

THE ECOLOGY OF MARINE MICROBENTHOS II. THE FOOD OF MARINE BENTHIC CILIATES

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ABSTRACT

The paper brings together knowledge on the food of marine benthic ciliates with the exception of sessile forms. References are given to 260 species of which 90 have been studied by the author.

The classification of ciliates according to their natural food and the specificity in choice of food is discussed and the ecological significance of discrimination of food according to size is emphasized.

INTRODUCTION

In a previous study (Fenchel, 1967) the quantitative importance of protozoa – especially ciliates – in marine microbenthos was investigated and it was concluded that the ciliates play an important role in certain sediments, viz. fine sands and sulphureta. A further analysis of the structure and function of the microfauna communities requires knowledge of factors which influence the animal populations. Of these food is probably one of the most important. Thus Fauré-Fremiet

(1950a, b, 1951a), Fenchel & Jansson (1966), Lackey (1961), Noland (1925), Perkins (1958), Picken (1937), Stout (1956) and Webb (1956) all stress the importance of the food factor for the structure of protozoan communities.

Although the physiology and biochemistry of nutrition probably are better known in ciliates such as *Tetrahymena* (references see Hall, 1967) than in any other animal, the knowledge of the food of the great majority of ciliates is very scanty, not least in marine forms. Sandon (1932) reviews what was then known on the food of protozoa, but since then many new marine species have been described.

Other information on the food of marine ciliates is mainly found scattered in the taxonomical literature, especially in the monographs of Borror (1963a), Dietz (1964), Dragesco (1960, 1963a), Kahl (1928, 1930-35), and Villeneuve-Brachon (1940). References to other taxonomical works with information on food is found in the special part of the present paper. Webb (1956) treats the food of ciliates as a main point in her description of the ciliate communities in a salt marsh. Detailed information on the feeding of histophagous ciliates is found in Fauré-Fremiet (1935), Mazoué (1935) and Mugard (1949). Dragesco (1962) gives valuable descriptions of the feeding mechanisms of a number of ciliates, mainly freshwater forms.

The purpose of the present paper is to bring together all available information – from the literature and from own observations – on the food of marine benthic ciliates, excluding the sessile forms. Reference is given to 260 species of which 90 species – selected to represent the most widely distributed and quantitatively most important forms – have been studied by me.

Food chains and community structure will be discussed in a later paper.

MATERIAL AND METHODS

The animals studied originate from localities listed in Fenchel (1967).

Information on the food of ciliates was obtained in three ways.

1. Observations on the contents of food vacuoles in ciliates from freshly collected samples, from samples left in the laboratory for some days or weeks, and from succession experiments with artificial sediments (the results of which will be reported in a later publication).
2. Direct observations of feeding ciliates under the dissection microscope or the compound microscope. In the latter case the animals were kept in the "Roto-Compressor" (see Heunert & Uhlig, 1966) where ciliates can be kept in good condition for hours or days under the microscope.
3. Several species were – for other purposes – kept in cultures. In many cases the animals were fed on "unnatural" food items (bakers yeast, peptone, planctonic algae, etc.) and information achieved from cultures is therefore often of restricted relevance to the natural food of the species.

Most information was achieved in the first mentioned way; a total of more than 500 individuals of various species were investigated for remains of food. Also the great majority of the information in the literature comes from observations of the contents of food vacuoles. The method has drawbacks, however, which must be considered in evaluations of the results.

Several food items, especially ingested ciliates, become unrecognizable very quickly in the food vacuoles. Some of the carnivorous ciliates digest their food very quickly and in species of such genera as *Litonotus* and *Loxophyllum* recognizable food is nearly never found. Even worse is the fact that some items become unrecognizable before others and the results of the investigation may therefore be biased. Frustules of diatoms, for example, are recognizable until the moment they are discharged while swallowed ciliates and flagellates, especially colourless forms, sometimes become unrecognizable within a few minutes. Sulphur bacteria leave sulphur grains long after the bacteria themselves have been digested and these bacteria will therefore have a better chance of being detected than other forms. *Remanella* contains various mineral inclusions which are not digested when the ciliates are eaten by a predator and these ciliates are therefore probably noted too frequently as prey for carnivorous ciliates. In carnivores it may often happen that the food remains of prey ciliates is left in the vacuoles of the predator after the prey is completely digested and this may also lead to misinterpretations.

Taxonomical problems give rise to serious difficulties in ciliate ecology. Several groups are badly in need of a systematical revision and in some genera (e.g. *Trachelocerca*, *Strombidium*, *Loxophyllum*, and others) satisfactory criteria for separation of the species are lacking. In many cases the identity of species mentioned under the same name in various works is not too convincing. In other cases one species has apparently been described under different names. Such cases are pointed out in the special part of this paper, but no attempts to solve them have been made. A number of undescribed species were found. They are not described here, but are only designated by their generic name, as are forms belonging to very difficult genera.

GENERAL PART

Mechanical properties of the food

It is well known that several parasitic ciliates, especially intestinal forms living in an environment rich in organic materials, are devoid of a mouth and hence are saprozoans. It is also known that a number of free-living ciliates (e.g. *Tetrahymena*) in sterile cultures can utilize and grow on dissolved substances. The ecological significance of this is not known but several facts indicate that saprozoic nutrition is of little if any importance in free-living ciliates. Concentrations of dissolved organic material are rarely if ever as high in natural environments as in the above mentioned cultures. Furthermore all free-living ciliates do possess a mouth and do

feed on particulate food in nature. For a long time it was impossible to grow *Paramecium* in chemically defined media, but Reilly (1964) showed that it could be grown on such media if inorganic particles with adsorbing properties were present. Thus this ciliate can satisfy its demands for food on particles with adsorbed nutrients, but not to a sufficient degree by transport of dissolved materials through the cell membrane.

It seems probable that small protophytes and especially bacteria with their large surface to volume ratio and high metabolic rate utilize dissolved organic materials in nature much more efficiently than do ciliates.

While it cannot at present be denied that saprozoic nutrition plays a small role for some free-living ciliates it can be stated that holozoic nutrition is by far the most important.

Ciliates are often divided into macro- and microphages according to the size of the food particles taken (see Dragesco, 1962), but the distinction is arbitrary.

The members of the order Gymnostomatida are all macrophages either eating large objects deposited on the substrate, e. g. diatoms, or hunting ciliates, flagellates or small metazoans; no ciliary organelles have evolved enabling these ciliates to feed on suspended material. The Trichostomatida comprises macro- as well as microphagous forms. The majority of the species treated in the present paper are macrophages but *Plagiopyla*, for example, feeds mainly on small particles: bacteria and protophytes.

The hymenostomes constitutes a varied group when feeding ecology is considered. Within the suborder Tetrahymenina bacteriophagous suspension feeders (e. g. *Uronema*, *Cardiostomella*) as well as macrophages (*Helicostoma*, *Ophryoglena*) are found. Within the Peniculina the paramecians are microphages while the frontonians, which have developed an expandable cytostome, are extreme macrophages feeding on objects which may exceed their own body size. The Pleuronematina comprises characteristic suspension feeders. When feeding they attach to a substrate and fold out their large undulating membrane through which they filter water propelled by the adoral membranelles (Fig. 10). From time to time the animals swim around to find a new place to feed.

The oral structures of the spirotrichs indicate that these ciliates are suspension feeders, but most forms living in soft sediments in fact find their food on the substrate. Some species, as *Spirostomum* and *Metopus*, feed on small objects, others, for example many species of *Strombidium*, feed only on large objects, and some forms are indifferent to the size of food items (e. g. *Uronychia*).

Ciliates feeding exclusively on small suspended particles are – with the exception of the pleuronematines – rare in soft sediments. The sessile or hemisessile suspension feeders (vorticellids, folliculinids, stentors), which are totally absent in sand and rare in detritus, dominate on hard substrates: rocks, plant leaves, etc.

The distinction between macrophages and microphages is – as mentioned earlier – arbitrary since many ciliates feed on items of very different sizes. The

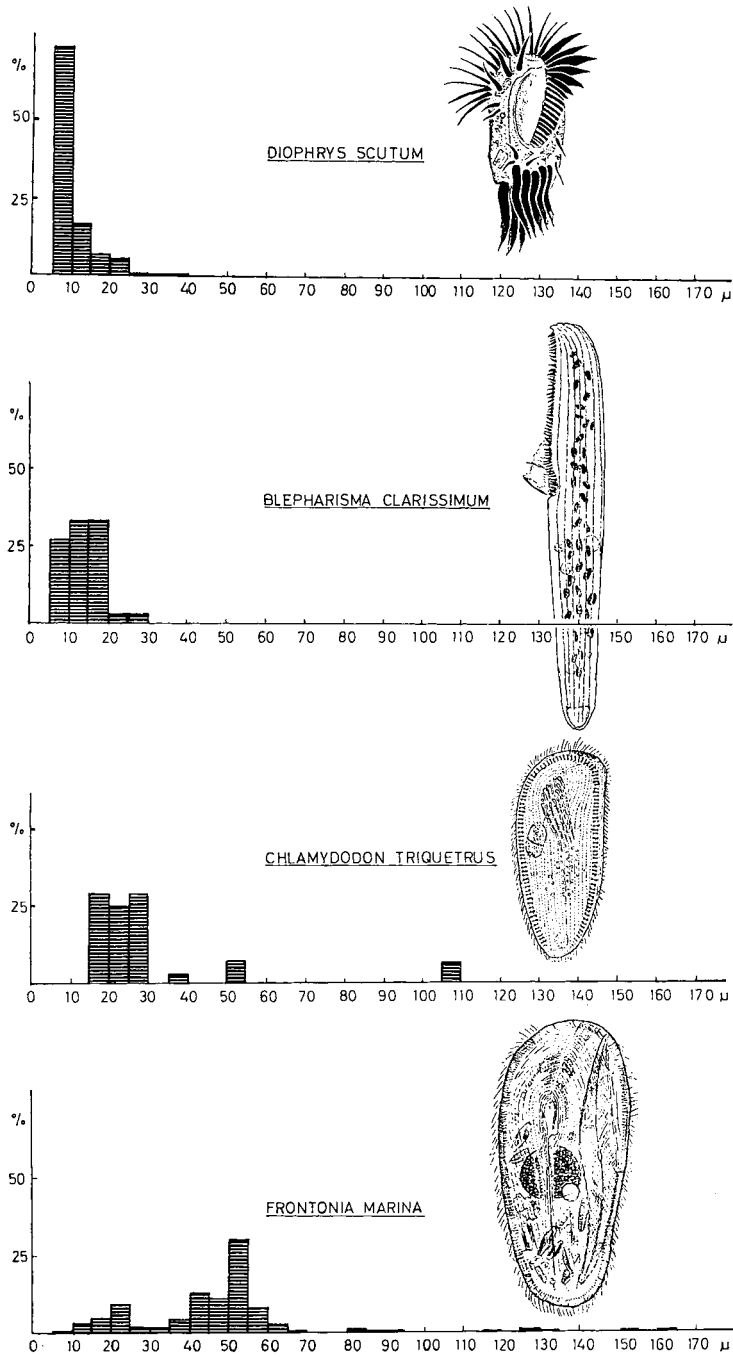


FIG. 1. Size distribution of diatoms found in four species of diatom-feeding ciliates coexisting in the surface layers of the sediments of Nivá Bay.

works of Kidder et al. (1940), Tuffrau (1959) and others have shown that populations of many species are polymorphic and that the morphology and size of the animals in a population depend on the food offered. Thus Kidder et al. showed that *Glaucoma vorax* may feed as a saprozoan or holozoically on bacteria, yeasts or other ciliates. If fed with the latter item the animals become larger and develop a larger mouth, thus enabling them to swallow the offered ciliates.

Nevertheless, discrimination of food particles according to size is evident in many species and this is of ecological significance. Fig. 1 shows the sizes of diatoms eaten by four species of ciliates which primarily eat diatoms. They often occur together, for example in the surface layers of the sediments of the Nivå Bay where they are the dominant diatom-feeders. Even though there is some overlapping it can be seen that each species prefers a certain size of diatoms. Fig. 2 shows the same for four species of *Remanella* which often occur together in the deeper layers of fine sand (only *R. gigas* is exclusively feeding on diatoms, but diatoms comprise about half of the natural diet of the other species).

Specificity in choice of food

There are many examples showing that some ciliates are remarkably specialized in their choice of food. It is, for example, well known that the carnivore *Didinium nasutum* only feeds on *Paramecium*. Furthermore, Burbanck & Eisen (1960) have shown that *Didinium* will only thrive on parameciums that have fed on special bacteria.

On the other hand many ciliate species feed on a great variety of food items. Species studied in more detail during the present investigation were often found to feed on a greater variety of food items than hitherto known. Fig. 3 shows the percentage of occurrences of different food items in the feeding vacuoles of four species. The representations do not give a completely correct picture of the relative importance of the different food items since some of these invariably occur more numerous in every individual than do others. Thus purple sulphur bacteria and diatoms play a larger quantitative role for *Parablepharisma pellitum* and *Frontonia arenaria* respectively than indicated on the diagrams.

