

Some Observations on the Ciliate Fauna of an Experimental Meat Digestion Plant

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Summary

A description is given of an experimental meat digestion plant consisting of an anaerobic digester and an oxidation pond. The ciliate fauna is identified and a description of the variation and encystment of *Vorticella microstoma* Ehrb. (syn. *V. hians* O. F. M.) is given. A new predacious ciliate, *Prorodon microstoma* n.sp. is described which feeds exclusively on *Vorticella microstoma*, and an account is given of its feeding behaviour and life history including encystment.

INTRODUCTION

SEWAGE plants have generally a characteristic ciliate fauna whose activity is often connected with the efficiency of the digestion process. The present plant was set up to treat meat wastes and consisted on an anaerobic digester and an oxidation pond. Samples from both the digester and the oxidation pond were forwarded periodically for examination. The plant was under the direction of Mr. R. A. Hicks, of the Auckland Metropolitan Drainage Board, to whom I am indebted both for the samples and the description of the digestion plant.

The ciliate species present proved to be characteristic polysaprobic and sewage species. An exception was a species of *Prorodon*, generally resembling *Prorodon griseus* in its life history, but feeding exclusively on *Vorticella microstoma* and resembling *Didinium nasutum* very closely in its feeding-behaviour.

DESCRIPTION OF THE DIGESTION PLANT

This description is based on information supplied by Mr. Hicks. "The anaerobic digester was maintained at 80° F. and fed daily with meat waste. The appearance of the raw meat waste was greenish-brown, opalescent, with much settleable solids and fat in small lumps. It had a typical meaty odour, like stale soup, and the pH was 7.5 to 12. After two days' digestion at 80° F. the waste was light to deep amber in colour, clear and bright initially, becoming turbid on standing and depositing solids with colloidal sulphur. It had a peculiar amine smell and some sulphides were present. The pH was 7.1 to 7.7. After ten days' retention in the oxidation pond the liquor was deep green, somewhat opalescent, with few stringy solids but some colloids. There was free ammonia at times but never any sulphides. The pH was 8.0 to 9.5. The Biochemical Oxygen Demand, in five days at 65° F., fell during digestion from 1553 in the raw waste, to 134 in the digester, to 53.2 in the oxidation pond. During this digestion, gas was evolved at the rate of 219,000 cubic feet per million gallons treated and at 37.17 cubic feet per pound of dry matter destroyed. The most important chemical transformations are, first, the conversion of organic sulphur bodies to sulphides and the oxidation of sulphides in the oxidation pond with complete removal in

less than half an hour, and, secondly, the conversion of protein nitrogen to ammoniacal nitrogen with the release of ammonia in the oxidation pond following the rise of pH.

“Biologically the raw wastes were virtually inactive, a few flagellates appearing occasionally. In the digester there were many active ciliates and flagellates, and chains of Cyanophyceae were formed on the surface of the liquor after shaking. Some vibrios and *Chlamydomonas* were identified. In the oxidation pond there was a dense population of *Chlorella* and many *Chlamydomonas*. In sunny weather particularly, *Paramecium* occurred in very great numbers”

In material forwarded to Cambridge (England), Dr. Pringsheim was able to identify *Chlorella saccharophila*, *Tetraedron* sp., *Polytoma uvella*, and *Sphaerotilus natans* in the digester fluid and *Chlorella*, *Chlamydomonas*, *Nitzschia* and *Monas* sp. in the oxidation pond fluid. *Clostridium* was also present in the oxidation pond sample which arrived in England in an anaerobic condition.

MATERIAL AND METHODS

Samples forwarded to Wellington were examined directly and also sub-cultured in petri dishes and Syracuse watch glasses with loops of bacteria (*Proteus* sp.) added as food for the ciliates. Altogether five sets of samples from both the digester and oxidation pond were examined over a period of six months.

