of new infection.

The more primitive Myxosporidia are coelozoic in the host's organs, such as the gall bladder, uriniferous tubules of the kidney, urinary bladder, etc. In these forms, the liberated amoebulae make their way into the specific organ and there grow into multinucleate amoeboid trophozoites which are capable of forming pseudopodia of various types. They multiply by exogenous or endogenous budding or plasmotomy. One to several spores are developed in the trophozoite.

The site of infections by Myxosporidia varies among different species. They have been found in almost all kinds of tissues and organs of host fish, although each myxosporidian has its special site of infection in one to several species of fish. The gills and gall bladder are most frequently parasitized by Myxosporidia in freshwater fishes, while the gall bladder and urinary bladder of marine fishes harbor one or more species of Myxosporidia. When the infection is concentrated in the fins or integument, the resulting changes are quite conspicuous (Fig. 129). The infection in the gills is usually manifest by whitish pustules which can be frequently detected with the unaided eye. When the wall of the alimentary canal, the mesentery, liver, and other organs are attacked, one sees considerable

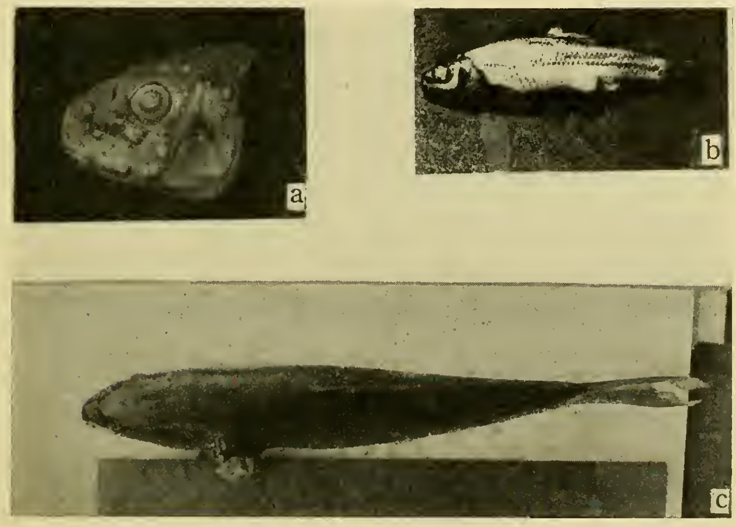


Fig. 129 External symptoms of myxosporidian infection in fish. (After Kudo). a. Head of the short-headed red-horse, *Moxostoma breviceps*, showing the cysts of *Myxobolus conspicuus*. One-half natural size. b. A blunt-nosed minnow, *Pimephales notatus*, showing three tumors which were caused by *Myxobolus notatus*. Five-eighths natural size. c. A sucker, *Catostomus commersonii*, with a large tumor due to an infection by *Myxosoma catostomi*. About one-third natural size.

changes in them. Heavy myxosporidian infection of the gall bladder or urinary bladder of the host fish may cause abnormal appearance and coloration or unusual enlargement of the organ, but under ordinary circumstances the infection is detected only by a microscopical examination of its contents.

Severe epidemic diseases of fishes are frequently found to be due to myxosporidian infections. According to Davis, the "wormy" halibut of the Pacific coast of North America is due to the myxosporidian, *Unicapsula muscularis*, which invades the muscular tissue of the host fish. The "boil disease" of the barbel, *Barbus barbus* and others, of European waters, is caused by *Myxobolus pfeifferi*. *Lentospora cerebralis* which attacks the supporting tissues of salmonoid fish, is known to be responsible for the so-called "twist disease," which is often fatal, especially to young fishes and which occurs in an epidemic form.

The Myxosporidia are divided into three suborders, as follows:

The largest diameter of the spore at right angles to the sutural plane; one polar capsule on each side of the plane; sporoplasm without iodinophilous vacuole .... Suborder 1 Eurysporea
The spore spherical or subspherical with one, two, or four polar capsules; sporoplasm without iodinophilous vacuole. Suborder 2 Sphaerosporea
The sutural plane coincides with, or is at an acute angle to, the largest diameter of the spore; one, two, or four polar capsules; sporoplasm with or without iodinophilous vacuole .... Suborder 3 Platysporea

Suborder 1 **Eurysporea** Kudo

Family **Ceratomyxidae** Doflein

Genus **Ceratomyxa** Thélohan. Shell-valves conical and hollow, attached on the bases; sporoplasm usually not filling the intrasporal cavity. The majority in the gall-bladder of marine fish. Numerous species.

Ceratomyxa mesospora Davis (Fig. 130, *a*). In the gall bladder of *Cestracion zygaena*. The dimensions of the spore: Sutural diameter 8 microns, width 50 to 65 microns.

Genus **Leptotheca** Thélohan. Shell-valves hemi-spherical. The majority live in the gall bladder or urinary bladder of marine fish and one in amphibians. Several species.

Leptotheca ohlmacheri (Gurley) (Fig. 130, *b-h*). In the uriniferous tubules of the kidney of frogs and toads. Dimensions of spore: Sutural diameter 9.5 to 12 microns; breadth 13 to 14.5 microns.

Genus **Myxoproteus** Doflein. Spores pyramidal with or without distinct processes at the base of the pyramid. Rare. In the urinary bladder of marine fish. Three species.

Myxoproteus cordiformis Davis (Fig. 130, *i*). In the urinary bladder of *Chaetodipterus faber*. The spore measures 12 microns long by 10 to 11 microns wide.

Genus **Wardia** Kudo. Spores isosceles triangle with two convex sides; oval in profile. Two large polar capsules. Tissue parasites of freshwater fish. Two species.

Wardia ovinocua Kudo (Fig. 130, *j*). In the ovary of *Lepomis humilis*. The spore measures 9 to 11 microns in sutural diameter by 10 to 12 microns in width.

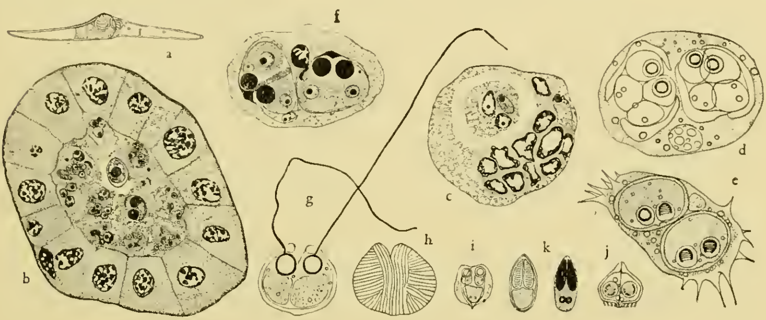


Fig. 130 a. *Ceratomyxa mesospora*, a fresh spore. ×500 (After Davis).
b–h. *Leptotheca ohlmacheri*. c–h, ×750. (After Kudo). b, section through a uriniferous tubule of *Rana pipiens*, showing the trophozoites in its lumen (×400); c, a trophozoite containing an endogenous gemmule; d, e, trophozoites, each containing two spores, from life; f, stained trophozoite with two spores; g, a spore with extruded polar filaments; h, surface view of a fresh spore.
i. A spore of *Myxoproteus cordiformis*. ×500 (After Davis).
j. A spore of *Wardia ovinocua*. ×665 (After Kudo).
k. A fresh and a stained spore of *Mitraspora elongata*. ×500 (After Kudo).

Genus **Mitraspora** Fujita. Spores circular or ovoidal in front view; somewhat flattened in profile. Two polar capsules; shell longitudinally striated; with or without posterior filaments. In the kidneys of freshwater fishes. This genus apparently includes border-line forms between this and the other suborders. Three species.

Mitraspora elongata Kudo (Fig. 130, *k*). In the kidney of *Lepomis cyanellus*. The spore is 15 to 17 microns long by 5 to 6 microns wide.

Suborder 2 **Sphaerosporea** Kudo

With four polar capsules........................Family 1 Chloromyxidae
With one or two polar capsules..................Family 2 Sphaerosporidae

Family 1 **Chloromyxidae** Thélohan

Genus **Chloromyxum** Mingazzini. Spore with four polar capsules, grouped at the anterior end. Surface often striated or with ridges. The sutural line is often obscure. Histozoic and coelozoic in freshwater and marine fishes and also in amphibians. Numerous species.

Chloromyxum leydigi Mingazzini (Fig. 131, *a*, *b*). In the gall bladder of various species of Raja, Torpedo, and Cestracion. The spore is 6 to 9 microns by 5 to 6 microns. Widely distributed.

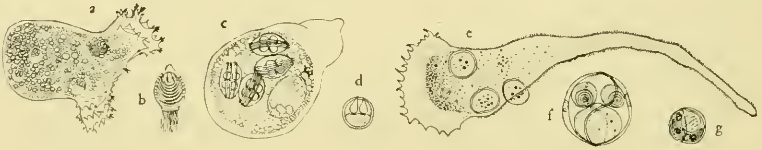


Fig. 131 a, b. *Chloromyxum leydigi*. (After Thélohan). a, trophozoite (×250); b, a spore (×500).
c. Trophozoite of *C. trijugum* with mature and developing spores. ×565 (After Kudo).
d. Spore of *Sphaerospora polymorpha*. ×500 (After Davis).
e, f. *Sinuolinea dimorpha*. (After Davis). e, a living trophozoite with three buds (×210); f, a spore (×465).
g. A spore of *Unicapsula muscularis*. ×830 (After Davis).

Chloromyxum trijugum Kudo (Fig. 131, *c*). In the gall bladder of *Lepomis megalotis*. The spore measures 8 to 10 microns by 5 to 7 microns.

Family 2 **Sphaerosporidae** Davis

Genus **Sphaerospora** Thélohan. The spore with two polar capsules. Histozoic or coelozoic parasites of marine and freshwater fish.

Sphaerspora polymorpha Davis (Fig. 131, *d*). In the urinary bladder of *Opsaus tau*. The spore measures 7 to 10 microns in diameter.

Genus **Sinuolinea** Davis. The spore with or without lateral processes. Sutural line sinuous; two polar capsules. In the urinary bladder of marine fish.

Sinuolinea dimorpha Davis (Fig. 131, *e*, *f*). In *Cynoscion regalis*. The spore is 15 microns in diameter.

Genus **Unicapsula** Davis. Spore with one polar capsule. Shell-valves asymmetrical; sutural line sinuous (?). Histozoic in marine fish. One species.

Unicapsula muscularis Davis (Fig. 131, *g*). The spore is about 6 microns in diameter. In the muscle fibers of the halibut on the Pacific coast of North America. The cause of the "wormy" halibut (Davis).

Suborder 3 **Platysporea** Kudo

Without iodinophilous vacuole
- Two polar capsules; one at each pole .... Family 1 Myxidiidae
- One polar capsule .... Family 2 Coccomyxidae
- 2 or 4 polar capsules at anterior end .... Family 3 Myxosomatidae

With an iodinophilous vacuole .... Family 4 Myxobolidae

Family 1 **Myxidiidae** Thélohan

Genus **Myxidium** Bütschli. The spore fusiform with pointed or rounded ends. Polar filament is comparatively long and fine. Coelozoic or histozoic in fishes and also in reptiles. Numerous species.

Myxidium lieberkühni Bütschli (Fig. 132, *a-d*). In the urinary bladder of various species of Lucius. The spore measures 18 to 20 microns by 5 to 6 microns. Widely distributed.

Genus **Sphaeromyxa** Thélohan. Spore fusiform, but ends are usually truncate. Polar filament short and thick. Trophozoites large and discoid. Coelozoic in marine fish and amphibians. Several species.

Sphaeromyxa balbianii Thélohan (Fig. 132, *e-g*). In the gall bladder of species of Motella and other marine fishes in Europe and of Siphostoma in the United States. The spore measures 15 to 20 microns long by 5 to 6 microns broad.

Sphaeromyxa sabrazesi Laveran and Mesnil (Fig. 132, *h*, *i*). In the gall bladder of Hippocampus, Motella, etc. The spore measures 22 to 28 microns long by 3 to 4 microns wide.

Genus **Zschokkella** Auerbach. The spore hemi-circular in front-view; fusiform in profile; circular in cross-section. Ends pointed obliquely. The polar capsules are large and spherical. The sutural line is usually in S-form. In organ-cavities of fish. A few species.

Zschokkella hildae Auerbach (Fig. 132, *j*, *k*). In the urinary bladder of varous species of Gadus. The spores measures 16 to 29 microns long by 13 to 18 microns wide.

Family 2 **Coccomyxidae** Léger and Hesse

The spore ellipsoidal, circular in cross-section. One polar capsule. Undoubtedly a border-line form between the Myxosporidia and the Microsporidia.

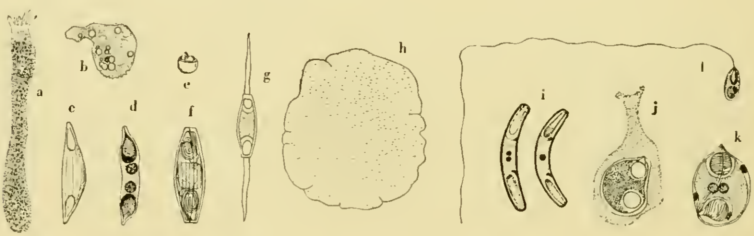


Fig. 132 a–d. *Myxidium lieberkühni.* a, large trophozoite (×110 after Lieberkühn); b, a small trophozoite from life (×500 after Kudo); c, d, fresh and stained spores (×700 after Kudo).
e–g. *Sphaeromyxa balbianii.* e, a living trophozoite (natural size after Thélohan); f, a spore (×700 after Davis); g, a spore with the extruded polar filaments (×420 after Thélohan).
h, i. *S. sabrazesi.* (After Schröder). h, a trophozoite from life (×5); i, two stained spores (×500).
j, k. *Zschokkella hildae.* (After Auerbach). j, a trophozoite (×300); k, stained spore (×530).
l. A spore of *Coccomyxa morovi.* ×330 (After Léger and Hesse).

Genus **Coccomyxa** Léger and Hesse. The polar filament long and fine. Coelozoic parasites in marine fish.

Coccomyxa morovi Léger and Hesse (Fig. 132, *l*). In the gall bladder of the sardine, *Clupea pilchardus*. The spore measures 14 microns long by 5 to 6 microns broad.

Family 3 **Myxosomatidae** Poche

Genus **Myxosoma** Thélohan. The spore ovoidal, flattened and more or less elongated. Two polar capsules. Histozoic parasites in freshwater and marine fishes. Several species.

Myxosoma catostomi Kudo (Figs. 28; 128; 129, *c*). In the muscle and connective tissue of the body of the sucker, *Catostomus commersonii*. The spore measures 13 to 15 microns by 10 to 11.5 microns.

Genus **Lentospora** Plehn. The spore circular to oval in front view. Two polar capsules. Histozoic parasites. Several species.

Lentospora cerebralis (Hofer) (Fig. 133, *a*, *b*). In the cartilage and perichondrium of the salmonoid fishes. Young fishes are especially affected by the infection. The disease is known as the

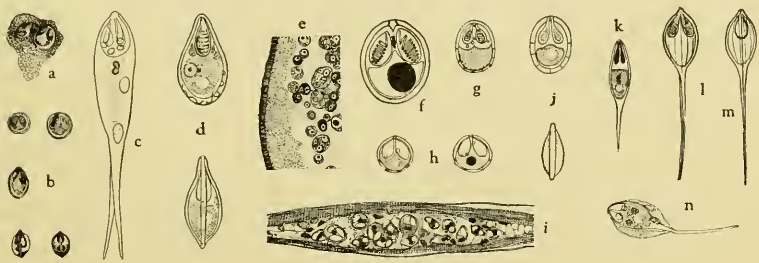


Fig. 133 a, b. *Lentospora cerebralis.* ×400 (After Plehn). a, trophozoite; b, five spores in different views.
c. A spore of *Agarella gracilis.* ×830 (After Dunkerley).
d. Two views of a spore of *Myxobolus notatus.* ×765. (After Kudo).
e–g. *Myxobolus pfeifferi.* e, part of section of a cyst; f, a spore treated with Lugol's solution (×890 after Keysselitz); g, a fresh spore (×500 after Thélohan).
h, i. *M. orbiculatus.* (After Kudo). h, a fresh spore and one treated with Lugol's solution (×500); i, infected host muscle (×300).
j. Spores of *M. conspicuus.* ×765 (After Kudo).
k. A spore of *Henneguya psorospermica.* ×665 (After Thélohan).
l–n. *H. mictospora.* (After Kudo). l, m, two spores in life (×665); a stained monosporous trophozoite (×565).

"twist-disease" (Drehkrankheit). The spore is 6 to 10 microns in diameter.

Genus **Agarella** Dunkerly. The spore is elongated oval. Four polar capsules at the anterior end. Shell is prolonged posteriorly into long processes. One species.

Agarella gracilis Dunkerly (Fig. 133, *c*). In the testis of South American lung-fish, *Lepidosiren paradoxa*.

Family 4 **Myxobolidae** Thélohan

Genus **Myxobolus** Bütschli. The spore ovoidal or ellipsoidal, flattened. One or two polar capsules at the anterior end. The sporoplasm contains an iodinophilous vacuole. Rarely with a posterior prolongation of the shell. Exclusively histozoic parasites in freshwater fishes and amphibians. Numerous species.

Myxobolus notatus Mavor (Fig. 129, *b*; 133, *d*). In the subdermal connective tissue of the blunt-nosed minnow, *Pimephales notatus*, and of *Leuciscus rutilus*. The tumor enclosing a trophozoite reaches a diameter of 7 mm. With a single polar capsule. Fresh spore 17 to 18 microns by 7.5 to 10 microns. The host tissue around the parasite becomes so highly changed that it appears as an epithelium.

Myxobolus pfeifferi Thélohan (Fig. 133, *e-g*). In the muscle and connective tissue of the body and various organs of *Barbus barbus*, *B. fluviatilis*, and *B. plebejus*. The tumor containing the parasites reaches a diameter of 7 cm. Most of the infected fish die from the effect (Keysselitz). The spore measures 12 to 12.5 microns long by 10 to 10.5 microns broad.

Myxobolus orbiculatus Kudo (Fig. 133, *h*, *i*). In the muscle of the minnow, *Notropis gilberti*. The preserved unstained spore measures 9 to 10 microns in diameter and 6.5 to 7 microns in thickness.

Myxobolus conspicuus Kudo (Fig. 133, *j*). In the corium of the head of the short-headed red-horse, *Moxostoma breviceps*. The trophozoites form tumors or cysts varying in diameter from one-half to 4 mm. (Fig. 129, *a*). The preserved spore measures 9 to 11.5 microns long by 6.5 to 8 microns broad.

Genus **Henneguya** Thélohan. The spore circular or ovoidal in front view; flattened. Two polar capsules at the anterior end. Each shell-valve is prolonged posteriorly into a long process. The sporoplasm contains an iodinophilous vacuole. Mostly histozoic (some coelozoic) parasites in freshwater fishes. Numerous species.

Henneguya psorospermica Thélohan (Fig. 133, *k*). In the gills of Lucius and Perca. Cyst formation. The total length of the spore 35 to 40 microns.

Henneguya mictospora Kudo (Fig. 133, *l-n*). In the urinary bladder of species of Lepomis and *Micropterus salmoides*. The spore measures 13.5 to 15 microns long, 8 to 9 microns broad, and 6 to 7.5 microns thick; caudel prolongation 30 to 40 microns long.

ORDER 2 **ACTINOMYXIDIA** STOLC

The Cnidosporidia placed in this order have been less frequently studied and, therefore, not so well known as the Myxosporidia. The spore is enveloped by a membrane, or shell, composed of three valves which are sometimes drawn out into simple or bifurcated processes. There are also three polar capsules in the spore and the polar filaments are plainly visible *in vivo*. Several sporoplasms occur as a rule in each spore. In the fully grown stage, the body is covered by a membrane and contains always eight sporoplasts which develop in turn into eight spores. Whether the pansporoblast is formed by the union of two cells or not, is yet to be confirmed. The nuclei and cytoplasm divide and isogamy takes place. The zygote thus formed is the sporont, from which a single spore is produced by repeated nuclear division combined with cytoplasmic differentiation.

The Actinomyxidia are parasitic in the body cavity or the gut-epithelium of fresh or salt water annelids.

The order is divided into two families as follows:

The spore with a double membrane; inner membrane a single piece and the outer trivalve. A single binucleate sporoplasm. Probably border-line forms between the Myxosporidia and the present order................................Family 1 Tetractinomyxidae

The spore membrane is a single trivalve shell. A single octonucleate sporoplasm or at least eight uninucleate sporoplasms.......
.....................................Family 2 Triactinomyxidae

Family 1 **Tetractinomyxidae**

Genus **Tetractinomyxon** Ikeda. Parasitic in the coelom of the sipunculid, *Petalostoma minutum*. The spore is tetrahedron in form and does not possess any processes. When the trophozoite reaches maturity, it is a rounded body, the pansporoblast, in which eight spores are developed.

Tetractinomyxon intermedium Ikeda (Fig. 134, *a*). and *T. irregulare* Ikeda. Parasitic in the coelom of the sipunculid, *Petalostoma minutum*.

Family 2 **Triactinomyxidae**

Genus **Triactinomyxon** Stolc. The three valves of the spore membrane are drawn out into long processes and the whole spore appears as an anchor. Parasitic in the gut-epithelium of oligochaetes.

Triactinomyxon ignotum Stolc (Fig. 134, *d*). Each spore possesses eight sporoplasms.

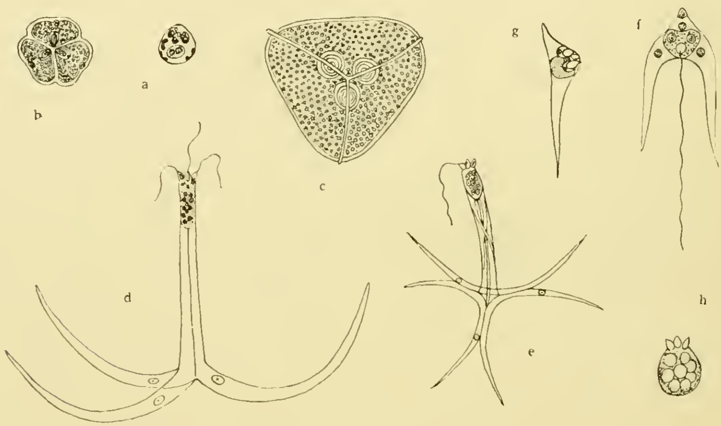


Fig. 134 a. Stained spore of *Tetractinomyxon intermedium*. ×600 (After Ikeda).
b. Spore of *Sphaeractinomyxon stolci*. ×450 (After Caullery and Mesnil).
c. Spore of *S. gigas*. ×500 (After Granata).
d. Spore of *Triactinomyxon ignotum*. ×200 (After Léger).
e. Spore of *Hexactinomyxon psammoryctis*. ×225 (After Stolc).
f, g. Polar and side view of spore of *Synactinomyxon tubificis*. ×450 (After Stolc).
h. A fresh spore of *Neoactinomyxum globosum*. ×650 (After Granata).

Triactinomyxon legeri Mackinnon and Adam. With 24 sporoplasms.

Triactinomyxon dubium Granata. With 32 sporoplasms.

Triactinomyxon mrazeki Mackinnon and Adam. With 50 sporoplasms. All in *Tubifex tubifex*, occurring in various parts of Europe.

Triactinomyxon magnum Granata. Each spore with 16 sporoplasms. In *Limnodrilus udekemianus*.

Genus **Sphaeractinomyxon** Caullery and Mesnil. Parasitic in the coelom of oligochaetes. The spore is rounded and without any processes. In the early stage of development, there are two uninucleate bodies surrounded by a binucleate envelope. The two inner cells multiply into 16 cells which unite in pairs. The nucleus of the zygote or sporont divides first into two. One of the nuclei divides into six nuclei which form three valves of the spore membrane and three polar capsules, while the other nucleus together with a portion of the cytoplasm remains outside the envelope, and undergoes multiplication. Later the multinucleate sporoplasm migrates into the spore. The sporoplasm later divides into a large number of uninucleate sporoplasms which, when the spore enters a new host, begin development.

Sphaeractinomyxon stolci Caullery and Mesnil (Fig. 134, *b*). The spore is spherical. Parasitic in *Clitellis arenarius* and *Hemitubifex benedii*.

Sphaeractinomyxon gigas Granata (Fig. 134, *c*). In the body cavity of *Limnodrilus hoffmeisteri*.

Genus **Hexactinomyxon** Stolc. Each of the three shell-valves is prolonged into two processes. Thus the spore appears as a six-armed anchor.

Hexactinomyxon psammoryctis Stolc (Fig. 134, *e*). In the gut-epithelium of *Psammoryctes barbatus*. The sporoplasm is multinucleate.

Genus **Synactinomyxon** Stolc. The spore with two prolonged shell-valves and one conical valve.

Synactinomyxon tubificis Stolc (Fig. 134, *f*, *g*). Parasitic in the gut-epithelium of *Tubifex tubifex*.

Genus **Neoactinomyxum** Granata. The three shell-valves without any process, but distended to hemi-sphere.

Neoactinomyxum globosum Granata (Fig. 134, *h*). Numerous sporoplasms. In the gut-epithelium of *Limnodrilus udekemianus*.

References

Auerbach, M. 1910 Die Cnidosporidien. Leipzig.

Caullery, M. and F. Mesnil. 1905 Recherches sur les Actinomyxidies. Arch. f. Protistenk., Vol. 6.

Davis, H. S. 1917 The Myxosporidia of the Beaufort region. Bull. U. S. Bureau Fish., Vol. 35.

Granata, L. 1924 Gli Attinomissidi. Arch. f. Protistenk., Vol. 50.

Kudo, R. 1920 Studies on Myxosporidia. Illinois Biol Monogr., Vol. 5.

CHAPTER XXV

ORDER 3 **MICROSPORIDIA** BALBIANI

THE MICROSPORIDIA are far more widely distributed as parasites among various animal phyla than are the Myxosporidia. They are, however, typically parasites of arthropods and fishes. Aside from one or two species, all Microsporidia invade and destroy host cells. Frequently these infected cells

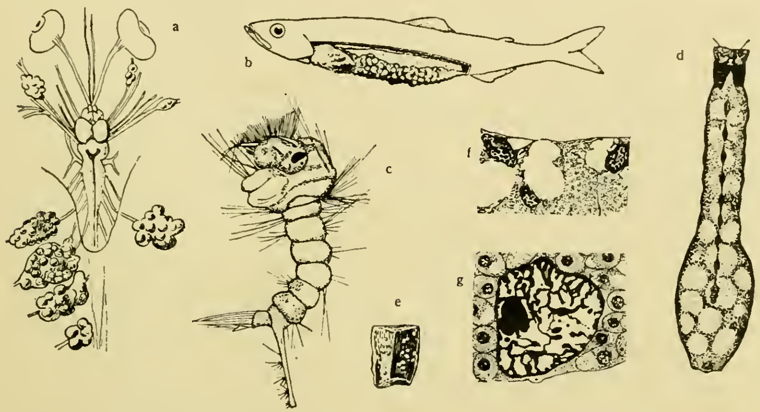


Fig. 135 Effects of microsporidian infection upon the hosts. (From Kudo).
a. The central nervous system of *Lophius piscatoris* infected by *Nosema lophii*.
b. A smelt showing a heavy infection by *Glugea hertwigi*.
c. A larva of *Culex territans* infected by *Thelohania opacita*. ×8.
d. A simulium larva infected by *T. multispora*. ×6.
e. Portion of the testis of *Barbus barbus* infected by *Plistophora longifilis*. Three-fourths natural size.
f, g. The normal and hypertrophied nuclei of the adipose tissue of larvae of *Culex pipiens*, the latter affected by *Stempellia magna*. ×750.

may show enormous hypertrophy of both the cytoplasmic body and the nuclei (Fig. 135), a characteristic feature of the host reaction toward this particular group of protozoan parasites.

The **microsporidian spore** is relatively small. In the vast majority it measures from 3 to 6 microns in length. The spore membrane, which is apparently of a single piece, envelops the sporoplasm and the polar filament, a very long and fine filament. The latter may directly be coiled in the spore or may be encased within a polar capsule which is similar to that of a myxosporidian or actinomyxidian spore in structure, but which is mostly obscure *in vivo*, because of the minuteness of the object.

When such spores are taken into the digestive tract of a specific host (Fig. 136), the polar filaments are extruded and perhaps anchor the spores to the gut-epithelium. The sporo-

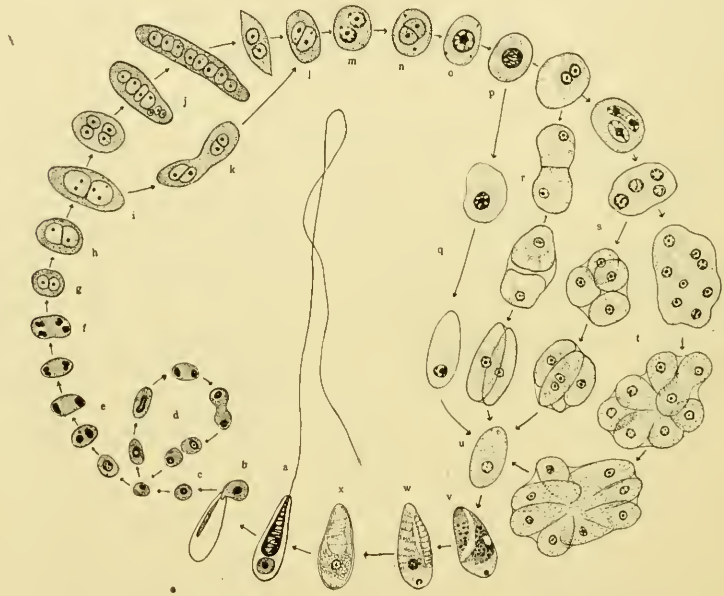


Fig. 136 Diagram showing the probable development of *Stempellia magna*. ×800 (After Kudo).

a, b, germination of spore in the mid-gut of culicine larva; c–k, stages in schizogony; l–p, sporont formation; q–t, formation of one, two, four and eight sporoblasts; u, a sporoblast; v–x, transformation of a sporoblast into a spore.

plasms emerge through the opening after the filaments become completely detached. By amoeboid movements they penetrate through the intestinal epithelium and enter the blood stream or body cavity and reach their specific site of infection. They then enter the host cells and undergo schizogonic multiplication at the expense of the latter. The schizonts become sporonts, each of which produces a number of spores characteristic of each genus. Some spores seem to be capable of germinating in the same host body, and thus the number of infected cells increases. When heavily infected, the host animal dies as a result of the degeneration of enormous numbers of cells thus attacked. Such fatal infections may occur in an epidemic form, as is well known in the case of the pébrine disease of silkworms, the nosema-disease of honey bees, microsporidiosis of mosquito larvae, etc.