A classification of the ciliates by their preferred food is thus sometimes difficult, but it is even more difficult to assign the species to trophic levels. Bacteriophages may feed on photoautotrophic, chemoautotrophic or heterotrophic bacteria. It is now known that heterotrophy is widely distributed among pigmented flagellates and algae living in sediments (see Wood, 1965 for references). During the present investigation pigmented dinoflagellates were often found to have a maximum in the aphotic zone several centimetres below the sediment surface and the same is the case with many diatom-feeding ciliates (these results will be described in detail in a later paper). Protophytes living at greater water depths obviously must live heterotrophically. Thus, ciliates classified as herbivores need not always occupy

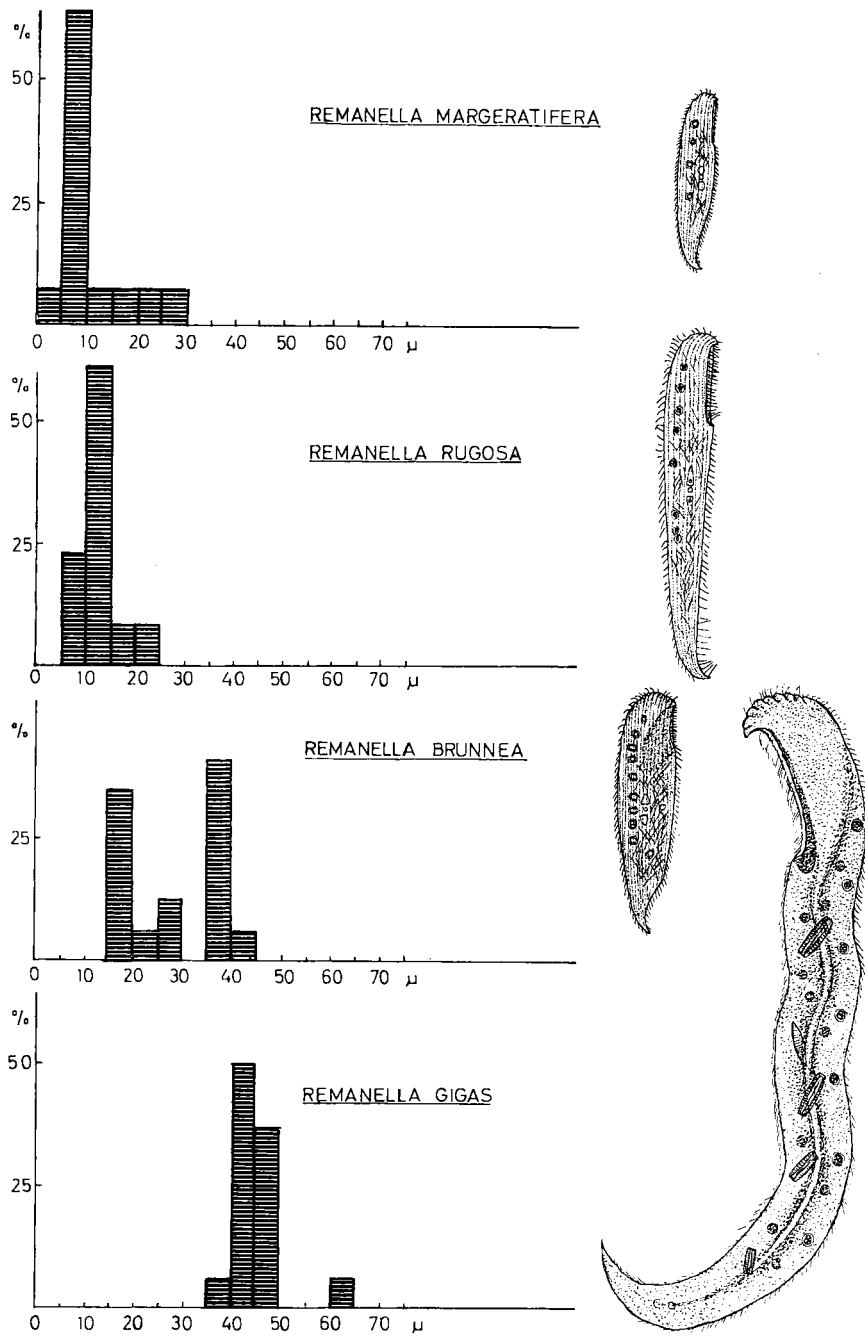


FIG. 2. Size distribution of diatoms found in four species of *Remanella* coexisting in fine sand.

the same trophic level in the community. Finally, many "carnivores" do not discriminate between pigmented and unpigmented flagellates and ciliates.

The ciliates can – according to their food – be classified as bacteriophages, herbivores, carnivores or histophages. It should be stressed once more, however, that a large number of forms, especially among the macrophages, feed on several types of food (diatoms, flagellates, ciliates, metazoans, large sulphur bacteria and algae), the items dominating the diet in any population being mainly dependent on food types available. Such forms do not, of course, lend themselves to the above mentioned "pidgeon hole system".

Bacteriophages

It is convenient to discuss the forms feeding on sulphur bacteria (Leucothiobacteriales and purple sulphur bacteria) separately. These bacteria are larger than other bacteria, and due to their contents of sulphur grains and sometimes of pigments they are easily recognizable in the feeding vacuoles of ciliates. *Thiobacillus* and other chemoautotrophs are possibly also eaten by ciliates that feed on the above mentioned sulphur bacteria, but this is not known since they cannot be recognized as chemoautotrophs under the microscope. The photoautotrophic Athiorhodacea are often eaten together with sulphur bacteria.

Several ciliate groups have specialized on sulphur bacteria and seem to be dependent on their presence. Within the holotrich ciliates the members of the family Plagiopylidae dominantly feed on these bacteria. Within the Dysteriidae *Trochiloides recta* has specialized on Leucothiobacteriales, especially *Beggiatoa*. The suspension feeding pleuronematines often feed on sulphur bacteria though most species are apparently not dependent on this food. A few species, e.g. *Cristigera media*, however, have specialized on sulphur bacteria.

Within the heterotrichs several groups have specialized on sulphur bacteria, e.g. several species of *Blepharisma*, *Parablepharisma*, *Peritromus* and the majority of the Metopidae and Caenomorphidae. Within other spirotrich orders fewer species feed on sulphur bacteria.

Many of these species will even discriminate between different kinds of sulphur bacteria, mainly according to size, but forms which mainly or solely feed on Leucothiobacteriales (e.g. *Trochiloides recta*) or on purples (e.g. *Parablepharisma pellitum*) are also found.

Ciliates feeding mainly or exclusively on other kinds of bacteria are found within the Hymenostomatida (Cohnilembidae, Philasteridae, Pleuronematidae and others), Hypotrichida (numerous forms within many families and probably all Aspidiscidae) and Odontostomatida. In addition there are also bacteriophages within other orders.

There is further evidence indicating that many bacteriophages have specialized on certain kinds of bacteria. Thus Burbank (1942) demonstrated that the division rate of *Colpidium colpoda* is dependent on the species of bacteria offered as food

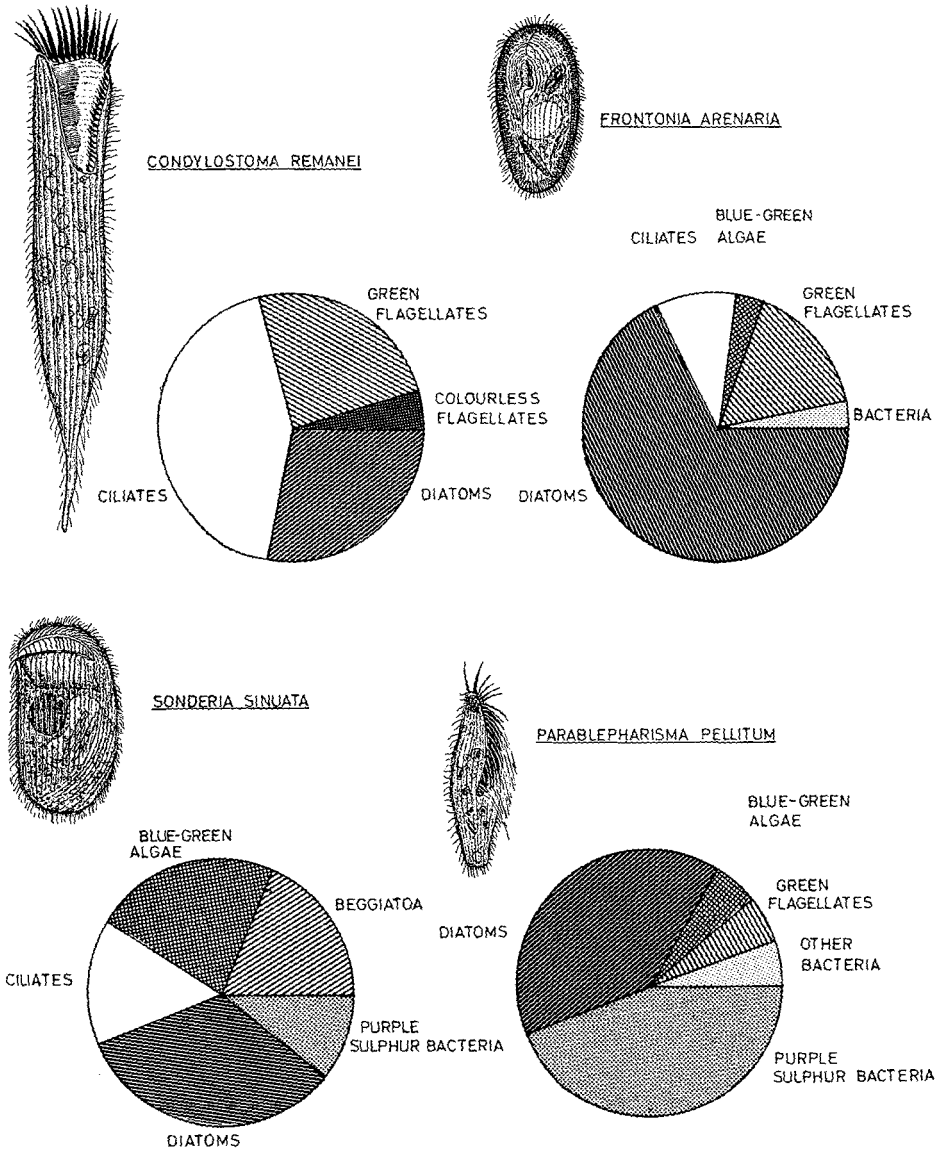


FIG. 3. Relative occurrence of food items in *Condylostoma remanei* (11 individuals studied with 21 findings of different items), *Frontonia arenaria* (29 individuals, 31 findings), *Sonderia sinuata* (11 individuals, 27 findings), and *Parablepharisma pellitum* (20 individuals, 36 findings).

and that no growth took place at all when certain bacteria were given. Similar observations were made by Kidder et al. (1940) on *Glaucoma vorax*. Lackey (1938) questioned the importance of the food factor for the distribution of ciliates since sometimes only very few species of bacteriophagous ciliates are present in environments rich in bacteria. It is, of course, obvious that food is not the sole important factor governing ciliate distribution, but specialization to different kinds of bacteria may well explain why a high number of bacteria is not always correlated with a high number of ciliate species.

During the present investigation these problems could not be studied in detail since I did not work with pure cultures of bacteria, and since bacteria can not be identified in the feeding vacuoles of the animals. Some information – mainly achieved from succession experiments with artificial sediments – can be given. Thus a number of ciliates are feeding on bacteria associated with the decomposition of animal and plant tissue, e. g. cohnilembids and bacteriophagous Philasteridae (especially in connection with decaying animal tissue), *Cyclidium* spp., *Aspidisca* spp., and some *Euplotes* and *Holosticha* spp. The two last mentioned groups also feed on colourless flagellates in such successions. All these forms can be cultured on the mixed bacterial flora living in peptone solutions. Other bacteriophages, for example *Pleuronema* spp. and *Cardiostomella*, do not occur in the beginning of successions with decaying organic material.

Herbivores

The suborder Cyrtophorina consists exclusively of macrophagous herbivores feeding mainly on large diatoms, filamentous blue-green algae or other large algae (and in a few cases on large sulphur bacteria). A large number of other ciliate groups have also specialized on algae, especially diatoms (rhabdophorine gymnostomes, many species; hymenostomes, for example *Frontonia* spp.; heterotrichs, for example *Blepharisma clarissimum*; oligotrichs, nearly all *Strombidium* spp.; hypotrichs, many species, for example *Diophrys scutum*). An even larger number of species feed on diatoms and other algae in addition to other items.

Phytoflagellates – mainly dinoflagellates but also euglenoids, cryptomonads and phytomonads – and the related colourless forms (*Peranema*, etc.) are also important in the diet of numerous ciliates; probably the majority of the rhabdophorines, many larger hymenostomes, several heterotrichs and larger hypotrichs feed mainly on phytoflagellates.

Carnivores

Formally the species feeding on small zooflagellates (*Bodo*, *Rhynchomonas*, and the like) should be classified as carnivores. The feeding ecology and taxonomical position of ciliates feeding on these organisms, however, speak in favour of classifying them together with bacteriophages. Examples are several species of *Euplotes* and *Holosticha*.

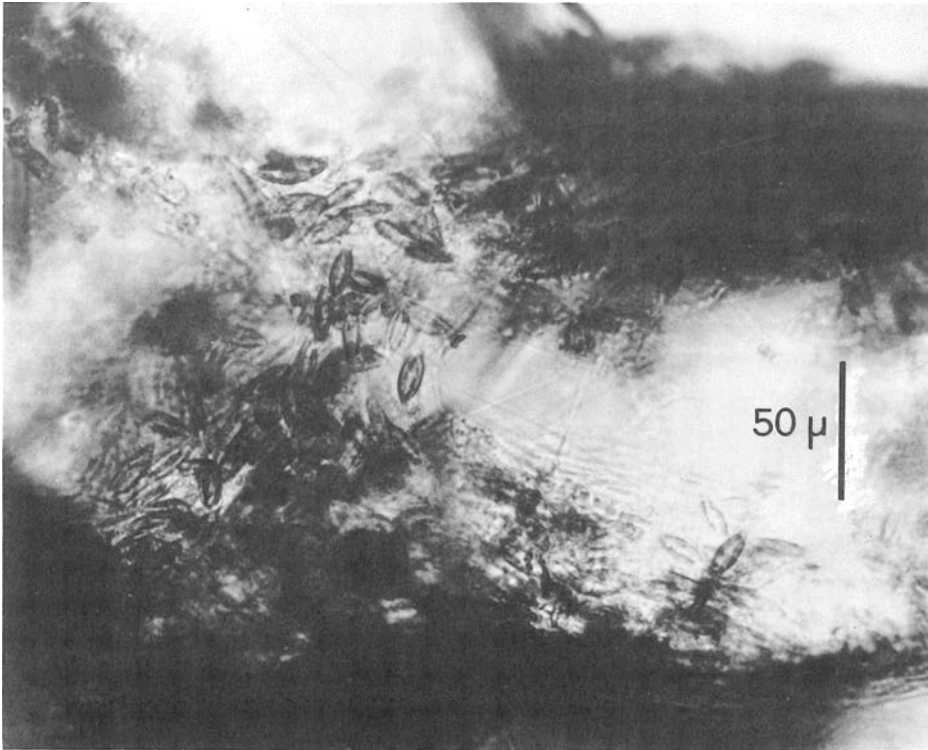


FIG. 4. The microflora on the surface of a sand grain from Nivå Bay.