The species identified are given in the following table:—

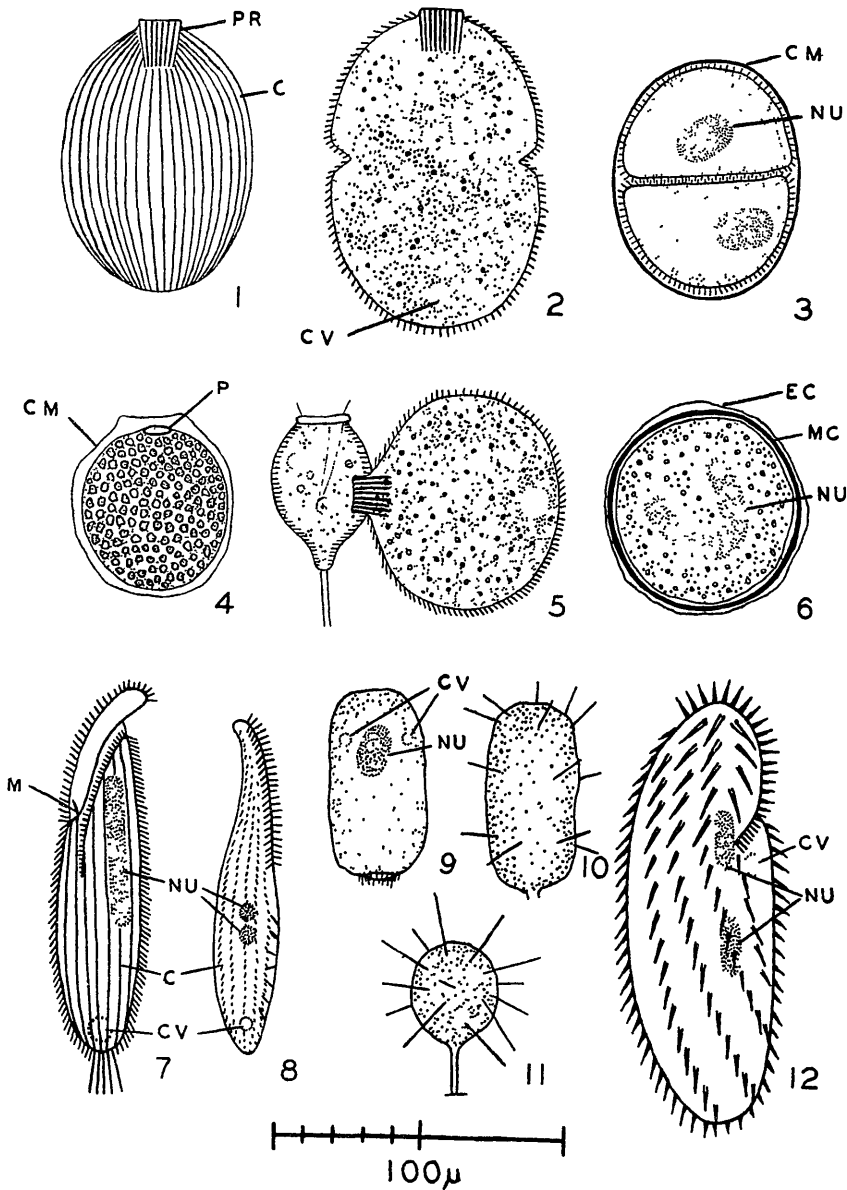
Species	Digester	Oxidation Pond
<i>Prorodon macrostoma</i> n.sp.	x	
<i>Enchelys</i> sp.	x	
<i>Lionotus</i> sp.		x
<i>Chilodonella</i> sp.		x
<i>Paramecium caudatum</i>		x
<i>Cyclidium glaucoma</i>	x	x
<i>Cohnilembus pusillus</i>	x	
<i>Metopus es</i>	x	
<i>Oxytricha pellionella</i>	x	x
<i>Kahlia simplex</i>	x	
<i>Euplotes aediculatus</i>		x
<i>Aspidisca lynceus</i>		x
<i>Vorticella microstoma</i>	x	
<i>Podophrya fixa</i>	x	x

Enchelys, *Prorodon*, *Metopus* and *Vorticella* were the only ciliates which occurred regularly in the digester and *Metopus* was the only active ciliate observed in direct examination of the digester fluid and conversely was the only ciliate which did not occur in aerobic cultures. *Paramecium* was the principal ciliate occurring in the oxidation pond and attained to very great numbers. The oxidation pond fluid was always densely green with *Chlorella* on which the *Paramecium* browsed.