According to the scheme of Léger and Hesse, the Microsporidia are divided into two suborders as follows:

The spore with a single polar filament..............Suborder 1 Monocnidea
The spore with two polar filaments...................Suborder 2 Dicnidea

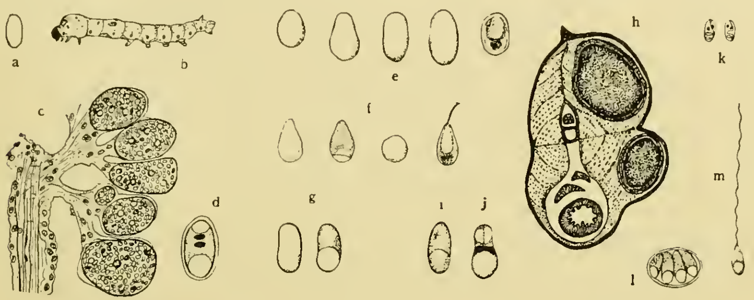


Fig. 137 a, b. *Nosema bombycis*. (After Kudo). a, a fresh spore (×1100); b, a silk-worm larva showing typical symptoms of heavy infection (one-half natural size).

c, d. *N. bryozoides*. c, portion of infected faniculus cut longitudinally (×200 after Braem); d, a stained spore (×900 after Schröder).

e. Four fresh spores and one stained spore of *N. apis*. ×1170 (After Kudo).

f. Four spores of *N. cyclopis*. ×1170 (After Kudo).

g. Two spores of *N. anophelis*. ×1200 (After Kudo).

h, i. *Glugea anomala*. h, cross-section of *Gasterosteus aculeatus* infected by the microsporidian (after Thélohan); a spore (×1125 after Stempell).

j. Stained spore of *G. hertwigi*. ×1250 (After Weissenberg).

k. Two spores of *Perezia mesnili*. ×600 (After Paillot).

l, m. A pansporoblast and a spore with its extruded polar filament of *Gurleya richardi*. ×900 (After Cépède).

Suborder 1 **Monocnidea** Léger and Hesse

This suborder will be divided into three families as follows:

The spore is oval, ovoid or pyriform; if subcylindrical, the length is less than four times the breadth . . . . Family 1 Nosematidae
The spore spherical or subspherical . . . . Family 2 Coccosporidae
The spore tubular or cylindrical (length is greater than five times the breadth) . . . . Family 3 Mrazekiidae

Family 1 **Nosematidae** Labbé

Genus **Nosema** Nägeli. Each sporont develops into a single spore. Numerous species.

Nosema bombycis Nägeli (Fig. 137, *a*, *b*). In all tissues of the egg, larva, pupa and adult of the silkworm, *Bombyx mori*. The cause of the pébrine disease.

Nosema bryozoides (Korotneff) (Fig. 137, *c*, *d*). In the germ cell and cavity of the bryozoans, *Plumatella fungosa* and *P. repens*. The spore is 7 to 10 microns long by 5 to 6 microns broad.

Nosema apis Zander (Fig. 137, *e*). In the honey bee. The spore measures 4 to 6 microns long by 2 to 4 microns wide.

Nosema cyclopis Kudo (Fig. 137, *f*). In *Cyclops fuscus*. The spore measures 4.5 microns by 3 microns.

Nosema anophelis Kudo (Fig. 137, *g*). In larvae of *Anopheles quadrimaculatus*. The spore measures 5 to 6 microns long by 2 to 3 microns.

Genus **Glugea** Thélohan. Each sporont develops into two spores. The infected host cells become much hypertrophied, producing the so-called **Glugea cysts.** Numerous species.

Glugea anomala (Moniez) (Fig. 137, *h*, *i*). In the connective tissue of the stickle back. The spore measures 4 to 6 microns long by 2 to 3 microns.

Glugea mülleri Pfeiffer. In the muscle of species of Gammarus. One of the several species of Microsporidia occurring in this host. The spore measures 5 to 6 microns by 2 to 3 microns.

Glugea hertwigi Weissenberg (Figs. 135, *b*; 137, *j*). In various tissue cells of the smelt, Osmerus. The spore measures 4 to 5.5 microns by 2 to 2.5 microns.

Genus **Perezia** Léger and Duboscq. Each sporont produces two spores as in Glugea, but the host cells are not hypertrophied. Four species.

Perezia mesnili Paillot (Fig. 137, *k*). In the cells of the silk glands and Malpighian tubules of the larva of *Pieris brassicae*. The spore measures 3.4 microns by 1.5 to 2 microns.

Genus **Gurleya** Doflein. Each sporont produces four sporoblasts and finally four spores. Rare.

Gurleya richardi Cépède (Fig. 137, *l*, *m*). In *Diaptomus castor*. The spore measures 4 to 6 microns long by 2.8 microns broad.

Genus **Thelohania** Henneguy. Each sporont develops into eight sporoblasts and ultimately into eight spores. The sporont membrane may degenerate at different times during development. Numerous species.

Thelohania legeri Hesse (Fig. 138, *a-f*). In the fat bodies of anopheline larvae. The spore measures 4 to 6 microns long by 3 to 4 microns broad. Widely distributed. Heavily infected larvae die without metamorphosing into adults.

Thelohania opacita Kudo (Figs. 135, *c*; 138, *g*, *h*). In the fat bodies of larvae of culicine mosquitoes. The spore measures 5.5 to 6 microns by 3.5 to 4 microns.

Genus **Stempellia** Léger and Hesse. Each sporont produces 1, 2, 4, or 8 sporoblasts and in turn 1, 2, 4, or 8 spores. Two species.

Stempellia magna Kudo (Figs. 135, *f*, *g*; 136; 138, *k-o*). In the fat bodies of various Culex larvae. The spore measures 12.5 to 16.5 microns long by 4 to 5 microns broad. The polar capsule is visible *in vivo*. The filament when extruded under mechanical pressure, reaches a length of 350 to 400 microns.

Genus **Duboscqia** Pérez. Each sporont produces 16 sporoblasts and later 16 spores. Only one species.

Duboscqia legeri Pérez. In the body cavity of *Termes lucifugus*. The spore measures 5 microns by 2.5 microns.

Genus **Plistophora** Gurley. Each sporont develops into many (more than 16) sporoblasts, each of which becomes a spore. Several species.

Plistophora simulii (Lutz and Splendore). In various species of Simulium larvae. The spore measures 4.5 to 8 microns long by 3 to 5 microns.

Plistophora longifilis Schuberg (Fig. 135, *e*; 138, *p*, *q*). In the testis of *Barbus fluviatilis*. The spore measures 3 microns by 2 microns up to 12 microns by 6 microns.

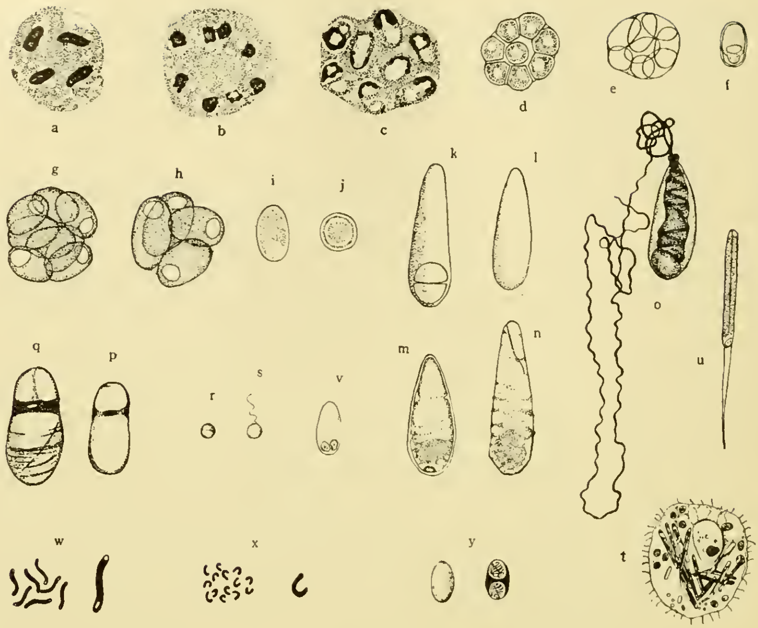


Fig. 138 a–f. *Thelohania legeri.* ×1180 (After Kudo). a–c, stages in sporogony; d, e, mature pansporoblasts; f, spore from life.

g–j. *T. opacita.* ×1180 (After Kudo). g, h, octosporous and tetrasporous pansporoblasts; i, j, fresh spores.

k–o. *Stempellia magna.* ×1180 (After Kudo). k–n, fresh spores; o, a spore with its extruded polar filament.

p, q. Stained spores of *Plistophora longifilis.* (After Schuberg).

r, s. Spores of Coccospora. ×1000 (After Léger and Hesse). s, a spore with its extruded polar filament.

t, u. *Mrazekia caudata.* t, an infected host cell (×350 after Mrazek); u, a spore (×875 after Léger and Hesse).

v. A spore of *Octosporea muscae-domesticae.* (After Chatton and Krempf).

w. Spores of *Spiroglugea octospora.* ×500; one ×1500. (After Léger and Hesse).

x. Spores of *Toxoglugea vibrio.* ×500; one ×1500. (After Léger and Hesse).

y. Fresh and stained spore of *Telomyxa glugeiformis.* ×1500 (After Léger and Hesse).

Family 2 **Coccosporidae** Kudo

(=**Cocconemidae** Léger and Hesse)

Genus **Coccospora** Kudo (=Cocconema Léger and Hesse). The spore is spherical or subspherical. Several species.

Coccospora slavinae (Léger and Hesse) (Fig. 138, *r*, *s*). In the gut-epithelium of *Slavina appendiculata*, an oligochaete worm. The spore is about 3 microns in diameter.

Family 3 **Mrazekiidae** Léger and Hesse

Genus **Mrazekia** Léger and Hesse. The spore straight tubular. The polar filament possesses a rod-like basal portion. Several species.

Mrazekia caudata Léger and Hesse (Fig. 138, *t*, *u*). In the lymphocyte of Limnodrilus and Tubifex. The spore measures 16 to 18 microns long by 1.3 to 1.4 microns broad.

Genus **Octosporea** Flu. The spore is cylindrical; more or less curved; ends similar. Two species.

Octosporea muscae-domesticae Flu (Fig. 138, *v*). In the gut and germ cells of the flies, Musca and Drosophila. The spore 5 to 8 microns long.

Genus **Spiroglugea** Léger and Hesse (=Spironema Léger and Hesse; Spirospora Kudo). The spore tubular and spirally curved. Polar capsule large. One species.

Spiroglugea octospora Léger and Hesse (Fig. 138, *w*). In the fat body of the larva of *Ceratopogon* sp. (Diptera). The spore measures 8 to 8.5 microns by 1 micron broad.

Genus **Toxoglugea** Léger and Hesse (=Toxonema Léger and Hesse; Toxospora Kudo). The minute spore is curved or arched in hemi-circle. One species.

Toxoglugea vibrio Léger and Hesse (Fig. 138, *x*). In the fat body of *Ceratopogon* sp. (Diptera). The spore measures 3.5 microns long by less than 0.3 microns broad.

Suborder 2 **Dicnidea** Léger and Hesse

Family **Telomyxidae** Léger and Hesse

Genus **Telomyxa** Léger and Hesse. The spore possesses two polar capsules. Each sporont produces 8, 16 or more sporoblasts and later spores. One species.

Telomyxa glugeiformis Léger and Hesse (Fig. 138, *y*). In the fat body of the larva of *Ephemera vulgata*. The spore measures 6.5 microns by 4 microns.

ORDER 4 **HELICOSPORIDIA**

This order has been created to include the interesting organism, Helicosporidium, observed by Keilin. Although quite peculiar in the structure of its spore, the organism seems to be best placed in the Cnidosporidia, if it is a protozoan.

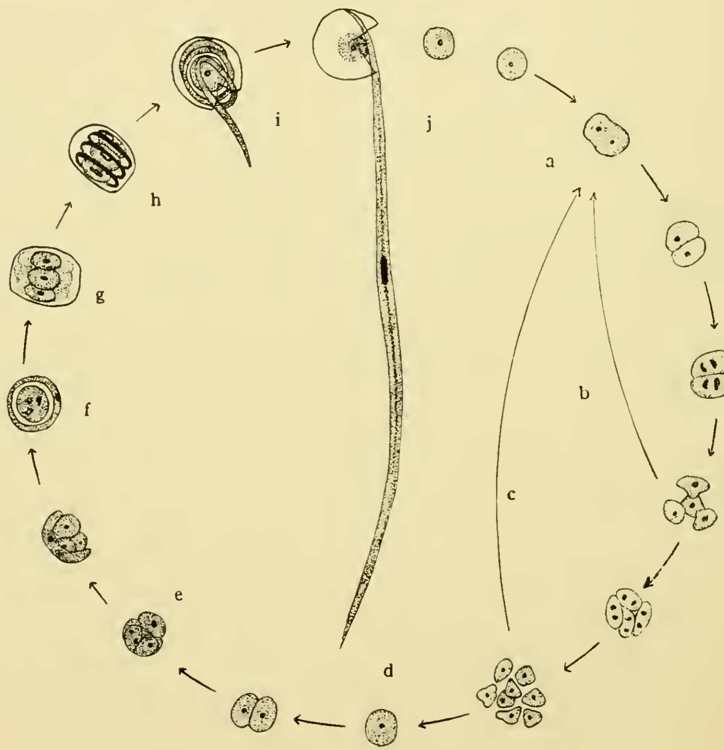


Fig. 139 Diagram showing the probable development of Helicosporidia. × about 1600. (After Keilin).

a–c, schizont and stages in schizogony; d, sporont (?); e, three stages in formation of four-celled stage; f, hypothetical stage; g, young spore before the spiral filament is formed; h, mature spore; i, j, opening of spore and liberation of sporozoites. a–h, in living host larva; i, j, in dead host larva.

The minute spore is composed of a thin membrane of one piece and of three uninucleate sporoplasms, around which is coiled a long thick filament. Young trophozoites are found in the host tissues or body cavity. They undergo schizogony, at the end of which uninucleate sporonts become differentiated. A sporont divides apparently twice and thus forms four small cells which develop into a spore. The complete life-history is still unknown.

Genus **Helicosporidium** Keilin. Parasitic in insects. Schizogony and sporogony. The spore with central sporoplasms and a single thick coiled filament. One species.

Helicosporidium parasiticum Keilin (Fig. 139). In the body cavity, fat body, and nervous sytem of the larva of *Dasyhelea obscura* (Diptera), also in *Mycetobia* *pallipes* (Diptera), and *Hericia hericia* (Acarina), all of which inhabits wounds of elm and horse-chestnut trees. The schizont is minute. The spore measures 5 to 6 microns in diameter; extruded filament 60 to 65 microns long by 1 micron thick.

References

Keilin, D. 1921 On the life-history of *Helicosporidium parasiticum*. Parasit., Vol. 13.

Kudo, R. 1924 A biologic and taxonomic study of the Microsporidia. Illinois Biol. Monogr., Vol. 9.

CHAPTER XXVI

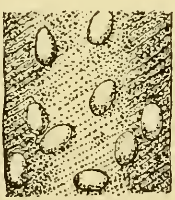
SUBCLASS 3 **ACNIDOSPORIDIA** CÉPÈDE

The sporozoa which are provisionally grouped here are mostly incompletely known, although some of them are widely distributed among the higher vertebrates. They possess spores which are quite simple in their structure, while their development is so far as is known wholly different from that of the Telosporidia. Two orders make up the subclass.

Muscle parasites of higher vertebrates	Order 1 Sarcosporidia
Parasites of invertebrates and fish	Order 2 Haplosporidia

ORDER 1 **SARCOSPORIDIA** BALBIANI

These Sporozoa are characteristic muscle parasites of mammals, although reptiles and birds have also been found to harbor them. The spore which has been known as "Rainey's


a

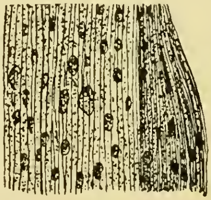

b

Fig. 140 a. *Sarcocystis tenella* in the wall of oesophagus of sheep.
b. *S. miescheriana* in the muscle of pig. Both natural size.
(After Schneidemühl from Doflein).

corpuscle," is crescent-shaped. One end is rounded and the other pointed. Near the former end there is a single nucleus, and the cytoplasm contains numerous granules. Infection of a new host begins with the entrance of spore into the digestive tract of a specific animal through the mouth. The delicate spore membrane ruptures and the sporozoite is liberated, which enters the gut-epithelium. After multiplying in this situation, the organism makes its way into the muscular tissue. At the beginning the parasitic mass is an elongated multinucleate body which may or may not divide into as many uninucleate bodies as there are nuclei. These become the centers of infection in other muscle fibers. Some trophozoites grow in size and the body becomes divided into parts, in each of which spores are formed (Fig. 141). According to some authors, the spores themselves are capable of fission. The host muscle fiber harboring the trophozoite, may vary in size from microscopic to as large as 5 centimeters (Fig.

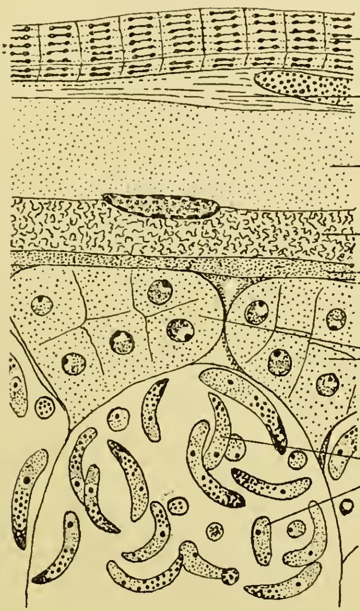


Fig. 141 Schematic drawing showing part of a cyst of *Sarcocystis tenella* in sheep. × about 1000 (After Alexeieff).

140). They are cylindrical with more or less pointed extremities and with a somewhat lobulated surface, and opaque whitish. They were formerly called "Miescher's tubes" (Fig. 140).

As to the pathogenic effect of the parasites upon the host animal, fatal cases are not uncommon. In heavily infected animals extensive muscular degeneration appears and the hosts die, soon or later, from the infection. One peculiarity of the Sarcosporidia is that these organisms contain certain toxin, to which Laveran and Mesnil gave the name **sarcotoxin,** and which when injected is highly toxic to other animals. The order is represented by one genus.

Genus **Sarcocystis** Lankester. Numerous species have been described from various mammals on the basis of difference in host species and slight difference in the dimensions of the spore. They are, however, morphologically indistinguishable from one another.

Sarcocystis lindemanni (Rivolta). In man.
Sarcocystis tenella Railliet (Figs. 140, *a*; 141). In sheep.
Sarcocystis miescheriana Kühn (Fig. 140, *b*). In pigs.
Sarcocystis muris Blanchard. In rats and mice.
Sarcocystis bertrami Doflein. In horses.
Sarcocystis cuniculi Brumpt. In rabbits.
Sarcocystis rileyi Stiles. In ducks.

ORDER 2 **HAPLOSPORIDIA** LÜHE

This order includes those sporozoans which produce simple spores. In some species the spores may resemble superficially those of the Microsporidia, but do not possess the polar capsule or the filament. The boundaries and affinities of this order to other groups are indistinctly known.

The Haplosporidia are cytozoic, histozoic, or coelozoic parasites of invertebrates and lower vertebrates. The spore is spherical or ellipsoidal in form and covered by a resistant membrane which may possess ridges or may be prolonged into a more or less long tail-like projection. In a few species the spore membrane possesses a lid which, when opened, will enable the sporoplasm to emerge as an amoebula. The sporoplasm is uninucleate and fills the intrasporal cavity.

The development of a haplosporidian, *Ichthyosporidium giganteum*, as worked out by Swarzcewsky, is as follows (Fig. 142): The spores germinate in the alimentary canal of the host fish and the sporoplasms make their way to the connective tissue of various organs (*a*). These amoebulae grow and their nuclei multiply in number, thus forming plasmodia. The plasmodia divide into smaller bodies, while the nuclei continue to divide (*b-e*). Presently the nuclei become paired (*f*, *g*) and the nuclear membranes disappear (*h*). The plasmodia now break up into numerous small bodies, each of which contains one set of the paired nuclei (*i*, *j*). This is the sporont (*j*) which develops into two spores by further differentiation (*k-o*).

Several genera have been recorded. A few genera will be briefly mentioned here.

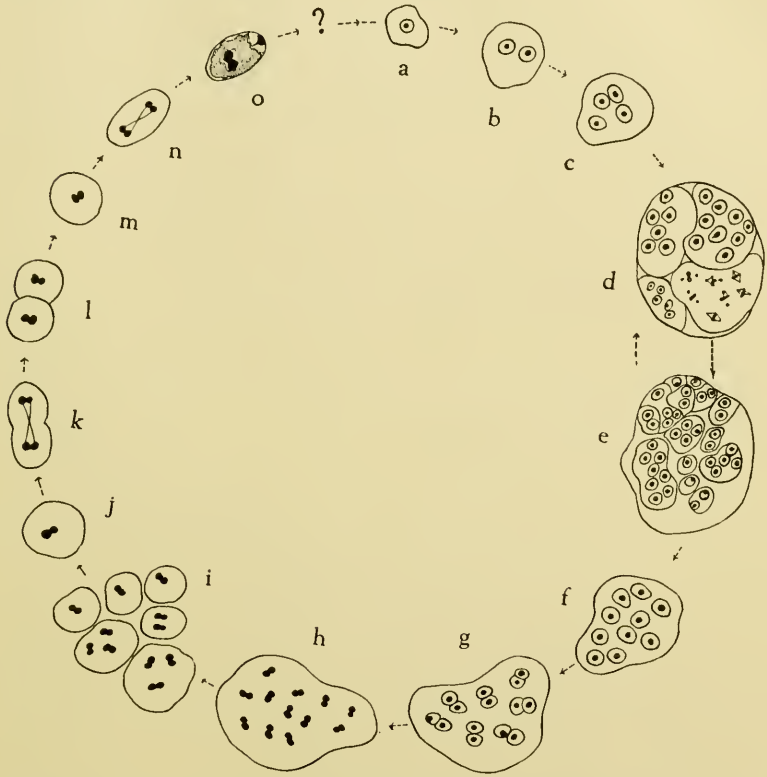


Fig. 142 The development of *Icthyosporidium giganteum*. Variously magnified. (After Swarczewsky).
a–e, schizogony; f–n, sporogony; o, a stained spore (× about 1275).

Genus **Haplosporidium** Caullery and Mesnil. After developing into a large form, the plasmodium divides into uninucleate bodies, each of which develops into a spore. The spore is truncate at one end where a lid occurs. The envelope is sometimes prolonged into processes. In salt and fresh water annelids and molluscs.

Haplosporidium chitonis (Lankester) (Fig. 143, *a, b*). In the liver and connective tissue of Chiton, *Craspido chilus cinereus.* The spore proper is oval and measures 10 microns by 6 microns. With two prolonged projections of envelope.

Haplosporidium limnodrili Granata (Fig. 143, *c*). In the gut-epithelium of *Limnodrilus udekemianus.* The spore measures 10 to 12 microns long by 8 to 10 microns wide.

Haplosporidium nemertis Debaisieux (Fig. 143, *d*). In the connective tissue of *Lineus bilineatus.* The spore is oval with a flat operculum, but without any projections, and measures 7 microns by 4 microns.

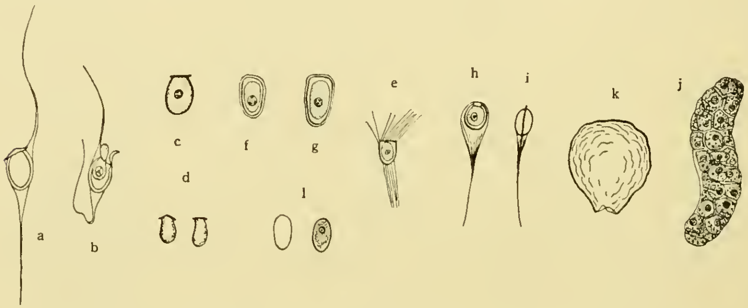


Fig. 143 a, b. *Haplosporidium chitonis.* ×500 (After Pixell-Goodrich). a, fresh and b, pressed and stained spore.
c. A spore of *H. limnodrili.* ×500 (After Granata).
d. Two spores of *H. nemertis.* ×500 (After Debaisieux).
e. A spore of *H. heterocirri.* ×500 (After Caullery and Mesnil).
f. A spore of *H. scolopli.* ×500 (After Caullery and Mesnil).
g. A spore of *H. vejdovskii.* ×500 (After Caullery and Mesnil).
h, i. Different views of spore of *Urosporidium fuliginosum.* ×500 (After Caullery and Mesnil).
j, k. *Bertramia asperospora.* ×520 (After Minchin). j, cyst with spores; k, empty cyst.
l. Spores of *Coelosporidium periplanetae.* ×750.

Haplosporidium heterocirri Caullery and Mesnil (Fig. 143, *e*). In the gut-epithelium of *Heterocirrus viridis.*

Haplosporidium scolopli Caullery and Mesnil (Fig. 143, *f*). In *Scoloplos mülleri.*

Haplosporidium vejdovskii Caullery and Mesnil (Fig. 143, *g*). In a fresh-water oligochaete, *Mesenchytraeus flavus.*

Genus **Urosporidium** Caullery and Mesnil. Similar to Haplosporidium, but the spheroidal spore with a long projection.

Urosporidium fuliginosum Caullery and Mesnil (Fig. 143, *h*, *i*). In the body cavity of the polychaete, *Syllis gracilis*. Not common.

Genus **Anurosporidium** Caullery and Chappellier. Similar to Haplosporidium, but the operculate spore is spherical.

Anurosporidium pelseneeri Caullery and Chappellier. In the sporocyst of a trematode parasitic in *Donax trunculus*. Schizogony intracellular; the cysts extracellular. The spore is small, about 5 microns long.

Genus **Bertramia** Caullery and Mesnil. Parasitic in aquatic worms and rotifers. Sausage-shaped bodies occur in the body cavity of the host. The spherical spores which develop in them, possess a uninucleate sporoplasm and a well-developed membrane.

Bertramia asperospora (Fritsch) (Fig. 143, *j*, *k*). Parasitic in the body cavity of rotifers (Brachionus, Asplanchna, Synchaeta, Hydatina, etc.). Fully grown vermicular body measures 70 to 90 microns and contains 80 to 150 spores.

Bertramia capitellae Caullery and Mesnil. Parasitic in the annelid, *Capitella capitata*. Spore very small; 2.5 microns in diameter.

Bertramia euchlanis Konsuloff. In the body cavity of the rotifier, belonging to the genus Euchlanis.

Genus **Ichthyosporidium** Caullery and Mesnil. Parasitic in fish. Often looked upon as Microsporidia, as the organism develops into large bodies in the body muscles, connective tissue, or gills, which appear as conspicuous "cysts." The latter are surrounded by a thick wall and contain numerous spores.

Ichthyosporidium giganteum (Thélohan) (Fig. 142). In the various organs of *Crenilabrus melops* and *C. ocellatus*. The cysts vary 30 microns to 2 mm. in diameter. The spore measures 5 to 8 microns long.

Ichthyosporidium hertwigi Swarczewsky. In *Crenilabrus paro*. The organism produces cysts which measure 3 to 4 mm. in diameter on the gills of the host fish. The spore measures 6 microns long.

Genus **Coelosporidium** Mesnil and Marchoux. Parasitic in the body cavity of Cladocera or the Malpighian tubules of the cockroach. Body small, forming cysts. The spore has a slight resemblance in its appearance to a microsporidian spore, but without a filament.

Coelosporidium periplanetae (Lutz and Splendore) (=*C. blattellae* Crawley) (Fig. 143, *l*). In the Malpighian tubules of various species of the cockroach. Common and cosmopolitan.

References

Alexeieff, A. 1913 Recherches sur Sarcosporidies. Arch. Zool. Exper., T. 51.

Caullery, M. and F. Mesnil. 1905 Recherches sur les Haplosporidies. Ibid., T. 4.

Crawley, H. 1914 The evolution of *Sarcocystis muris* in the intestinal cells of the mouse. Proc. Acad. Nat. Sci., Philadelphia. Vol. 66.

Lambert, S. W. Jr. 1927 Sarcosporidial infection of the myocardium in man. Amer. Jour. Path., Vol. 3.

Swarczewsky, R. 1914 Ueber den Lebenscyklus einiger Haplosporidien. Arch. f. Protistenk., Vol. 33.