Many of the macrophagous forms feeding on phytoflagellates and diatoms also often feed on other ciliates or even small metazoans as rotifers (many rhabdophorines, *Trachelocerca*, *Proroden*, etc.; hymenostomes, *Frontonia* spp.; heterotrichs, *Condylostoma* spp.; large hypotrichs, *Uronychia transfuga*). In addition some rhabdophorine groups, Amphileptidae, Tracheliidae, *Lacrymaria* spp., *Helicoprorodon* spp. and others, are specialized ciliate hunters. They possess toxic trichocysts (Dragesco, 1962; Dragesco et al., 1965) with which they kill the prey prior to swallowing. These ciliate hunters often kill more ciliates than they eat because they do not always manage to find the prey after it is killed by the trichocysts. In cultures of *Lacrymaria marina* I observed that only about half of the ciliates (*Uronema marina*) that were killed were swallowed. The same was observed in cultures of *Litonotus lamella*. In contrast to this facultative carnivores like *Condylostoma* and *Uronychia* swallow their prey in a living state and the prey animals will sometimes stay alive for several minutes in the food vacuoles of the predator.

Histophages

This term covers species feeding on living or dead tissue of dying or mechanically damaged animals. They fall taxonomically as well as ecologically into two groups. A) Several species representing different groups within the rhabdophorine gymnostomes: *Coleps* spp., *Prorodon discolor*, *Paraspathidium fuscum*, *Plagiopogon loricatus* and some others. These ciliates are facultative histophages and feed also on ciliates, flagellates, etc. The histophagous habit is derived from macrophagy in this group. B) Representatives of three families within the tetrahymenine hymenostomes: Cohnilembidae, Philasteridae and Ophryoglenidae. Here the histophages have developed from microphagous bacteriovores specializing on bacteria in decaying animal tissue. Some cohnilembids and philasterids are bacteriophages and histophages at the same time.

Finally it should be mentioned that several species often contain sand grains in their feeding vacuoles (*Strombidium* spp., *Discocephalus ehrenbergi* and others). This is probably due to the fact that many micro-organisms (bacteria, small pennate diatoms, blue-green algae, etc.) live attached to the sand grains as noted by Meadows & Anderson (1966) (see also Fig. 4). By swallowing sand grains some macrophagous ciliates are probably able to utilize these attached micro-organisms as food.

SPECIAL PART

(The systematics follows Corliss (1961) in the main).

Order GYMNOSTOMATIDA

This large order, which comprises many species in the mesopsammon, is composed of macrophagous forms. The cytopharynx is equipped with trichites in accordance with this form of feeding. Oral ciliature, found in a few groups, is never developed as an apparatus for suspension feeding.

Suborder RHABDOPHORINA

The suborder comprises a rather heterogenous assemblage of ciliate families. The members of the group are mainly carnivores, eating flagellates or other ciliates, or they feed on diatoms. Species more or less specialized as histophages are found within several genera.

Family COLEPIDAE

Genus *Coleps*

The freshwater species of this genus are dominantly histophagous but they also feed on small algae and on other infusorians (Dragesco, 1962; Kahl, 1930-35). Little information is available on marine species. According to Borror (1963a) *C. pulcher* Spiegel is feeding on diatoms and *C. spiralis* Noland on unicellular algae.

A few specimens of *C. tessellatus* Kahl from sandy bottom (5 m depth) from Øresund and from shallow water (Nivå Bay and Askö) contained what was probably remains of dinoflagellates and also clear refringent masses which may well have originated from animal tissue.

Family ENCHELYIDAE

Genus *Chaena*

C. vorax Quennerstedt is a carnivore (Kahl, 1930-35; Dragesco, 1960, 1962). According to the latter author it feeds mainly on *Uronema*, *Cyclidium* and *Cohniembus* while species of *Euplotes* are rejected as food.

Genus *Enchelydon*

According to Kahl (1930-35) all species of this genus are carnivores. *E. laevis* (Quennerstedt) is a carnivore according to Dragesco (1960) who cultured the ciliate on species of *Strombidium*, *Cyclidium* and other small ciliates. *E. sulcatus* Kahl is considered to feed on ciliates (Kahl, 1930-35). *E. vacuolatus* Dragesco feeds on cryptomonads, dinoflagellates and diatoms according to Dragesco (1960).

Genus *Helicoprорodon*

H. gigas Kahl is a carnivore. Four specimens from fine sand from the Øresund contained remains of 1-3 ciliates. In two cases the prey could be identified as *Remanella brunnea* and *R. margaritifera* respectively. In addition a specimen of *H. gigas* was observed – under the dissection microscope – to swallow a specimen of a *Kentrophorus* sp., a process which very much resembled *Lacrymaria marina* swallowing ciliates.

In addition two specimens of *H. minutus* Bock were studied. One contained an 80 μ long diatom (may have originated from a prey ciliate) and the other did not contain any remains.

Dragesco (1960) mentions a *Helicoprорodon* sp. that contained a *Remanella* sp.



FIG. 5. *Lacrymaria marina* swallowing a specimen of *Uronema marina*.

Genus *Holophrya*

H. biconica Sauerbrey eats unicellular brown algae (Kahl, 1930-35), and *H. vorax* Dragesco eats diatoms and flagellates (Dragesco, 1960).

Genus *Lacrymaria*

The species within this genus are mainly ciliate hunters, they are all fast swimmers. Dragesco (1960) considers the sand-dwelling species to feed on ciliates like *Pleuronema*, *Cyclidium*, *Frontonia*, etc. The numerous species of *Lacrymaria* described in the literature are not too well defined.

Borror (1963a) observed *L. versatilis* Quennerstedt feeding on *Uronema marina*. *L. coronata* Claparède & Lachmann eats small ciliates (Dragesco, 1960), small ciliates, flagellates and amoebae (Kahl, 1930-35), and "protozoa" (Webb, 1956). *L. pupula* O.F.M. feeds on ciliates (Kahl, 1930-35). Dragesco (1960) found sand grains in *L. delamarei* Dragesco and in *L. trichocystis* Dragesco. *L. lagenula* Claparède & Lachmann feeds on protozoa (Webb, 1956). The last mentioned author described *L. marina* Dragesco (as *L. olor* (O.F.M.)) in more detail. She found it to feed on holotrich ciliates like *Cohnilembus* but only reluctantly on hypotrichs. In cultures it would feed on cysts of *Nassula citrea* and on dinoflagellates (*Glenodinium*).

I have also studied *L. marina*, which is common in several sandy localities in the Sound, in some detail. Specimens from freshly collected samples sometimes contained dinoflagellates, and sometimes what was probably remains of ciliates.

In one case 50 diatoms about 15 μ long were found which did not seem to originate from prey ciliates.

L. marina was easy to culture when fed on *Uronema marina*. In cultures *Lacrymaria* can be seen to swim swiftly around swinging its long contractile proboscis in all directions. When an *Uronema* is touched by the tip of the proboscis, on which the mouth is situated, the prey is immediately paralyzed by a trichocyst discharge and usually swallowed a few seconds later (Fig. 5). During the few minutes it takes for the prey to pass the proboscis it may still be identified, but very shortly after this is impossible due to digestion. In accordance with Webb, I observed that *L. marina* would not eat *Euplotes vannus* which did not even react when touched by the tip of the proboscis of the carnivore.

A few specimens of another *Lacrymaria* sp. from sand, probably *L. delamarei*, were studied but no recognizable food remains were found.

Genus *Placus*

P. luciae Kahl feeds on flagellates, especially euglenoids, and small ciliates (Kahl, 1930-35). *P. salinus* Dietz feeds on flagellates (Dietz, 1964) and *P. socialis* Fabre-Domergue is a histophage but it also eats diatoms and bacteria (Webb, 1956). Kahl (1930-35) described a population of *P. socialis* which practically only fed on the ciliate *Mesodinium*.

Genus *Plagiocampa*

P. margaritata Kahl feeds on purple sulphur bacteria and small algae, *P. posticeconica* Kahl, on peridineans but also on other small algae and purple bacteria, and *P. rouxi* Kahl feeds on small algae (Kahl, 1930-35).

An unidentified *Plagiocampa* from the beach at Helsingør was found to be histophagous since it was attracted to and ate living tissue of a piece of a polychaete worm. Another *Plagiocampa* sp. commonly found at the same beach occurred in great numbers in succession experiments with decomposing sea weeds, apparently feeding on colourless flagellates.

Genus *Plagiopogon*

P. loricatus Kahl, which was found in large numbers in reducing, sulphide-containing sediments, was studied in some detail. Most individuals contained remains of dinoflagellates and clear material of animal origin, sometimes also unicellular green algae. In sediment samples the ciliates quickly gather around oligochaetes, harpacticoids, etc. which have been damaged mechanically. This species is thus at the same time histophagous and feeds on phytoflagellates and other protista, a rather common combination within the rhabdophorine gymnostomes.

Genus *Prorodon*

This genus consists of species mainly feeding on protophytes (according to Sandon (1932) also bacteria, but this hardly seems probable) but in at least two species (*P. discolor*, *P. teres*) histophagous habits have evolved.

Kahl (1930-35) believed that *P. discolor* (Ehrenberg) eats algae, Dragesco (1960) that it eats flagellates, and Webb (1956) that it is a histophage. All these views are correct. I have studied a large number of specimens from Askö Harbour, Nivå Bay and Julebæk Beach. In dishes *P. discolor* devoured tissue of metazoans, and freshly collected specimens nearly always contain remains of dinoflagellates (*Gymnodinium*, *Amphididium*, etc.), phytomonads and diatoms besides contents of animal origin. In one case 6 *Gymnodinium* with a diameter of about 20 μ and a number of smaller flagellates were found in one specimen. In a sample from the Julebæk Beach kept for about a week in the laboratory some of the ciliates contained – in addition to flagellates – complete specimens of the rotifer *Enentrum marinum*. These had probably been swallowed dead since the rotifer, which was numerous when the sample was collected, died when the sample became anoxic.

A few specimens of *P. morgani* Kahl were studied by me. They all contained remains of phytoflagellates, in one case these were dinoflagellates.

P. marinus Claparède & Lachmann feeds on dinoflagellates and cryptomonads, and *P. ovum* Ehrenberg and *P. arenarius* Dragesco on diatoms (Dragesco, 1960). *P. luteus* Kahl and *P. mimeticus* Kahl feed on small dinoflagellates (Kahl, 1930-35). *P. teres* Ehrenberg feeds on diatoms, dead nematodes and possibly purple sulphur bacteria, and in waste water on starch grains (Kahl, 1930-35).

Genus *Pseudoprorodon*

Corliss (1961) places this genus and the genus *Paraspathidium* in the trichostome family Coelostomidae. I do not agree with this action since both genera are typical rhabdophorine gymnostomes and they are here placed in the Enchelyidae and Spathidiidae respectively as also done by Dragesco (1960). It is, however, possible that the species *Pseudoprorodon arenicola* should be transferred to the spathidids since it shows close resemblance to *Paraspathidium*.

This genus comprises many carnivorous freshwater species (Sandon, 1932).

The large sand-dwelling species *P. arenicola* Kahl feeds on flagellates and algae (Dragesco, 1960). My observations agree with this since most specimens contained vacuoles with green, brownish or yellow pigments, probably remains of dinoflagellates. In one case I found what was probably remains of a ciliate.

P. soosiae Dietz feeds on diatoms (Dietz, 1964).

Genus *Stephanopogon*

S. colpoda Entz sen. feeds on diatoms (Dragesco, 1963; Kahl, 1930-35) and *S. mesnili* Lwoff on diatoms and cryptomonads (Kahl, 1930-35).

Family TRACHELOCERCIDAE

In spite of great efforts (Dragesco, 1960, 1963a; Raikov, 1962) it has not been possible to define the apparently numerous species in a satisfactory way. Thus Dragesco (1963a) writes: "La multiplicité du nombre d'espèces du genre *Tracheloraphis*, la difficulté de leur détermination exacte, l'extrême variabilité de certaines de leurs structures, nous font penser que les critères systématique que nous employons sont à réviser et que, peut-être, bien des espèces ne représentent que des stades d'un polymorphisme probable."

I have studied a large number of individuals but have only in a few cases been able to identify any of them with any described form in a convincing way. In the citations given below the specific names are given in accordance with the cited author. My own observations are given without specific names.

The trachelocercids are typical ciliates of the marine benthos, especially in sand, but they are also found in detritus. They are macrophages eating ciliates, flagellates and diatoms.

Genus *Trachelocerca*

T. gracilis Dragesco eats diatoms but also other ciliates (*Remanella*) (Dragesco, 1960).

Genus *Tracheloraphis*

T. dracontoides (Bullington) and *T. angustivittatus* Borror feed on algae and diatoms (Borror, 1963a). *T. phoenicopterus* (Cohn) feeds on ciliates (Kahl, 1930-35), mostly on diatoms (Raikov, 1962) and on green algae, flagellates, eggs of annelids and masses of bacteria? (Morgans, 1926). Kiesselbach (1936) described a population feeding on *Lacrymaria coronata*. The observation by Perkins (1958) that *Tracheloraphis* feeds on bacteria is probably due to a misinterpretation. *T. subviridis* (Sauerbrey) feeds on protozoa (Webb, 1956), *T. prenanti* Dragesco on flagellates and *T. gracilis* Dragesco, 1960 on diatoms (Dragesco, 1960).