No amoebae were observed in the digester, which is in agreement with previous observations (Barritt, 1940).

DESCRIPTION OF THE FAUNA

Most of the species recorded are typical sewage or soil species (Watson, 1946). *Enchelys* sp. is very similar to a common soil species which may be *E. farcimen*



TEXT-FIG. 1—1-6, *Prorodon microstoma* n. sp. 1, showing ciliary meridians and pharyngeal rods; 2, beginning to divide; 3, two ciliates encysted, following division (?); 4, temporary cyst, with thin cyst membrane; 5, about to engulf a vorticellid; 6, permanent cyst, with thick mesocyst and thin ectocyst. 7, *Metopus es*, showing ciliary rows and oral membrane. 8, *Lionotus* sp., showing ciliary rows and trichites. 9-11, *Podophrya fixa*. 9, free-swimming larva, with terminal ciliary ring; 10, larva settling and regular development of tentacles; 11, adult form. 12, *Kahlia simplex*, size of the cilia slightly exaggerated.

C, ciliary meridians or rows. CM, cyst membrane. CV, contractile vacuole. EC, ectocyst. MC, mesocyst. NU, nucleus. M, oral membrane. P, pharynx. PR, pharyngeal rods.

All figures were drawn with the aid of a camera lucida.

O. F. M.-Ehrb. (Sandon, 1927). *Lionotus* sp. (Text-fig. 1, fig. 8) is distinguished from *L. fasciola* Ehrb.-Wrzeseniowski, which it otherwise closely resembles, in possessing five, and not fourteen, ventral ciliary rows (Kahl, 1926). *Chilodonella* sp. is very similar to *C. uncinata* Ehrb. (Kahl, 1931), differing in the size of the oral basket and the number of ciliary rows. Considering the intra-specific variation of the genus (MacDougall, 1929, 1931; Krascheninnikow, 1951) they are probably identical.

Metopus es (O. F. M.) (syn. *Metopus sigmoides* Clap. and L.) is commonly recorded from Imhoff tanks and is an obligate anaerobe (Lackey, 1938). Noland (1927) studied the conjugation and encystment of this species. The present material (Text-fig. 1, fig. 7) is very similar to Noland's. Neither conjugation nor division of this species was observed, nor did it long survive under aerobic conditions.

Cohnilembus pusillus (Quennerstedt) Kahl (syn. *Lembus pusillus* Q.) and *Cyclidium glaucoma* O. F. M. are well described by Hoare (1927) who remarks: "it is of course a matter of common knowledge that ciliates occur in infusions of all sorts . . . (but) the ciliates here described show a predilection for organic matter in a state of advanced decomposition to a degree not observed in the case of most other free-living ciliates".

Although *Paramecium caudatum* Ehrb. is often stated to be widespread in nature (Kudo, 1947), this assertion is misleading. Bary (1950), in a survey of typical fresh water ponds and reservoirs, recorded the species only once, and then in small numbers. It is generally associated only with polluted water (Lackey, 1938; Gray, 1951, 1952). It has been recorded in very great numbers by Green (1925) in an open sewer and by Hassall (1850, 1855) in the Thames near sewer mouths.

Oxytricha pellionella (O. F. M.) is a common soil species (Sandon, 1927). *Aspidisca lynceus* Ehrb. and *Podophrya fixa* (O. F. M.) (Text-fig. 1, figs 9-11) are both recorded from trickling filter and activated sludge by Lackey (1938). Although the adult of the present *Podophrya* is identical in size and proportions with *P. fixa*, the larva is dissimilar. It is elongate flattened with one surface convex and the other slightly concave or flat. Cilia are restricted to the ultimately stalked end. The nucleus is ovoid but there are two contractile vacuoles at this stage (Fig. 9). The tentacles appear to develop in three regular rings (Fig. 10). Finally the suctorian is transformed into the spherical stalked form with irregularly disposed tentacles (Fig. 11). This material is provisionally identified with *P. fixa* although it may prove to be a separate species. *Euplotes aediculatus* Pierson is well described by Pierson (1943). The only other occasion when it has been identified was in a sample of drain water when it was taken with *Paramecium caudatum*, *Lembadion bullinum* and *Vorticella strata*.