Teichmann, E. 1912 Sarcosporidia. Prowazek's Handbuch der Path. Protozoen., Vol. 1.

Weissenberg, R. 1921 Fischhaplosporidien. Ibid., Vol. 3.

CHAPTER XXVII

SUBPHYLUM 2 **CILIOPHORA** DOFLEIN

THE CILIOPHORA possess cilia which serve as cell-organs of locomotion and food-capture. In Suctoria the cilia are absent in the adult stage, but always present during the developmental stages. The members of this subphylum possess a unique organization not seen in the Plasmodroma. Except a small group (Protociliata), the Ciliophora contain two kinds of nuclei, the macronucleus and the micronucleus. The former is large and massive, and controls the metabolic activities of the organism, while the latter is minute and usually vesicular or less compact, and is concerned with the reproductive processes. Nutrition is holozoic or parasitic. Sexual reproduction is mainly by conjugation. Asexual reproduction is by binary fission or budding. The majority are free-living and free-swimming, while the Suctoria are ordinarily attached forms. A number of parasitic forms occur also within this group.

The Ciliophora are ordinarily subdivided into two classes:

Cilia present throughout trophic life........................Class 1 Ciliata
Adult with tentacles; cilia only while young.................Class 2 Suctoria

CLASS 1 **CILIATA** BÜTSCHLI

The class Ciliata includes Protozoa of various habitats and body structures. All members possess cilia or cirri during the trophic stage of life. They inhabit all sorts of fresh and salt water bodies by free-swimming, creeping, or being attached to other objects. Some are parasitic in animals. Free-swimming forms are usually spherical to elliptical, while the creeping forms are, as a rule, dorso-ventrally flattened.

The **cilia** are extremely fine and comparatively short, and are arranged in rows. In some forms they diminish in number and are replaced by **cirri.** The cilia are primarily the organelles of locomotion, but secondarily through their movements bring the food matter into the cytostome. The food of Ciliata consists of small plant and animal organisms which ordinarily abound in the water. Thus their nutrition is holozoic. The ciliates vary in size from less than 10 microns up to 2 mm. in large forms (as in an extended Spirostomum). The cytoplasm is distinctly differentiated into the ectoplasm and the endoplasm. The ectoplasm gives rise to cilia and trichocysts and is covered by a pellicle. The endoplasm contains nuclei, food vacuoles, contractile vacuoles, pigment granules, crystals, etc. In the majority of the ciliates, the anterior and posterior extremities are permanent and distinct. In all cytostome-possessing forms, the oral and aboral surfaces are distinguishable, while in numerous creeping forms the dorsal and ventral sides are differentiated.

The body is covered by a very thin yet definite membrane, the **pellicle,** which is ordinarily uniformly thin and covers the entire body surface so closely that it is not recognizable in life. In some forms, such as Coleps, it develops into numerous platelets and in others, such as Trichodina, into hook-like processes. The outer half of the ectoplasm may show alveolar structure which, in section, exhibits radiating and parallel lines. In this portion the myonemes are lodged. The deeper layer of the ectoplasm is structureless and free from granules. In the ectoplasm are embedded the basal granules of cilia, which are arranged in longitudinal, oblique, or spiral rows. The cilia may fuse to form cirri, membranellae, and undulating membranes which are invariably present in certain groups. In Euciliata contractile vacuoles with one to several radiating canals are one of the prominent structures. The endoplasm is more fluid in nature and the ground substance is finely granulated or reticulated. It undergoes rotation movement, called cyclosis.

Two types of nuclei are present in all Euciliata. The massive **macronucleus** is of various forms. In Paramecium it is oblong; in Vorticella it is band-form, often curved; in Stentor it is beaded. The chromatin granules fill compactly the intranuclear space. The macronucleus multiplies by amitosis as was stated before. The **micronucleus** is ordinarily so minute that it is difficult to see in a living specimen. It is spherical and usually vesicular in structure, although in some it appears to be compact, and consists of a centrally located endosome, the nucleoplasm, and the membrane. The number of the micronucleus present in an individual varies: thus, one in *Paramecium caudatum*; two in *P. aurelia*; three in Spirochona; four in *Paramecium multimicronucleatum*; up to as many as 28 in *Stentor roeseli*. At the time of reproduction it increases in size and divides mitotically. During conjugation it apparently undergoes a meiotic division.

The Protociliata possess from one to many hundreds of nuclei of a uniform structure and numerous ovoid or spindle-shaped bodies, the nature of which is open to speculation. Some authors think that they are nuclei—micronuclei (after Hickson) or macronuclei (after Konsuloff). Metcalf considers that each nucleus possesses both metabolic chromatin and reproductive chromatin, the former being seen as large flattened peripheral masses and the latter, as smaller spheroidal granules.

In all except a comparatively small number of astomous forms, there is a **cytostome** located either at the anterior end or between this point and the middle of the body. In its simplest form the cytostome is represented by a small opening on the pellicle, which may or may not be closed when the animal is not feeding. The cytostome opens into the **cytopharynx** (or gullet), a canal which ends in the deeper portion of the endoplasm. In the cytopharynx there may be present an undulating membrane to facilitate the intaking of the food. Occasionally the cytostome is surrounded by trichites (p. 34). When the cytostome is not at the anterior region as for instance in Paramecium, there is a **peristome** (or oral groove) which starts at the anterior end and runs posteriorly. The ridges of the peristome are ciliated so that food particles are thrown down along it and ultimately into the cytostome which is located at its posterior end. Solid waste particles are extruded from the **cytopyge**, or cell-anus, which is usually noticeable only at the time of actual defecation (p. 34).

Following Metcalf, the Ciliata are here divided into two subclasses:

Two to many nuclei of one type; sexual reproduction copulation..... ....Subclass 1 Protociliata
Nuclei of two types: macronucleus and micronucleus; sexual reproduction conjugation..........................Subclass 2 Euciliata

SUBCLASS 1 **PROTOCILIATA** METCALF

The members of this group are parasitic in the intestine of Amphibia with the exception of a few species which occur in the intestine of a fish. The body is leaf-like or ellipsoidal, and covered uniformly by cilia of equal length. There is no cytostome and the nutrition is parasitic. The number of nuclei varies from two to several hundreds, and the nuclei are of one type. Asexual reproduction is by binary fission. In a number of species copulation of the gametes has been observed. Encystment is common. One family.

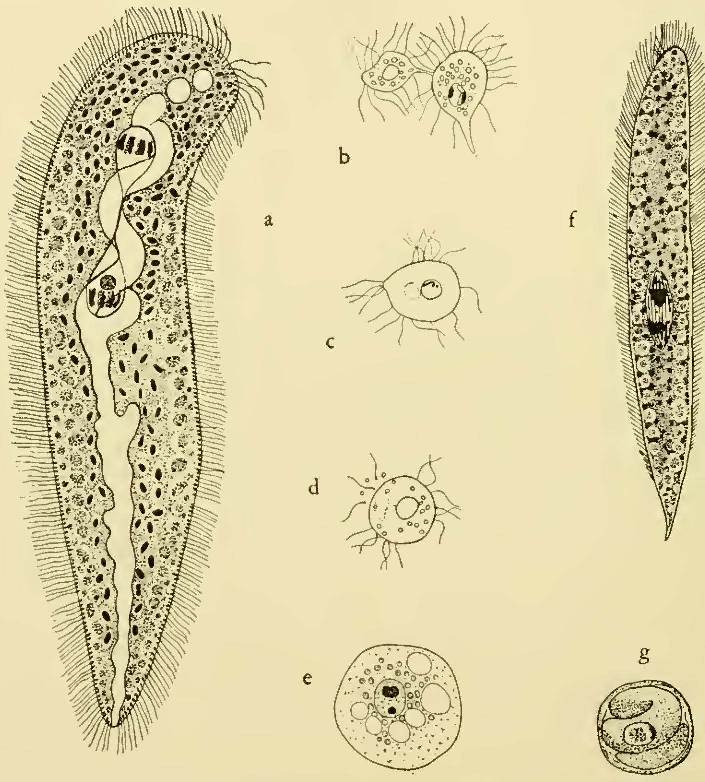


Fig. 144 a–e. *Protoopalina intestinalis.* (After Metcalf). a, stained trophozoite (×265); b–e, stages in anisogamy. f, g. *P. saturnalis.* ×400 (After Léger and Duboscq). g, cyst.

Family **Opalinidae** Claus

Genus **Protoopalina** Metcalf. The body cylindrical or spindle-shaped, circular in cross-section. Two similar nuclei which are invariably in a stage of mitotic division, are conspicuously present. In the rectum of various species of Amphibia with one exception.

Protoopalina intestinalis (Stein) (Fig. 144, *a-e*). In the intestine of various species of frogs and toads.

Protoopalina saturnalis Léger and Duboscq (Fig. 144, *f, g*). In the intestine of the marine fish, *Box boops*.

Protoopalina mitotica (Metcalf) (Fig. 145, *a*). Body 300 microns long by 37 microns broad. In the intestine of *Ambystoma tigrinum*.

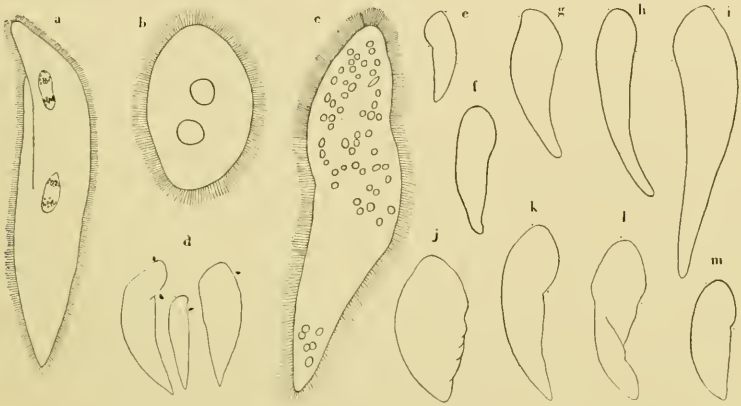


Fig. 145 a. *Protoopalina mitotica.* ×150.
b. *Zelleriella scaphiopodos.* ×150.
c. *Cepedia cantabrigensis.* ×150.
d. *Opalina hylaxena.* ×150.
e–m. *O. obtrigonoidea.* ×40. e–i, from *Bufo fowleri;* j–m, from *Rana pipiens.* (All after Metcalf).

Genus **Zelleriella** Metcalf. The body is greatly flattened. Two similar nuclei which are in a mid-mitotic condition. All in Amphibia.

Zelleriella scaphiopodos Metcalf (Fig. 145, *b*). In *Scaphiopus solitarius*. Body about 150 microns long by 90 microns broad by 13 microns thick.

Genus **Cepedia** Metcalf. The body is cylindrical or pyriform as in Protoopalina, but contains many similar nuclei. All in Amphibia.

Cepedia cantabrigensis Metcalf (Fig. 145, *c*). In *Rana cantabrigensis*. Length 350 microns, width 84 microns.

Genus **Opalina** Purkinje and Valentin. Body highly flattened. Multinucleate. In amphibians. Numerous species.

Opalina hylaxena Metcalf (Fig. 145, *d*). In *Hyla versicolor*. Larger individuals measure about 420 microns in length, 125 microns in width, and 28 microns in thickness.

Opalina obtrigonoidea Metcalf (Fig. 145, *e–m*). Length 400 to 840 microns, breadth 175 to 180 microns, thickness 20 to 25 microns. In various species of frogs and toads (Rana, Hyla, Bufo, Gastrophryne, etc.).

References

Calkins, G. N. 1926 The biology of the Protozoa. Philadelphia.

Doflein, F. and E. Reichenow. 1929 Lehrbuch der Protozoenkunde. Jena.

Kent, W. S. 1880 to 1882 A manual of Infusoria.

Metcalf, M. M. 1923 The opalinid ciliate infusorians. Smithsonian Inst., U. S. Nat. Museum, Bull., No. 120.

Stein, F. 1867 Der Organismus der Infusionsthiere. Vol. 2.

Stokes, A. C. 1888 A preliminary contribution toward a history of the fresh-water Infusoria of the United States. Jour. Trenton Natural Hist. Soc., Vol. 1.

CHAPTER XXVIII

SUBCLASS 2 **EUCILIATA** METCALF

THE EUCILIATA are subdivided into five orders according to the arrangement of the cilia, cirri, and adoral zone:

Without adoral zone . . . . Order 1 Holotrichida
With adoral zone
  Adoral zone turns to left
    Cilia over the entire body . . . . Order 2 Heterotrichida
    Cilia on body absent or a few . . . . Order 3 Oligotrichida
    Cilia or cirri on the ventral side only . . . . Order 4 Hypotrichida
  Adoral zone turns to right . . . . Order 5 Peritrichida

ORDER 1 **HOLOTRICHIDA** STEIN

The members of this order possess cilia which are uniformly distributed over the entire body surface. A cytostome may or may not be present. Adoral zone is never present. The position of the cytostome varies among different forms. In connection with the cytostome, there may be a proboscis in some forms and in one group the so-called pharyngeal apparatus may be well developed. Mode of nutrition is holozoic or parasitic. Asexual reproduction is usually by transverse fission. Sexual reproduction is ordinarily isogamous conjugation. Encystment is common. These Euciliata are parasites or free-living in all sorts of freshwater body and less frequently in marine water.

The order is here divided into three suborders.

Without cytostome . . . . Suborder 1 Astomina
With cytostome
  Cytostome usually closed; oral membrane absent . . . .
  . . . . Suborder 2 Gymnostomina
  Cytostome usually opened; oral membrane present . . . .
  . . . . Suborder 3 Trichostomina

Suborder 1 **Astomina** Cépède

Genus **Rhizocaryum** Caullery and Mesnil. One species, *R. concavum* (Fig. 146, *a*), an intestinal inhabitant of the marine worms, *Polydora caeca* and *P. flava*. Body ovoid with depressed ventral surface. Macronucleus branches out characteristically.

Genus **Bütschliella** Awerinzew. Body elongate cylindrical. Macronucleus elongated; several contractile vacuoles arranged in a longitudinal row.

Bütschliella opheliae Awerinzew (Fig. 146, *b*). In the marine worm, *Ophelia limacina*.

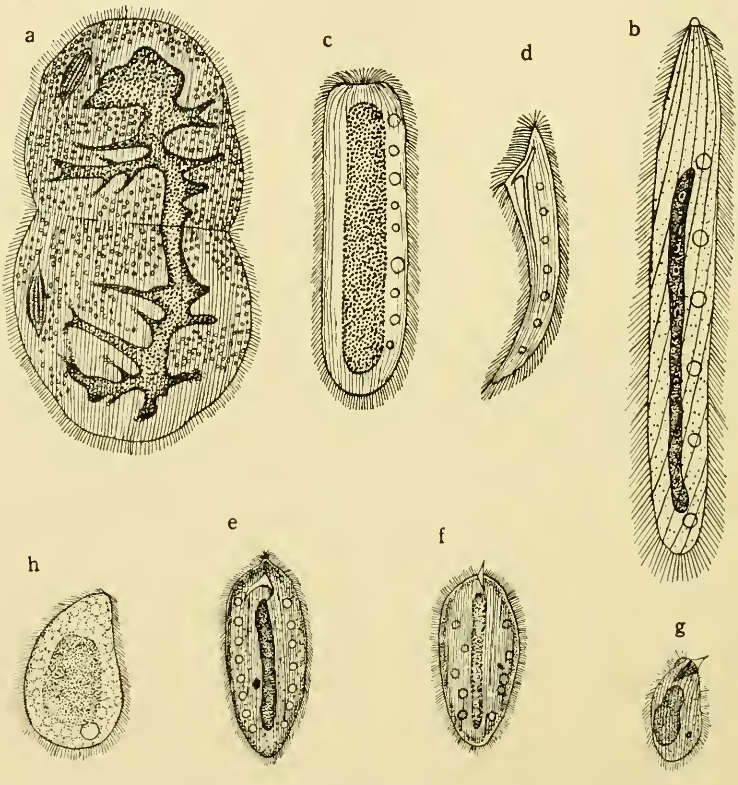


Fig. 146 a. *Rhizocaryum concavum*, dividing form. ×665.
b. *Bütschliella opheliae*. ×350.
c. *Anoplophrya naidos*. ×200.
d. *Mesnilella clavata*. ×200.
e. *Hoplitophrya lumbrici*. ×140.
f. *Maupasella nova*. ×280.
g. *Schultzellina mucronata*. ×665.
h. *Kofoidella eleutheriae*. ×265 (All from Cépède).

Genus **Anoplophrya** Stein. Body elongated vermiform with rounded ends. An elongated macronucleus irregularly outlined. Micronucleus small. Parasitic in the intestine of Annelida, Gastropoda, and Crustacea.

Anoplophrya naidos (Dujardin) (Fig. 146, *c*). In the digestive tract of the polychaete, *Nais serpentina*. Body about 200 microns long.

Genus **Mesnilella** Cépède. Elongated body similar to Anoplophrya, but containing a rigid rod.

Mesnilella clavata (Leidy) (Fig. 146, *d*). Found in the intestine of *Lumbricus variegatus*. Length up to 160 microns. With a number of contractile vacuoles arranged in a longitudinal row.

Genus **Hoplitophrya** Stein. Body oval. There is a protrusible chitinous structure embedded in the cytoplasm, which serves for attachment of the body to the intestinal epithelium of the host. Parasites of Lumbricus.

Hoplitophrya lumbrici (Dujardin) (Fig. 146, *e*). In the intestine of *Lumbricus terrestris*.

Genus **Maupasella** Cépède. With a spinous fixing cell-organ at the anterior end of the body. A number of myonemes run inward from the base. Parasitic in the intestine of Lumbricus.

Maupasella nova Cépède (Fig. 146, *f*). In the intestine of an African Lumbricus.

Genus **Schultzellina** Cépède. Similar to Maupasella, but attaching cell-organ making some angles with the main axis of the body.

Schultzellina mucronata Cépède (Fig. 146, *g*). In the intestine of the earthworm, *Allurus tetraedurus*.

Genus **Kofoidella** Cépède. Broadly pyriform organism, 30 to 80 microns long. A large macronucleus; a contractile vacuole in the posterior third.

Kofoidella eleutheriae Cépède (Fig. 146, *h*). Commonly found in the gastrovascular cavity of the medusa, *Eleutheria dichotoma*.

Genus **Intoshellina** Cépède. Body elongate, and ciliary rows are slightly spiral. Macronucleus long. Contractile vacuoles five to seven in number. A cell-organ of attachment, vestigial cytostome and cytopharynx at the anterior end.

Intoshellina maupasi Cépède (Fig. 147, *a*). In the intestine of *Tubifex* sp.

Genus **Haptophrya** Stein. Body elongate, uniformly ciliated; anterior end without neck-like constriction. On the ventral side there is a circular sucker surrounded by one or two rows of cilia; but no other fixing cell-organ. In the intestine of Amphibia.

Haptophrya michiganensis Woodhead (Fig. 147, *b*). In the intestine of the four-toed salamander, *Hemidactylium scutatum*. Frequent. Length 1.1 to 1.6 mm.

Genus **Sieboldiellina** Collin. Similar to Haptophrya, but with neck-like constriction and there is a single row of cilia around the ventral sucker. Without other fixing organ.

Sieboldiellina planariarum (Stein) (Fig. 147, *c*). In the gastrovascular cavity of Tuberllaria.

Genus **Lachmannella** Cépède. Without sucker, but fixing organ is present.

Lachmannella recurva (Claparède and Lachmann) (Fig. 147, *d*) in the gastro-vascular cavity of the turbellarian, *Planaria limacina*.

Genus **Steinella** Cépède. Sucker without encircling cilia; with two fixing cell-organs. One species in Tuberllaria.

Genus **Lada** Vejdovsky. Antero-ventral portion bears a large sucker surrounded by a thick ciliated horseshoe-shaped rim.

Lada wrzesniowskii Vejdovsky. In the oligochaete, *Phreatothrix pragensis*.

Genus **Cepedella** Poyarkoff. Body small, pyriform with a pointed anterior end, where there is a concavity for fixation of body, from which longitudinal myonemes arise. No contractile vacuole. Macronucleus globular.

Cepedella hepatica Poyarkoff. Body 16 to 26 microns long; intracellular parasite of the liver of *Sphaerium corneum*, a cyclad mollusc of France.

Genus **Herpetophrya** Siedlecki. Body ovoid, anterior end possesses a pointed, mobile, tactile (non-ciliated) cone. Contractile vacuoles absent. Macronucleus globular.

Herpetophrya astoma Siedlecki. In the body cavity of an annelid worm, Polymnia.

Genus **Perezella** Cépède. Body ovoid, the ventral surface is concave and serves as a sucker. Macronucleus ellipsoidal; a contractile vacuole at the posterior end.

Perezella pelagica Cépède (Fig. 147, *e*). A coelomic parasite of copepods (Clausia, Acartia, and Paracalanus).

Fig. 147 a. *Intoshellina maupasi.* ×280 (After Cépède).
b. *Haptophrya michiganensis.* ×34 (After Woodhead).
c. *Sieboldiellina planariarum.* × about 100 (After Cépède).
d. *Lachmannella recurva.* ×95 (After Cépède).
e. *Perezella pelagica.* ×340 (After Cépède).
f. *Collinia circulans.* (After Balbiani).
g, h. *Protophrya ovicola.* (From Cépède). h, a young *Littorina rudis* with *P. ovicola.* ×80.
i. *Orchitophrya stellarum.* ×865 (After Cépède).
j. *Monomastix ciliatus.* ×665 (After Roux).

Genus **Collinia** Cépède. Body ovoid; without cytostome. Cilia are arranged in longitudinal rows. One to several contractile vacuoles. Parasites in the coelom of fresh-water Crustacea (Gammarus, Neoniphargus, and Asellus.)

Collinia circulans (Balbiani) (Fig. 147, *f*). Polymorphic. In the blood vessel of *Asellus aquaticus*.

Genus **Protophrya** Kofoid. Body ellipsoidal to pyriform. Macronucleus elliptical; a micronucleus; contractile vacuole at the posterior end. One species.

Protophrya ovicola Kofoid (Fig. 147, *g*, *h*). Body about 60 microns long. Parasitic in the uterus of the mollusc, *Littorina rudis*.

Genus **Isselina** Cépède. Similar to Protophrya. One species in the mantle cavity of *Littorina obtusata*.

Genus **Orchitophrya** Cépède. Body pyriform; ciliary rows are curved. Macronucleus spherical.

Orchitophrya stellarum Cépède (Fig. 147, *i*). In the gonads of the echinoderm, *Asteracanthion* (*Asterias*) *rubens*.

Genus **Monomastix** Roux. Elongated cylindrical; body flattened; ciliation uniform. Pointed anterior end with trichites and a long flagellum. Two macronuclei and micronuclei. Free-living. Saprozoic.

Monomastix ciliatus Roux (Fig. 147, *j*). Body about 75 microns long by 14 microns broad. In stagnant water.

Suborder 2 **Gymnostomina** Bütschli

The Holotrichida placed in this suborder possess a cytostome which is closed except at the time of actual food taking. In several genera longer cilia form a peristomal ring; the cytostome is, as a rule, terminal. The body form is usually definite, a distinct pellicle being present in all forms, and in some, platelets are developed.

The suborder is divided into four families:

Thick cortex on various parts of body; peristome narrow and long;
    all parasitic..............................Family 1 Nicollellidae
No thick cortex
  With terminal cytostome......................Family 2 Holophryidae
  Cytostome not terminal
    Anterior end with proboscis..................Family 3 Trachelinidae
    Usually with an oral basket; no proboscis......Family 4 Chilodontidae

Family 1 **Nicollellidae** Chatton

Genus **Nicollella** Chatton and Pérard. Body elongate ovoid. The thickened cortex on the anterior half of the oral surface.

Nicollella ctenodactyli Chatton and Pérard (Fig. 148, *a*). In the caecum and large intestine of *Ctenodactylus gundi* of Tunisia.

Genus **Collinella** Chatton and Pérard. Body form similar to Nicollella, but the thickened cortex reaches the posterior end on the oral surface.

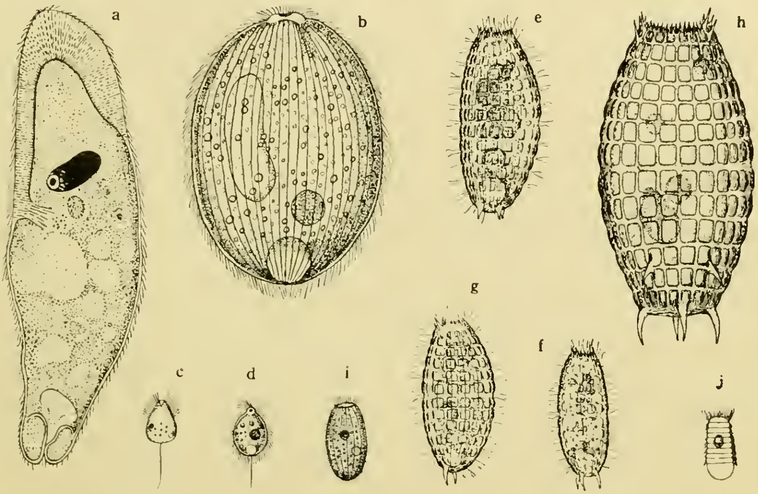


Fig. 148 a. *Nicollella ctenodactyli.* ×125 (After Chatton and Pérard).
b. *Holophrya discolor.* ×250 (After Bütschli).
c. *Balanitozoon agile.* ×400 (After Stokes).
d. *Urotricha farcata.* ×350 (After Lieberkühn from Bütschli).
e. *Coleps hirtus.*
f. *C. elongatus.*
g. *C. bicuspis.*
h. *C. octospinus.* All four ×400 (After Noland).
i. *Plagiopogon coleps.* ×125 (After Perty).
j. *Metacystis truncata.* ×200 (After Cohn).

Collinella gundii Chatton and Pérard. In the caecum and large intestine of *Ctenodactylus gundi.*

Genus **Pycnothrix** Schubotz. Elongated body with thickened cortex on both oral and aboral surfaces.

Pycnothrix monocystoides Schubotz. In the intestine of *Procavia capensis* of Africa.

Family 2 **Holophryidae** Schouteden

Genus **Holophrya** Ehrenberg. Body ovate or globose. Ciliation uniform. Cytostome simple, without any special ciliary ring around it. Fresh or marine water.

Holophrya discolor Ehrenberg (Fig. 148, *b*). Body ovoid to subspherical, about 150 microns long. In still fresh water.

Genus **Balanitozoon** Stokes. Oval or rounded triangular in shape. Cilia only on the anterior half. A single nucleus, contractile vacuole, and cytopharynx. A long seta at the posterior extremity. Swimming as well as leaping movement. Fresh water.

Balanitozoon agile Stokes (Fig. 148, *c*). Body small, about 15 microns long. In standing water with Sphagnum.

Genus **Urotricha** Claparède and Lachmann. Body oval or ellipsoidal in form; ciliation uniform; one or more posterior setae as long as the body. A small circular cytostome at anterior end. Contractile vacuole posterior. Fresh water.

Urotricha farcata Claparède and Lachmann (Fig. 148, *d*). Length about 24 microns. Holozoic on bacteria. Pond-water and infusion.

Genus **Actinobolus** Stein. Body ovate or spherical. Cilia are uniformly short; extensible tentacles among the cilia. Contractile vacuole conspicuous; macronucleus a curved band.

Actinobolus radians Stein. In fresh water among Lemnae.

Genus **Coleps** Ehrenberg. Body barrel-shaped and constant; covered with platelets which are variously sculptured. Spinous projections often at the posterior end. The cytostome is surrounded by slightly larger cilia. Division stages common. Fresh or salt water. Several species.

Coleps hirtus (Müller) (Fig. 148, *e*). Body 40 to 65 microns long. 20 longitudinal rows of platelets and 3 posterior spines.

Coleps elongatus Ehrenberg (Fig. 148, *f*). Body slender, 40 to 55 microns long. 13 rows of platelets; 3 posterior spines.

Coleps bicuspis Noland (Fig. 148, *g*). Body about 55 microns long. With two posterior spines and 16 longitudinal rows of platelets.

Coleps octospinus Noland (Fig. 148, *h*). Body large, 100 to 110 microns long. With eight posterior spines. All fresh water.

Genus **Tiarina** Bergh. Somewhat similar to Coleps, but the posterior end pointed. Marine. Rare.

Genus **Plagiopogon** Stein. Similar to Coleps, but with rounded posterior end. Fresh or salt water.

Plagiopogon coleps Stein (Fig. 148, *i*). Body about 80 microns long.

Genus **Metacystis** Cohn. Body oblong, symmetrical, definite; the entire surface ciliated, except the posterior end. Ciliary circle around the cytostome.

Metacystis truncata Cohn (Fig. 148, *j*). About 40 microns long. Among decaying marine algae.

Genus **Trachelocerca** Ehrenberg. Body highly extensible, flask-shaped; the anterior portion forms a long flexible neck-like process. The cytostome is often quadrangular in form. Numerous contractile vacuoles irregularly situated.

Trachelocerca phoenicopterus Cohn (Fig. 149, *a*). In salt water. Body extended measures 1.7 mm. in length.

Genus **Trachelophyllum** Claparède and Lachmann. Elongated, ribbon-like, flexible. Peristomal ciliary ring is well developed. A knob on the end of a neck-like proboscis. Contractile vacuole at the posterior end. Numerous micronuclei. Fresh or salt water.

Trachelophyllum clavatum Stokes (Fig. 149, *b*). Length about 180 microns. In fresh water.