Own observations: A population of a *Trachelocerca* sp. (resembling *T. tessieri* Dragesco, 1960) living in fine sand from beaches in the northern part of the Sound feeds on other ciliates. In most cases the ciliates in the feeding vacuoles could not be identified but in four cases they were *Remanella margaritifera*. A large brownish form, possibly identical with *T. kahli* Raikov, which is commonly found on the diatom rich sediment surfaces in the Isefjord, Nivå Bay and Askö Harbour, was found mainly to feed on diatoms (up to 45 μ in length, but usually around 10 μ) and dinoflagellates. Another form living in the same localities, but deeper in the sediments, also feeds on diatoms, up to 25 μ in length. One individual, however, was observed swallowing a specimen of *Euplotes elegans*.

A *Tracheloraphis* sp., commonly found in the Helsingør Beach, was found to contain mainly dinoflagellates (*Amphidinium*) and also small ciliates.

Family SPATHIDIIDAE

Macrophages, mainly carnivores according to Kahl (1930-35).

Genus *Homalozoon*

H. caudatum Kahl feeds on flagellates and algae according to Dragesco (1960). The few specimens of this common ciliate studied by me did not contain any remains of food.

Genus *Paraspathidium*

P. obliquum Dragesco feeds on prey of vegetable nature (Dragesco, 1963a).

P. fuscum (Kahl) feeds on algal debris and euglenoid flagellates (Kahl, 1928), but is considered to feed on ciliates by Kahl (1930-35).

This ciliate, which is often of quantitative importance in sand and especially in sulphureta, was studied at several occasions. It is a histophage which is quickly attracted to small metazoans torn to pieces with needles. The vacuole contents of 33 individuals from Nivå Bay, the Helsingør Beach, a beach further north in the Sound, and Askö Harbour were investigated. In most cases they contained material of animal origin, in one case a bristle of the oligochaete *Paranais littoralis*. Often the vacuoles also contained material of vegetable origin, mostly dinoflagellates, rarely diatoms, and in some cases the vacuoles contained remains of ciliates.

Genus *Spathidium*

S. fresenburgii Kahl feeds on euglenoids (Kahl, 1928, 1930-35) and *S. curvatum* Kahl on infusoria and colourless flagellates (Kahl, 1928).

Genus *Perispira*

P. ovum Stein feeds mainly on *Euglena viridis* and other green flagellates (Kahl, 1928, 1930-35).

Family DIDINIIDAE

The well known predator *Didinium nasutum* O.F.M. belongs to this family. In sediments the small species of the genus *Mesodinium* play a role but their feeding ecology is poorly known.

Genus *Mesodinium*

M. pulex Claparède & Lachmann and *M. acarus* Stein feed on bacteria (Webb, 1956).

M. pupula Dragesco, which is often very numerous below the sediment surface in sandy localities, feeds on dinoflagellates and other green flagellates (Dragesco, 1963a). A few specimens studied by me also contained green pigments.

Family AMPHILEPTIDAE

This family consists exclusively of carnivorous forms which mostly feed on other ciliates, a few are recorded to feed on flagellates or small metazoans. The amphileptids digest their food very quickly and are therefore usually found without food remains in nature. Statements in the literature that amphileptids eat diatoms or other algae (Sauerbrey, 1928 for *Loxophyllum vermiforme*, Ozaki & Yagiu, 1943 for *L. multinucleatum*) is probably due to misinterpretations of food remains of the prey animals.

Genus *Litonotus*

Often misspelled as *Lionotus* (see Corliss, 1961).

L. lamella (Ehrenberg) is a common and well known carnivore living in sea- as well as freshwater. Dragesco (1962) kept the freshwater form in culture on *Tetrahymena* and *Colpidium* and gave a fine description of the feeding behaviour. He (1960) states that the food of the marine form consists of ciliates such as *Pleuronema*, *Cristigera*, *Uronema*, etc. I have kept *L. lamella* in culture on *Uronema marina* and could confirm the observations of Dragesco concerning the killing and swallowing of the prey. One specimen was found to eat 4 *Uronema* within 45 minutes (20°C) but the prey is unidentifiable within a few minutes after swallowing so it is understandable that amphileptids are mostly found without food remains in nature.

L. fasciola (Ehrenberg) and *L. cygnus* (O. F. M.) feed on protozoa (Webb, 1956).

Genus *Hemiophrys*

H. filum Gruber which is rather frequent in fine sand on the Helsingør Beach probably feeds on ciliates, but direct observations are lacking.

Genus *Heminotus*

H. caudatus Kahl feeds on flagellates and diatoms (Dragesco, 1960).

Genus *Loxophyllum*

Probably all *Loxophyllum* spp. are ciliate hunters; as mentioned earlier the algal contents of *L. vermiforme* Sauerbrey and *L. multinucleatum* Ozaki & Yagiu has probably been misinterpreted. *L. setigerum* Quennerstedt, *L. undulatum* Sauerbrey, *L. meleagris* Dujardin, *L. helus* (Stokes), *L. fasciolatum* Kahl all feed on protozoa according to Webb (1956). She observed *L. setigerum* eating *Diophrys appendiculatus* and its cysts.

In a sand sample from Nivå Bay I observed *L. variabilis* Dragesco, 1954 eating a small unidentified ciliate.

Family TRACHELIIDAE

Genus *Dileptus*

This genus consists of carnivorous ciliates feeding on other ciliates and small metazoans (Kahl, 1930-35, Dragesco, 1963b). In his memoir on this genus, Dragesco (1963b) describes the feeding biology of some freshwater species. Unfortunately no information could be found on the food of marine species in the literature. Some specimens of *D. estuarinus* Dragesco from the Øresund were investigated but no recognizable food remains were found. There can be little doubt, however, that marine *Dileptus* spp. are also carnivores.

Family LOXODIDAE

The members of this family are all specialized to interstitial life, especially in fine sand. They are omnivorous macrophages feeding on diatoms and other unicellular algae, flagellates, small ciliates, and sometimes large bacteria.

Genus *Ciliofaurea*

All specimens of *C. mirabilis* (Dragesco) from 5 m depth in fine sand from the Øresund contained remains of dinoflagellates. Dragesco (1960) also mentions flagellates as food.

Genus *Remanella*

This is one of the quantitatively most important ciliate genera in fine marine sand, sometimes comprising more than 50 % of all ciliates present. The *Remanella* spp. only thrive in chemically reducing environments (Eh: 0 — +200 mV), thus never occurring at the sediment surface; mostly they have their maximum between 5 and 20 cm below the sediment surface in relatively clean sand. The diatoms and flagellates which comprise the most important part of their diet are thus heterotrophic.

R. margaritifera Kahl, which is the most common species (up to 2000 individuals per cm² in fine sand), eats different kinds of algae (Dragesco, 1960). I studied the food contents of 28 individuals from various localities in the Sound. Of these 7 contained diatoms, the majority of which measured 5-10 μ (see Fig. 2), 15 contained flagellates, mostly dinoflagellates but also euglenoids and phytomonads, 1 contained a small ciliate, and 1 contained bacteria measuring 2-3 μ .

R. rugosa Kahl feeds on diatoms (Borror, 1963a). I studied 11 specimens of which 8 contained diatoms, the majority of which measured 10-15 μ (see Fig. 2), 6 contained flagellates (dinoflagellates and euglenoids), and one contained a specimen of *Remanella margaritifera*.

R. brunnea Kahl from the Sound contained diatoms and dinoflagellates equally frequently. The diatoms ranged from 15 to 45 μ in length (see Fig. 2). In a few cases chlorophytes, colourless flagellates and ciliates were found.

R. brunnea was described by Kahl without any illustration. Dragesco (1960) therefore claimed *R. brunnea* to be a nomen nudum, but in a later paper (Dragesco, 1965a) he described another *Remanella* species as *R. brunnea* Kahl. This form, however, cannot be identical with the species described by Kahl and should have another name. Among other things it differs from *R. brunnea* in possessing composite "corpscules of Müller". The specimens which I found regularly in fine sand at several localities in the Sound correspond perfectly with the description given by Kahl: 400-500 μ long, 10-12 simple corpscules of Müller, strongly developed brown pigmentation and nucleus of the "margaritifera type".

R. gigas Dragesco was the most rare species of *Remanella* and it was only found in samples from deeper water (5-15 m). It feeds on diatoms according to Dragesco (1960). Diatoms, 35-65 μ long, were also the only food item found in 5 specimens studied by me (see Fig. 2).

The food of *R. minuta* Dragesco is not known, which is unfortunate since it is a very common species. A few specimens studied did not contain any recognizable remains of food.

Information on the food of some less common species is found in the literature. *R. obtusa* Fauré-Fremiet feeds on diatoms (Fauré-Fremiet, 1951 b). According to Dragesco (1960) *R. faurei* Dragesco, *R. trichocystis* Dragesco and *R. swedmarki* Dragesco also feed on diatoms, *R. multinucleata* Kahl feeds on flagellates, and *R. caudata* Dragesco feeds on other *Remanella*. Finally Borrer (1963a) mentions that an unidentified *Remanella* feeds on bacteria.

Addendum to LOXODIDAE

The peculiar genus *Kentrophorus* is placed in the Amphileptidae by Kahl (1930-35) and Dragesco (1960) and in the Loxodidae by Corliss (1961).

The *Kentrophorus* spp. are confined to interstitial life in fine sands where they may sometimes be numerous. The most characteristic feature of the genus is the flatness and especially the dense cover of symbiotic sulphur bacteria on the non-ciliated side. The ecological and physiological significance of these bacteria is unknown. The mouth, if present at all, has never been observed and the true systematic position of these animals is therefore unknown.

Normally there are no inclusions originating from food particles in the cytoplasm of these animals but sometimes, however, small diatoms are found (a cytostome is thus present). Fauré-Fremiet (1950a) found diatoms in *K. fistulosa* Fauré-Fremiet, and Dragesco (1960) observed diatoms in *K. grandis* Dragesco. I also noted diatoms in *K. fasciolata* Sauerbrey while no food remains were found in a few specimens of *K. latum* Raikov.

The ecology and physiology of these species are worth a more detailed study. The *Kentrophorus* spp. live as do *Remanella* spp. in reducing environments. This may be important for the understanding of the role of the symbiotic bacteria.

Family GELEIIDAE

Genus *Corlissia*

C. picta (Dragesco) feeds on dinoflagellates and algae according to Dragesco (1960).

Genus *Geleia*

This genus consists of sand-dwelling species. As suggested by Nouzarede (1965) and Raikov (1962) it should probably be removed from the Gymnostomatida due to the complex structure of the mouth.

Both Dragesco (1960) and Nouzarede (1965) consider protophytes as the most important prey of the *Geleia* species. I found, however, that other ciliates are also important in the diet.

G. decolor Kahl feeds on up to 30 μ long diatoms (Borror, 1963a) and flagellates (Dragesco, 1960). I only studied 4 specimens, of which 3 contained remains of dinoflagellates and 2 contained remains of ciliates (in one case *Remanella margaritifera*).

Event though *G. fossata* Kahl is the most commonly found species no references to its food could be found in the literature. I studied 18 specimens of this species. Of these 4 contained diatoms (20-80 μ in length), 4 contained dinoflagellates or euglenoids, and 12 contained from 1 to 4 ciliates (see Fig. 9D, p. 105). In 7 cases the ciliates were *Remanella* spp. In addition some unidentifiable food remains were often found.

Four specimens of *G. orbis* Fauré-Fremiet were studied. One specimen from a locality in the northern Sound contained remains of several *Remanella margaritifera*. Three specimens from Julebæk Beach all contained a large number of ciliates; in some cases they could be identified as *Strombidium sauerbreyae* which is common on this locality.

G. nigriceps Kahl was also only studied in four individuals from a locality in the northern part of the Sound. All contained diatoms (10-40 μ long) and in three cases remains of flagellates.

A specimen of an unidentified *Geleia* sp. from the Helsingør Beach contained remains of several ciliates.

Dragesco (1960) notes that *G. gigas* Dragesco feeds on protophytes, *G. swedmarki* Dragesco on diatoms and dinoflagellates, and *G. luci* Dragesco on flagellates; none of the three species were found by me.

Suborder CYRTOPHORINA

The second suborder within the Gymnostomatida is a much more homogeneous group than the rhabdophorines from a morphological as well as an ecological

point of view. The great majority of the cyrtophorines are macrophagous herbivores feeding on large diatoms, filamentous cyanophyceans or other algae and in a few cases on large sulphur bacteria.

Family NASSULIDAE

Genus *Chilodontopsis*

C. elongata Kahl was studied in a number of individuals from the Isefjord and from Julebæk Beach. All contained diatoms (up to 13 per individual) 11 to 72 μ long, the majority measuring 40-50 μ . No other item was found. Webb (1956) mentions diatoms and bacteria as food, but the latter have probably just been some of the clear granules often present in the cytoplasm of cyrtophorines.

C. vorax (Stokes) feeds on diatoms (Kahl, 1930-35; Dragesco, 1960) as does *C. transversa* Kahl (Kahl, 1928).

Four species described by Ozaki & Yagui (1941) also feed on diatoms: *C. hisioensis*, *C. numerosa*, *C. acuta* and *C. simplex* according to the original descriptions.

Genus *Nassula*

The species of this genus feed mainly on cyanophyceans. *N. aurea* Ehrenberg feeds on *Oscillatoria* (Kahl, 1930-35) as does *N. citrea* Kahl according to Webb (1956). *N. halophila* Gurwitsch feeds on cyanophyceans (Dietz, 1964) and *N. elegans* Ehrenberg on *Oscillatoria limosa* (Dragesco, 1962). Ozaki & Yagui (1941) found that *N. hesperida* Entz sen. also feeds on cyanophyceans while three new species described in the same paper feed on other items: *N. longissima* and *N. terminalis* on large diatoms, and *N. renalis* on "minute particles of sea weed".

Genus *Orthodon*

O. hamatus Gruber feeds on diatoms according to Kahl (1930-35) and Ozaki & Yagui (1941) as does *O. macrocephalus* Ozaki & Yagui according to the original description (1943).