Horvath (1932) described *Kahlia acrobates* and later (Horvath, 1934, 1936) a second species, *K. simplex*. These two species differ slightly in size, in ciliation and in nuclear detail. Both are soil and saprobic species. The cilia are arranged in even longitudinal rows, both frontally and ventrally. The anterior frontals are larger than the other cilia. Horvath depicted six ventral rows in *K. acrobates* (Fig. 2) and four in *K. simplex* (Fig. 2). However there is considerable variation in the different figures of the two species. Horvath also described dorsal ciliary rows in both species, but these cilia are depicted as much finer than the ventral

cilia. The adoral zone is well developed with a strong row of adoral cilia. Horvath described an undulating membrane in both species. A third species, *K. costata*, was described by Kahl (1932). It is generally similar to Horvath's species but has five ventral ciliary rows. The present material (Text-fig. 1, fig. 12) closely resembles *K. acrobates* and *K. simplex* in general proportions. The frontal and ventral cilia are arranged in four rows. The history of the nucleus is similar to that described by Horvath (1936). There are, however, no dorsal cilia, nor was an undulating membrane identified. Despite these inconsistencies the present material is provisionally identified with *K. simplex*, which it otherwise resembles so closely. Horvath (1936) described encystment in this species and the present material appeared to survive in the digester fluid principally in the encysted state and to excyst and divide in the sub-cultures. In this it resembled both *Vorticella microstoma* and *Prorodon*.

Vorticella microstoma Ehrenberg was the most common species encountered. It is common in soil (Sandon, 1927) and in infusions, and is one of the most common sewage protozoa (Dr. S. C. Pillai, Indian Institute of Science, personal communication). Lackey (1938) recorded it only in a polluted stream, an activated sludge chamber, a trickling filter and an Imhoff tank. It was recorded from muds, "shown to be oxygen-free", by Kolkwitz and Marsson (1909). In the present material only cysts were found upon direct examination of the digester fluid. These cysts were larger than those occurring in aerobic cultures and, when placed in air, they excysted and divided rapidly. In air, when the food was exhausted, they encysted. The addition of bacteria caused the ciliates to excyst, to increase in size and to multiply until the bacteria were consumed, when they encysted again. If a very heavy inoculum of bacteria was added the vorticellids encysted before the bacteria were consumed, and in this case they formed large cysts as were initially found in the digester fluid. These cysts, like the cysts from the digester, excysted on aeration.

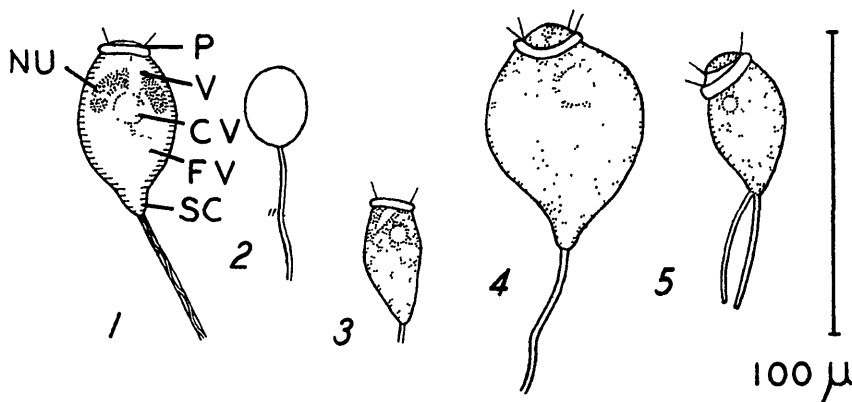
The vorticellids multiply rapidly in the presence of bacteria, dividing six times in twenty-four hours at room temperatures. They also increase in size, and the large tropic vorticellid is quite distinct from the normal form. It was first described from infusions as *V. hians* by Muller (1773)—"Vorticella simplex citriformis retortili". Subsequently Kent (1880-1882) figured this species and described it as "body elongate, pyriform or lemon-shaped, widest and inflated posteriorly, about twice as long as broad, pedicle very short, scarcely as long as the body". But Kent added that this description fits only one type of *V. hians* and that the stalk may be of normal length.