Genus **Lacrymaria** Ehrenberg. Body flask-shaped but changeable, with a comparatively long contractile proboscis. Posterior end is rounded. Cytostome round. There is a neck-like constriction with a circle of longer cilia around the cytostome. Cytopharynx. Fresh or salt water.

Lacrymaria olor Müller (Fig. 149, *c*, *d*). Highly contractile. When extended the body measures 400 microns in length. Fresh water.

Lacrymaria lagenula Claparède and Lachmann (Fig. 149, *e*, *f*). Length 90 to 160 microns. Marine.

Lacrymaria coronata Claparède and Lachmann (Fig. 149, *g*). Length 85 microns. Marine.

Genus **Chaenia** Quennerstedt. Elongated body highly contractile; inconspicuous cytostome widely dilated during the passage of food material. Peristomal ciliary circle present, but no neck-like constriction, nor proboscis.

Chaenia teres Dujardin (Fig. 149, *h*). Length about 250 microns. In salt water.

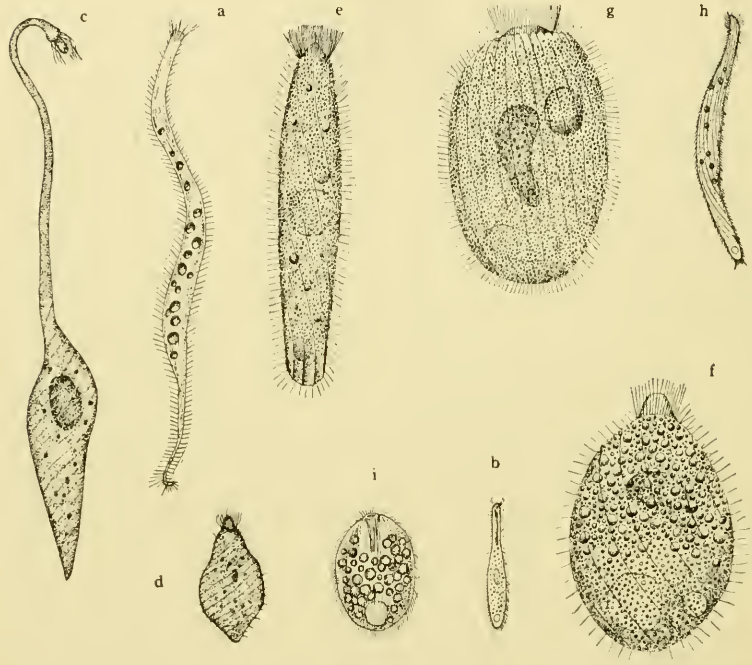


Fig. 149 a. *Trachelocerca phoenicopterus.* ×40 (After Calkins).
b. *Trachelophyllum clavatum.* ×75 (After Stokes).
c, d. *Lacrymaria olor.* ×200 (After Calkins).
e, f. *L. lagenula.* ×300 (After Calkins).
g. *L. cornata.* ×400 (After Calkins).
h. *Chaenia teres.* ×140 (After Quennerstedt).
i. *Prorodon griseus.* ×250 (After Conn).

Genus **Prorodon** Ehrenberg. Body constant in form; ovate; rounded at the extremities. Cytopharynx conspicuous often with rod-like structures. A single contractile vacuole posterior. A massive macronucleus oval or band-form. Fresh or salt water.

Prorodon griseus Claparède and Lachmann (Fig. 149, *i*). Body oblong, about 50 to 70 microns long. Fresh water.

Genus **Ichthyophthirius** Fouquet. Body oval. Ciliation uniform; pellicle longitudinally striated. Cytostome at or near the anterior end, followed by a short cytopharynx with cilia. A single horseshoe-shaped macronucleus and a small micronucleus. Multiplication by binary fission during the actively motile

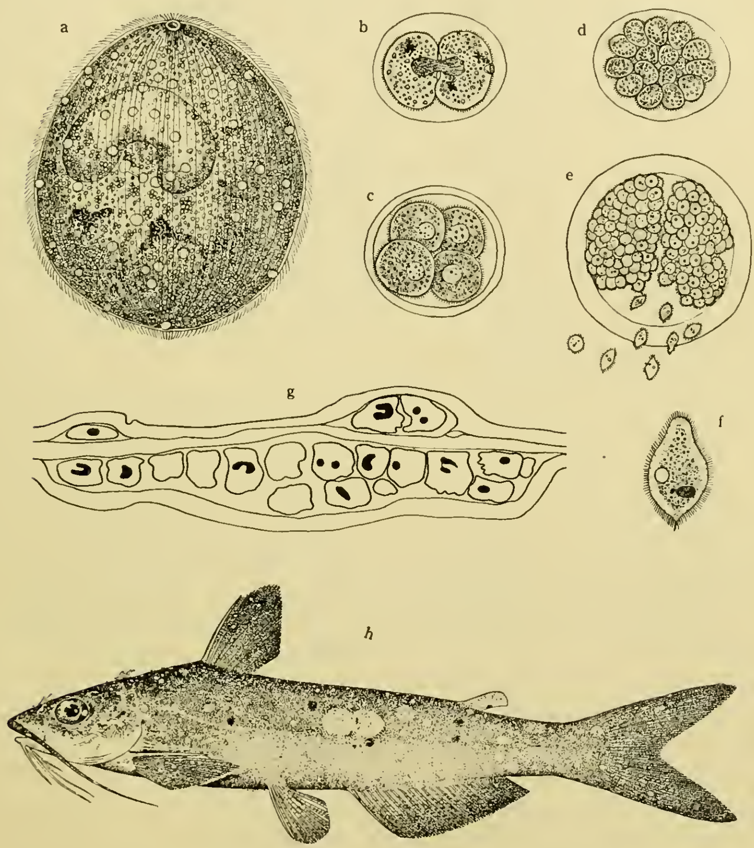


Fig. 150 *Ichthyophthirius multifiliis.* a, free-swimming individual (×75 after Bütschli); b–e, development within cyst; f, a young individual (×400 after Fouquet); g, section through fin of a carp showing numerous parasites (×10); h, a catfish, *Ameiurus albidus*, heavily infected by the parasites (after Stiles).

phase or by multiple division in the encysted condition, which produces two hundred or more individuals (30 to 45 microns long). Conjugation is also reported. Parasitic in the integument of numerous freshwater fishes in small ponds or especially in aquaria. Widely distributed.

Ichthyophthirius multifiliis Fouquet (Fig. 150). Body measures 300 to 800 microns in length. The ciliate attacks the epidermis or gills and forms pustules. When heavily infected, the host fish dies apparently from the infection.

Genus **Enchelys** Ehrenberg. The anterior portion is drawn out into flask-shaped body which is obliquely truncated. Peristomal cilia are more conspicuous than those of the general body surface. Free-living in fresh water. Several species.

Enchelys teres (Stokes) (Fig. 151, *a*). About 170 to 200 microns long. In standing water among decaying vegetation.

Enchelys truncata (Stokes) (Fig. 151, *b*). About 125 microns long. In fresh water among dead leaves.

Genus **Enchelyodon** Claparède and Lachmann. Similar to Enchelys, but with long trichites around the cytopharynx. In salt or fresh water.

Enchelyodon farctus Claparède and Lachmann (Fig. 13, *d*). Body about 240 microns long. In marshes.

Genus **Lagynus** Quennerstedt. Body elongated; anterior end sharply truncated. The cytopharynx is rather conspicuous. Encystment observed. In fresh or salt water.

Lagynus elegans Engelmann (Fig. 151, *c*). Body about 85 to 175 microns long. Fresh water.

Genus **Spathidium** Dujardin. Flask- or sack-shaped; anterior end is slightly narrowed into a neck with a truncate extremity. Cytostome occupies the whole of the end and is ordinarily closed. Contractile vacuole posterior; elongate macronucleus and several micronuclei. Trichites around the cystotome and also scattered throughout the endoplasm (Fig. 13, *c*).

Spathidium spathula (Ehrenberg) (Fig. 151, *d*, *e*). Body up to 250 microns in length. Fresh water.

Genus **Didinium** Stein. Body barrel-shaped. Two girdles of long cilia, but no other cilia. The anterior end possesses a proboscis-like elevation, at the end of which is located an expansible cytostome. Macronucleus is horseshoe-shaped. A contractile vacuole posterior. Feeding on other ciliates, especially Paramecium. Fresh water.

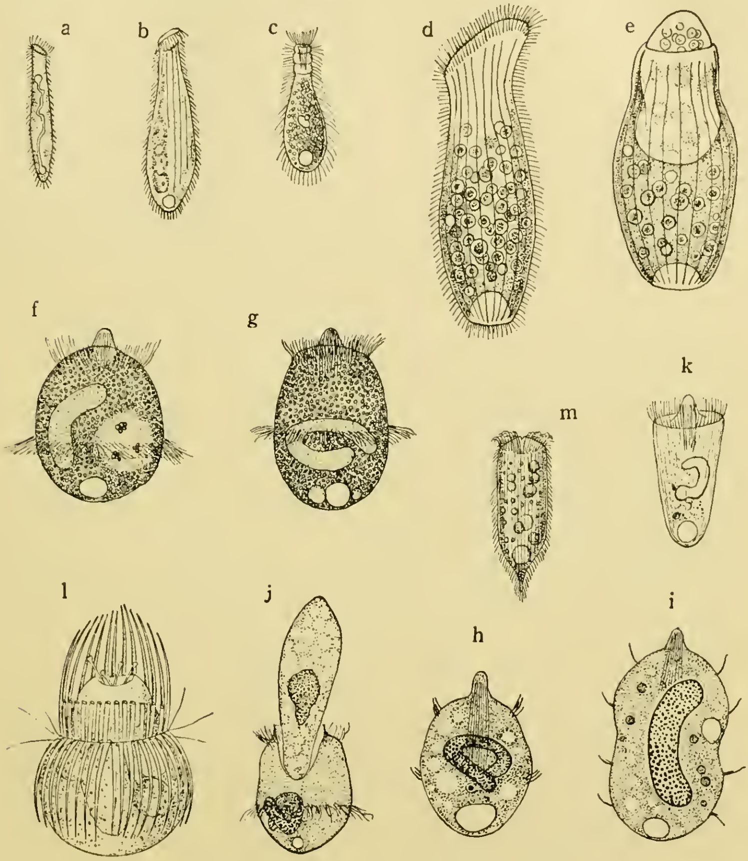


Fig. 151
- a. *Enchelys teres.* ×100 (After Stokes).
- b. *E. truncata.* ×200 (After Stokes).
- c. *Lagynus elegans.* ×165 (After Engelmann).
- d, e. *Spathidium spathula.* ×200 (After Woodruff and Spencer). e, individual swallowing a Colpidium.
- f–j. *Didinium nasutum.* ×165. f, g, living specimens; h, a stained specimen; i, dividing form, stained; j, an individual swallowing *Paramecium caudatum.*
- k. *Monodinium balbianii.* ×285 (After Bütschli).
- l. *Mesodinium pulex.* ×665 (After Calkins).
- m. *Dinophrya lieberkühni.* ×300 (After Bütschli).

Dinidium nasutum (Müller) (Fig. 151, *f–j*). Body length 80 to 200 microns. Cysts common. In fresh water; often abundantly found in Paramecium cultures.

Genus **Monodinium** Fabre. Body somewhat similar to Didinium, but with a single girdle of cilia located at the anterior end.

Monodinium balbianii (Bütschli) (Fig. 151, *k*). About 70 microns long. Fresh water.

Genus **Mesodinium** Stein. Body spherical with a deep constriction, in which are located strong cilia. Anterior end is conical. Cytostome is connected with a cytopharynx. Four tentacle-like retractile processes occur around the cytostome. Nuclei similar to those of Didinium. Fresh or marine water.

Mesodinium pulex Claparède and Lachmann (Fig. 151, *l*). Length about 35 microns. In salt water.

Genus **Dinophrya** Bütschli. Body elongate; posterior end drawn out. Anterior end conical with a cytostome at its extremity. Besides being ciliated on general body surface, several girdles of long cilia near the anterior end. Ellipsoidal macronucleus central; a contractile vacuole posterior. Fresh water.

Dinophrya lieberkühni Bütschli (Fig. 151, *m*). Length 70 to 80 microns. In fresh water.

Family 3 **Tracheliidae** Kent

Cilia occur uniformly over the entire body surface except in a few forms in which they are considerably reduced. Anterior end is drawn out into a proboscis. The location of the cytostome is not constant, it may be on the proboscis, dorsal side, or ventral side.

Genus **Trachelius** Schrank. Body large, spherical to ellipsoidal. The anterior region is drawn out into a massive dorsally bent moveable proboscis. The cytostome is located on the ventral side at the base of the proboscis. Cytopharynx basketlike. Contractile vacuoles numerous; macronucleus central and simple or band-form. Movement slow. With spherical cyst.

Trachelius ovum Ehrenberg (Fig. 152, *a*). Body about 350 microns long. Fresh water.

Genus **Dileptus** Dujardin. Body much elongated, anterior end is drawn out into a long proboscis, on the ventral side of which is a row of long cilia. The open circular cytostome is situated at the base of the proboscis. Numerous contractile vacuoles on the dorsal side or scattered. The body surface is uniformly ciliated. Macronucleus moniliform. Conjugation. Spherical cysts. Fresh or salt water.

Dileptus anser Müller (Figs. 4, *b;* 152, *b*). Extended body 1 mm. or more in length. In fresh or salt water.

Genus **Lionotus** Wrzesniowski. Body elongated and flattened. Ventral surface flat, dorsal surface convex. The anterior end is drawn out into a proboscis and the posterior end terminates usually in a cone. A row of long cilia on the proboscis. The long slit-like cytostome is located on the ventral side of the proboscis and is ordinarily closed. One to many contractile vacuoles. Two spherical macronuclei. Fresh or salt water. Several species.

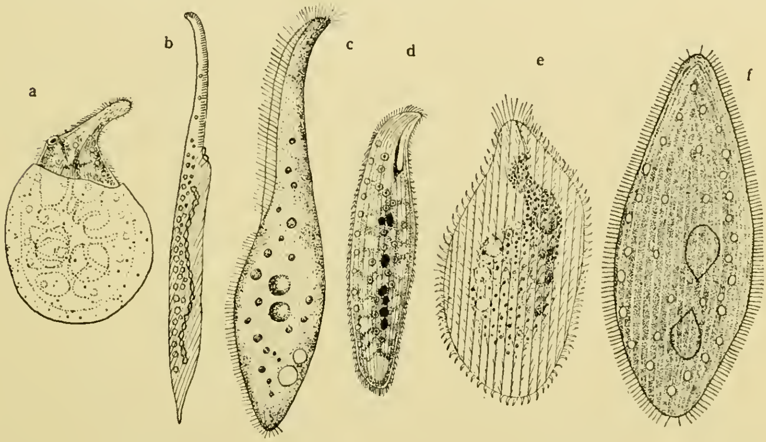


Fig. 152 a. *Trachelius ovum* emerging from a cyst. ×65 (After Bütschli).
b. *Dileptus anser.* ×50 (After Bütschli).
c. *Lionotus fasciola.* ×100 (After Calkins).
d. *Loxodes rostrum.* ×100 (After Bütschli).
e. *Loxophyllum setigerum* var. *armatum.* ×350 (After Calkins).
f. *Amphileptus branchiarum.* ×370 (After Wenrich).

Lionotus fasciola Ehrenberg (Fig. 152, *c*). Body large 200 to 600 microns long. In fresh or salt water.

Genus **Loxodes** Ehrenberg. Body elongated, flattened, and more or less constant in form. Ventral surface flattened with longitudinal rows of cilia, the dorsal surface convex. Stronger cilia are present on the margin. Anterior end is bent toward one side and just below it is a slit-like cytostome. Cytopharynx is small and indistinct. Numerous nuclei and contractile vacuoles. Fresh water.

Loxodes rostrum Müller (Fig. 152, *d*). Body about 300 to 375 microns long. In stagnant water.

Genus **Loxophyllum** Dujardin. Body flattened; ventral surface flat; dorsal surface convex. Anterior end narrowed; hyaline cytoplasm asymmetrically arranged. Cytostome straight slit-like with trichocysts on the border in papilla-like groups or scattered. Nucleus simple to moniliform. One to many contractile vacuoles, posterior. Fresh or salt water.

Loxophyllum setigerum var. *armatum* (Claparède and Lachmann) (Fig. 152, *e*). Body about 100 microns long. In salt water.

Loxophyllum meleagris Ehrenberg. Pond water.

Genus **Amphileptus** Ehrenberg. Body flask-shaped, somewhat compressed. Anterior end is drawn out into an acute proboscis at the base of which is located the cytostome. Contractile vacuole one to many. One or two macronuclei. Fresh or salt water.

Amphileptus claparedei Stein. Fresh or salt water.

Amphileptus branchiarum Wenrich (Fig. 152, *f*). On the skin and gills of the tadpole of common frogs (Rana). Swimming individuals killed with iodine, measure 100 to 135 microns long by 40 to 60 microns broad.

Family 4 **Chilodontidae** Bütschli

Body is usually flattened. Ciliation seems to be limited to the oral surface. Cytostome is surrounded by trichites, presenting a basket-like appearance. Free-living; a few parasitic.

Genus **Chilodon** Ehrenberg. Body small to medium large; on the whole dorso-ventrally flattened, flexible. Dorsal surface convex, ventral surface flat. Uniformly ciliated. Cytostome in the center of the anterior half and toward the left. Pharyngeal basket is protrusible beyond the cytostomal aperture. Contractile vacuole variable in number; macronucleus oval, central. Cysts oval. Common in fresh or salt water infusion.

Chilodon cucullulus Müller (Fig. 153, *a*). Length 100 to 300 microns. Fresh or salt water.

Chilodon vorax Stokes (Fig. 153, *b*). Length about 200 microns. Fresh water among algae.

Chilodon caudatus Stokes (Fig. 153, *c*). About 40 microns long. In standing water.

Chilodon fluviatilis Stokes (Fig. 153, *d*). About 50 microns long. Fresh water.

Chilodon cyprini Moroff (Fig. 153, *e*). Body about 50 to 70 microns long by 30 to 40 microns broad. In the integument and gills of the cyprinoid fishes. The organism, if freed from the host skin, dies in from 12 to 24 hours.

Genus **Nassula** Ehrenberg. Body large, oval to elongate, flexible. Usually brightly colored. Often flattened dorso-ventrally. The extremities are equally rounded. Cytostome toward the left side. In some a poorly developed adoral zone may occur. The cytopharynx is conspicuous by the presence of a pharyngeal basket. Spherical macronucleus central. Contractile vacuole one to several. Cysts are spherical. Fresh or salt water. Several species.

Nassula aurea Ehrenberg (Fig. 153, *f*). About 200 to 250 microns long. Fresh water.

Nassula microstoma Cohn (Fig. 153, *g*). About 100 microns long. Marine.

Genus **Opisthodon** Stein. Body medium large, ovoid or pyriform. Dorsal surface convex, ventral flat. Cytostome located at about one-fourth from the posterior end of body. Pharyngeal basket is conspicuous. Two spherical macronuclei; one contractile vacuole. Ciliation uniform. Fresh water.

Opisthodon niemeccensis Stein (Fig. 153, *h*). Body about 200 microns long. In fresh water.

Genus **Orthodon** Gruber. Body, oval, medium-large, contractile and colorless. Much flattened; anterior end is curved toward the left, while the posterior end rounded. Ventral side is distinctly striated and ciliated. Dorsal surface is also finely ciliated, although the striation is less distinct. Cytostome on the right side margin. Cytopharynx with a conspicuous basket. Oval macronucieus central; one contractile vacuole terminal. Salt or fresh water.

Orthodon hamatus Gruber (Fig. 153, *i*). Length about 150 to 180 microns. In salt water.

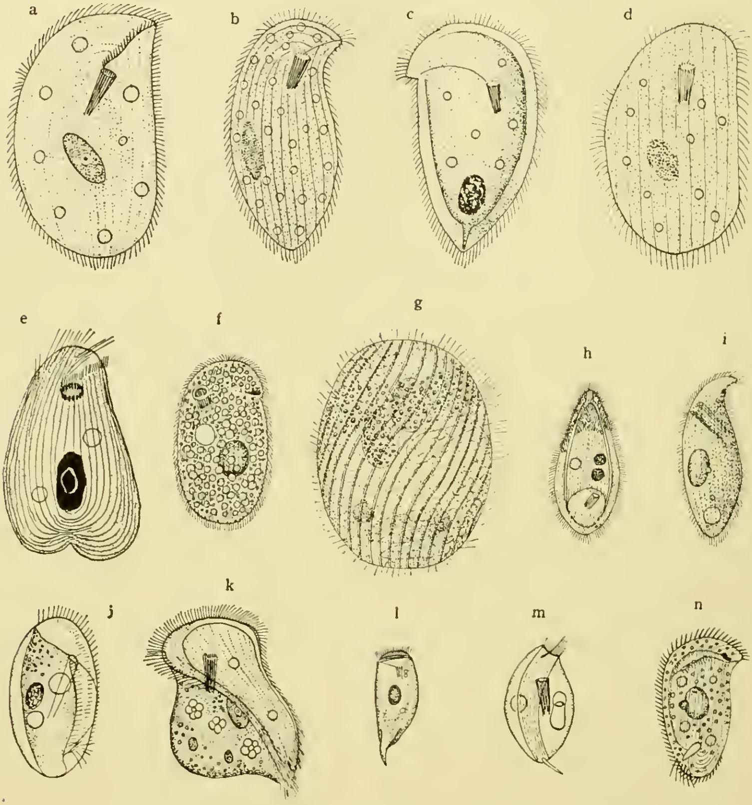


Fig. 153 a. *Chilodon cucullulus.* ×200 (After Stein).
b. *C. vorax.* ×150 (After Stokes).
c. *C. caudatus.* ×750 (After Stokes).
d. *C. fluviatilis.* ×600 (After Stokes).
e. *C. cyprini.* ×500 (After Moroff).
f. *Nassula aurea.* ×90 (After Bütschli).
g. *N. microstoma.* ×500 (After Calkins).
h. *Opisthodon niemeccensis.* ×100 (After Stein).
i. *Orthodon hamatus.* ×120 (After Entz).
j. *Dysteria lanceolata.* ×400 (After Calkins).
k. *Phascolodon vorticella.* ×250 (After Stein).
l. *Scaphidiodon navicula.* ×100 (After Stein).
m. *Trochilia palustris.* ×300 (After Stein).
n. *Aegyria oliva.* ×165 (After Entz).

Genus **Dysteria** Huxley. Body ovoid on the whole, constant. Colorless or variously colored. Ventral side narrowly ciliated. Cytostome toward one side near the anterior end with a distinct basket. A spinous projection from a point near the posterior end. A globular macronucleus; contractile vacuoles several. Marine.

Dysteria lanceolata Claparède and Lachmann (Fig. 153, *j*). Body 45 to 70 microns long. Marine.

Dysteria armata Huxley. Body length 40 to 100 microns. Marine.

Genus **Phascolodon** Stein. Body rounded; anterior end broadly truncate and curved dorsally; posterior end narrowed. Dorsal surface convex; ventral surface flattened. Ciliation general. Cytostome near the anterior end on the ventral side and with a pharyngeal basket. Two contractile vacuoles ventral. Fresh water.

Phascolodon vorticella Stein (Fig. 153, *k*). About 80 to 90 microns long. Fresh water.

Genus **Scaphidiodon** Stein. Body spheroid or boat-shaped; colorless. Dorsal surface convex; ventral surface flat. Posterior end drawn out into a spinous projection; the anterior edge possesses a lip-like border. Cytostome near the anterior end with a pharyngeal basket. Macronucleus oval, central. Contractile vacuoles. Marine.

Scaphidiodon navicula Stein (Fig. 153, *l*). About 150 microns long. In salt water.

Genus **Trochilia** Dujardin. Body small, ovate. Dorsal surface convex; ventral surface flat. Anterior portion bent toward the left. There is a movable spinous structure attached at the posterior end. Cilia confined to a subcentral, curved, band-like area on the ventral surface. Cytostome in the anterior half of the body. Cytopharynx visible. There is a long cirrus near the cytostome. Fresh or salt water.

Trochilia palustris Stein (Fig. 153, *m*). Body about 30 microns long. Fresh water.

Genus **Aegyria** Claparède and Lachmann. Body medium large. General appearance similar to Chilodon. Colorless or variously colored. Ventral side flattened or slightly convex, longitudinally striated. At the posterior end, there is a movable caudal style. Cytostome antero-ventral. Pharyngeal basket short. Salt or fresh water. Rare.

Aegyria oliva Claparède and Lachmann (Fig. 153, *n*). About 100 microns long. Marine.

Suborder 3 **Trichostomina** Bütschli

The cytostome is a permanent opening and is located at the posterior end of the **peristome** (oral groove). There is one (or more) undulating membrane which runs into the cytopharynx or borders the cytostome. The membrane is inconspicuous in many, but in others it is a large sail-like expansion apparently used for capturing the food. The cilia are usually uniformly developed and distributed, although in some they may be much reduced. The group contains both free-living and parasitic forms.

The suborder is divided into six families:

Cilia on two broad zones and on the posterior tip.....Family 1 Urocentridae
Cilia not arranged in zones
  With small circular or ellipsoidal peristome
    Cystotome in the anterior half of body.......Family 2 Ophryoglenidae
    Cytostome in the posterior half of body......Family 3 Microthoracidae
  With large peristome
    Undulating membrane in the cytopharynx.....Family 4 Parameciidae
    Huge undulating membrane in peristome.....Family 5 Pleuronematidae
    Parasitic in the digestive tract of mammals....Family 6 Isotrichidae

Family 1 **Urocentridae** Schouteden

Genus **Urocentrum** Nitzsch. Somewhat short cocoon-shaped, with a constriction slightly behind the middle. Two broad zones of cilia and a conspicuous tuft of fused cilia at the posterior end. Large and oval cytostome posterior; with a distinct cytopharynx. Macronucleus horseshoe-shaped and a micronucleus. A contractile vacuole at the posterior end with four radiating canals. Movement rapid. Fresh water.

Urocentrum turbo Müller (Fig. 154, *a*). About 100 microns long. Fresh water.

Family 2 **Ophryoglenidae** Kent

The body uniformly ciliated, with or without peristome. Cytostome is at the anterior half of the body.

Genus **Ophryoglena** Ehrenberg. Body elliptical or somewhat cylindrical. Ends are equally rounded or attenuated. Cytostome usually crescentic, near the anterior fourth. An undulating membrane. Contractile vacuole one or more and with numberous radiating canals. Macronucleus elongated or band-form; micronucleus fusiform.

Ophryoglena flava Ehrenberg (Fig. 154, *b*). Body 500 to 550 microns long. Stagnant water.

Genus **Cyrtolophosis** Stokes. Body oblong; secretes mucilaginous envelope in which the organism lives, but from which it emerges at will. A tuft of curved vibratile coarse cilia at the anterior end. Cytostome at the end of a short peristome and circular. Long cilia on the peristome. Macronucleus central and spherical. A posterior contractile vacuole. Fresh water.

Cyrtolophosis mucicola (Fig. 154, *c*). Body 25 to 30 microns long. In infusion of dead leaves.

Genus **Loxocephalus** Eberhard. Body elliptical; anterior end obliquely truncate and bent to one side. Near this end, one or more short, curved setae on one or both sides. Usually one (sometimes more) long caudal setae at the posterior extremity. The cytostome below the bent anterior portion, indistinct. Macronucleus ovoid, central; one contractile vacuole. Fresh water.

Loxocephalus granulosus Kent (Fig. 154, *d*). Body about 50 to 60 microns long. In decaying vegetation.

Genus **Uronema** Dujardin. Body elongate ovoid. Cytostome ventral; oblong with an extensible trap-like membrane. Ciliation uniform. One or more caudal setae at the posterior end. A contractile vacuole posterior. Fresh or salt water.

Uronema marina Dujardin (Fig. 154, *e*). Body about 30 to 50 microns long. Common in decaying algae.

Genus **Dallasia** Stokes. Body elongate-ovate, subcylindrical, produced posteriorly into a more or less retractile tail-like prolongation. One side convex, the other flattened. Cytostome near the anterior end and roughly triangular with two undulating membranes. Nucleus oblong, central. One contractile vacuole.

Dallasia frontata Stokes (Fig. 154, *f*). Body 65 to 140 microns long. Polymorphic. Fresh water.

Genus **Frontonia** Ehrenberg. Elongated cylindrical; extremities rounded or pointed. Ciliation and striation uniform. Cytostome near the anterior end, oblong; surrounded by elevated ridges which extend posteriorly for some distance. Cytopharynx short with rods and two undulating membranes. Macronucleus ellipsoidal; several micronuclei. One or two contractile vacuoles with radiating canals. Trichocysts. Fresh or salt water.

Frontonia leucas Ehrenberg (Fig. 154, *g*). Body 250 to 300 microns long. In infusion.