Family CHLAMYDONTIDAE

Genus *Chilodonella*

C. calkinsi Kahl feeds on diatoms (Kahl, 1928; Webb, 1956) as does *C. psammophila* Dragesco according to the describer.

Genus *Chlamydon*

C. triquetrus (O.F.M.) eats diatoms (Kahl, 1930-35; Webb, 1956), small diatoms (Ozaki & Yagui, 1941) and green algae and diatoms (Borror, 1963a). I studied 9

individuals of this species which is often common on the surface of sediments where diatoms are numerous. The only food item found was diatoms (up to 6 per individual) ranging in size from 17 to 108 μ (see Fig. 1).

C. obliquus Kahl feeds on algae (Borror, 1963a), which sort of algae, however, is not clear. I studied some specimens living on mats of *Oscillatoria* and *Vaucheria* in Nivå Bay and noticed, as did Kahl (1930-35), flakes brilliantly coloured in different shades of green in the feeding vacuoles. These remains could not originate from cyanophyceans or diatoms.

C. mnemosyne Ehrenberg feeds on cyanophyceans and small algae (Dietz, 1964), unicellular algae and bits of sea weed (Ozaki & Yagiu, 1941) and diatoms (Webb, 1956; Dragesco, 1960). I found the ciliate in Nivå Bay. It always contained remains of cyanophyceans and the ciliate was observed feeding on *Oscillatoria* – filaments. *C. cyclops* Entz sen. feeds on diatoms (Kahl, 1930-35). Two species described by Ozaki & Yagiu (1941): *C. exocellatus* and *C. rectus* feed on “minute particles of sea weed” and small sized diatoms and on bacteria and bits of algae respectively according to the authors.

Genus *Cryptopharynx*

C. setigerus Kahl feeds mostly on purple sulphur bacteria but also on diatoms, green algae and other material (Kirby, 1934), mostly purple sulphur bacteria and also small algae (Kahl, 1928, 1930-35) and diatoms and bacteria (Webb, 1956). A few specimens observed by me in samples from Nivå Bay were not studied for contents of the feeding vacuoles.

Genus *Lynchella*

L. gradata Kahl is sometimes rather numerous in fine sand from deeper water in the northern part of the Øresund. All specimens investigated contained diatoms, 6 to 45 μ long.

Family CLATHROSTOMATIDAE

Genus *Paranassula*

P. brunnea (Fabre-Domergue) feeds on filamentous cyanophyceans (Fauré-Fremiet, 1962).

Family DYSTERIIDAE

Genus *Dysteria*

D. oblongnucleata Ozaki & Yagiu, 1943 feeds on diatoms according to the authors.

Genus *Trochiloides*

T. recta Kahl feeds exclusively on *Beggiatoa* according to Kahl (1928, 1930-35). I studied several specimens from Askö Harbour and from Nivå Bay where it is sometimes very numerous on mats of *Beggiatoa* and I also observed the feeding. The most important food item is without doubt *Beggiatoa*-filaments but also other Leucothiobacteriales as *Thiovolum* and *Macromonas* are eaten, and in one specimen diatoms were observed.

Order TRICHOSTOMATIDA

Family COELOSOMIDIDAE

Genus *Coelosmides*

C. marina Anigstein feeds on algae and filamentous bacteria (Fauré-Fremiet, 1950a) and dinoflagellates (Dragesco, 1960). *C. tessieri* Dragesco, 1954 eats algae, especially diatoms (Dragesco, 1960).

Family MICROTHORACIDAE

Genus *Discotricha*

D. papillifera Tuffrau – a sand-dwelling species – feeds on diatoms according to Tuffrau (1954). Studies of a few specimens from the Øresund confirmed this.

Family PLAGIOPYLIDAE

The members of this family are largely confined to sulphureta, living in or above reducing – sulphide-containing – sediments and their most important food item is sulphur bacteria.

Genus *Plagiopyla*

P. ovata Kahl feeds on purple sulphur bacteria (Dietz, 1964) and on “dark bacteria” (sulphur bacteria?) according to Osaki & Yagiu (1941). *P. vestita* Kahl feeds exclusively on purple sulphur bacteria (Kahl, 1928).

P. frontata Kahl, 1931 was the *Plagiopyla* species most commonly found during the present investigation. A total of 11 specimens from Nivå Bay, the Helsingør Beach and the Isefjord were studied. The food consists of purple sulphur bacteria (*Lamprocystis*, *Chromatium*), Leucothiobacteriales (*Macromonas*), and colourless bacteria, but also small (less than 20 μ long) diatoms and unicellular cyanophytes.

Genus *Sonderia*

The members of this genus seem to be restricted to chemically reducing environments, in sulphureta and in the sulphide layers of sandy localities, some times as deep as 20 cm below the sediment surface. The species feed primarily on sulphur bacteria but many other items are also eaten. In contrast to the *Plagiopyla* spp. the *Sonderia* spp. feed on large objects.

S. schizostoma Kahl feeds mainly on *Beggiatoa* but also on rhodobacteria according to Kahl (1931), and mainly on *Beggiatoa* and more rarely on diatoms according to Fenchel & Jansson (1966). A large number of specimens from Nivå Bay and the Askö Harbour was studied. Large coils of *Beggiatoa* are always found in this ciliate (see Fig. 6). Similar coils of *Oscillatoria* and other filamentous cyanophyceans are also found. Other food items observed were the sulphur bacterium *Achromatium* and diatoms up to 30 μ in length.

S. pharyngea Kirby, which resembles *S. schizostoma*, feeds on green and blue-green algae, diatoms, "granular rods" (*Macromonas?*), and long filamentous algae (Kirby, 1934).

S. vorax Kahl has a varied diet: cyanophyceans, diatoms, purple sulphur bacteria, euglenoids and more rarely other ciliates (Kahl, 1928, 1931, 1930-35), purple sulphur bacteria (Dietz, 1964), and flagellates, diatoms and bacteria (Fenchel & Jansson, 1966). I have studied 15 individuals from Askö Harbour, Nivå Bay, the Isefjord and the Helsingør Beach. Eleven of these contained diatoms (up to 60 per individual) ranging in size from 9 to 48 μ , 5 contained flagellates, 4 contained filamentous cyanophyceans, 4 contained purple sulphur bacteria, 2 contained *Beggiatoa* filaments, 2 contained bits of decaying algae, and 1 contained some sand grains.

S. sinuata Kahl feeds on diatoms and *Oscillatoria* (Kahl, 1931, 1930-35). I studied 11 specimens from Nivå Bay of which 10 contained diatoms (up to 54 μ long), 5 contained cyanophyceans, 1 contained flagellates, 3 contained purple sulphur bacteria (*Lamprocystis*), 3 contained *Beggiatoa*, 1 contained unidentifiable remains of sulphur bacteria, and 4 contained ciliates.

S. cyclostoma Kahl feeds exclusively on purple sulphur bacteria (Kahl, 1931). A few specimens from Nivå Bay and from the Helsingør Beach all contained grains of sulphur.

S. mira Kahl, *S. vestita* Kahl and *S. macrochilus* Kahl were not found by me. The two first-mentioned feed on purple sulphur bacteria while the last mentioned species feeds on cyanophyceans, purple sulphur bacteria and *Beggiatoa* (Kahl, 1928, 1931, 1930-35).

Unassigned trichostome genus: *Conchostoma*

C. longissimum Fauré-Fremiet feeds on phytoflagellates and sulphur bacteria Fauré-Fremiet (1963). I found the species regularly in the Helsingør Beach and



FIG. 6. *Sonderia schizostoma* containing filaments of *Beggiatoa*.

rarely in Nivå Bay. A few specimens from the first mentioned locality contained remains of dinoflagellates.

Order HYMENOSTOMATIDA

Within this large order nearly every type of feeding ecology may be found.

Suborder TETRAHYMENINA

Beside the family Tetrahymenidae three families are recognized in Corliss (1961): Cohnilembidae, Philasteridae and Ophryoglenidae. The representatives of these families show different stages in the evolution from bacteriophages to histophages and parasites. The systematical relationship between the families still has to be clarified in detail.

The two first-mentioned families comprise forms feeding on bacteria, especially those living on decaying animal tissue (e. g. *Uronema*, *Paralembus*). The Philasteridae comprise both bacteriophages and forms feeding directly on living or decaying tissue (*Philaster*, *Philasterides*) and also more specialized histophages like *Helicostoma notatum*. The last-mentioned species has a polymorph life cycle comprising a quickly swimming swarmer (tomite), which searches for an injured animal, a feeding stage (trophont), which is able to increase its volume surprisingly, followed by a fission stage (tomont) giving rise to new tomites. This type of life cycle allows the ciliates to make the most of the food when it is present.

The ophryoglenids are all histophages (e. g. *Ophryoglena*) or parasites (the well known *Ichthyophthirus*) all with a life cycle as described above. The biology of the philasterids is described in detail in Fauré-Fremiet (1935) and Mazoué (1935), and that of the ophryoglenids in Mugard (1949).

Family COHNILEMBIDAE

Genus *Uronema*

This genus consists of bacteriophages. *Uronema marina* Dujardin feeds on bacteria (Kahl, 1930-35; Morgans, 1926; Borror, 1963; Parkins, 1958 and Dietz, 1964).

U. marina will gather and multiply around dead and decaying animals within a few hours in any sample of marine (or limnic) sediment. Due to the rapid reproduction (generation time at 20°C: 2-3 hours) this ciliate will initiate any ciliate succession on decaying material. When the supply of bacteria is exhausted *U. marina* forms cysts which excyst when a new mass occurrence of bacteria appears. *U. marina* is easy to culture on bacteria grown in peptone solutions (Fig. 7).

U. acutum von Buddenbrock and *U. filificum* Kahl also feed on bacteria (Borror, 1963a, b).

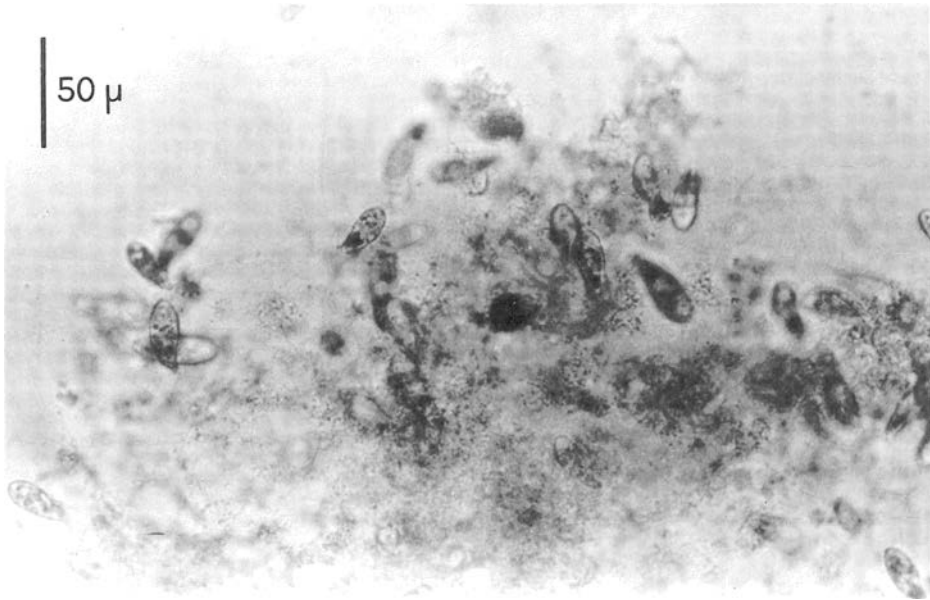


FIG. 7. *Uronema marina* browsing on bacteria.

Genus *Cohnilembus*

C. verminus (O. F. M.) feeds on bacteria (Dietz, 1964; Borror, 1963a). According to the latter author it can be cultured on filtered sea-water with rice grains.

C. pusillus (Quennerstedt) also feeds on bacteria (Dietz, 1964; Webb, 1956). Kahl (1928) found this species and *C. stichotricha* (Kahl) to feed especially on purple sulphur bacteria in the Oldesloe salines.

Genus *Paralembus*

P. digitiformis Kahl and *P. rostratus* Kahl feed on bacteria and cellular debris from decaying animals (actinians) (Fauré-Fremiet, 1935).

Genus *Anophrys*

A. sarcophaga Cohn is a histophage but may also appear as a facultative parasite in the body fluids of crabs (Poisson, 1930).

Family PHILASTERIDAE

Genus *Philaster*

P. digitiformis Fabre-Domergue feeds on tissues of metazoans (sponges, asteroids) (Kahl, 1930-35; Fauré-Fremiet, 1935).

Genus *Philasterides*

P. armata (Kahl) feeds on decaying animals (Fauré-Fremiet, 1935).

Genus *Helicostoma*

H. oblongum Cohn feeds on organic debris but may also feed on suspended bacteria when swimming freely in the water (Fauré-Fremiet, 1935).

H. notatum (Möbius) is an obligate histophage (Fauré-Fremiet, 1935; Dragasco, 1960). Mazoué (1935), who gave a detailed description of the feeding and the life cycle, found that it is unable to feed on fine particles.

I found the species in several localities, most commonly in the harbour of Askö. Here an oligochaete worm cut with a needle would attract several specimens in a few minutes.

Addendum to PHILASTERIDAE

During the investigation Dr. G. Møller Christensen drew my attention to an undescribed philasterid which invades unmetamorphosed lamellibranch larvae (*Spisula*) in her cultures. The ciliates feed on the living tissue and form large populations while the bivalve is still living (see Fig. 8). The ciliate was easily cultured on bits of mussel meat. It has a simple life cycle.

Family OPHRYOGLENIDAE

Genus *Ophryoglena*

The members of this genus are all histophages. The life cycle and feeding biology is outlined earlier. I found some unidentified *Ophryoglena* on several occasions. They are sometimes common in the sand of the "splash zone" of beaches where they feed on plankton organisms filtered from the waves by the sand. In the harbour of the Askö Laboratory they were also common. I observed how one specimen of *Ophryoglena* sp. completely emptied a nearly 1 mm long oligochaete in about 30 minutes.