Fauré-Frémiet (1905) was the first to connect this infusion species with *V. microstoma* Ehrenberg. He considered it an anaerobic variety of the latter species and described his material as "ovoid and more often pyriform, swollen at the base and very narrow at the apex". The size of his material was 90 μ by 53 to 60 μ and the peristome width 22 μ compared with 27 μ in Fauré-Frémiet's normal form. He also recorded abnormalities of colour, peristome and nucleus in *V. hians*.

The dramatic change in the form of *V. microstoma* which is effected by the addition of bacteria is shown in Text-fig. 2.

The average size of a normal *V. microstoma* is 55 μ by 35 μ and the peristome width 16 μ . The ratio of length to breadth is therefore 1.6 to 1. The

striations are clearly marked and so too is the line of the posterior ciliary wreath. This form is well described by Noland and Finley (1931). When starved the ciliate is thinner and therefore appears more elongate. This form is 40 μ by 20 μ and the peristome width 15 μ . The ratio of length to breadth is therefore 2:1. When fed on bacteria this form changes dramatically. The ciliate becomes markedly swollen and pyriform and greatly increased in body volume. The striations are no longer clearly visible. These forms are over 70 μ long and up to 55 μ in breadth. The ratio of length to breadth is then 1.3:1. The peristome width is 23 μ .



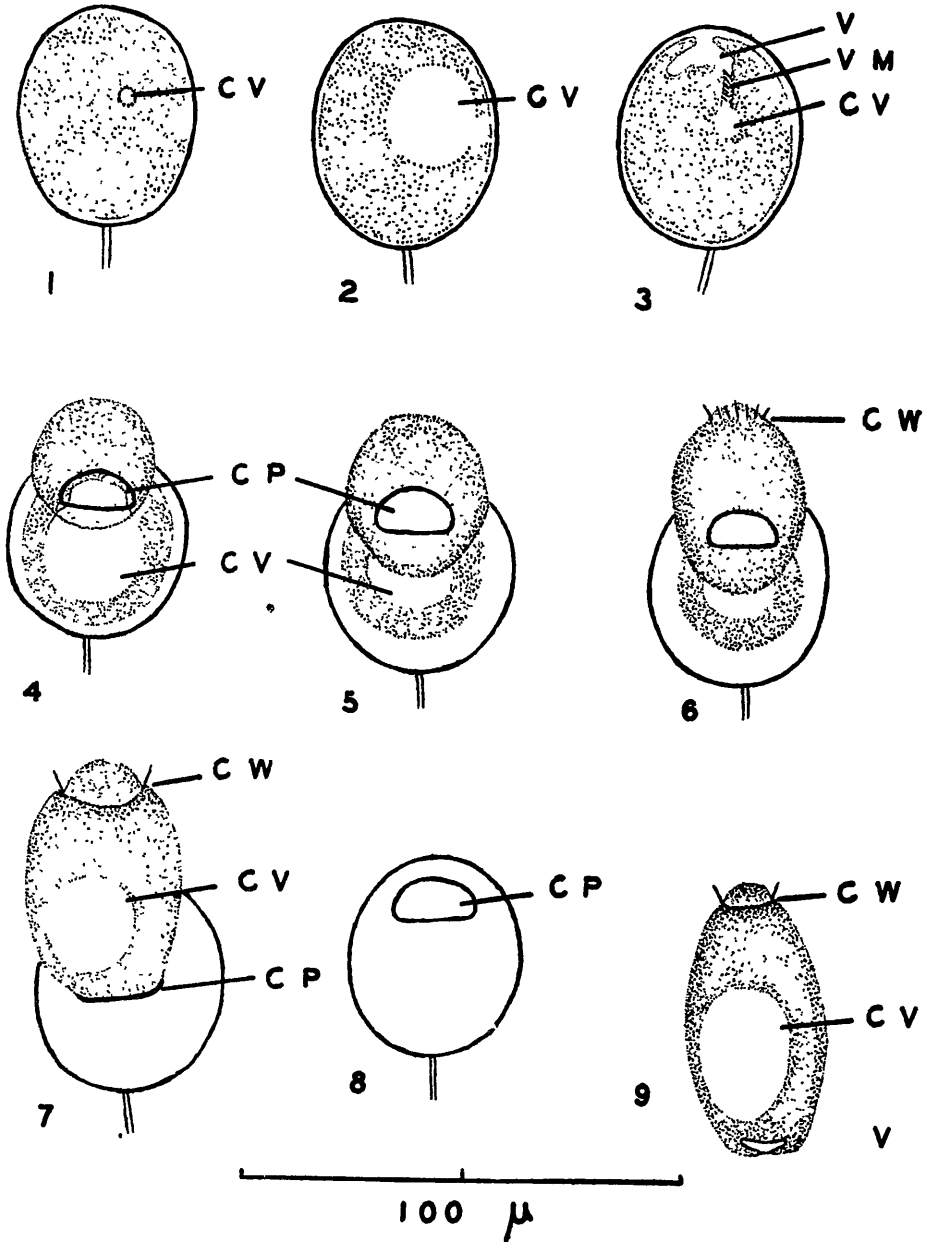
TEXT-FIG. 2.—Variation in form of *Vorticella microstoma*. 1, normal form of *Vorticella microstoma*, 2, cyst from starved culture; 3, recently excysted form, 4, form fed on bacteria for twenty-four hours, 5, form with two stalks.