Genus **Glaucoma** Ehrenberg. Body ovoid, ventral surface flattened; dorsal surface convex. Cytostome about one-fourth from the anterior end; triangular or crescent in form, with

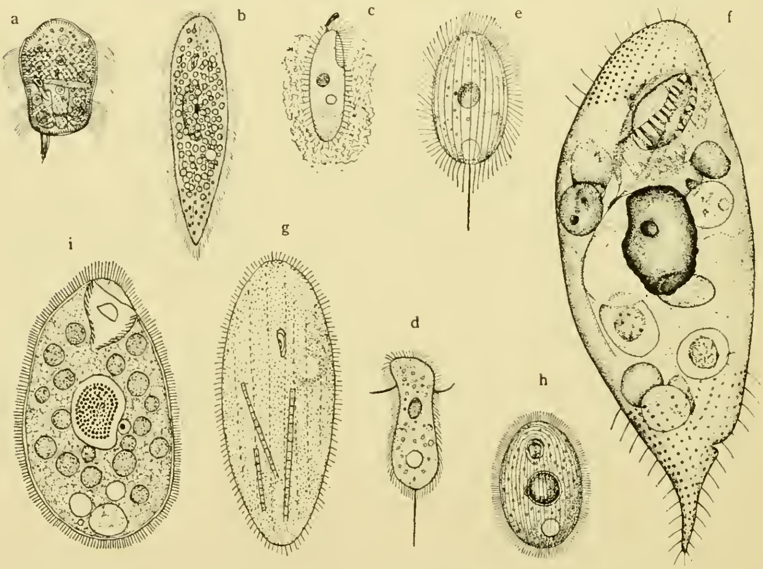


Fig. 154 a. *Urocentrum turbo.* ×150 (After Bütschli).
b. *Ophryoglena flava.* ×55 (After Bütschli).
c. *Cyrtolophosis mucicola.* ×500 (After Stokes).
d. *Loxocephalus granulosus.* ×300 (After Kent).
e. *Uronema marina.* ×350 (After Calkins).
f. *Dallasia frontata.* ×580 (After Calkins and Bowling).
g. *Frontonia leucas.* ×150 (After Edmondson).
h. *Glaucoma scintillans.* ×180 (After Bütschli).
i. *G. pyriformis.* ×1000 (After McArthur).

two undulating membranes. Ciliation and striation uniform. Macronucleus central and spherical. A single micronucleus.

Glaucoma scintillans Ehrenberg (Fig. 154, *h*). Body 90 to 100 microns long. Pond water and infusion.

Glaucoma pyriformis MacArthur (Fig. 154, *i*). In the body cavity of larvae of the mosquito, *Theobaldia annulata.*

Genus **Colpoda** Müller. Body kidney-shaped, laterally compressed; aboral surface hemi-circular, oral surface somewhat flattened. Cytostome some distance from the anterior end. Long cilia around the opening. Contractile vacuole often terminal. Macronucleus central and rounded. Fresh water. Common in infusion.

Colpoda helia (Stokes) (Fig. 155, *a*). Body about 85 to 95 microns long. In standing water with algae.

Colpoda campyla (Stokes) (Fig. 155, *b*). Body about 50 to 60 microns long. In standing water with dead leaves.

Colpoda cucullus Müller (Fig. 155, *c*). Body about 90 microns long. In infusion.

Colpoda inflata (Stokes) (Fig. 155, *d*). Body about 40 to 50 microns long. In standing water.

Genus **Colpidium** Stein. Similar to Colpoda. Body oval to reniform, elongated, but not so compressed. Peristome shallow, nearer the anterior end, with an undulating membrane. Cytostome roughly triangular. Cytopharynx short. Macronucleus central and spherical. A single micronucleus. One contractile vacuole in the posterior half. Fresh or salt water. Very common in infusion.

Colpidium striatum Stokes (Fig. 155, *e*). Length about 50 microns. In infusion of decaying vegetation.

Colpidium colpoda Ehrenberg (Fig. 155, *f*). The figure shows a marine form, 45 microns long by 20 microns wide. Fresh or salt water.

Genus **Lambornella** Keilin. Body oval; dense ciliation; small cytostome fusiform near the anterior end (?). A spherical macronucleus and a micronucleus. Cysts hemi-spherical. Parasitic. One species.

Lambornella stegomyiae Keilin (Fig. 155, *g*, *h*). In the coelom of *Stegomyia scutellaris.* Body about 50 to 70 microns long.

Cysts 30 to 40 microns in diameter, 20 microns in width. Keilin studied preserved material.

Genus **Entorhipidium** Lynch. Large and colorless body pyriform, flattened. Anterior end broadly rounded, posterior end drawn out. Permanently opened cytostome on the dorsal surface near the right border in a depression. Cytopharynx indis-

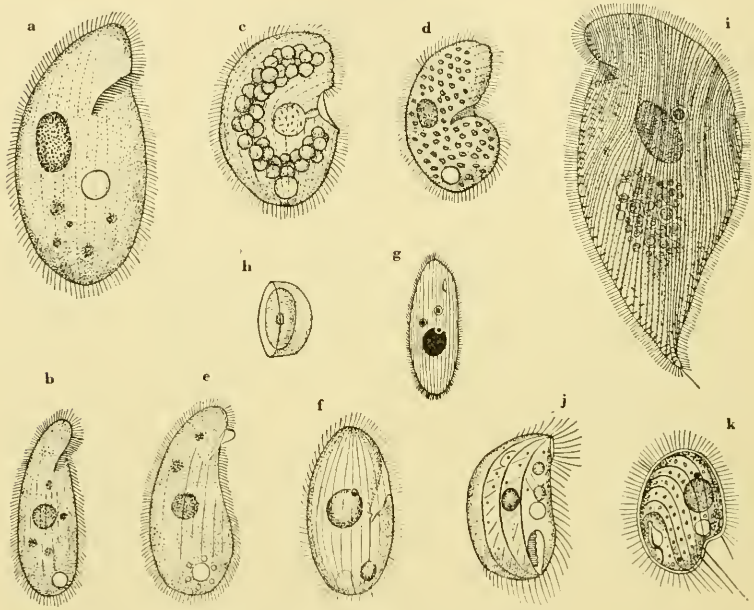


Fig. 155 a. *Colpoda helia.* ×400 (After Stokes).
b. *C. campyla.* ×400 (After Stokes).
c. *C. cucullus.* ×400 (After Maupas from Bütschli).
d. *C. inflata.* ×400 (After Stokes).
e. *Colpidium striatum.* ×500 (After Stokes).
f. *C. colpoda* from salt water. ×500 (After Calkins).
g, h. Trophozoite and cyst of *Lambornella stegomyiae.* ×250 (After Keilin).
i. *Entorhipidium echini.* ×200 (After Lynch).
j. *Microthorax sulcatus.* ×400 (After Engelmann).
k. *Cinetochilum margaritaceum.* ×400 (After Schewiakoff).

tinct. Trichocysts present. A single macronucleus and one to several micronuclei; several "excretory" vacuoles. Several species in the intestine of sea urchins belonging to the genus Strongylocentrotus.

Entorhipidium echini Lynch (Fig. 155, *i*). Large, 253 microns long. With a single micronucleus.

Family 3 **Microthoracidae** Schouteden

Genus **Microthorax** Engelmann. Body small, up to 60 microns in length. Roughly ovoid; ventral side flat, dorsal side convex. Cytostome at the posterior end, with an undulating membrane. Cilia few. Rounded macronucleus central. A contractile vacuole between the macronucleus and cytostome. Fresh water.

Microthorax sulcatus Engelmann (Fig. 155, *j*). 45 to 60 microns long. In pond water and infusion.

Genus **Cinetochilum** Perty. Body irregularly ovoid or lenticular. With deep spiral furrows. Beginning at the posterior end on the ventral surface, there is a short oral groove, at the anterior end of which a cytostome surrounded by an undulating membrane, is located. Macronucleus rounded, central; a contractile vacuole. Fresh water.

Cinetochilum margaritaceum Ehrenberg (Fig. 155, *k*). Body about 40 microns long. Fresh water.

Family 4 **Parameciidae** Grobben

Genus **Paramecium** Hill (=Paramaecium O. F. Müller). Cigar-shaped; circular or ellipsoidal in cross-section. With a single macronucleus and one to many micronuclei which are either vesicular or compact. The peristome long, broad, and conspicuous. Cosmopolitan and common in the stagnant water and infusion. Several species of which nine are here described briefly.

Paramecium caudatum Ehrenberg (Fig. 156, *a*). The most widely distributed and, therefore, most frequently observed species. Length 200 to 260 microns. With a compact micronucleus and a massive macronucleus. Two contractile vacuoles on the aboral surface. Posterior end bluntly pointed.

Paramecium aurelia Müller (Fig. 156, *b*). Length 120 to 250 microns. Two small vesicular micronuclei and a massive macronucleus. Two contractile vacuoles on the aboral surface. The posterior end is more rounded than *P. caudatum*.

Paramecium multimicronucleatum Powers and Mitchell (Fig. 156, *c*). Body as a rule is slightly larger than *P. caudatum*. With three to seven contractile vacuoles. Four or more vesicular micronuclei and a single macronucleus.

Paramecium bursaria (Ehrenberg) (Fig. 156, *d*). Foot-shaped, somewhat compressed. Body about 100 to 200 microns long by 50 to 60 microns broad. Containing Zoochlorellae as symbionts. A single compact micronucleus; two contractile vacuoles.

Paramecium putrinum Claparède and Lachmann (Fig. 156, *e*). Similar to *P. bursaria*, but a single contractile vacuole and an elongated macronucleus. No Zoochlorellae. Body about 80 to 150 microns long.

Paramecium calkinsi Woodruff (Fig. 156, *f*). Foot-shaped; posterior end broadly rounded. Body 100 to 130 microns long by 50 microns broad. With two vesicular micronuclei. Two contractile vacuoles. The rotation of the body is clockwise, viewed from the posterior end. Fresh or brackish water.

Paramecium trichium Stokes (Fig. 156, *g*). Body oblong; somewhat compressed; about 70 to 100 microns long. A single compact micronucleus. Two contractile vacuoles deeply situated, each with a convoluted outlet.

Paramecium polycaryum Woodruff and Spencer (Fig. 156, *h*). Body form similar to *P. bursaria*. Length 70 to 110 microns. Two contractile vacuoles. Vesicular micronuclei three to eight in number.

Paramecium woodruffi Wenrich (Fig. 156, *i*). Similar to *P. polycaryum*. Length 150 to 210 microns. Two contractile vacuoles. Three or four micronuclei, vesicular. Brackish water.

Although Paramecium occurs widely in various fresh-water bodies and has been studied extensively by numerous investigators by mass or pedigree culture method, there are only a few observations concerning the process of encystment. Bütschli considered that Paramecium was one of the Protozoa in which encystment did not occur. But stages of encystment have been observed in 1899 in *P. bursaria* (by Prowazek) and in *P. putrinum* (by Lindner). In recent years, three observers recorded their findings on the encystment of Paramecium. Curtis (1927) gives figures showing the encystment in Paramecium (*P. caudatum*?) (Fig. 157, *a–c*), while Cleveland (1927) injected Para-

Fig. 156 Semi-diagrammatic drawings of nine species of Paramecium in oral surface view, showing distinguishing characteristics taken from fresh and stained specimens. ×230 (Combined after several authors).

a. *P. caudatum*
b. *P. aurelia*
c. *P. multimicronucleatum*
d. *P. bursalia*
e. *P. putrinum*
f. *P. calkinsi*
g. *P. trichium*
h. *P. polycaryum*
i. *P. woodruffi*

mecium culture (species not mentioned) into the rectum of frogs and observed that the ciliate encysted within a thin membrane. Michelson (1928) found that if *Paramecium caudatum* is kept in Knop-agar medium, the organism becomes ellipsoidal, later spherical to oval, losing all cell-organs except the nuclei, and develops a thick membrane. The fully formed cyst is elongated and angular, and resembles a sand particle (Fig. 157, *d–f*). Michelson considers its resemblance to a sand grain as the chief cause of the cyst having been overlooked by workers.

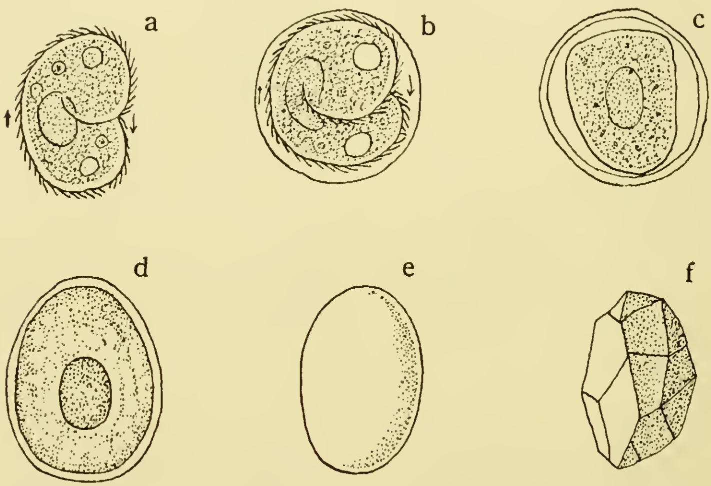


Fig. 157 a–c. Encystment in a species of Paramecium (after Curtis). d–f. Encystment of *Paramecium caudatum*. × about 380 (After Michelson). d, e, young cysts; f, old cyst.

Family 5 **Pleuronematidae** Kent

One or more well developed undulating membranes are conspicuously present.

Genus **Pleuronema** Dujardin. Body medium large; elliptical to lenticular, compressed. The ends are equally rounded. Peristome is a long groove starting at the anterior extremity, from which is expanded a conspicuous membrane. Longitudinal rows of long cilia. Trichocysts are said to be occasionally present.

Macronucleus ovoid; contractile vacuole near the posterior end. Fresh or salt water.

Pleuronema chrysalis Ehrenberg (Fig. 158, *a*). Body about 50 to 70 microns long. In fresh or salt water.

Genus **Cyclidium** Ehrenberg. Body small ovoid, slightly compressed. Cytostome ventral; peristome narrow, with a conspicuous membrane. One caudal filament. Fresh or salt water.

Cyclidium glaucoma Ehrenberg (Fig. 158, *b*). Body about 20 to 30 microns long. Fresh water.

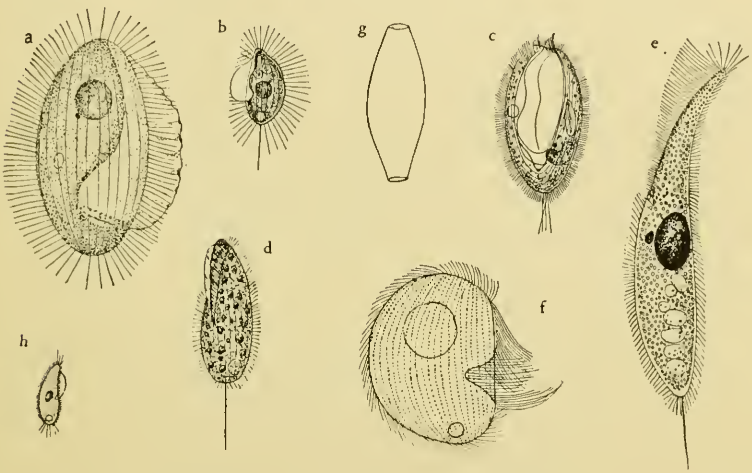


Fig. 158 a. *Pleuronema chrysalis.* ×400 (After Calkins).
b. *Cyclidium glaucoma.* ×500 (After Schewiakoff).
c. *Lembadion bullinum.* ×150 (After Schewiakoff).
d. *Lembus pusillus.* ×550 (After Calkins).
e. *L. infusionum.* ×550 (After Calkins).
f. *Pleurocoptes hydractiniae.* ×350 (After Wallgren).
g, h. *Calyptotricha inhaesa.* (After Kellicott).
g, lorica (×100); h, the body (×250).

Genus **Lembadion** Perty. Body medium large; form constant. Oval, slightly flattened dorso-ventrally. Peristome very large and with a large membrane. Cytostome at the end of the peristome. Macronucleus reniform near the posterior end where several long and firm cilia are located. A single contractile vacuole towards the right side near the middle. Fresh water.

Lembadion bullinum Perty (Fig. 158, *c*). About 100 to 150 microns long. Fresh water.

Genus **Lembus** Cohn. Body rather small; elongated and flexible. Peristome narrow and possesses one or two (?) membranes. There are one or more long caudal filaments. Marine.

Lembus pusillus Quennerstedt (Fig. 158, *d*). About 26 to 30 microns long. In marine infusion.

Lembus infusionum Calkins (Fig. 158, *e*). 70 to 75 microns long by 10 to 12 microns wide. Marine.

Genus **Pleurocoptes** Wallengren. Body ovoid. Dorsal side hemi-spherical, ventral side flattened or concave. Peristome large; cytostome near one-third from the posterior end; cytopharynx indistinct. Longer cilia along peristome. Macronucleus spherical; several micronuclei. A contractile vacuole posterior. Ectoparasitic on Hydractinia.

Pleurocoptes hydractiniae Wallengren (Fig. 158, *f*). Body measures 60 to 70 microns long. On *Hydractinia echinata*.

Genus **Calyptotricha** Phillips. Resembles Pleuronema, but dwelling in a lorica which is opened on both ends. The body is actively motile. Fresh water.

Calyptotricha inhaesa (Kellicott) (Fig. 158, *g*, *h*). In swamp water. Attached laterally to filamentous algae. Lorica 180 to 210 microns long; body about 30 microns long.

Family 6 **Isotrichidae** Schouteden

The majority of the members of this family live in the midgut of ruminants and are covered by a thick pellicle. Ciliation uniform and thick.

Genus **Isotricha** Stein. Body ovoid. Ciliation heavy and uniform. Cytostome is either at the anterior end or somewhat toward one side. Oblong macronucleus nearer the anterior end, with a micronucleus. Contractile vacuoles numerous. Cytopyge is usually noticeable at the posterior extremity. Two species in the stomach of cattle and sheep.

Isotricha prostoma Stein (Fig. 159, *a*). 80 to 200 microns long.

Isotricha intestinalis Stein (Fig. 159, *b*). 97 to 130 microns long.

Genus **Dasytricha** Schuberg. Body regularly ovoid. Cytostome at the anterior end with a curved cytopharynx. A macronucleus and a micronucleus. A single contractile vacuole. One species.

Dasytricha ruminantium Schuberg (Fig. 159, *c*). In the rumen of cattle and sheep. 50 to 75 microns long.

Genus **Conchophthirus** Stein. Body colorless and not contractile. Oval in profile; ventral side less convex. Peristome occurs towards the right side. Cytostome large, in the middle or near the posterior end. Cytopharynx distinct. Usually a few

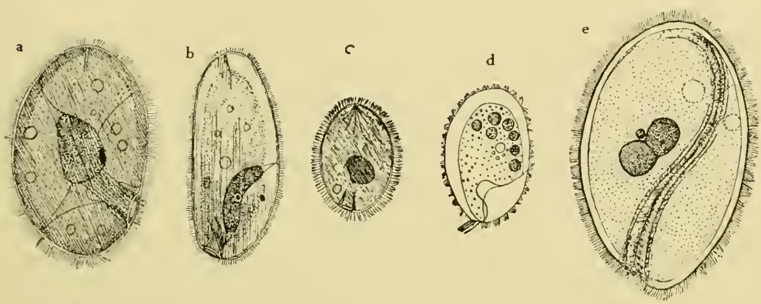


Fig. 159 a. *Isotricha prostoma.* ×375 (After Becker and Talbott).
b. *I. intestinalis.* ×375 (After Becker and Talbott).
c. *Dasytricha ruminantium.* ×245 (After Becker and Talbott).
d. *Conchophthirus steenstrupii.* ×100 (After Quennerstedt).
e. *Buxtonella sulcata.* ×295 (After Jameson).

longer cilia at the posterior end. Occasionally adoral zone in the anterior portion of the peristome. Macronucleus spherical, several. Free-living in fresh water or parasitic in the mucous membrane of various molluscs.

Conchophthirus steenstrupii Quennerstedt (Fig. 159, *d*). About 175 microns long.

Genus **Buxtonella** Jameson. Body oval. A prominent curved ridge runs from one end to the other on the dorsal side, and extends to the ventral side, where a cytostome is located. In the caecum of cattle.

Buxtonella sulcata Jameson (Fig. 159, *e*). Body 55 to 124 microns long by 40 to 72 microns broad.

References

Becker, E. R. and Mary Talbott. 1927 The protozoan fauna of the rumen and reticulum of American cattle. Iowa State Coll. Jour. Sci., Vol. 1

Calkins, G. N. 1926 The biology of the Protozoa. Philadelphia.

Cépède, C. 1910 Recherches sur les Infusoires astomes. Arch. Zool. Expér., T. 3.

Conn, H. W. 1905 A preliminary report of the Protozoa of the fresh-water of Connecticut. Conn. State Geol. and Nat. Hist. Survey, Bull. No. 2.

Doflein, F. and E. Reichenow. 1929 Lehrbuch der Protozoenkunde. Jena.

Edmondson, C. H. 1906 The Protozoa of Iowa. Proc. Davenport Acad. Sci., Vol. 11.

Kahl, A. 1926 Neue und wenige bekannte Formen der holotrichen und heterotrichen Ciliaten. Arch. f. Protistenk., Vol. 55.

———. 1927 Neue und ergänzende Beobachtungen holotricher Ciliaten. Ibid., Vol. 60.

Michelson, E. 1928 Existenzbedingungen und Cystenbildung bei *Paramecium caudatum* Ehrenberg. Ibid., Vol. 61.

Noland, L. E. 1925 Factors influencing the distribution of fresh-water ciliates. Ecology, Vol. 6.

Penard, E. 1922 Etudes sur les Infusoires d'eau douce. Geneva.

Wenrich, D. H. 1928 Eight well-defined species of Paramecium. Trans. Amer. Micr. Soc., Vol. 47.

Wenyon, C. M. 1926 Protozoology. Vol. 2. London.

CHAPTER XXIX

ORDER 2 **HETEROTRICHIDA** STEIN

THIS ORDER includes those Euciliata which possess an adoral zone that is wound to the left. The adoral zone is composed either of strong cilia or membranellae. As a rule, the body is covered by delicate cilia which, however, may be reduced in some forms. The cytopharynx possesses a conspicuous undulating membrane. In one group Tintinnoinea, the animal secretes a lorica. Free-living or parasitic.

Following an extensive study of Kofoid and Campbell, the Euciliata which were formerly placed in the family Tintinnidae, are removed from Oligotrichida into the present order. The Heterotrichida are, therefore, divided into two suborders as follows:

Without a lorica........................Suborder 1 Gymnoheterotrichina
With a lorica..................................Suborder 2 Tintinnoinea

Suborder 1 **Gymnoheterotrichina**

The group will be divided into six families:

Adoral zone parallel to the main body axis
  Peristome is narrow and long................Family 1 Plagiotomidae
  Peristome is wide, triangular, and deep............Family 2 Bursariidae
Adoral zone not parallel to the main body axis
  Body funnel-shaped; adoral zone strong
    Cytopharynx tubular; free-living................Family 3 Stentoridae
    Cytostome not permanently open; ectoparasitic....Family 4 Boveriidae
  Body form medusoid........................Family 5 Caenomorphidae
  Body asymmetrical; sapropelic; cilia reduced.........Family 6 Epalcidae

Family 1 **Plagiotomidae** Poche

Genus **Plagiotoma** Dujardin. Body form constant, ovoid; convex dorsally, flattened ventrally. Peristome extends from the anterior end to the middle of the body, where a cytostome is located. Cytopharynx distinct. There is a single bristle extending out of the cytostome. Parasitic.

Plagiotoma lumbrici Dujardin (Fig. 160, *a*). In the intestine of the common earthworm, *Lumbricus terrestris*. Length 130 to 210 microns.

Genus **Nyctotherus** Leidy. Body oval or reniform, more or less compressed dorso-ventrally. Body surface uniformly ciliated. Peristome begins a little back of the anterior end of the body, winding slightly toward the middle of the body, and forms the cytostome, from which a small cytopharynx continues down. The macronucleus is oval or sausage-shaped and anteriorly located. Contractile vacuole at the posterior end, where a permanent cytopyge is present. Several species.

Nyctotherus ovalis Leidy (Fig. 160, *b*, *c*). In the colon of the cockroach. Common. Body length up to 350 microns.

Nyctotherus cordiformis Stein (Fig. 160, *d*, *e*). In the large intestine of frogs and toads. Length about 165 to 240 microns.

Genus **Blepharisma** Perty. Body medium large, constant in form; often reddish in color. Anterior part compressed, pointed, sickle-shaped, and curved toward the left. Peristome deep, oblique, but straight; with an adoral zone and undulating membrane at the posterior part. Cytopharynx inconspicuous, curved. Striation spiral and uniform. Macronucleus elongate or spherical; contractile vacuole near the posterior end. Fresh water.

Blepharisma lateritia Ehrenberg (Fig. 160, *f*). Body rose-red due to the presence of zoopurpurin (p. 23). 50 to 150 microns long. Fresh water, often in infusion.

Genus **Spirostomum** Ehrenberg. Body highly elastic and contractile. When extended it is quite long. Cylindrical or slightly flattened. Anterior end rounded, posterior end truncate. Peristome narrow and long. Adoral zone on the left side ridge; no undulating membrane. Cytostome and cytopharynx small. Contractile vacuole canal-like with a large reservoir near the posterior end. Uniform ciliation. Fresh or salt water.

Spirostomum ambiguum Ehrenberg (Fig. 160, *g*). Cosmopolitan in fresh water and infusion. Some authors distinguish varieties, based chiefly upon the dimensions. Thus, Roux holds that var. *major* is more than 2 mm. long when extended and that var. *minor* seldom reaches 500 microns in length. Kahl adds to them var. *inflatum* which measures 300 to 400 microns in length. For our purpose, we ignore the varieties. Length 500 microns to 2 mm. when extended. The macronucleus moniliform.

Spirostomum teres Claparède and Lachmann (Fig. 160, *h*). In habitats similar to the last species. Smaller with an oblong macronucleus. Length 150 to 400 microns.

Fig. 160 a. *Plagiotoma lumbrici.* ×140 (After Stein).
b, c. *Nyctotherus ovalis.* ×130 (After Stein). c, cyst.
d, e. *N. cordiformis.* ×130 (After Stein). e, cyst.
f. *Blepharisma lateritia.* ×100 (After Stein).
g. *Spirostomum ambiguum.* ×70 (After Stein).
h. *S. teres.* ×125 (After Stein).
i–k. *Metopus sigmoides.* i, from life (×100 after Stein); j, a stained specimen (×250 after Noland); k, encysted exconjugant after life (×210 after Noland).

Genus **Metopus** Claparède and Lachmann. Body elastic. When extended it is oblong or fusiform, with rounded extremities. Circular or oval in cross-section. Anterior part of the body spirally twisted. Peristome with an adoral zone on its left side;

undulating membrane on the right. When contracted, the peristome is much spirally coiled. The cytostome with a short cytopharynx at the end of the peristome. Body ciliation uniform, with longer cilia at the extremities. Contractile vacuole posterior; macronucleus elongated. Fresh or salt water. Numerous species.

Metopus sigmoides Claparède and Lachmann (Fig. 160, *i-k*). Fresh or rarely salt water. Body about 200 microns in length.

Family 2 **Bursariidae** Kent

Peristome is wide, more or less triangular, and of variable length. The adoral zone is on the left margin of the peristome. The right side ridge may or may not bear an undulating membrane. Free-living or parasitic.

Genus **Bursaria** Müller. Body ovoid with the truncate anterior end. Dorsally convex, ventrally flattened. Deep peristome begins at the anterior end, and forms on the ventral side a slit reaching the middle where it passes into a long cytopharynx. Adoral zone. No undulating membrane. Striation and ciliation uniform. Macronucleus elongated band, often curved. Micronucleus numerous. Contractile vacuole when visible, numerous and scattered. Cysts are spherical with a double thick membrane, the inner cover being connected at places with the outer. Fresh water.

Bursaria truncatella (Fig. 161, *a*). 500 to 600 microns long. Pond or marshy water.

Genus **Balantidium** Claparède and Lachmann. Body large, oval to subcylindrical, slightly truncate anteriorly. Peristome medium wide and slightly oblique in direction. At its posterior end, is located a cytostome with a short cytopharynx. Ciliation uniform. Macronucleus elongated. One or more contractile vacuoles. A cytopyge. Several species. Parasitic in the intestine of man, mammals and amphibians.

Balantidium coli (Malmsten) (Fig. 161, *b*, *c*). In the intestine of pigs and man. Body about 50 to 100 microns long by 30 to 70 microns broad. The infection in man is presumably acquired from the cysts produced in pigs, and is responsible for a serious intestinal disturbance in the unfortunate patient.

Genus **Balantidiopsis** Bütschli. Body ovoid. Cytostome a narrow slit, opening at the anterior end. One contractile vacuole at the posterior end. Macronucleus spherical and posterior. Parasitic.

Balantidiopsis duodeni (Stein) (Fig. 161, *d*). Body about 110 microns long. In the mid-gut of various frogs (Rana).

Genus **Condylostoma** Dujardin. Body colorless and oval to cylindrical or club-shaped. Contractile; flattened slightly dorsoventrally. Peristome short at the anterior region, the left margin bears the adoral zone and the right ridge an undulating membrane. Macronucleus moniliform. One or several contractile vacuoles. If one is present, there is a long canal leading into it. Cytopyge posterior. Fresh or salt water.

Condylostoma patens Müller (Fig. 161, *e*). Body large 350 to 550 microns long. Salt water.

Condylostoma vorticella Ehrenberg (Fig. 161, *f*). 150 microns long. Fresh water.

Family 3 **Stentoridae** Claus

The anterior end is broad and at about right angles to the longitudinal axis of the body. Almost all of them free-living.

Genus **Stentor** Oken. Attached or free-swimming. When extended, the body is cylindrical or trumpet-shaped. Occasionally with a mucilaginous lorica. When free-swimming, the body is oval to pyriform. The anterior end possesses a peristome which is spiral in its course and at its end is located a cytostome. A row of strong cilia marks the peristomal ridge. Ciliation fine and regular. Macronucleus rounded to elongate or moniliform. Several micronuclei indistinguishable *in vivo*. The cytopyge is located near the left end of the adoral spiral. A single contractile vacuole which is usually present near the anterior end possesses a long canal which runs posteriorly in a more or less straight course. Sometimes with chlorophyll. Fresh or salt water. Johnson (1893) distinguishes the following species.