Investigations should be carried out to determine the quantitative importance of histophagous ciliates as scavengers in nature.

Unassigned tetrahymenine genera

Genus *Cardiostomella*

C. vermiforme Kahl feeds on colourless bacteria and small purple sulphur bacteria (Kahl, 1930-35), and on bacteria and algae (Borror, 1963a).

This ciliate, which is common in most sandy localities and in sulphureta, is a

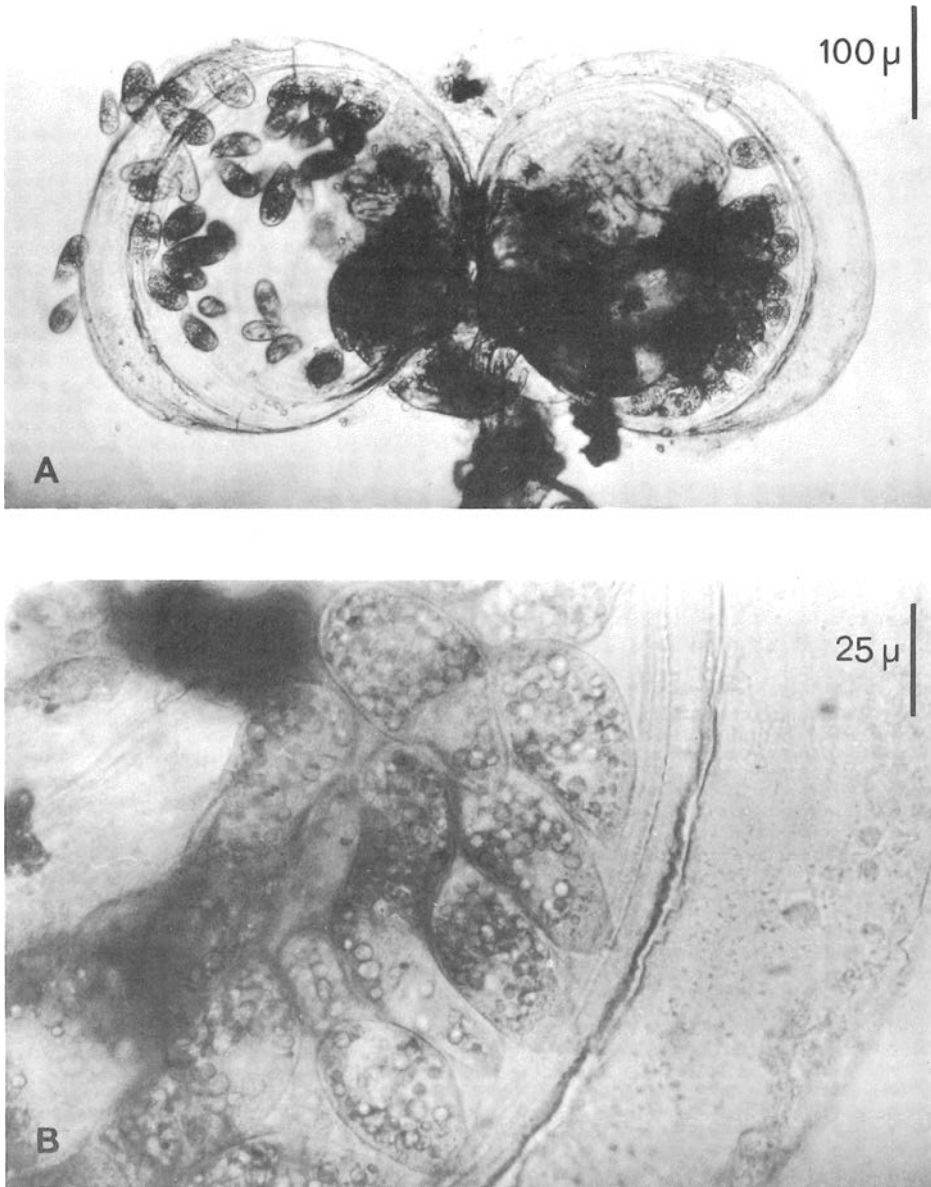


FIG. 8. Philasterids feeding on a (living) larva of the lamellibranch *Spisula subtruncata*.

microphage. I have studied 8 individuals from various localities and found bacteria, sulphur bacteria and small diatoms (less than 10 μ long) in the animal. In addition I often observed some yellow or orange spheres a few microns in diameter but the nature of these spheres is unknown.

C. mononucleata Dragesco was found once but no food contents were noted.

Genus *Platynematum*

P. denticulatum Kahl was found gathering round a decaying amphipod in a sample of sand from a beach in the northern Øresund. The ciliates were apparently feeding on bacteria and possibly on the animal tissue.

Suborder PENICULINA

Family PARAMECIIDAE

The only genus within this family, *Paramecium*, comprises mainly freshwater species. The paramecians are filter feeders.

A few species of the "bursaria group" occur in salt and especially in brackish water. According to Kahl (1930-35) all species of this group feed on purple sulphur bacteria, *Thiovolum*, small blue-green and green algae, and flagellates.

I occasionally found *P. calkinsi* Woodruff in samples from Nivå Bay left in the laboratory for some days. Here the ciliates were feeding on sulphur bacteria: *Thiovolum*, *Macromonas*, *Chromatium*.

Family FRONTONIIDAE

Genus *Frontonia*

Macrophages and mainly herbivores. Due to their expansive cytostome these ciliates can swallow diatoms, filamentous cyanophyceans and animal prey of the same size or larger than themselves. Several species are common in marine benthos.

F. marina (Fabre-Domerque) feeds on diatoms and cyanophyceans (Dietz, 1964), diatoms half as long as the animal (Borrer, 1963a), and diatoms and bacteria (Webb, 1956).

F. marina was found commonly in coarse sediments and especially on the diatom- and cyanophycean-rich surface of the sediments in Nivå Bay and Askö Harbour. Fourteen specimens were studied for vacuole contents. All contained diatoms which is quantitatively the most important food item, and 120 diatoms (20-40 μ long) have been found in one specimen. *F. marina* feeds on diatoms of all sizes (Figs. 2 and 9). Specimens of *Pleurosigma* up to 200 μ long and colonies of *Licmophora* and *Melosira* are often found in ciliates measuring about 230 μ in length. Two specimens contained *Oscillatoria* (up to 350 μ long), 2 contained

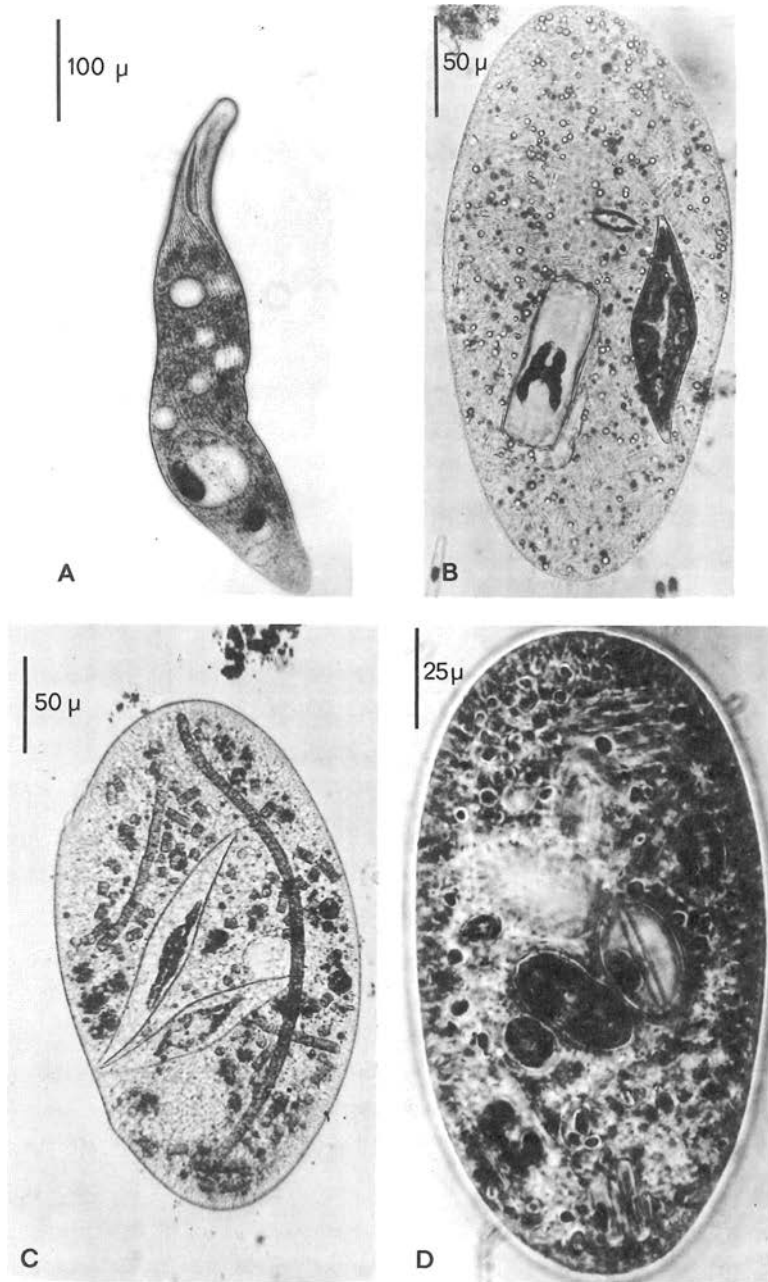


FIG. 9. A, *Geleia fossata* with a partly digested ciliate in a feeding vacuole; B-C, diatoms and *Oscillatoria* in *Frontonia marina*; D, diatoms in *Frontonia arenaria*.

Beggiatoa filaments, and 3 contained remains of other sulphur bacteria (in one case *Thiovolum*). Two contained dinoflagellates and one a unicellular cyanophycean. Two specimens contained ciliates (in one case *Trochiloides recta*), and one contained a complete rotifer (*Cohurella* sp.).

F. microstoma Kahl feeds on large diatoms according to Borror (1963a), Kahl (1930-35) and Fenchel & Jansson (1966).

This ciliate was found regularly in Askö Harbour and Nivå Bay. It lives directly in the sulphide zone of the sediments. A number of specimens from the above mentioned localities contained only large diatoms.

F. algivora Kahl feeds on *Oscillatoria* according to Kahl (1930-35). The species was found in great numbers on *Vaucheria-Oscillatoria* carpets in Nivå Bay. Four specimens contained much *Oscillatoria*, 3 specimens also contained diatoms up to 26 μ in length.

F. arenaria Kahl was common in the surface of fine sand on several localities in the Sound. Twentynine specimens were studied for contents of food. The relative numbers of findings of various food items can be seen in Fig. 3, but the diatoms are actually more important than indicated since they always constitute the most numerous item in the animals. A maximum of 29 diatoms measuring up to 70 μ in length was found per ciliate.

Suborder PLEURONEMATINA

The species within this suborder are suspension feeders securing food by means of their large undulating membrane and adoral membranelles (Fig. 10). The smaller species feed mainly on bacteria, the larger forms also on small flagellates, diatoms, etc.

Family PLEURONEMATIIDAE

Genus *Pleuronema*

P. marinum Dujardin feeds on purple sulphur bacteria and dinoflagellates (Kahl, 1930-35), diatoms (Borror, 1963a) and bacteria (Webb, 1956).

Several specimens from Nivå Bay and from fine sand from the northern part of the Sound contained purple sulphur bacteria, flagellates and especially small diatoms (usually less than 20 μ in length; in one case a diatom measuring 40 μ was found).

P. crassum Dujardin feeds on bacteria (Webb, 1956) and on bacteria and small algae (Kahl, 1930-35). *P. setigera* Calkins feeds "partly on bacteria" (Borror, 1963a), and *P. grassei* Dragesco feeds on small algae (Dragesco, 1960).

P. coronatum Kent feeds mainly on bacteria (Kahl, 1930-35), exclusively on bacteria (Dietz, 1964), but on diatoms according to Borror (1963a).

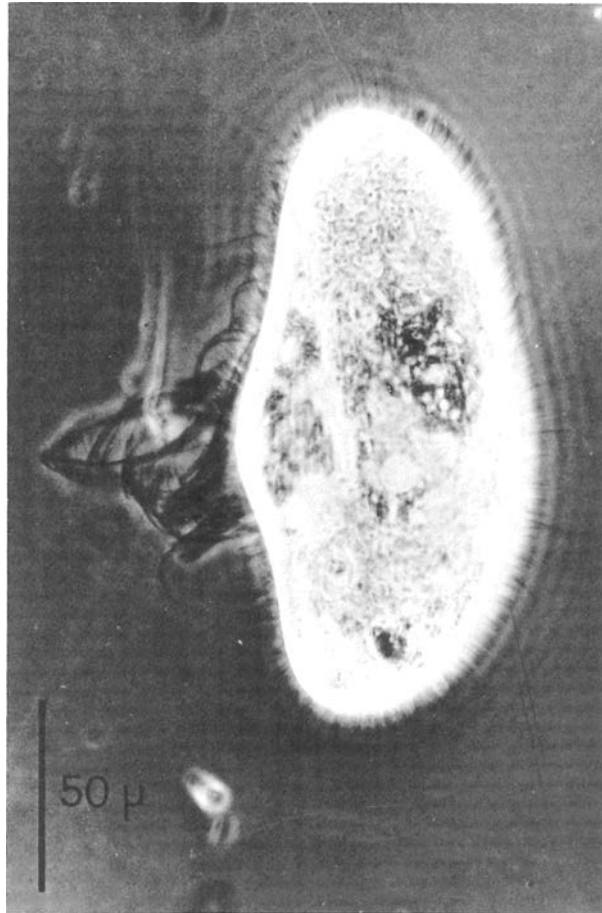


FIG. 10. Suspension-feeding *Pleuronema marinum*.