CV, contractile vacuole. FV, food vacuole. NU, nucleus. P, peristome. SC, scopula. V, vestibule.

The cysts of *V. microstoma* also vary in size, depending upon the previous history of the culture. Cysts formed under well aerated conditions ranged from 28.8 μ to 40.0 μ in diameter and averaged 35.2 μ . Cysts in the anaerobic digester ranged from 33.6 μ to 46.4 μ in diameter and averaged 38.4 μ . Cysts from starved cultures were even smaller.

Division of *Vorticella* is by longitudinal fission of the trophic form (Finley, 1936). This is slightly unequal. One daughter remains on the parent stalk and the other metamorphoses into a telotroch, separates, becomes free-swimming, and later settles and grows its own stalk. Mass cultures of *Vorticella microstoma* fed with loops of bacteria showed considerable variation of body form. The most bizarre individual was one which developed two stalks. This is shown in Text-fig. 2. These stalks were not observed to contract. The sexual cycle described by Finley (1936, 1939) was only rarely observed. It did not occur regularly as described by Finley in his cultures.

Excystment of *Vorticella microstoma* is shown in Text-fig. 3. It commences with the formation of the contractile vacuole which pulsates and becomes very large. The ciliate escapes from the cyst membrane through a cyst pore which is forced open by hydrostatic pressure due to the activity of the contractile vacuole. The ciliate differentiates as a telotroch, becomes free-swimming, and finally settles as a normal trophic vorticellid. The whole process as illustrated



TEXT-FIG 3—Excystment of *Vorticella microstoma* 1-7, excystment and formation of the telotroch; 8, cyst membrane. 9, telotroch

CV, contractile vacuole V, vestibule. VM, vestibular membrane CP, ciliary pore. CW, ciliary wreath.

in Text-fig. 3, takes place within an hour, from the first signs of the contractile vacuole to the escape of the ciliate from the cyst membrane. Normally the ciliate is still undifferentiated when it escapes from the cyst membrane, but occasionally a fully differentiated telotroch has been observed still within the cyst membrane from which it has failed to escape. Text-fig. 3 also shows that the vestibule is early differentiated, although feeding does not take place until the telotroch has settled and metamorphosed into the sessile form.

The development of *Vorticella* under aerobic conditions was markedly affected by the presence of *Prorodon*. This *Prorodon* species (Text-fig. 1, figs. 1-6) is very similar to *P. griseus*, whose morphology and life history are well described by Tannreuther (1926). The body is oval to sub-spherical, plastic and symmetrical. There is a well-developed and protrusible pharynx supported by rods or trichites, and the body is uniformly covered with about fifty ciliary meridians. The size of the ciliate ranges from 50 μ to 200 μ with well fed individuals about 100 μ to 150 μ in length. The macronucleus, as with *P. griseus*, is variable in shape but in most resting cysts is curved band-shaped although at other times it is oval. Because the body is normally stuffed with food it is difficult to study nuclear and other details.