Stentor igneus Ehrenberg (Fig. 161, *g*). On plants in freshwater. When extended 350 microns long.

Stentor pyriformis Johnson (Fig. 161, *h*). Fresh water. When extended 500 microns long, diameter of the anterior end 200 microns.

Stentor roeseli Ehrenberg. Standing fresh water among decaying vegetation. Body colorless; when extended, reaches over 1 mm. The posterior end often in a tubular envelope.

Stentor polymorphus (Müller) (Fig. 161, *i*). Among freshwater plants. Extended body measures 1.25 mm.

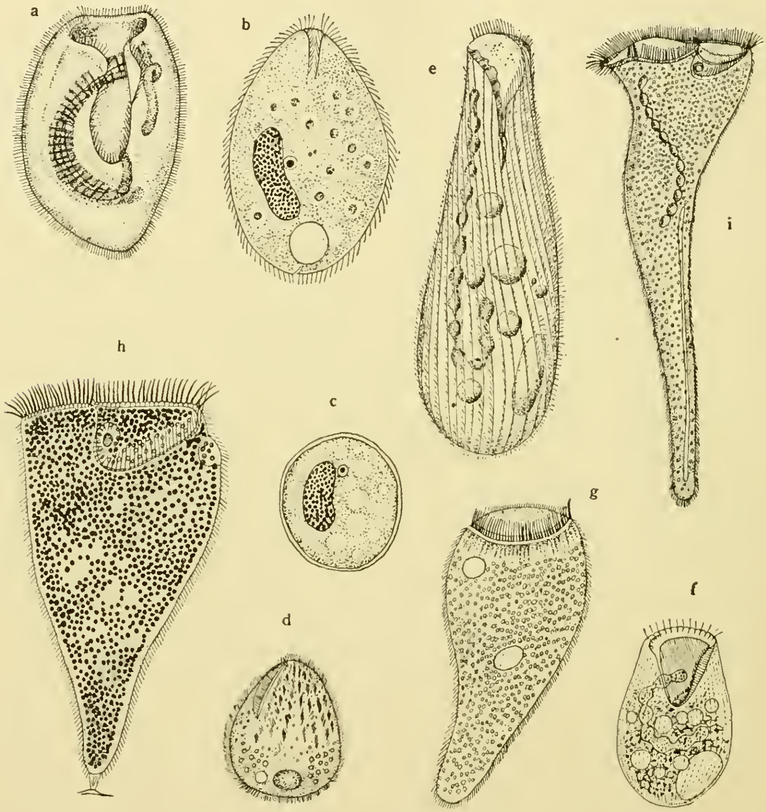


Fig. 161 a. *Bursaria truncatella.* ×50 (After Calkins).
b, c. *Balantidium coli.* ×400. c, a cyst.
d. *Balantidiopsis duodeni.* ×125 (After Stein).
e. *Condylostoma patens.* ×135 (After Calkins).
f. *C. vorticella.* ×160 (After Bütschli).
g. *Stentor igneus.* ×115 (After Stein).
h. *S. pyriformis.* ×115 (After Johnson).
i. *S. polymorphus.* ×50 (After Stein).

Stentor coeruleus Ehrenberg. In fresh water. Body bluish in color and measures 130 to 265 microns in length.

Stentor multiformis (Müller). In salt water. Social. Extended body measures about 140 microns in length.

Genus **Folliculina** Lamarck. Peristome is drawn out; with two wings; with a membranella. With an elongated pseudochitinous lorica. Marine.

Folliculina ampulla Müller (Fig. 162, *a*). Body more than 1 mm. in length when extended. Salt water.

Genus **Climacostomum** Stein. Medium large. Colorless or green with Zoochlorellae. Body form constant, compressed dorso-ventrally; right side convex. Peristome conspicuous;

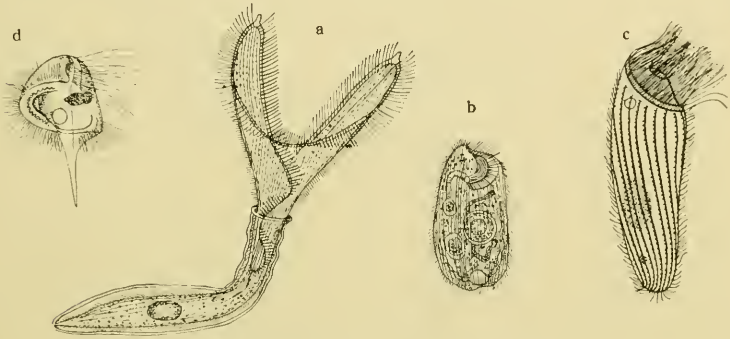


Fig. 162 a. *Folliculina ampulla.* ×125 (After Stein).
b. *Climacostomum virens.* ×75 (After Stein).
c. *Boveria teredinidi.* ×410 (After Pickard).
d. *Caenomorpha medusula.* ×150 (After Blochmann).

cytopharynx long and curved. Contractile vacuole posterior with two radiating canals. Macronucleus band-form, central. Cysts pyriform or oval. Fresh water.

Climacostomum virens (Ehrenberg) (Fig. 162, *b*). Body about 250 microns long.

Family 4 **Boveriidae** Pickard

Genus **Boveria** Stevens. Ectoparasitic on gills of various marine animals, such as Teredo, Bankia, Tellina, Capsa, and Holothuria. Body conical, adoral zone conspicuous. One macronucleus central and one micronucleus. One contractile vacuole.

Boveria teredinidi Pickard (Fig. 162, *c*). Body about 27 to 173 microns long. On gills of *Teredo navalis*.

Family 5 **Caenomorphidae** Poche

Genus **Caenomorpha** Perty (=Gyrocoris Stein). Body constant and colorless. Free-swimming. The anterior portion bell-shaped, posterior half drawn out. Peristome long, oblique with strong cilia. Elongated macronucleus with a constriction. A single contractile vacuole. Fresh or salt water. Several species.

Caenomorpha medusula Perty (Fig. 162, *d*). Fresh water. Body about 100 to 130 microns long.

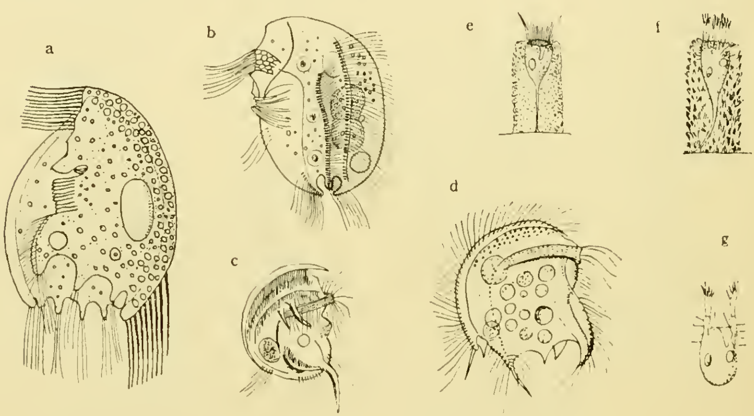


Fig. 163 a. *Epalxis mirabilis*. ×900 (After Roux).
b. *Pelodinium reniforme*. ×450 (After Lauterborn).
c. *Discomorpha pectinata*. ×165 (After Kahl).
d. *Saprodinium dentatum*. ×320 (After Kahl).
e. *Tintinnidium fluviatile*. ×100 (After Kent).
f, g. *T. semiciliatum*. ×100 (After Sterki).

Family 6 **Epalcidae** Wetzel

Asymmetrical body discoid, compressed laterally; cilia reduced. Spines and comb-like structures about the cytostome. Sapropelic.

Genus **Epalxis** Roux. Body rounded triangular; anterior end bluntly pointed, posterior end drawn out into 7 or 8 blunt processes. Dorsal surface convex. Cytostome at the anterior third with comb-like structure posterior to it. Oval macronucleus dorsal. Fresh water.

Epalxis mirabilis Roux (Fig. 163, *a*). Body 32 to 40 microns long by 27 to 30 microns broad.

Genus **Pelodinium** Lauterborn. Body form constant. Similar to Epalxis, but the posterior end narrowed.

Pelodinium reniforme Lauterborn (Fig. 163, *b*). Body 40 to 50 microns long.

Genus **Discomorpha** Levander. Anterior end with a ventrally pointed spine. There are two spines on the right side of the body.

Discomorpha pectinata Levander (Fig. 163, *c*). Body 60 to 80 microns long.

Genus **Saprodinium** Lauterborn. With six or eight posterior spines, but none on the sides.

Saprodinium dentatum Lauterborn (Fig. 163, *d*). Body 80 microns by 72 microns.

Suborder 2 **Tintinnoinea** Kofoid and Campbell

These Hetrotrichida possess a conical or trumpet-like body, attached inside a lorica which is composed of gelatinous or pseudochitinous substances and which varies in shape. Body with several longitudinal rows of cilia, and two macronuclei and two micronuclei are present in the majority. The organisms are mostly pelagic, a few inhabiting brackish or fresh water. Kofoid and Campbell distinguished more than 300 species and placed them in 12 families and 51 genera, of which 23 genera were established by them. Here a fresh water genus is mentioned.

Genus **Tintinnidium** Kent. With an elongated lorica, highly irregular in form; soft in consistency. Aboral end closed or with a minute opening. Wall viscous and freely agglomerates foreign objects. Salt or fresh water.

Tintinnidium fluviatile (Stein) (Fig. 163, *e*). Lorica about 125 microns high by 45 microns broad. Widely distributed on aquatic plants in fresh water.

Tintinnidium semiciliatum (Sterki) (Fig. 163, *f*, *g*). Body length 40 to 60 microns. Widely distributed on aquatic plants in fresh water.

References

CALKINS, G. N. 1926 The biology of the Protozoa.

JOHNSON, H. P. 1893 A contribution to the morphology and biology of the stentors. Jour. Morph., Vol. 8.

KAHL, A. 1927 Neue und ergänzende Beobachtungen heterotricher Ciliaten. Arch. f. Protistenk., Vol. 57.

KENT, W. S. 1881–1882 A manual of Infusoria. Vol. 2. London.

KOFOID, C. A. AND A. S. CAMPBELL. 1929 A conspectus of the marine and fresh-water Ciliata, belonging to the suborder Tintinnoinea, with descriptions of new species principally from the Agassiz Expedition to the eastern tropical Pacific 1904 to 1905. Uni. California Publ. Zool., Vol. 34.

STEIN, F. 1867 Der Organismus der Infusionstiere. Vol. 2.

CHAPTER XXX

ORDER 3 **OLIGOTRICHIDA** BÜTSCHLI

The cilia are greatly reduced in number in the Oligotrichida. The adoral zone which is invariably present, is a complete ring bordering the left-side margin of the peristome which is at right angles to the main body axis. The Oligotrichida are chiefly parasitic forms.

The order is divided into two families as follows:

Free-living small forms............................Family 1 Halteriidae
Parasitic in the digestive tract of mammals....Family 2 Ophryoscolecidae

Family 1 **Halteriidae** Claus

Genus **Halteria** Dujardin. Small spherical body. Adoral zone at the anterior end. Near the middle of the body there is a circle of long cirri which serve for springing movement. No other cilia. Macronucleus spherical or oval; a single contractile vacuole. Fresh water.

Halteria grandinella Müller (Fig. 164, *a*). Body length 20 to 30 microns. Common in infusion, pond, and stagnant water.

Genus **Strombidium** Claparède and Lachmann. Similar to Halteria, but without springing cirri. Sometimes yellowish in color. The adoral zone is protrusible; frequently with trichocysts. A single cilium or a few cilia may be present on the ventral side. Salt or fresh water.

Strombidium typicum (Lankester) (Fig. 164, *b*). About 35 microns in length. Marine.

Family 2 **Ophryoscolecidae** Claus

Genus **Ophryoscolex** Stein. In the stomach of ruminants. Body more or less pyriform. Posterior end is drawn out into a number of processes; at the anterior end there is a conspicuous ring of cirri which continues through the cytostome into the cytopharynx. A little toward the back there is an incomplete circle of cirri. With numerous contractile vacuoles.

Ophryoscolex caudatus Eberlein (Fig. 164, *c*). In the stomach of cattle. Body about 200 microns in length.

Genus **Entodinium** Stein. In the stomach of ruminants. Body ovoid; anterior end with a spiral row of cirri extending through the cytostome into the cytopharynx; posterior end drawn out into one or several processes. Macronucleus rod-shaped, micronucleus small. One contractile vacuole.

Entodinium caudatum Stein (Fig. 164, *d*). About 50 to 80 microns long. In cattle and sheep.

Genus **Diplodinium** Schuberg. In the stomach of ruminants. Body oblong. Cytostome is located near the anterior end at one side and surrounded by a peristome with a spiral row of cirri. Towards the dorsal side, there is another spiral of cirri. The posterior end of the body is with or without prolongations. An elongated macronucleus with a closely associated micronucleus, is situated near the dorsal surface. Two contractile vacuoles; a cytopyge at the posterior end of body.

Diplodinium bursa Fiorentini (Fig. 164, *e*). In the stomach of cattle. Body 100 to 150 microns long.

Genus **Spirodinium** Fiorentini. Body oblong; with about three turns of a spiral row of cirri. Macronucleus oblong.

Spirodinium equi Fiorentini (Fig. 164, *f*). In the caecum of the horse. About 230 microns long.

Genus **Triadinium** Fiorentini. Body is rounded at the anterior end, and pointed at the posterior end. With three rings of cirri, and a caudal tuft of cilia. Macronucleus elongate.

Triadinium caudatum Fiorentini (Fig. 164, *g*). In the caecum of the horse. About 130 microns long.

Genus **Cycloposthium** Bundle. Body large, barrel-shaped. Cytostome is in the center of a conical elevation at the anterior end, surrounded by a circle of cirri. Near the posterior end there are two groups of long processes. Macronucleus elongate. Several contractile vacuoles in a row along the macronucleus.

Cycloposthium bipalmatum (Fiorentini) (Fig. 164, *h*). In the caecum of the horse. About 255 microns long.

Genus **Tripalmaria** Gassovsky. Body oblong, similar to Cycloposthium, but three bundles of long processes, two on the sides near the posterior end and one on the dorsal side near the anterior end. Two longitudinal ridges.

Fig. 164 a. *Halteria grandinella.* ×400 (After Schewiakoff).
b. *Strombidium typicum.* ×800 (After Bütschli).
c. *Ophryoscolex caudatus.* ×250 (After Becker and Talbott).
d. *Entodinium caudatum.* ×375 (After Becker and Talbott).
e. *Diplodinium bursa.* ×250 (After Becker and Talbott).
f. *Spirodinium equi.* ×130 (After Gedoelst).
g. *Triadinium caudatum.* ×170 (After Gedoelst).
h. *Cycloposthium bipalmatum.* ×225 (After Bundle).
i. *Tripalmaria dogieli.* ×135 (After Gassovsky).
j. *Tetratoxum unifasciculatum.* ×135 (After Gassovsky).
k. *Cochliatoxum periachtum.* ×65 (After Gassovsky).
l. *Ditoxum funinucleum.* ×135 (After Gassovsky).

Tripalmaria dogieli Gassovsky (Fig. 164, *i*). In the colon of the horse. About 100 to 200 microns long.

Genus **Tetratoxum** Gassovsky. Body oblong slightly compressed and medium in size. There are four arched membranes, two being near each end. Slit-like cytostome surrounded by cilia at the anterior end. There are six to eight longitudinal ridges. Macronucleus band-form. A contractile vacuole near the macronucleus.

Tetratoxum unifasciculatum (Fiorentini) (Fig. 164, *j*). In the colon of the horse.

Genus **Cochliatoxum** Gassovsky. Similar to Tetratoxum; body much larger; two contractile vacuoles.

Cochliatoxum periachtum Gassovsky (Fig. 164, *k*). In the colon of the horse. About 400 to 500 microns long.

Genus **Ditoxum** Gassovsky. Somewhat similar to Tetratoxum, but with a single posterior arched membrane. Macronucleus elongated.

Ditoxum funinucleum Gassovsky (Fig. 164, *l*). In the colon of the horse. Body about 145 to 225 microns long.

References

Becker, E. R. and Mary Talbott. 1927 The protozoan fauna of the rumen and reticulum of American cattle. Iowa State Coll. Jour. Sci., Vol. 1.

Dogiel, V. 1925 Die Geschlechtsprozess bei Infusorien. Arch. f. Protistenk., Vol. 50.

Gassovsky, G. 1918 Ueber die Mikrofauna des Pferdedarms. Trav. Soc. Nat. Petrograd. Vol. 49.

CHAPTER XXXI

ORDER 4 **HYPOTRICHIDA** STEIN

The members of this order are usually dorso-ventrally flattened and cilia or cirri are restricted to the ventral surface. In some forms there occur dorsal processes which apparently are used as tactile organelles. Peristome possesses an adoral zone which is a left-handed spiral. The undulating membrane often occurs. According to their location, the cirri may be called frontals, ventrals, laterals or marginals, anals, and caudals (Fig. 10, *b*). There are usually two macronuclei and two micronuclei. Contractile vacuoles vary in number and do not possess radiating canals.

Asexual reproduction is by binary fission and sexual reproduction through isogamous conjugation is common. Encystment often takes place. Mostly free-living in fresh or salt water, undergoing creeping movement. A few are parasitic.

The order is divided into the following five families:

With ventral cilia; adoral zone conspicuous..........Family 1 Peritromidae
With cilia and cirri..............................Family 2 Oxytrichidae
With cirri only
  With frontals, ventrals, anals, marginals..........Family 3 Euplotidae
  With frontals, ventrals, anals; without laterals......Family 4 Aspidiscidae
  Frontals and ventrals much reduced.............Family 5 Psilotrichidae

Family 1 **Peritromidae** Stein

Genus **Peritromus** Stein. Simplest form of the Hypotrichida. Cilia present uniformly and densely on the ventral surface. No stouter cilia nor cirri. Marine.

Peritromus emmae Stein (Fig. 165, *a*, *b*). In salt water. Body about 90 microns long.

Family 2 **Oxytrichidae** Kent

Genus **Oxytricha** Ehrenberg. Flexible body ellipsoid, rounded at the extremities. Ventral surface flat; dorsal convex. 8 frontals, 5 ventrals, 5 anals, and short caudals. Numerous species.

Oxytricha fallax Stein (Fig. 165, *c*). In fresh or salt water. About 150 to 180 microns long.

Genus **Stylonychia** Ehrenberg. Inflexible body, ovoid or reniform. Ventral surface flat; dorsal convex. Peristome broadly triangular. 8 frontals, 5 ventrals, 5 anals. Usually 3 caudals which break up the marginal rows of cilia. Fresh or salt water.

Stylonychia mytilus (Müller) (Fig. 165, *d*). Fresh water and infusion. Body about 85 to 350 microns in length.

Stylonychia pustulata Ehrenberg (Fig. 165, *e*). Fresh or salt water. Body about 85 to 210 microns long.

Stylonychia putrina Stokes (Fig. 165, *f*). Fresh water. 125 to 150 microns long.

Stylonychia notophora Stokes (Fig. 165, *g*). Standing water. Body about 125 microns long.

Genus **Urostyla** Ehrenberg. Flexible body ellipsoidal; ends rounded. Ventral surface flattened, covered with 5 to 7 longitudinal rows of fine cilia, besides two marginal rows. Dorsal side curved. Peristome triangular. Frontals 3 or more, anals 5 to 12. A single contractile vacuole and a single macronucleus. Fresh or salt water.

Urostyla grandis Ehrenberg (Fig. 165, *h*). Fresh water. Body 400 to 420 microns in length.

Genus **Kerona** Ehrenberg. Body reniform. No caudals. Six oblique rows of ventral cilia. Fresh water.

Kerona pediculus (Müller) (Fig. 165, *i*). On various species of freshwater Hydra. Body 120 to 210 microns in length.

Genus **Epiclintes** Stein. Spoon-shape; ventral side flat with 5 or 6 rows of cilia. Without caudals. Salt water.

Epiclintes radiosa Quennerstedt (Fig. 165, *j*). Body about 45 microns long. In salt water.

Genus **Amphisia** Sterki. Ovate or ellipsoidal. Two rows of marginal cirri; 2 or 3 rows of ventral cirri; 3 to 5 frontals; 5 to 10 anals. Macronucleus double; a single contractile vacuole. Peristome long and narrow; with an undulating membrane on the right margin. Fresh or salt water.

Amphisia kessleri Wrzesniowski (Fig. 165, *k*). Marine. About 135 microns long.

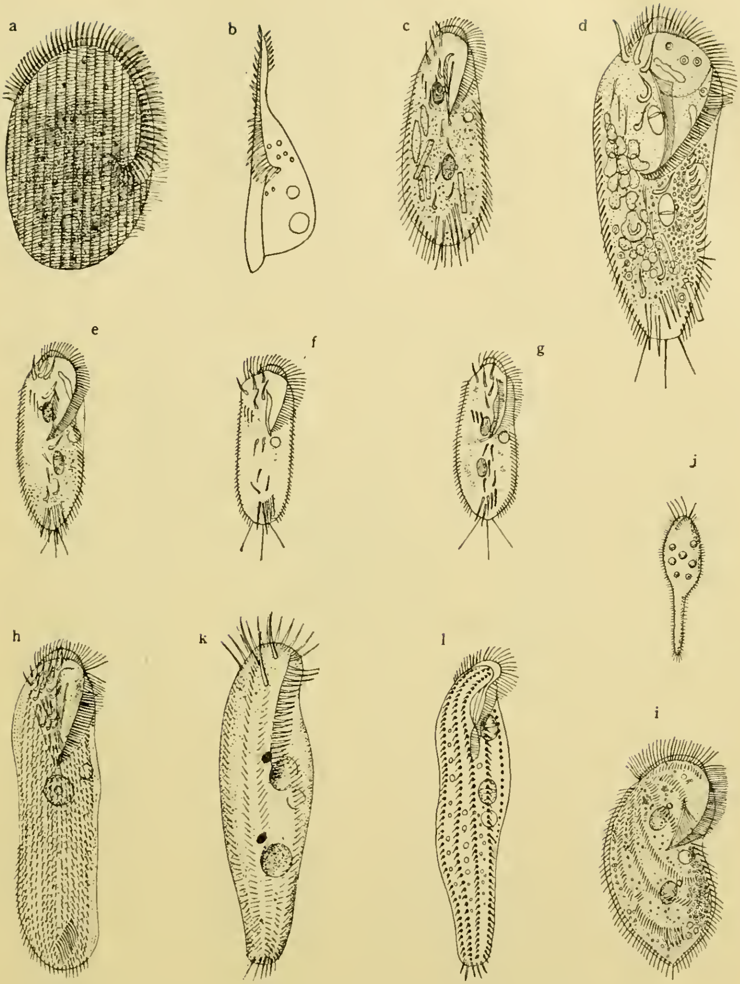


Fig. 165 a, b. *Peritromus emmae.* ×330 (After Calkins).
c. *Oxytricha fallax.* ×170 (After Stein).
d. *Stylonychia mytilus.* ×150 (After Stein).
e. *S. pustulata.* ×100 (After Stein).
f. *S. putrina.* ×150 (After Stokes).
g. *S. notophora.* ×150 (After Stokes).
h. *Urostyla grandis.* ×100 (After Stein).
i. *Kerona pediculus.* ×140 (After Stein).
j. *Epiclintes radiosa.* ×400 (After Calkins).
k. *Amphisia kessleri.* ×300 (After Calkins).
l. *Holosticha rubra.* ×200 (After Entz).

Genus **Holosticha** Enz. Two ventral and two marginal rows of cirri. Caudals. Salt or fresh water.

Holosticha rubra Ehrenberg (Fig. 165, *l*). Marine. Body about 180 microns long.

Genus **Stichotricha** Perty. Body contractile, elongate cylindrical. Long peristome reaches the middle of the body. Rows of cilia spiral. Sometimes tube-dwelling, then colonial. Fresh or salt water.

Stichotricha secunda Perty (Fig. 166, *a*). Fresh water. About 180 to 200 microns long.

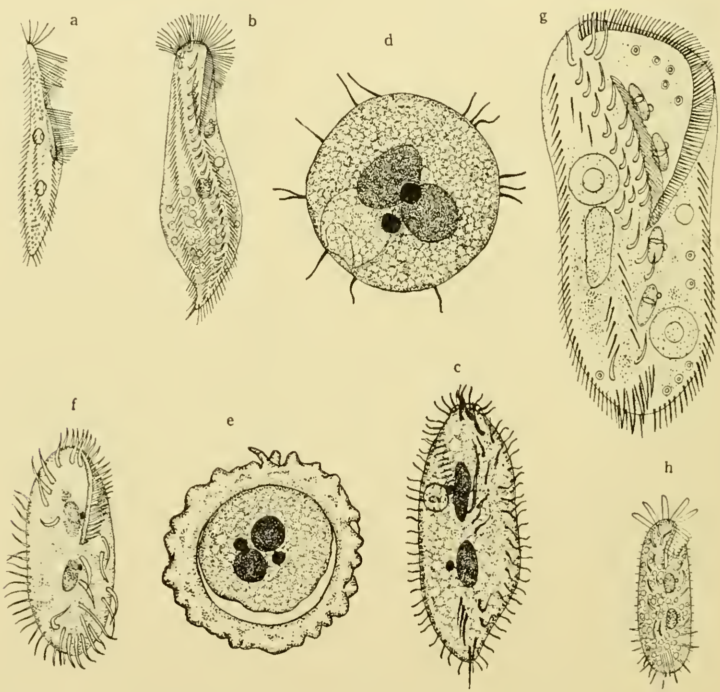


Fig. 166 a. *Stychotricha secunda.* ×150 (After Stein).
b. *Uroleptus musculus.* ×180 (After Stein).
c–e. *Pleurotricha lanceolata.* ×275 (After Meanwell). c, active form; d, encysting form; e, encysted individual.
f. *Gastrostyla steini.* ×200 (After Calkins).
g. *Onychodromus grandis.* ×170 (After Stein).
h. *Actinotricha saltans.* ×200 (After Maupas from Bütschli).

Genus **Uroleptus** Ehrenberg. Body sometimes rose or violet in color. Elongate to cylindrical. The anterior end rounded, posterior end more or less drawn out. Three frontals; 4 or 5 rows of ventral cirri, but no posterior cirri. Peristome about one-third the length of the body. Fresh or salt water.

Uroleptus musculus Ehrenberg (Fig. 166, *b*). Fresh water. Body about 130 to 210 microns long.

Genus **Pleurotricha** Stein. Body oblong with rounded ends. Marginal rows of cilia continuous. Five anals. Ventral cilia in two rows or somewhat irregular. Between the ventral and marginal rows are 1 to 3 rows of coarse cilia. Peristome broad, one-third the body length. Fresh water.

Pleurotricha lanceolata (Ehrenberg) (Fig. 166, *c–e*). Fresh water. Body measures 100 to 165 microns long.

Genus **Gastrostyla** Engelmann. Body flexible; with broken rows of ventral cirri. Fresh or salt water.

Gastrostyla steini Engelmann (Fig. 166, *f*). Body about 220 microns long by 80 microns broad.

Genus **Onychodromus** Stein. Inflexible body large, somewhat rectangular. Anterior end truncate; posterior end rounded. Ventral surface flat; dorsal convex. Peristome broadly triangular. Three frontals. Parallel to the right ridge of the peristome run three rows of cirri in oblique direction. Five or six anals. Marginals uninterrupted. Four to eight macronuclei; one contractile vacuole.

Onychodromus grandis (Fig. 166, *g*). Fresh water. Body about 100 to 350 microns long.

Genus **Actinotricha** Cohn. Body colorless, flexible; peristome small. Its left border bears a small number of large membranellae arranged in the form of a fan. Marine.

Actinotricha saltans Cohn (Fig. 166, *h*). Salt water. Body about 100 microns long.

Family 3 **Euplotidae** Claus

Genus **Euplotes** Ehrenberg. Inflexible body ovoid; ventral surface flattened; dorsal surface convex. Longitudinally ribbed. Peristome broadly triangular and large; its right edge is slightly drawn out. Nine or more frontal-ventrals, 5 anals, 4 scattered caudals. Band-like macronucleus and a micronucleus. Contractile vacuole single. Salt or fresh water.

Euplotes charon (Müller) (Fig. 167, *a*). Fresh or salt water. Body about 80 to 100 microns long.

Euplotes patella (Müller) (Fig. 167, *b*). Fresh or salt water. Body about 130 microns long.

Genus **Uronychia** Stein. Without frontals or caudals. Marine.

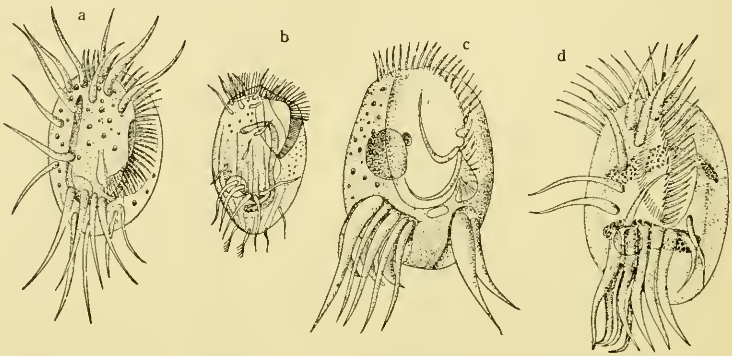


Fig. 167 a. *Euplotes charon.* ×500 (After Calkins).
b. *E. patella.* ×150 (After Stein).
c. *Uronychia setigera.* ×650 (After Calkins).
d. *Diophrys appendiculatus.* ×500 (After Calkins).