Dragesco (1960) showed that what was previously described as *P. coronatum* is in reality 4 species, viz. *P. arenicola* Dragesco, *P. oculata* Dragesco, *P. simplex* Dragesco, and *P. coronatum*. These forms can only be identified with certainty by silver impregnations of the mouth and I have made no attempts to distinguish between them. The presence of several distinct species in the samples is probable since "*Pleuronema coronatum*" were found under the most different conditions: in some places only in sulphide-containing sediments, and in other places only in the oxidized surface sand. In sulphureta the ciliate mostly feeds on sulphur bacteria: *Thiovolum*, *Macromonas*, etc. but also on flagellates – pigmented and colourless – and small diatoms. In cleaner sand it feeds mostly on colourless bacteria and small diatoms. In Julebæk Beach the diet was dominated by small (about 10 μ long) diatoms and small dinoflagellates.

Genus *Histobalantidium*

H. marinum Kahl was found once in fine sand from the northern part of the Sound. The only specimen studied contained large diatoms.

Genus *Cyclidium*

These small forms are mostly bacteriophages. *C. citrullus* Cohn feeds on bacteria (Dietz, 1964), an observation I could confirm, and so does *C. glaucoma* O.F.M. according to Morgan (1926). *C. candens* Kahl feeds mainly on purple sulphur bacteria (Kahl, 1928) while *C. marinum* Borror eats small flagellates and algae in addition to bacteria (Borror, 1963a).

Genus *Cristigera*

This genus also consists of bacteriophages. *C. media* Kahl feeds on purple sulphur bacteria (Kahl, 1928, 1930-35). Observations on specimens from Nivå Bay confirm this, but other types of sulphur bacteria (*Macromonas*) and colourless bacteria were also found.

Order HETEROTRICHIDA

Family SPIROSTOMIDAE

Mostly microphagous forms.

Genus *Blepharisma*

B. clarissimum Anigstein was found commonly in Askö Harbour, Nivå Bay and the Isefjord. Only 6 individuals were studied, and they all contained small diatoms. Up to 120 diatoms per individual were found, mostly about 10 μ long, rarely more than 20 μ (Fig. 1). In 3 of the individuals a few unicellular algae or flagellates were found, in 4 some remains of sulphur bacteria, and in one case a piece of a filamentous blue-green alga.

A related, undescribed species was found regularly in fine-sand localities in the Sound. It also mainly feeds on diatoms (9-13 μ in length), and a unicellular chlorophyte was observed once.

B. salinarum (Florentin) feeds on purple sulphur bacteria (Kahl, 1930-35) and bacteria, detritus and diatoms (Webb, 1956). The species occurred regularly in samples from Nivå Bay and Askö Harbour. Of a total of 17 individuals 13 contained sulphur bacteria (*Chromatium*, *Macromonas*) or sulphur grains only, 2 contained other bacteria, and 2 contained diatoms measuring 8-9 μ in length.

B. tardum Kahl, *B. dileptus* Kahl and *B. vestitum* Kahl all feed on purple sulphur bacteria according to Kahl (1930-35) and so does *B. melana* Borror (1963a).

Genus *Gruberia*

G. lanceolata (Gruber) has diatoms in the food vacuoles (Borror, 1963a). *G. aculeata* Ozaki & Yagiu feeds on bacteria according to the original description (1941).

A few specimens of an undescribed *Gruberia* sp. which is regularly found in the Nivå Bay – especially in patches of purple sulphur bacteria – were studied. They contained numerous diatoms (in one case several hundreds) measuring 20-30 μ in length, in addition to pieces of *Beggiatoa* and *Oscillatoria* and large masses of *Lamprocystis*. Two specimens were observed feeding on *Uronema marina*, but they could not multiply on this diet.

Genus *Parablepharisma*

P. pellitum Kahl feeds mostly on rhodobacteria but also on other bacteria, cyanophyceans and diatoms. Twentyone specimens of this species – which only occurs in reduced sediments with rich growth of sulphur bacteria – were investigated. The relative number of findings of various food items is shown on Fig. 3. Here the purple sulphur bacteria are underrepresented since they are always more numerous in the food vacuoles than any of the other items. The cyanophyceans were all unicellular forms and the diatoms all smaller than 20 μ .

P. chlamydophorum Kahl which also was found commonly in sulphide-containing sediments always contains colourless bacteria. *P. bacteriophaga* Villeneuve-Brachon feeds above all on sulphur bacteria (Villeneuve-Brachon, 1940) but on algae and diatoms according to Borror (1963a).

Genus *Protoctruca*

P. tuzeti Villeneuve-Brachon feeds on sulphur bacteria in nature but will feed on all sorts of bacteria in cultures (Villeneuve-Brachon, 1940).

Genus *Spirostomum*

This genus consists of freshwater species but one species also occurs in brackish water.

S. teres Claparède & Lachmann feeds on bacteria and diatoms (Noland, 1925; Webb, 1956) and on bacteria (Villeneuve-Brachon, 1940). During the present study *S. teres* was found numerously in the Askö Harbour (the Baltic Sea, salinity: about 6 ‰) but not in any of the Danish localities where the salinity is always above 10 ‰. The specimens studied all contained small diatoms, desmidiaceans and bacteria.

Family CONDYLOSTOMATIDAE

Genus *Condylostoma*

Large marine ciliates which all are macrophagous omnivores, feeding on diatoms, flagellates, green algae, other ciliates and small metazoans. Several species have been described, the delimitation of which is not quite clear.

C. remanei Spiegel feeds on diatoms and dinoflagellates (Dragesco, 1960), mostly diatoms and also bacteria (Villeneuve-Brachon, 1940) and, according to Kahl (1928), euglenoids, ciliates, unicellular algae and purple bacteria.

I studied 11 individuals from various localities. The diet of the species is very varied. Specimens from Julebæk Beach contained ciliates (in one individual 6 *Strombidium* were found), large dinoflagellates (*Gymnodinium*, *Amphidinium*), diatoms, and chlorophytes (*Chlamydomonas* or similar organisms). Specimens from a locality with fine sand in the northern part of the Sound contained ciliates (mainly *Remanella margaritifera*), up to 6 specimens in one ciliate, diatoms (up to 55 μ in length, but mostly around 20 μ), up to 70 per ciliate, and remains of various phytoflagellates. Individuals from the Askö Harbour mainly contained *Gymnodinium* but ciliates and diatoms were also found in the vacuoles. *C. remanei* was observed feeding on small ciliates (e.g. *Uronema*) in the laboratory.

C. arenarium Spiegel feeds on small diatoms and probably also ciliates and flagellates, in sapropelic environments also on rhodobacteria (Kahl, 1930-35), on diatoms, dinoflagellates, small algae, and bacteria (Villeneuve-Brachon, 1940), on algae (Borror, 1963a), and on flagellates and small diatoms (Kiesselbach, 1936). Two specimens of this species from the Askö Harbour contained large diatoms, remains of cyanophyceans, chlorophytes, many *Gymnodinium*, and unidentifiable remains of ciliates.

C. patens (O. F. M.) feeds on diatoms (Webb, 1956) or on diatoms (and copepod eggs!) (Perkins, 1958).

C. patulum Claparède & Lachmann feeds on diatoms and bacteria (Webb, 1956), sulphur bacteria (Dragesco, 1963), and according to Kahl (1930-35) on diatoms, especially *Pinnularia*.

I studied 6 specimens from the Nivå Bay. They contained diatoms (up to 150 in one ciliate, measuring up to 80 μ), flagellates: *Gymnodinium*, euglenoids and phytomonads, ciliates, unicellular cyanophyceans and sometimes bits of *Beggiatoa* and *Oscillatoria* and masses of *Lamprocystis*. The ciliate was cultured on *Dunaliella*.

Loosanoff (1959) described how an unidentified *Condylostoma* sp. (400-900 μ in length) fed on larvae of lamellibranchs. Judging from the photo in the paper of Loosanoff the ciliate may well have been *C. patulum*.

C. acuta Dragesco feeds on different flagellates (Dragesco, 1960), *C. ancestralis* Villeneuve-Brachon on diatoms and also on bacteria and algal debris, while *C. vorax* Villeneuve-Brachon feeds on dinoflagellates and holo- and hypotrichous ciliates (Villeneuve-Brachon, 1940).

C. tenuis Fauré-Fremiet was found once but its vacuole contents were not noted. This species is unusual in being a psammophilous ciliate with zoochlorellae (phytomonads), see Dragesco (1963a).

Family STENTORIDAE

Genus *Climacostoma*

A freshwater genus but one species *C. virens* (Ehrenberg) occurs in brackish water. Kahl (1930-35) states that it feeds on algae and infusoria. I found a few specimens of this species in Askö Harbour.

Genus *Fabrea*

F. salina Henneguy feeds on dinoflagellates, bacteria, diatoms, "small red rod-like bacteria" (= *Chromatium* ?) and may also be cannibalistic (Kirby, 1934). Villeneuve-Brachon (1940) found dinoflagellates, *Dunaliella*, diatoms, and bacteria, especially sulphur bacteria, in the vacuoles.

Family CHATTONIDAE

Genus *Chattonidium*

C. setense Villeneuve-Brachon feeds on dinoflagellates, diatoms, bacteria and small ciliates, especially *Coleps* (Villeneuve-Brachon, 1940).

Family PERITROMIDAE

Genus *Peritromus*

P. faurei Kahl feeds on algae and diatoms (Borror, 1963a). I studied seven individuals from various stations in the Nivå Bay. All of these contained sulphur bacteria (in 3 cases *Lamprocystis*, in 3 cases *Achromatium* and in one case only the sulphur grains were left). Four specimens contained diatoms (10-20 μ in length), one contained chlorophytes and one contained blue-green algae.

P. kahli Villeneuve-Brachon feeds – above all – on sulphur bacteria but also on small algae and diatoms (Villeneuve-Brachon, 1940).

P. emmae Stein feeds on algae, *P. minor* Ozaki & Yagiu on bacteria, *P. montanus* Kahl on bacteria and small diatoms, and *P. tetramacronucleatus* Ozaki & Yagiu on small diatoms and "minute particles of sea weed" (Ozaki & Yagiu, 1941).

Families METOPIDAE and CAENOMORPHIDAE

Jankowski (1964) has shown how the Metopidae have evolved from the most primitive heterotrichs: *Blepharisma*, and that the Metopidae have given rise to the caenomorphids as well as to the order Odontostomatida. This is noteworthy since

several *Blepharisma* spp. as well as all metopids, caenomorphids and the members of the Odentostomatida are "sapropels" which live in reduced sulphide-containing environments and are anaerobes. Even though Jankowski's work is based on comparative morphological studies it shows the value of ecological considerations in phylogenetical work. The biology of these groups seems to be as conservative as the morphological features of systematical significance. Here the systematics proposed by Jankowski will be used.

The metopids, caenomorphids and odontostomatids have far more species in freshwater than in the sea.

Family METOPIDAE

Genus *Metopus*

Microphages feeding mainly on sulphur bacteria.

M. contortus (Quennerstedt) feeds on purple sulphur bacteria (Kahl, 1928, 1930-35), on bacteria, especially sulphur bacteria (Villeneuve-Brachon, 1940), and on colourless bacteria (Fenchel & Jansson, 1966). The ciliates congregate in regions of high bacterial concentration (Borrer, 1963 a).

I have studied 16 specimens (Nivå Bay, the Isefjord, Askö) which all contained bacteria. In 12 cases sulphur-bacteria of some sort was dominating (purples, *Lamprocystis*, *Chromatium*; Leucothiobacteriales, *Macromonas*, *Achromatium*). In addition nearly all specimens contained unidentifiable colourless bacteria and one contained a representative of the Athiorhodacea. Eight specimens contained some diatoms less than 15 μ long.

A few specimens of *M. vestitus* Kahl from Nivå Bay contained remains of purple and white sulphur-bacteria.

M. brachoni n. nov. (for *M. vestitus* Villeneuve-Brachon, 1940) feeds only on bacteria, especially sulphur bacteria (Villeneuve-Brachon, 1940). *M. halophilus* Kahl feeds on purple sulphur-bacteria and also on other bacteria (Kahl, 1928, 1930-35).

M. verrucosus (Cunha) was found in deep sulphide-containing layers (10-15 cm below the sediment surface) of a sandy bottom at 10 m depth in the Sound. The food contents were not noted. Kirby (1934) states that it feeds on bacteria.

Genus *Copemetopus*

C. subsalsus Villeneuve-Brachon has a varied diet: dinoflagellates, diatoms and bacteria (Villeneuve-Brachon, 1940).

Family CAENOMORPHIDAE

Genus *Caenomorpha*

These forms are all microphages feeding on sulphur bacteria and other bacteria according to Kahl (1930-35).

C. levandri Kahl was the only species found by me. It occurs regularly and sometimes numerously in sulphide-containing sediments (Askö, Nivå Bay, Isefjord, Helsingør Beach, and in samples from deeper water).

A number of specimens from Nivå Bay, Askö and from artificial laboratory sulphureta all contained small colourless bacteria.

Order ODONTOSTOMATIDA

The species of this small order are – as mentioned earlier – all confined to anaerobic environments. There are only a few species described from sea-water. According to Kahl (1930-35) the species feed on small cocci and bacilli.

Family EPALXELLIDAE

Genus *Saprodinium*

S. halophilum Kahl was regularly found in sulphide-containing sediments at Nivå and Askö. The food contents always consisted of small colourless bacteria.

Family MYELOSTOMATIDAE

Genus *Myelostoma*

M. bipartitum Gourret & Roeser was also common in reducing sediments from Nivå Bay. According to Kahl (1928) it feeds on very minute food particles but may also feed on very thin filaments of beugatoans and blue-green algae.

Order OLIGOTRICHIDA

Family HALTERIIDAE

Genus *Strombidium*

The species of this genus are very common in marine sediments, especially in sand. Identification of the species is difficult, probably because too many have been described, and the genus is therefore in need of a revision.

The large majority of the species feed on diatoms that often measure more than half the length of the ciliates (see Fig. 11).

S. latum Kahl is a rather well-defined species which feeds on diatoms (Kahl,

1930-35). The species is common in Julebæk Beach where it feeds on diatoms varying between 10 and 70 μ in length, the majority measuring 30-40 μ . A few spheric, unicellular blue-green algae were sometimes also found.

S. sauerbreyae Kahl feeds on diatoms (Kahl, 1930-35) and diatoms and sand grains (Dragesco, 1960). Most specimens of *Strombidium* found during the present investigation probably belong to this species. Ten specimens from different localities (Nivå Bay, Julebæk Beach, fine sand at 5 m depth in the northern Øresund) all contained nothing but diatoms. As many as 31 diatoms per animal were found (measuring up to 45 μ but mostly only measuring 20-30 μ).

An unidentified *Strombidium* sp. from Askö Harbour contained only sand grains.

S. sulcatum Claparède & Lachmann feeds on diatoms according to Borror (1963a), but mostly on bacteria and rarely on diatoms according to Kahl (1930-35). *S. viride* Stein feeds on diatoms (Borror, 1963a) as do *S. macronucleatum* Dragesco (Dragesco, 1960), *S. cinctum* Kahl (Kahl, 1930-35), *S. styliferum* Levander (Kahl, 1928; Webb, 1956), and *S. elegans* Florentin (Webb, 1956). *S. calkinsi* Kahl feeds on dinoflagellates and *Cyclidium* (Kahl, 1930-35), and *S. faurei* Dragesco on sand grains (Dragesco, 1960). *S. purpureum* Kahl feeds on rhodobacteria (Kahl, 1930-35).

Family STROBILIIDAE

Mainly planktonic forms.

Genus *Strobilidium*

S. conicum Kahl, 1932 is probably a pelagic species but it nevertheless occurred regularly in small numbers in surface samples from the Nivå Bay. It feeds on small diatoms.

Order HYPOTRICHIDA

Family OXYTRICHIDAE

Many species belonging to this large family occur commonly on and in the sea bottom. Unfortunately there are species within several genera which are difficult to identify and many forms were therefore not identified by me.

Genus *Amphisiella*

A. milnei Kahl feeds on diatoms and on other ciliates (Kahl, 1930-35). *A. thiophaga* (Kahl) feeds on the sulphur bacterium *Thiovolum* (Kahl, 1928, 1930-35), and *A. annulata* (Kahl) feeds on small diatoms (Kahl, 1930-35; Borror, 1963a).

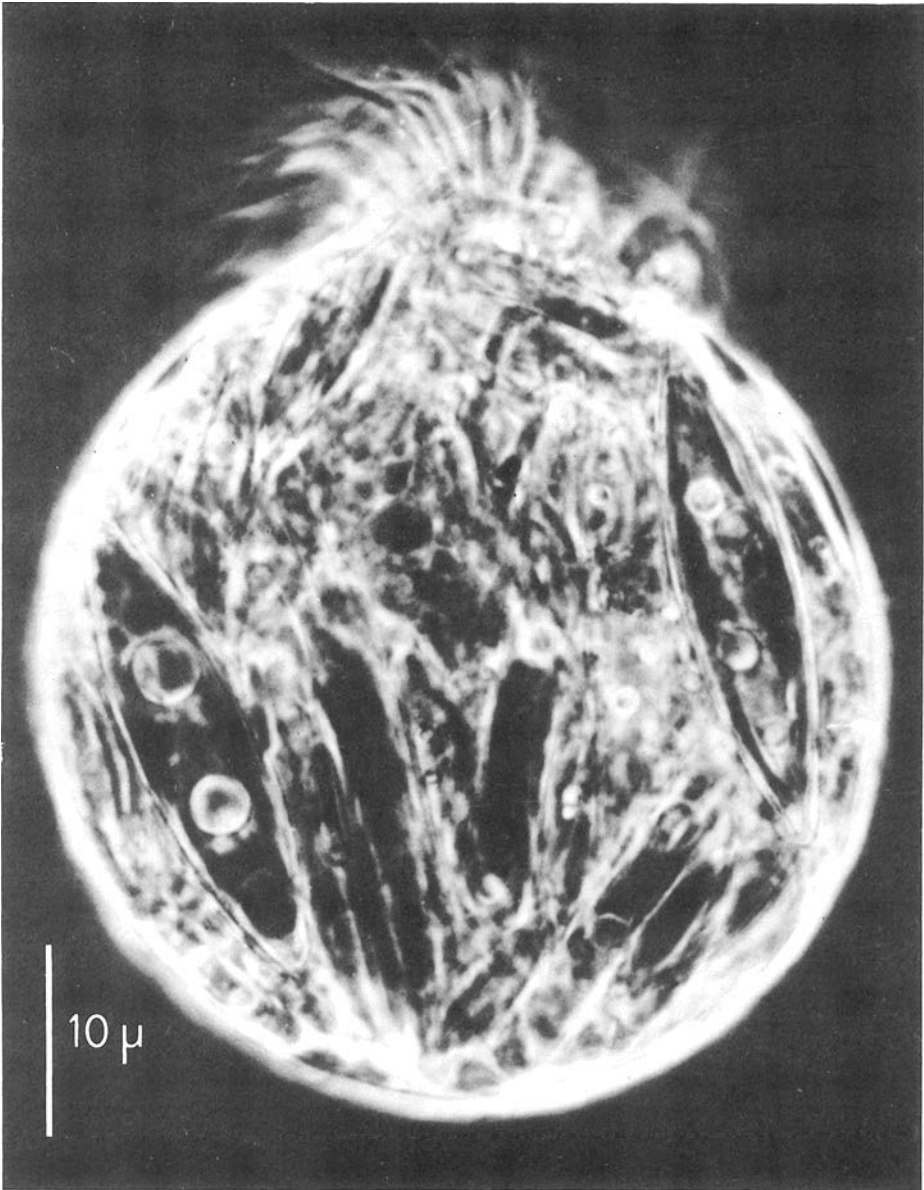


FIG. 11. *Strombidium* sp. containing diatoms.

Genus *Balladyna*

B. euplotes Dragesco feeds on flagellates (Dragesco, 1950).

Genus *Banyulsella*

B. viridis Dragesco feeds "possibly on flagellates" (Dragesco, 1960).

Genus *Epiclintes*

E. ambiguus (O. F. M.) feeds on diatoms according to Borror (1963a).

Genus *Gastrostyla*

G. pulchra (Perejaslawzewa) feeds on diatoms and algae (Borror, 1963b).

Genus *Holosticha*

H. arenicola Kahl feeds on colourless flagellates (Kahl, 1930-35). The ciliate was found in great numbers in sand from the Helsingør Beach during periods when great amounts of sea weed were mixed with the sand and in artificial sediments consisting of *Fucus* bits mixed with clean sand. The ciliate can be cultured in peptone solutions with a mixed microflora. In all cases it feeds on small zooflagellates and bacteria.

H. kessleri (Wrzesiowski) feeds on diatoms (Kahl, 1930-35) and diatoms and detritus (Webb, 1956). I occasionally found the species in the surface layers of Nivå Bay samples. The ciliate allways contained diatoms and also some sulphur grains indicating that sulphur bacteria contribute to the diet.

H. diademata (Rees) feeds on bacteria and other microflora (Borror, 1963a). *H. alveolata* Kahl feeds on diatoms (Kahl, 1930-35) and diatoms and blue-green algae (Borror, 1963a). *H. manca* Kahl also feeds on diatoms (Kahl, 1930-35) while *H. violacea* Kahl feeds on purple sulphur bacteria (Kahl, 1928).

Genus *Keronopsis*

K. flavicans Kahl feeds on *Oscillatoria*, *K. globulifera* Kahl on diatoms, *K. coronata* (Gourret & Roeser) on diatoms, algae and bacteria, and *K. ovalis* Kahl on diatoms and sand grains, all according to Kahl (1930-35). *K. multistilata* (Kahl) feeds on diatoms (Kahl, 1928), *K. arenivorus* Dragesco on cryptomonads (Dragesco, 1960), and *K. rubra* (Ehrenberg) on algae and diatoms (Borror, 1963b). I have isolated this species from aquaria of the Helsingør laboratory and cultured it successfully on cultures of *Phaeodactylum*.

Genus *Oxytricha*

O. stenocephala Borror feeds only on diatoms (Borror, 1963 a).

Genus *Strongylidium*

S. arenicolus Dragesco feeds on flagellates (Dragesco, 1960).

Genus *Trachelostyla*

T. pediculiformis (Cohn) feeds on bacteria (Borror, 1963 a). My observations on this ciliate – which is common in all sorts of sediments, also detritus – confirm this.

Genus *Urostrongylum*

U. caudatum Kahl is a typical ciliate of sulphureta and was found – sometimes numerous – in samples from the Nivå Bay and the Isefjord. The only food item found in a number of specimens from the first mentioned locality was diatoms (up to 20 per individual, 9 to 17 μ long).

Genus *Urostyla*

U. marina Kahl feeds on small diatoms (Kahl, 1930-35).

Family EUPLOTIDAE

Genus *Euplotes*

E. harpa Stein feeds “willingly on rhodobacteria” (Kahl, 1930-35) and on bacteria, diatoms and detritus according to Webb (1956). Some specimens studied by me at Askö contained mainly diatoms. *E. vannus* (O. F. M.) feeds on bacteria and other colourless microflora (Borror, 1963 a). Specimens isolated from the Nivå Bay were cultured in peptone solutions where they fed on bacteria and colourless flagellates (*Bodo* or similar forms). It could also be successfully cultured in suspensions of bakers yeast.

E. balteatus (Dujardin) and *E. moebiusi* Kahl feeds on bacteria and colourless microflora according to Borror (1963 a). I could confirm this for the last mentioned species which was found in samples from the Helsingør Beach.

E. trisulcatus Kahl feeds “partly on algae” (Borror, 1963 a), *E. charon* (O. F. M.) on bacteria (Webb, 1956), and *E. violacea* Kahl on rhodobacteria (Kahl, 1928).

E. elegans Kahl was found regularly in Nivå Bay samples and in artificial laboratory sulphureta. Diatoms (smaller than 20 μ) and sulphur bacteria (*Thiovolum*, *Macromonas* and *Chromatium*) were found in the food vacuoles.

Genus *Discocephalus*

D. ehrenbergi Dragesco was found regularly but always in small numbers in several sandy localities in the Øresund. The individuals studied always contained sand grains, 2-3 μ long phytoflagellates, and often some unidentifiable black pigment. The most important food item, however, seems to be diatoms 7 to 23 μ long; as many as 12 diatoms were noted in this small ciliate.

Genus *Swedmarkia*

S. arenicola Dragesco feeds on protophytes, especially diatoms and dinoflagellates (Dragesco, 1960, 1965b). I found it in small numbers in fine to median sand from 10 m depth off the Helsingør laboratory. All investigated specimens contained remains of dinoflagellates.

Genus *Diophrys*

D. scutum Dujardin feeds on diatoms together with bacteria, sand grains and unidentified spicules and cysts (Borror, 1963a) and on diatoms and bacteria (Webb 1956).

This species occurs in high numbers on the surface of diatom-rich sediments (Askö Harbour, Nivå Bay). Fourteen individuals all contained diatoms, 8 contained blue-green algae (bits of *Oscillatoria* and unicellular forms), 2 contained ciliates (in one case *Saprodinium halophila* and in the other case a *Cyclidium* sp.), 5 contained sulphur bacteria (*Lamprocystis*, *Thiovolum*), 5 contained flagellates (dinoflagellates and colourless forms), 1 contained sand-grains, and 1 contained a green alga. Of all these items diatoms are by far the most important. As many as 200 and usually about 50 diatoms were found per individual while the other items occurred in small amounts only. The ciliate prefers small diatoms measuring 5-10 μ in length (see Fig. 1).

D. scutum was cultured on small diatoms, bakers yeast or *Dunaliella*. Best growth occurred with small planktonic diatoms (*Phaeodactylum*) while pennate benthic diatoms of the same size (approximately 10 μ long) gave slower growth. The explanation may be that is difficult for the ciliates to remove the firmly attached pennates from the smooth glass surface of the culture vessels. Fed with *Dunaliella* and yeast the cultures grew rather slow and the generation time increased after some generations, probably due to "microstarvation". *Isochrysis* would not support growth of cultures even though the animals ingested large numbers of this flagellate.

D. scutum was once observed feeding on long filaments of blue-green algae.

D. appendiculata (Ehrenberg) feeds on diatoms (Borror, 1963a). Webb (1956) found that the species feeds on yeast, bacteria, *Chlorococcus*, starch grains and

especially on small diatoms in culture experiments. I found the ciliate regularly on different localities but did not study the contents of the feeding vacuoles.

D. irmgard Mansfield feeds on diatoms (Borror, 1963a) as does *D. oligothrix* Borror (Borror, 1965).

Genus *Uronychia*

U. transfuga (O. F. M.) feeds on algae and protozoa (Kahl, 1930-35) mainly on diatoms (Borror, 1963b), on bacteria, diatoms detritus, and other ciliates (Webb, 1956), and on diatoms (Perkins, 1958).

This ciliate seems to be completely omnivorous. In most cases it was found to feed on small ciliates (*Uronema*, *Cyclidium*, *Strombidium*, etc.). One specimen contained 14 *Uronema marina*, of which two were still swimming around in the vacuoles. At other occasions *U. transfuga* was observed feeding on *Thiovolum*, diatoms, flagellates, green algae etc.

Family ASPIDISCIDAE

Genus *Aspidisca*

Representatives of this genus occur numerously in the oxidized surface layers of sediments. The *Aspidisca* spp. feed on bacteria according to Kahl (1930-35). I also found only bacteria in the food vacuoles of the species investigated: *A. mutans* Kahl, *A. pulcherrima* Kahl, *A. fusca* Kahl, *A. angulata* Bock, and *A. major* Madsen. *A. angulata* was easily cultured on a mixed bacterial flora in peptone solutions, and this species as well as *A. major* and an unidentified small species occurred in great numbers in artificial sediments consisting of sand and bits of *Fucus*.

A. steini (von Buddenbrock) also feeds on bacteria according to Borror (1963) as does *A. crenata* Fabre-Domergue, but according to Webb (1956), the latter species also eats diatoms.

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