Uronychia setigera Calkins (Fig. 167, *c*). Salt water. Body about 40 microns long.

Genus **Diophrys** Dujardin. Peristome long, reaching the row of anal ciri. Three posterior giant cirri; 7 to 8 frontal-ventrals. Marine.

Diophrys appendiculatus Stein (Fig. 167, *d*). Marine. Body about 50 microns long.

Family 4 **Aspidiscidae** Stein

Genus **Aspidisca** Ehrenberg. Body small, inflexible, oval. Right side convex. Ventral side flattened; dorsal side convex. Adoral zone runs more or less straight. Seven ventrals; 5 anals. Macronucleus ring or horseshoe shape. A single contractile vacuole. Salt or fresh water.

Aspidisca lynceus Ehrenberg (Fig. 168, *a*). Body about 45 to 50 microns long. Fresh or salt water.

Aspidisca hexeris Quennerstedt (Fig. 168, *b*). Body about 68 microns long. Salt water.

Aspidisca polystyla Stein (Fig. 168, *c*). Body about 36 microns long. Salt water.

Family 5 **Psilotrichidae** Bütschli

Genus **Psilotricha** Stein. Body oblong, compressed. Anterior end broad, posterior end more constricted. Two rows of longitudinal cirri; two macronuclei. Peristome very broad. Fresh water.

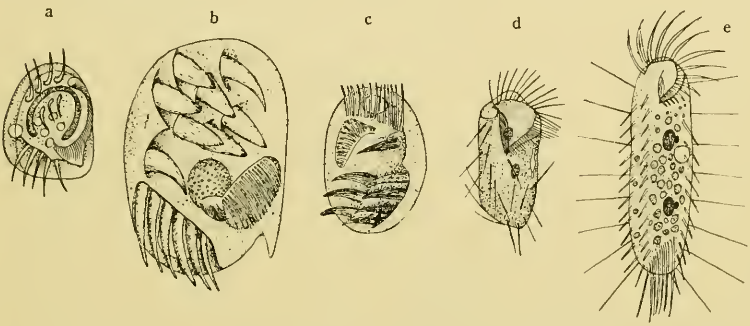


Fig. 168 a. *Aspidisca lynceus.* ×220 (After Stein).
b. *A. hexeris.* ×500 (After Calkins).
c. *A. polystyla.* ×500 (After Calkins).
d. *Psilotricha acuminata.* ×170 (After Stein).
e. *Balladina elongata.* ×600 (After Roux).

Psilotricha acuminata Stein (Fig. 168, *d*). Body length 85 to 100 microns. Fresh water.

Genus **Balladina** Kowaleski. With numerous elongated cirri. Fresh water.

Balladina elongata Roux (Fig. 168, *e*). Fresh water. Body 32 to 35 microns long by 11 to 12 microns broad.

References

STEIN, F. 1867 Der Organismus der Infusionstiere. Vol. 2.

STOKES, A. C. 1888 A preliminary contribution toward a history of the fresh-water Infusoria of the United States. Jour. Trenton Nat. Hist. Soc., Vol. 1.

CHAPTER XXXII

ORDER 5 **PERITRICHIDA** STEIN

The PERITRICHIDA possess a much enlarged disc-like anterior end which is conspicuously ciliated. The adoral zone is a right-handed spiral unlike those of the other orders mentioned in the preceding pages. Aside from a few genera such as Trichodinopsis and young free-swimming individuals of the stalked forms, the general body surface is not ciliated. Both free-swimming and stalked forms occur. The latter produce colonial forms. A test occurs among the members of Cothurnia.

Asexual reproduction is by binary fission and sexual reproduction occurs commonly. The majority are free-living, often attached to various aquatic animals and plants, although a few are parasitic.

The order is here divided into four families:

Without stalk; body barrel-shaped.................Family 1 Trichodinidae
With stalk; body more or less conical
  Peristome not spirally rolled
    Free-living attached forms; posterior end inflexible. Family 2 Vorticellidae
    Attached; posterior end flexible...............Family 3 Licnophoridae
  Peristome spiral; sessil, with or without stalk....Family 4 Spirochonidae

Family 1 **Trichodinidae** Claus

Genus **Trichodina** Ehrenberg. Body barrel-shape with a row of posterior cilia. Posterior end forms a sucking disc. Adoral zone at the anterior end. Nucleus band-form; a contractile vacuole. All ectoparasitic.

Trichodina pediculus Ehrenberg (Fig. 169, *a*). On Hydra, tadpole, etc. Body diameter 55 to 70 microns.

Trichodina sp. Diller. On the skin and gills of the tadpoles of Rana and Bufo. Body 30 to 40 microns in diameter.

Trichodina asterisci Gruber. On starfish.

Genus **Cyclochaeta** Jackson. Body on the whole similar to

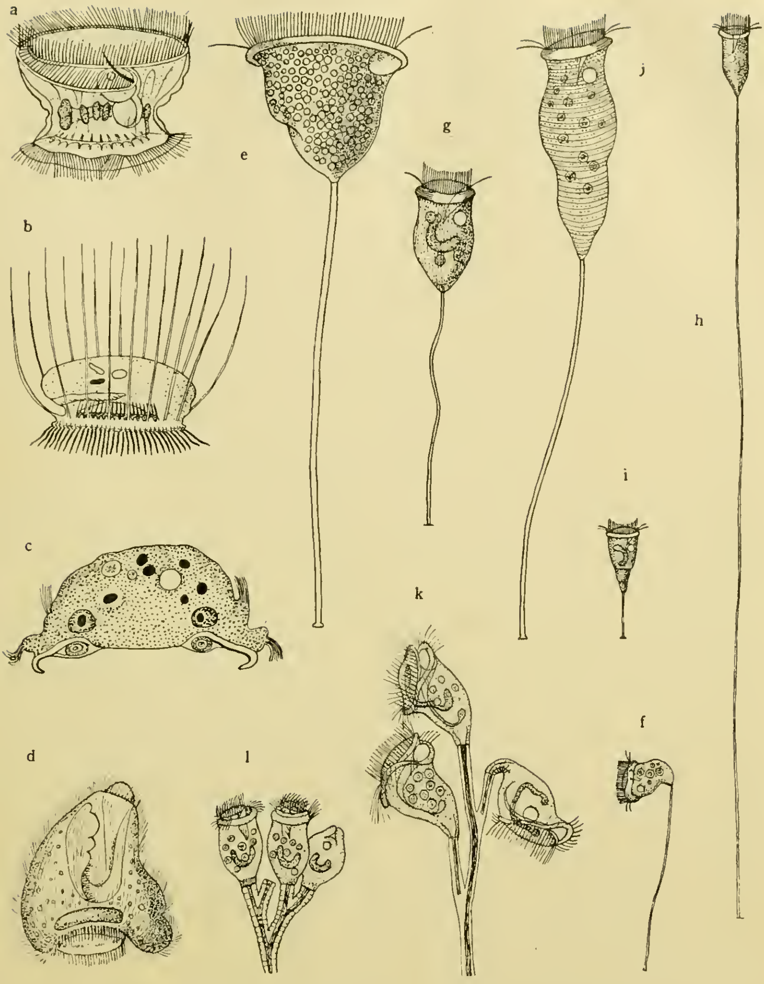


Fig. 169 a. *Trichodina pediculus.* ×400 (After James-Clark).
b. *Cyclochaeta spongillae.* ×450 (After Jackson).
c. *C. domerqui.* ×600 (After Wallengren).
d. *Trichodinopsis paradoxa.* ×200 (After Claparède and Lachmann).
e. *Vorticella campanula.* ×150.
f. *V. nutans.* ×150.
g. *V. alba.* ×150.
h. *V. longifilum.* ×150.
i. *V. telescopa.* ×150.
j. *V. quadrangularis.* ×150. (e–j, after Kent).
k. *Carchesium polypinum.* ×150 (After Stein).
l. *Zoothamnium arbuscula.* ×150 (After Stein).

Trichodina, but with rigid bristles external to the posterior girdle of cilia.

Cyclochaeta spongillae Jackson (Fig. 169, *b*). In the interstices of the freshwater sponge, *Spongilla fluviatilis*.

Cyclochaeta domerqui Wallengren (Fig. 169, *c*). In the integument of freshwater fishes. Body about 55 microns in diameter.

Genus **Trichodinopsis** Claparède and Lachmann. Body conical in form; oral end much constricted; body surface covered with long cilia.

Trichodinopsis paradoxa Claparède and Lachmann (Fig. 169, *d*). Inhabit the gut and respiratory cavity of *Cyclostoma elegans*. When extended about 140 microns long.

Family 2 **Vorticellidae** Fromental

Genus **Vorticella** Linnaeus. Body inverted bell-form; colorless, yellowish, or greenish; peristome more or less outwardly extended. Pellicle frequently annulated. Always with a contractile stalk. Adoral zone prominent; a single macronucleus curved band-form; one micronucleus; one or two contractile vacuoles. Solitary, never colonial. Free-living in fresh or salt water. Numerous species. Specific identification is very difficult because of variation.

Vorticella campanula Ehrenberg (Fig. 169, *e*). Fresh water. Body about 150 microns long; stalk thick, usually 5 to 6 times the body length.

Vorticella nutans Müller (Fig. 169, *f*). Fresh water. About 40 to 85 microns long when extended. The body is curved characteristically toward the base of the stalk.

Vorticella alba Fromentel (Fig. 169, *g*). Fresh water. 45 to 55 microns long.

Vorticella longifilum Kent (Fig. 169, *h*). Fresh water. The stalk is 10 to 15 times the body length.

Vorticella telescopa Kent (Fig. 169, *i*). Fresh water. With two annular grooves in the posterior part. About 45 to 50 microns long.

Vorticella quadrangularis Kent (Fig. 169, *j*). Fresh water. Body about 200 microns long.

Genus **Carchesium** Ehrenberg. Individuals similar to those of Vorticella, but colonial; individuals are all alike. The myonemes in the stalks are not continuous, and, therefore, individual stalks contract independently. The macronucleus is a curved band; one contractile vacuole. Attached to animals and plants. Some reach 4 mm. in height. Fresh or salt water.

Carchesium polypinum Ehrenberg (Fig. 169, *k*). Ordinarily in fresh, sometimes in salt, water. Body about 45 to 60 microns long.

Genus **Zoothamnium** Ehrenberg. Similar to Carchesium except that the contractile myonemes of all stalks are continuous with one another, so that the entire colony contracts or expands. Sometimes several millimeters high. Fresh or salt water.

Zoothamnium arbuscula Ehrenberg (Fig. 169, *l*). In fresh or salt water. Individuals about 60 microns long; colonies often more than 6 mm. high.

Genus **Epistylis** Ehrenberg. Body similar to that of Vorticella, but usually in a dichtomous colonial form, resembling superficially Carchesium; but the stalk not contractile. Attached to fresh or salt water animals. Colonies may reach several millimeters in height.

Epistylis plicatilis Ehrenberg (Fig. 170, *a*). Fresh water. Body about 90 to 100 microns long. Colony often 3 mm. in height.

Epistylis flavicans Ehrenberg. On fresh water plants. Body about 130 to 360 microns long.

Genus **Ophrydium** Ehrenberg. Colonial. The whole is embedded in a common mucilaginous mass. Stalk not contractile. Fresh or salt water.

Ophrydium sessile Kent (Fig. 170, *b*, *c*). Attached to freshwater plants. Body fully extended about 300 microns long. Ovoid colony measures 5 mm. by 3 mm.

Genus **Opercularia** Stein. The peristome end is oblique; with an undulating membrane in the persitome. Short, not contractile stalk branched and rigid. Fresh water. Several species.

Opercularia stenostoma Stein (Fig. 170, *d*). Fresh water; often attached to Crustacea. When extended the body measures about 125 microns long.

Fig. 170 a. *Epistylis plicatilis.* ×150 (After Stein).
b, c. *Ophrydium sessile.* (After Kent). b, an entire colony, natural size; c, a colony more magnified (×50).
d. *Opercularia stenostoma.* ×100 (After D'Udekem).
e. *Gerda vernalis.* ×120 (After Stokes).
f. *Scyphidia constricta.* ×270 (After Stokes).
g. *Glossatella tintinnabulum.* ×300 (After Kent).
h. *Rhabdostyla vernalis.* ×240 (After Stokes).
i. *Astylozoon fallax.* ×125 (After Engelmann).
j. *Hastatella aesculacantha.* ×380 (After Jarocki).
k. *Cothurnia crystallina.* ×200 (After Calkins).
l. *C. nodosa.* ×350 (After Calkins).
m. *Vaginicola crystallina.* ×100 (After Kent).
n. *Lagenophrys ampulla.* ×150 (After Stein).
o. *Licnophora macfarlandi.* ×625 (After Calkins).
p. *Spirochona gemmipara.* ×225 (After Hertwig).

Genus **Gerda** Claparède and Lachmann. Body elongated and cylindrical, highly contractile. Cytostome at the anterior end; adoral zone spiral, leading into the cytostome. Macronucleus band-form. A contractile vacuole. No stalk; not firmly attached.

Gerda vernalis Stokes (Fig. 170, *e*). In shallow freshwater ponds in early spring. About 250 microns long when extended.

Genus **Scyphidia** Dujardin. Somewhat similar to Gerda. Posterior end drawn out and suctorial in function. Stalk is non-contractile. Attached. Fresh water. Several species.

Scyphidia constricta Stokes (Fig. 170, *f*). Pond water, often attached in clusters of 2 to 4 to Nais. Body about 55 microns long.

Genus **Glossatella** Bütschli. Non-contractile stalk rudimentary. An enormously large undulating membrane around the peristomal margin. Often attached to Triton larvae.

Glossatella tintinnabulum (Kent) (Fig. 170, *g*). On the epidermis and gills of the young Triton. Body about 40 microns long.

Genus **Rhabdostyla** Kent. Solitary with non-contractile stalk. Attached to aquatic animals. Fresh or salt water. Several species.

Rhabdostyla vernalis Stokes (Fig. 170, *h*). Attached to Cypris and Cyclops in the pools in early spring. Body about 50 microns long.

Genus **Astylozoon** Engelmann. Without stalk, two posterior setae. Free-swimming. Rare.

Astylozoon fallax Engelmann (Fig. 170, *i*). Fresh water. Body about 70 to 100 microns long.

Genus **Hastatella** Erlanger. With several conical projections. Free-swimming. Fresh water. Two species.

Hastatella aesculacantha Jarocki and Jakubowska (Fig. 170, *j*). In stagnant water. Extended body 30 to 52 microns long by 24 to 40 microns wide.

Genus **Cothurnia** Ehrenberg. Vorticella-like body in pseudochitinoid lorica which is attached directly, or by a short stalk, to submerged objects. Salt or fresh water.

Cothurnia crystallina Ehrenberg (Fig. 170, *k*). Fresh or salt water. Lorica 70 to 200 microns in length.

Cothurnia nodosa Claparède and Lachmann (Fig. 170, *l*). Cup 75 microns long; stalk 35 to 40 microns long.

Genus **Vaginicola** Lamarck. Body elongate and cylindrical; ciliation and peristomal structure similar to those of Vorticella, but with a vase-like lorica. Several species in fresh water.

Vaginicola crystallina Ehrenberg (Fig. 179, *m*). On freshwater plants. Lorica about 120 microns long.

Genus **Lagenophrys** Stein. Similar to Vaginicola, but the aperture of the lorica narrow and thickened. Attached to freshwater animals.

Lagenophrys ampulla Stein (Fig. 170, *n*). Attached to Gammarus and Asellus. Diameter of the sheath 50 to 70 microns.

Family 3 **Licnophoridae** Stevens

Genus **Licnophora** Claparède. Spiral girdle left-handed and ciliated. Adoral sucker surrounded by a circle of cilia. Salt water.

Licnophora macfarlandi Stevens (Fig. 170, *o*). Attached to various marine invertebrates, such as medusae, polychaetes, etc. Body length about 60 microns.

Family 4 **Spirochonidae** Grobben

Genus **Spirochona** Stein. A delicate spiral membrane at the anterior end of the body. The posterior end serves for adhesion, often showing pseudopodial lobes. Exogenous budding. One macronucleus, one to three micronuclei. Attached to Crustacea. Several species.

Spirochona gemmipara Stein (Fig. 170, *p*). Attached to fresh-water crustaceans. Body 40 to 110 microns in length.

References

Kent, W. S. 1881–1882 A manual of the Infusoria. Vol. 2.

Stein, F. 1868 Der Organismus der Infusionstiere. Vol. 2.

Stokes, A. C. 1881 A preliminary report toward a history of the fresh-water Infusoria of the United States. Jour. Trenton Nat. Hist. Soc., Vol. 1.

CHAPTER XXXIII

CLASS 2 **SUCTORIA** BÜTSCHLI

THE SUCTORIA, which are also called the Acineta, Acinetaria, Tentaculifera, etc., do not possess any cilia or any other cell-organs of locomotion in the mature stage. The cilia are present only on young individuals which are capable of free-swimming, and are lost with the development of a stalk or an attaching disc, and of **tentacles.** Therefore, an adult suctorian is incapable of active movement. The body is covered with a pellicle and occasionally possesses a lorica. There is no cytostome, and the food-capturing is carried on exclusively by the tentacles. Tentacles are of two kinds. One is suctorial in function and bears a rounded knob on the extremity. It is found in many genera. The other kind of tentacle is for piercing and is, more or less, sharply pointed, as in Ephelota. These tentacles may be confined to limited areas or may be formed from the entire body surface. The prey is usually small ciliates. Nutrition is holozoic.

The body of a suctorian may be spherical, elliptical, dendritic, etc. Asexual reproduction is by binary fission or budding. The buds which are formed by either exogenous or endogenous gemmation are ciliated, and swim around actively after leaving the parent individual. Finally becoming attached to a suitable object, they metamorphose into adult forms. Sexual reproduction is through copulation. The Suctoria live attached to animals, plants, or non-living matter submerged in fresh or salt water.

According to Collin, the Suctoria are here divided into eight families as follows:

Adult without cilia
  With Suctorial tentacles only
    Body irregular or branching
      Without proboscis or special arms. Body form highly variable; often with stolon; but usually without a stalk..........
Family 1 Dendrosomidae

With proboscis or special arms
With a retractile proboscis which bears tentacles...........
Family 2 Ophryodendridae
With special arms with tentacles.......Family 3 Dendrocometidae
Body somewhat bilaterally symmetrical
Exogenous budding and division............Family 4 Podophryidae
Endogenous budding
With delicate pellicle. With or without cup-like test; with or without stalk.......................Family 5 Acinetidae
With tough pellicle; tentacles may be small in number and variable in form; stalk short and stout...Family 6 Discophryidae
With both suctorial and prehensile tentacles; with or without test; exogenous budding; ectoparasitic on marine hydroids........
Family 7 Ephelotidae
Adult with cilia................................Family 8 Hypocomidae

Family 1 **Dendrosomidae** Bütschli

Genus **Trichophrya** Claparède and Lachmann. Body small and form variable. Without stalk. Tentacles in fascicles. No branches. Attached usually to animals in both fresh and salt water. About ten species known.

Trichophrya epistylidis Claparède and Lachmann (= *T. sinuosa* Stokes) (Flg. 171, *a*). Fresh water. About 40 microns in length.

Trichophrya salparum Entz (Fig. 171, *b*). Living on the external body surface of various tunicates, such as *Molgula manhattensis*.

Genus **Astrophrya** Awerinzew. Body with eight processes, each with a fascicle of tentacles.

Astrophrya arenaria Awerinzew (Fig. 171, *c*). Found in the plankton of the Volga. The main body measures 145 to 188 microns in diameter; the length of the processes 86 to 190 microns.

Genus **Lernaeophrya** Pérez. Body large; with numerous short prolongations bearing very long fascicled tentacles. With a branching nucleus.

Lernaeophrya capitata Pérez (Fig. 171, *d*). Attached to the stalk of the hydrozoan, *Cordylophora lacustris*. Body 400 to 500 microns long; tentacles 400 microns long.

Genus **Dendrosoma** Ehrenberg. Large form often 2 mm.

in height. Body ramification more advanced, with basal stolon and upright branches which are branched.

Dendrosoma radians Ehrenberg (Fig. 171, *e*). On plants in rivers and ponds. Fully grown form measures 1.2 to 2.5 mm. in height.

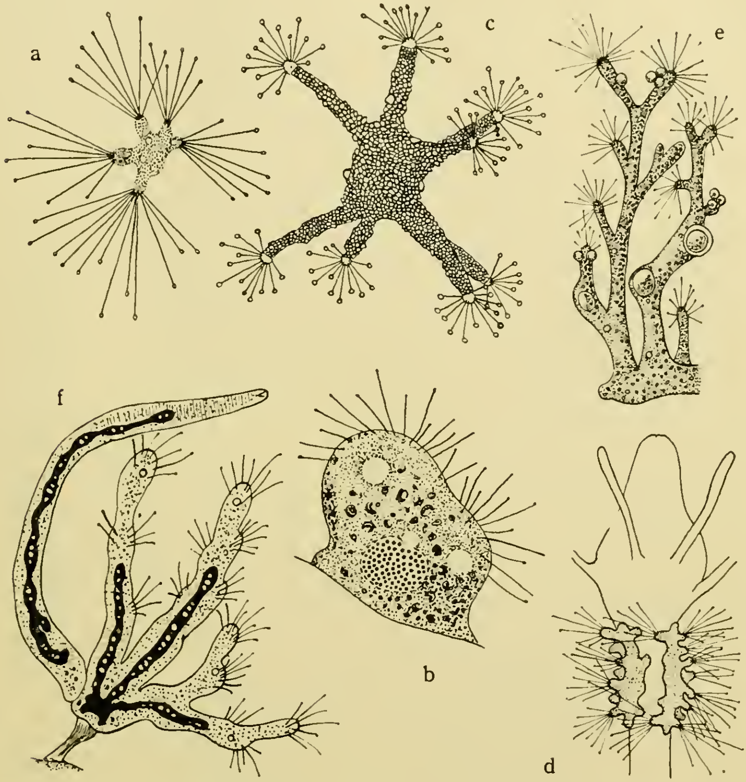


Fig. 171 a. *Trichophrya epistylidis.* ×250 (After Stokes).
b. *T. salparum.* ×165 (After Collin).
c. *Astrophrya arenaria.* ×65 (After Awerinzew).
d. *Lernaeophrya capitata.* ×35 (After Pérez).
e. *Dendrosoma radians.* ×35 (After Kent).
f. *Dendrosomides paguri.* ×200 (After Collin).

Genus **Dendrosomides** Collin. Branched body similar to Dendrosoma, but with a peduncle. Reproduction by budding of vermicular individual.

Dendrosomides paguri Collin (Fig. 171, f). Length about 200 to 300 microns; vermicular individuals measure 350 microns in length. Attached to the hermit crabs, *Eupagurus excavatus* and *E. cuanensis*.

Genus **Rhabdophrya** Chatton and Collin. Body cylindrical or rod-shaped with a short peduncle. Not branched. Tentacles distributed over the entire body surface. The macronucleus ellipsoidal and the micronucleus small. Two or three contractile vacuoles.

Rhabdophrya trimorpha Chatton and Collin (Fig. 172, *a*).

Family 2 **Ophryodendridae** Stein

Genus **Ophryodendron** Claparède and Lachmann. With a retractile proboscis which bears suctorial tentacles. Several species; attached to Crustacea, Annelida, etc.

Ophryodendron porcellanum Kent (Fig. 172, *b*). Attached to Crustacea, especially *Porcellana platycheles*.

Family 3 **Dendrocometidae** Stein

Genus **Dendrocometes** Stein. The arms are branched and each branch terminates in a sucker.

Dendrocometes paradoxus Stein (Fig. 172, *c*). Fresh water. On amphipods. Body about 85 microns in diameter.

Genus **Stylocometes** Stein. Each of the arms which are not branched, terminates in a sucker.

Stylocometes digitatus Stein.

Family 4 **Podophryidae** Bütschli

Genus **Podophrya** Ehrenberg. Body subspherical, normally with a rigid stalk. Suctorial tentacles in fascicles or distributed over the entire body surface. Encystment common. Specific identification is often difficult. Several species.

Podophrya fixa (Müller) (Fig. 172, *d*, *e*). In fresh water among vegetation.

Podophrya gracilis Calkins (Fig. 172, *f*). Stalk long and filiform, not rigid. One or two contractile vacuoles. A single nucleus near the attachment of the stalk. Body 8 microns in diameter; stalk 40 microns long. Rare. Salt water.

Genus **Sphaerophrya** Claparède and Lachmann. Body spherical, without a peduncle or stalk. Suctorial tentacles radiating. Several species; free-living and two parasitic species.

Sphaerophrya stentoris Maupas. Parsitic in various Euciliata such as Bursaria, Stentor, etc.

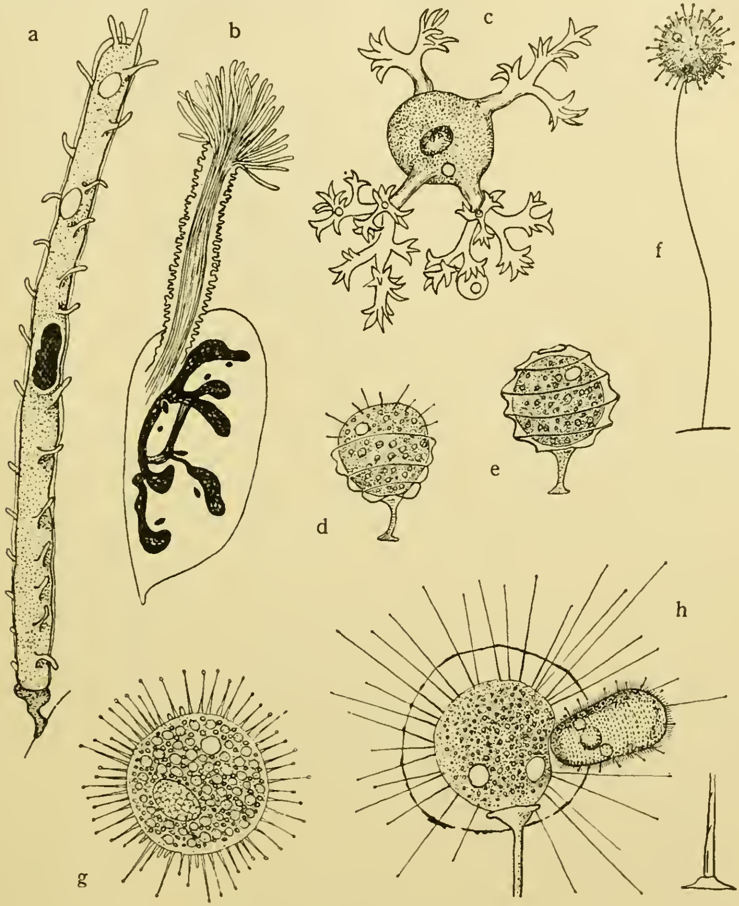


Fig. 172 a. *Rhabdophrya trimorpha.* ×645 (After Collin).
b. *Ophryodendron porcellanum.* ×330 (After Collin).
c. *Dendrocometes paradoxus.* ×265 (After Wrzesnowski).
d, e. *Podophrya fixa.* ×330 (After Collin).
f. *P. gracilis.* ×1000 (After Calkins).
g. *Sphaerophrya soliformis.* ×200 (After Lauterborn).
h. *Paracineta limbata.* A bud is just escaping. Stalk on right. ×460 (After Collin).

Sphaerophrya soliformis Lauterborn (Fig. 172, *g*). Saplopelic. Diameter about 100 microns.

Genus **Paracineta** Collin. Body covered by a closely fitting delicate test. Stalked; several species. Many which had been called Acineta have been placed in this genus by Collin.

Paracineta limbata (Maupas) (Fig. 172, *h*). Marine; among algae, bryozoans, hydrozoans, etc.

Genus **Metacineta** Bütschli. Test coarse; with fasciculated tentacles.

Metacineta mystacina (Ehrenberg) (Fig. 173, *a*). Fresh or salt water.

Genus **Urnula** Claparède and Lachmann. Tentacles one to three in number.

Urnula epistylidis Claparède and Lachmann.

Family 5 **Acinetidae** Bütschli

Genus **Acineta** Ehrenberg. Body usually pyramidal, and encased in a cup- or funnel-like stalked test. The test has no free margin. Suctorial tentacles in groups or scattered at the non-stalked end. More than twenty species recorded.

Acineta divisa Fraipont (Fig. 173, *f*). Salt water. Body 27 microns long; tentacles 65 microns long; length of stalk 100 microns .

Acineta tuberosa Ehrenberg (Fig. 173, *g*). Salt water. Body large, 330 microns long.

Genus **Tokophrya** Bütschli. Stalked; body pyriform or pyramidal; with fasciculated tentacles. Numerous species.

Tokophrya infusionum (Stein) (Fig. 173, *b–d*).

Tokophrya cyclopum Claparède and Lachmann (Fig. 173, *e*). Attached to Cyclops, Diaptomus, Gammarus, etc.

Genus **Thecacineta** Collin. Body more or less elongated. The stalked test rigid and shows free margin. Suctorial tentacles from the anterior end. Several species.

Thecacineta cothurnioides Collin (Fig. 173, *h*). Attached to the copepod, *Cletodes longicaudatus*.

Genus **Periacineta** Collin. Close-fitting test elongated and attachment by a short narrowed test or stalk(?). The other end is open without free margin. Fasciculated tentacles at the anterior end.

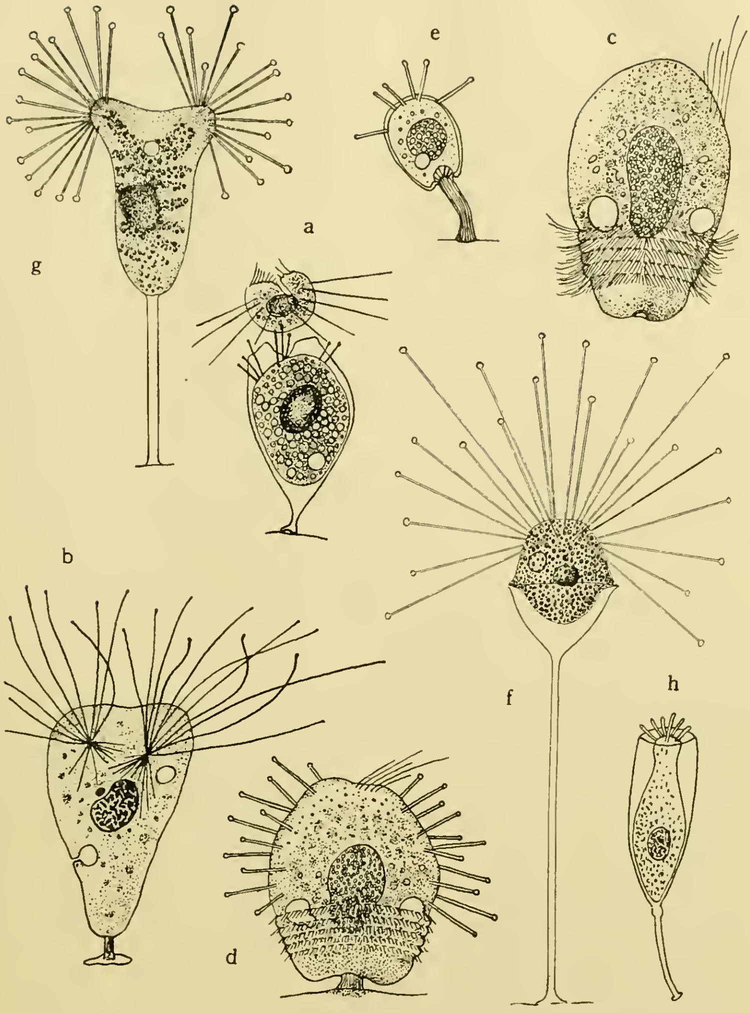


Fig. 173 a. *Metacineta mystacina*, capturing *Halteria grandinella.* ×400 (After Collin).

b–d. *Tokophrya infusionum.* b, an adult organism (×400); c, free-swimming bud (×800); d, a young attached form (×800). (After Collin).

e. A young *T. cyclopum.* ×500 (After Collin).

f. *Acineta divisa.* ×465 (After Calkins).

g. *A. tuberosa.* ×665 (After Calkins).

h. *Thecacineta cothurnioides.* ×400 (After Collin).

Periacineta buckei (Kent) (Fig. 174, *a*). Attached to Lymnaea, etc.

Genus **Hallezia** Sand. Without test; with or without a short stalk; body variable in form. Tentacles in fascicles.

Hallezia brachypoda (Stokes) (Fig. 174, *b*). Standing water with dead leaves. Body about 34 to 42 microns in diameter.

Genus **Solenophrya** Claparède and Lachmann. Body not filling the cup-like test. Attached by the base of the test.

Solenophrya inclusa Stokes (Fig. 174, *c*). Standing fresh water. Lorica subspherical and about 44 microns in diameter.

Solenophrya pera Stokes (Fig. 174, *d*). Test satchel-shaped; 44 microns high. Body about 35 microns long. Standing fresh water.

Genus **Acinetopsis** Robin. Close-fitting test polyhedral and short stalked. One to six long and active tentacles in the center of the anterior end.

Acinetopsis tentaculata Root (Fig. 174, *e*, *f*). Attached to species of Obelia. Test 185 microns long; stalk 285 microns long; body about 138 microns by 100 microns.

Genus **Tachyblaston** Martin. Ectoparasitic on Ephelota. No contractile vacuoles.

Tachyblaston ephelotensis Martin (Fig. 174, *g*, *h*).

Genus **Dactylophrya** Collin. Test with a short stalk. 12 to 15 arm-like tentacles, each terminating in a sucker, extended from the anterior end.

Dactylophrya roscovita Collin (Fig. 174, *i*). Rare; on the stalk of the hydrozoan, *Diphasia attenuata*.

Genus **Pseudogemma** Collin. Parasitic in other Suctoria, such as Acineta or Paracineta.

Pseudogemma pachystyla Collin (Fig. 174, *j*). In *Acineta tuberosa*.

Genus **Endosphaera** Engelmann. Body spherical and without axial differentiation. Tentacles and stalk absent. Endoparasitic in other Protozoa.

Endosphaera engelmanni Entz. In *Trichodina pediculus*, *Didinium nasutum*, Vorticellidae, etc.

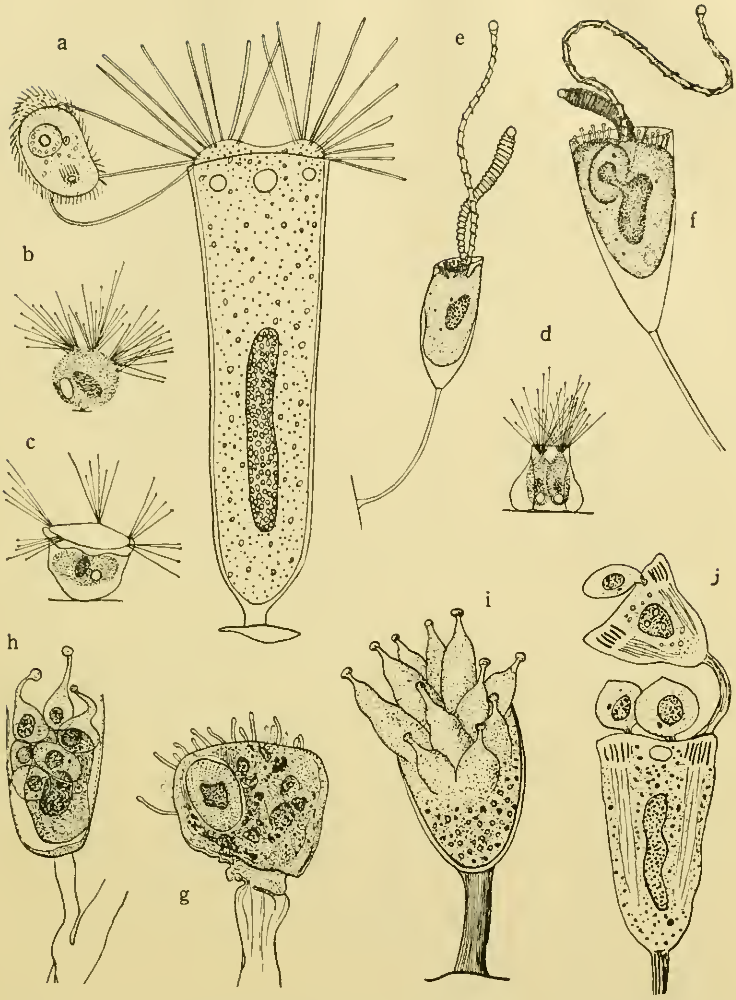


Fig. 174 a. *Periacineta buckei* with *Chilodon* sp. ×530 (After Collin).
b. *Hallezia brachypoda.* ×200 (After Stokes).
c. *Solenophrya inclusa.* ×225 (After Stokes).
d. *S. pera.* ×225 (After Stokes).
e, f. *Acinetopsis tentaculata.* e, ×125; f, with a bud, ×230. (After Root).
g, h. *Tachyblaston ephelotensis.* (After Martin). g, a young individual in Ephelota (×255); h, adult individual (×500).
i. *Dactylophrya roscovita.* ×830 (After Collin).
j. *Pseudogemma pachystyla.* ×400 (After Collin).

Family 6 **Discophryidae** Collin

Genus **Discophrya** Lachmann. Body triangular to ellipsoidal. Attached with a short stalk. Tentacles fasciculated or distributed.

Discophrya elongata (Claparède and Lachmann) (Fig. 175, *a*). Attached to the shell of *Vivipara contecta.*

Genus **Thaumatophrya** Collin. Tentacles numerous and each tapers toward the free end.

Thaumatophrya trold (Claparède and Lachmann) (Fig. 175, *b*). Salt water. Body diameter about 70 microns.

Genus **Rhynchophrya** Collin. Body oblong, bilaterally symmetrical. A short stalk. One main tentacle and a few secondary tentacles.

Rhynchophrya palpans Collin (Fig. 175, *c*). Body 85 microns long by 50 microns broad; tentacles 10 to 200 microns; style 20 microns by 10 microns.

Genus **Choanophrya** Hartog. Body spheroidal with a stalk. Tentacles expansible at their distal ends to engulf voluminous food particles.

Choanophrya infundibulifera (Hartog) (Fig. 175, *d*).

Genus **Rhyncheta** Zenker. Protoplasmic body is attached directly to an aquatic animal. With a long mobile tentacle bearing a sucker at its end.

Rhyncheta cyclopum Zenker (Fig. 175, *e*, *f*). On species of Cyclops. When extended the body measures about 170 microns long.

Family 7 **Ephelotidae** Sand

Genus **Ephelota** Wright. No test; with or without stalk. Ectoparasitic on hydroids.

Ephelota coronata Wright (Fig. 175, *g*). Salt water. On hydroids, algae, bryozoans, etc. Body 90 to 200 microns long.

Ephelota sessilis Collin. Attached to the ascidian, *Pyrosoma elegans*.

Genus **Podocyathus** Kent. Conspicuous test and stalk. Salt water.

Podocyathus diadema Kent (Fig. 175, *h*). Salt water. Lorica about 42 microns long.

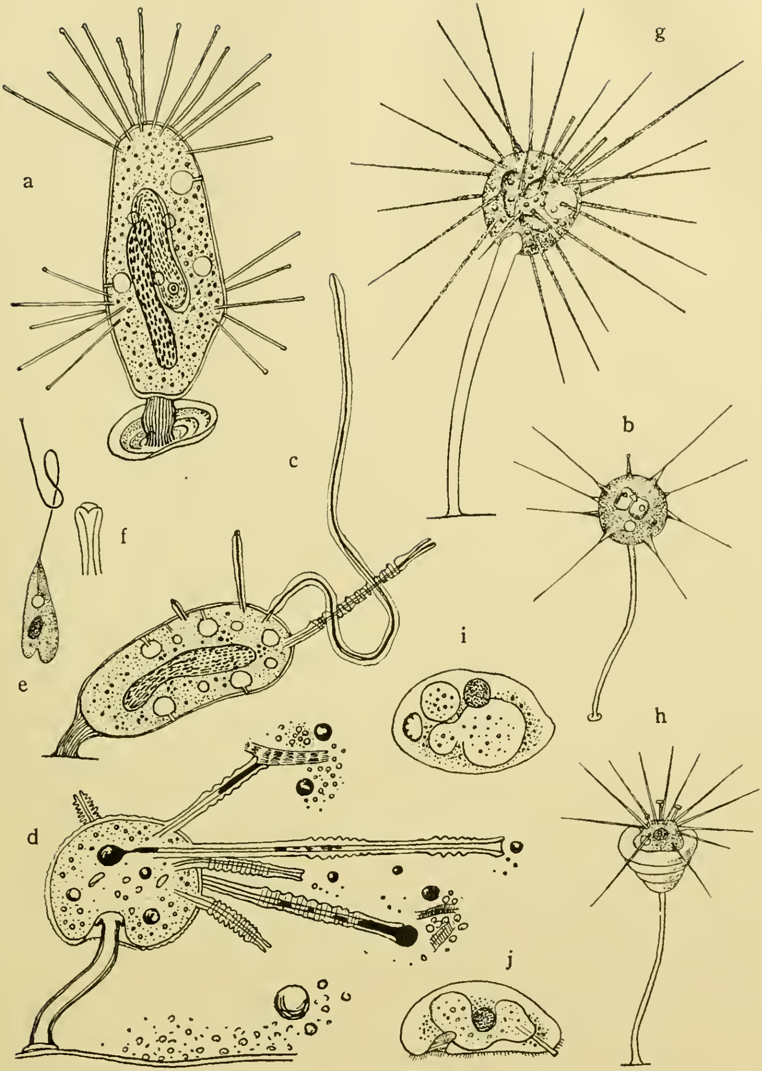


Fig. 175 a. *Discophrya elongata.* ×435 (After Collin).
b. *Thaumatophrya trold.* ×115 (After Claparèd eand Lachmann).
c. *Rhynchophrya palpans.* ×435 (After Collin).
d. *Choanophrya infundibulifera,* feeding on disintegrated parts of a Cyclops. ×400 (After Collin).
e, f. *Rhyncheta cyclopum.* e, the whole organism (×100); f, end of tentacle enlarged (×400). (After Zenker).
g. *Ephelota coronata.* ×65 (After Calkins).
h. *Podocyathus diadema.* ×200 (After Kent).
i, j. Dorsal and side view of *Hypocoma acinetarum.* ×400 (After Collin).

Family 8 **Hypocomidae** Bütschli

Genus **Hypocoma** Gruber. The cilia are present throughout the life-cycle.

Hypocoma acinetarum Collin (Fig. 175, *i, j*). Ectoparasitic on *Acineta papillifera* and *Ephelota gemmipara.*

References

Collins, B. 1912 Étude monographique sur les Acinétiéns. Arch. Zool. Expér., T. 51.

APPENDIX

COLLECTION, CULTIVATION, AND OBSERVATION OF PROTOZOA

Collection

IN THE FOREGOING chapters it has been pointed out that the various species of Protozoa have characteristic habitats and that many of the free-living forms are widely distributed in bodies of water: fresh, brackish, and salt; while the parasitic forms are limited to specific host organisms. Of the free-living Protozoa, certain species may occur in large numbers within a small area under favorable conditions, but the majority are present in comparatively small numbers. If a student who has become acquainted with the representative forms intends to make collections, it is well to carry a compound microscope to the field in order to avoid bringing back numerous jars containing much water but few organisms. Submerged plants, decaying leaves, surface scum, ooze, etc., should be examined with the microscope. When desired forms are found, they should be collected together with a quantity of the water in which they occur.

When the collected material is brought into the laboratory, it is often desirable to concentrate the organisms in a relatively small volume of water. For this purpose the material may be partly filtered rapidly through a fine milling cloth or an ordinary filter paper and the residue quickly poured back into a suitable glass container before the filtration is completed. The container should be placed in a cool, well-lighted room to allow the organisms to become established in the new environment. Euglena and other stigma-bearing Phytomastigina will then be found on the side of the container facing the strongest light, just below the surface of the water, and members of the Sarcodina will be found among the debris on the bottom. Many forms will not only live for several weeks under these conditions in the laboratory, but also increase in number.

In order to collect parasitic forms, one must, of course, find the host animals that harbor them. Various species of frogs, tadpoles, cockroaches, etc., which are of common occurrence or easily obtained and which are hosts to numerous species of Protozoa, are useful material for class work. In the case of intestinal Protozoa of vertebrates, freshly voided fecal matter should be collected in a clean and dry container, and microscopical examination should be made immediately.

Cultivation

For extensive study or for class work, large numbers of a certain species of Protozoa are frequently desirable, and this makes it necessary to provide favorable conditions for their growth and multiplication. Success in culturing Protozoa depends upon several factors. First, an abundant supply of proper food material is needed to enable the organisms to grow and multiply more rapidly than under natural conditions. For example, several species of Paramecium live almost exclusively on bacilli, while Coleps, Didinium, and allied forms depend on other ciliates as sources of food supply. For cultivating the Phytomastigina successfully, good light and a fairly large amount of inorganic substances are necessary. In the second place, the temperature and chemical constituents of the medium seem to have a far greater influence on the multiplication of protozoans than was thought heretofore. As a rule, a lower temperature seems to be much more favorable for culture than a higher one, although this is not the case with the parasitic forms occurring in warm-blooded animals. Recent investigations show also the importance of a proper hydrogen ion concentration. In the third place, both protozoans and metazoans which prey upon the forms under cultivation must be excluded from the culture. For instance, it is necessary to remove *Didinium nasutum* in order to obtain a rich culture of Paramecium.

Mixed cultures of several free-living forms are comparatively easily maintained by adding a small amount of cut-up hay to the water, although the protozoan population changes a great deal from time to time. Amoeba, Vahlkampfia, Arcella, Peranema, Bodo, Paramecium, Stylonychia, and many other forms often multiply abundantly in such cultures. To obtain large numbers of a single species, individuals are taken out by means of a finely drawn pipette and transferred to a suitable ripe culture medium which contains proper food material.

Aside from the successful cultures of blood-inhabiting Protozoa, the so-called protozoan cultures are by no means "pure" cultures in the bacteriological sense, even if only one species of Protozoa is present, since bacteria and other Protophyta are invariably present abundantly in them.

Some of the more commonly used culture media will here be mentioned.

Cultivation of Free-living Forms

Euglena, Phacus, and other holophytic Mastigophora.—These flagellates usually do not live long in ordinary collection jars, but rich cultures of them may be obtained in Zumstein's medium, which is made up as follows:

Peptone	0.5 to 1 gm.
Grape sugar	0.4 to 0.5 gm.
Citric acid	0.2 to 0.4 gm.
Magnesium sulphate	0.2 gm.
Potassium phosphate	0.05 gm.
Ammonium nitrate	0 to 0.05 gm.
Distilled water	100 c.c.

Gonium, Eudorina, and other Phytomonadida.—Several authors have obtained excellent results with one of the following media:

Knop's solution:	Magnesium sulphate	0.25 gm.
	Calcium nitrate	1.0 gm.
	Potassium phosphate	0.25 gm.
	Potassium chloride	0.12 gm.
	Iron chloride	Trace
	Distilled water	1000 c.c.
Benecke's solution:	Ammonium nitrate	0.3 gm.
	Calcium chloride	0.15 gm.
	Potassium phosphate	0.15 gm.
	Magnesium sulphate	0.15 gm.
	Iron chloride	One drop
	Distilled water	1500 c.c.

Peranema, Chilomonas, and other holozoic or saprozoic Mastigophora.—Although ripe hay infusion is frequently adequate for these flagellates, it is often worth while to prepare the following medium. Mix 10 gm. of peptone and 5 gm. of sodium chloride and dissolve in 1000 c.c. of distilled water. Add 3 gm. of Liebig's beef-extract and 1.5 gm. of shredded agar, to the solution and boil the whole slowly, stirring frequently until the agar is dissolved. Add distilled water to make up for the loss by evaporation. The reaction should be slightly alkaline (pH 7.4). Filter while hot through cotton in a steam sterilizer. Then divide the filtrate into a number of test tubes, insert cotton plugs, and autoclave for 15 minutes under 15 pounds pressure. The tubes thus sterilized can be kept indefinitely. Before using, each test tube is heated and the melted contents poured into a Petri dish and allowed to cool.

Amoeba proteus and allied forms.—These amoebae feed on diatoms, bacteria, protozoans, and not infrequently small metazoans. Hay infusion makes a satisfactory medium if a few wheat grains are added. Knop's and Benecke's solutions mentioned above are also suitable for culturing these free-living holozoic amoebae. Some workers recommend cutting and boiling aquatic plants, such as Elodea, for this purpose. Upon cooling, pour the plants and extract into a deep, wide-mouthed, glass jar and add aerated rain water. A weaker solution is, on the whole, much better than a stronger one, although the development of amoebae may be slow. After leaving the jar standing exposed for several days, introduce into it the amoebae that have been previously collected. The inoculated jar should be kept in a cool, well-lighted place.

Vahlkampfia, Naegleria, etc.—These small mono- or di-phasic amoebae which feed on bacteria can easily be cultivated on the agar medium mentioned above for Peranema and others. A similar medium, devised by Musgrave and Clegg, and modified by Walker, consists of the following:

Agar	2.5	gm.
Sodium chloride	0.05	gm.
Liebig's beef-extract	0.05	gm.
Normal NaOH solution	2.0	gm.
Distilled water	100	c.c.

By subcultures, almost a pure culture with bacteria can be obtained. Hay infusion is also excellent for these small free-living amoebae.

Arcella and other Testacea.—These forms commonly multiply in a mixed culture in hay infusion. Hegner cultivated Arcella by the following method: Pond water and weeds are collected. In the laboratory they are shaken up violently and filtered through eight thicknesses of cheese cloth, which apparently prevents passage of particles larger than Arcella. The filtrate is distributed among Petri dishes, and when the suspended particles settle down to the bottom of the dish, Arcella are introduced. They multiply rapidly.

Actinophrys, Actinosphaerium, etc.—Bělař cultivated these heliozoans successfully in Knop's solution.

Paramecium, Euplotes, Stylonychia, and other ciliates.—All these ciliates are easily cultivated in a weak solution of hay infusion, with or without wheat grains. The crystallization jars containing the medium should be left standing uncovered for several days to allow a rich bacterial growth in them. Seed them with material such as submerged leaves or scum containing these ciliates. When once started, separate cultures can be easily made and maintained by the isolation method. If desired, a culture can be started with a single individual. Subcultures should be made from time to time. Mixtures of beef-extract and hay infusion have also been used for cultivating free-living holozoic ciliates.

Cultivation of Parasitic Forms

Embadomonas, Trichomonas, Chilomastix, etc.—There are numerous media which have been used for successful cultivation of these flagellates *in vitro*. For *Trichomonas hominis* and *T. vaginalis*, Lynch used nutrient broth with 0.05 per cent acetic acid, incubated at 30° C., making subcultures every two to three days. Hogue's ovo-mucoid medium is made as follows: Whites of six eggs are broken in a sterile flask with beads. Add 600 cc. of 0.7 per cent salt solution and cook the whole for 30 minutes over a boiling water bath, shaking the mixture constantly. Filter through a coarse cheese cloth and through cotton-wool with the aid of a suction pump. Put 5 c.c.

of the filtrates in each test tube. Autoclave the test tubes for 15 minutes under 15 pounds pressure. After cooling, a small amount of fresh fecal matter containing the flagellates is introduced into the tubes. Incubation at 37° C.

Lophomonas blattarum and L. striata.—A mixture of one part sterile egg albumen and three parts autoclaved Ringer's solution, to which a small amount of yeast cake has been added, is excellent for the culture of these cockroach flagellates. Incubation is at room temperature, and subcultures are made every fourth day.

Trypanosoma and Leishmania.—Blood-agar medium, commonly called N.N.N. medium because it was originally developed by Novy and MacNeal and simplified by Nicolle, is prepared in the following manner: 14 gm. of agar and 6 gm. of sodium chloride are dissolved by heating in 900 c.c. of distilled water. When the mixture cools to about 50° C., 50 to 100 c.c. of sterile defibrinated rabbit blood is gently added and carefully mixed so as to prevent the formation of bubbles. The blood agar is now quickly distributed among sterile test tubes to the height of about 3 cm., and the test tubes are left in a sloping position until the medium becomes solid. The tubes are then incubated at 37° C. for 24 hours to determine sterility and further to hasten the formation of condensation water. Sterile blood containing Trypanosoma or Leishmania is introduced by a Pasteur pipette to the condensation water, in which the organisms multiply. This medium is also good for intestinal flagellates and amoebae of vertebrates.

Entamoeba barreti.—Barret and Smith used a mixture of 9 parts of 0.5 per cent sodium chloride and 1 part of human blood serum. After inoculation the culture is incubated at from 10 to 15° C.

Entamoeba histolytica and other intestinal amoebae.—Since Boeck and Drbohlav (1925) successfully cultivated *Entamoeba histolytica* by using a medium composed of Locke's solution, egg, and human blood serum, several authors have repeated their experiments and have obtained positive results. This method has been modified and simplified in various ways. Perhaps the simplest of all is that proposed by Craig as salt-serum (or S.S.) medium, in which 0.85 per cent sodium chloride solution is autoclaved for 15 minutes under 15 pounds pressure and cooled; then to seven parts of the solution is added one part of inactivated human blood serum. In this culture medium, the dysentery amoeba undergoes active multiplication. Some investigators find that N.N.N. medium given above for Trypanosoma is also suitable for intestinal amoebae.

Plasmodium.—Bass' method is as follows: 10 c.c. of defibrinated human blood containing Plasmodium and 0.1 c.c. of 50 per cent sterile dextrose solution are mixed in test tubes and incubated at 40° C. The cultures are centrifuged to separate the erythrocytes, which sink to the bottom, from the leucocytes, which become collected above. The erythrocytes are now transferred to fresh culture tubes. Several modifications have been made.

Balantidium coli—Barret and Yarbrough's method is as follows: The medium consists of 16 parts of 0.5 per cent sodium chloride and 1 part of inactivated human blood serum. It is divided among test tubes. Introduce a small amount of the fecal matter containing the cilitate to the bottom of the tubes and incubate at 37°C. Maximum development is reached in from 48 to 72 hours. Subcultures should be made every second day. Reese used a mixture of 16 parts of Ringer's solution and 1 part of Löffler's dehydrated blood serum.

Observation

Protozoa should be studied as much as possible in life. In making fresh preparations care should be exercised to avoid any deformities which might occur owing to the pressure of the coverglass. If small bits of detritus or debris are included in the preparation, the coverglass will be supported by them and the organisms will not receive any mechanical pressure. Although ordinary plain slides are used for this purpose, it is often advantageous to use depression slides instead. To make a fresh preparation with a depression slide, the following procedure may be followed: By means of a fine pipette, a small drop of water containing the desired protozoans is placed on a large square coverglass, and is covered with a small circular coverglass, which in turn is covered by a depression slide smeared with vaseline along the edge of the depression, so as to make an air-tight compartment. In turning over the whole, in order to examine the preparation through the square coverglass, care must be taken to prevent the small circular coverglass from touching any part of the slide; for this would allow the water to run down into the depression. In such a preparation, individual protozoans can be observed and studied for several days without further treatment.

The members of the Sarcodina give little trouble to an observer, since they are not actively motile. To retard the active movement of the Mastigophora and the Ciliata, various methods have been advocated. Most of them, however, cause abnormality in form, structure, or behavior of the organisms, and should be avoided as much as possible. Addition of a solution of picric acid often will retard the movements of an actively moving protozoan without causing any deformity. When the organisms are obtainable in large numbers some of them may be stained on a plain slide by adding a drop of Lugol's solution in order to bring out the number, location, or arrangement of cilia, cirri, or flagella. Lugol's solution consists of 1 gm. of iodine, 5 gm. of potassium iodide, and 500 c.c. of distilled water.

Living protozoans, when treated with highly diluted watery solutions of certain dyes, exhibit some of their parts stained without being injured or killed by the treatment. This *intra-vitam* staining is accomplished either by adding a drop of the dye solution to the edge of the coverglass, or by allowing a drop of the dye solution to dry on the slide before the water containing the protozoans is added. Some of the dyes used for this purpose are as follows:

Auramin (1:2,000) to stain the nucleus.

Bismarck brown (1:3,000 to 30,000) to stain the cytoplasm yellowish and the granules reddish brown.

Brilliant cresyl blue (1:10,000) to stain many granules in the cytoplasm violet or blue. This dye frequently shows the endosome of the nucleus. It may also be used for blood parasites such as trypanosomes, haemogregarines, etc.

Congo red (1:1,000) to test the alkalinity and the presence of organic acids (reddish color) and mineral acids (bluish).

Methylene blue (1:10,000) to stain cytoplasmic granules, structures in the nucleus, and also protoplasmic projections.

Neutral red (1:3,000 to 30,000) to stain the nucleus and to test the alkalinity (yellowish red) or acidity (cherry red) of food vacuoles.

Parasitic Protozoa should be studied in the tissue or body fluid of the host animals in which they occur. When these are unavailable or too small in amount to make a suitable preparation, one of the following solutions may be substituted:

Physiological salt solution. The standard concentration of the solution of sodium chloride is 0.7 per cent for cold-blooded animals and 0.85 per cent for warm-blooded animals.

Ringer's solution. Various modifications have been proposed. The commonly used one consists of the following:

Sodium chloride	0.8 gm.
Potassium chloride	0.02 gm.
Calcium chloride	0.02 gm.
Sodium bicarbonate	0.02 gm.
Distilled water	100 c.c.

References

Bělař, K. 1928 Untersuchung der Protozoen. Methodik der wiss. Biologie. Vol. 1.

Doflein, F. and E. Reichenow. 1929 Lehrbuch der Protozoenkunde. Jena.

Gatenby, J. B. and E. V. Cowdry. 1928 Bolles Lee's microtomist's vade mecum. London.

Hegner, R. and J. Andrews. 1930 Problems and methods of research in protozoology. New York.

McClung, C. E. 1929 Handbook of microscopical technique. New York.

INDEX

Numbers in bold-face type indicate pages on which are given the definitions, explanations, and discussions of technical terms; the explanations or differentiations of taxonomic subdivisions; or the descriptions of genera and species. Since the technical terms and names of systematic subdivisions are in **bold-face type in the text,** this combination serves the purpose of a glossary.

Numbers in italics indicate pages on which appear those illustrations that could not be placed on the same pages as the related text matter.

A

THIS BOOK

HANDBOOK OF PROTOZOOLOGY

was set, printed and bound by The Collegiate Press of Menasha, Wisconsin. The cover design is by The Decorative Designers of Chatham, New Jersey. The type face is Binney Old Style. The type is set 10 on 12 point (Monotype) 21E. The type page is 24 x 40 picas. The paper is 60 pound Special English Finish. The end sheets are 80 pound White Schuylkill. The jacket is 25 x 38–80—Gray Dull Coated Polychrome. The binding is Holliston Extra Colors 236 L W pattern.