The life history of this *Prorodon* is very similar to that of *P. griseus*. The ciliate spends the greater part of its life as a cyst, and is trophic for only short periods when food is in good supply. Two types of cyst may be distinguished, a temporary cyst and a permanent cyst. The temporary cyst (Fig. 4) has a very thin and flexible membrane within which the ciliate continues to rotate. After a short time, less than an hour, it breaks out to begin feeding again or it may again encyst. Occasionally division may take place within a temporary cyst. In the permanent cyst the membrane is thicker and there is generally a second inner cyst membrane (mesocyst, Fig. 6) as well. The ciliate ceases to rotate, dedifferentiates and will not excyst for twenty-four hours or more. Although the ciliates encyst fairly readily the factors stimulating encystment and excystment are uncertain. With adequate food supply the ciliates continue to feed and divide and may reach considerable numbers. One slide was observed with over a thousand active trophic ciliates. In the absence of food they generally encyst, but may excyst again within forty-eight hours, without any apparent stimulus. Single individuals suspended in hanging drops encyst as readily as crowded individuals, when deprived of food. The ciliates encyst, however, when the cytoplasm is still filled with food particles and when they are about 100 μ in diameter. The average diameter of the permanent cysts is about 60 to 100 μ , while the temporary cysts are generally larger as the ciliate does not dedifferentiate in them. On the other hand, starved individuals, about 50 μ in length, may continue active in the absence of food and fail to encyst. Absence of food, however, does seem the most important factor as neither temporary nor permanent cysts are formed in the presence of an adequate food supply. Crowding appears to be of less significance but staling of the medium may be of some importance. With the exception of the temporary cysts, which excysted without any apparent stimulus, excystment is most readily obtained with fresh bacterial suspensions. Neither yeast nor hay extracts proved effective. Excystment under these conditions never took less than twenty-four hours and often took longer; nor was every cyst stimulated to excyst. In excystment of permanent cysts the inner cyst membrane appears to be dissolved and the outer membrane, similar

to the single membrane of the temporary cysts but often thicker, is fractured, as with a temporary cyst, and the ciliate escapes fully differentiated. It immediately commences searching for food.

Division generally takes place while the ciliate is free-swimming, although rarely a temporary cyst may be formed. It is presaged by the lengthening of the ciliate and the appearance of a transverse median cleft (Text-fig 1, fig. 2). Subsequently, the cleft increasingly separates the anterior and posterior parts of the body. The latter develops a pharynx and pharyngeal rods, and the former a contractile vacuole. The parts then separate as two ciliates which recommence their search for food. The process of division takes less than twenty minutes and a ciliate well supplied with food may divide six times in forty-eight hours. Conjugation has never been observed at any stage of the life history.

The food of *Prorodon* is, as far as can be ascertained, solely trophic *Vorticella microstoma*. The sub-spherical *Prorodon*, rotating in counterclockwise direction, darts vigorously to and fro until it finally strikes a vorticellid with its extended mouth and pharynx. The rotary movement then ceases and the *Prorodon* proceeds to swallow the vorticellid withdrawing it gradually within its pharynx. The whole process may take place within thirty seconds and the *Prorodon* immediately swims off until it again chances on another vorticellid, or else it remains stationary, rotating vigorously, and secreting around itself a temporary membrane through which it can later break. Its feeding behaviour is as dramatic as that of the well-known *Didinium nasutum*, and it appears to be even more selective in its food requirements. For this latter reason the ciliate has been named *Prorodon microstoma* n.sp. This predatory habit separates it absolutely from all other species of *Prorodon* (Kahl, 1930; Sandon, 1932). The similarities and dissimilarities to closely related species are summarised in Table 1.

TABLE I.
Comparison of *Prorodon microstoma* n.sp. with related species

	<i>P. discolor</i>	<i>P. griseus</i>	<i>P. microstoma</i> n.sp.	<i>Didinium</i> <i>nasutum</i>
Shape	Ovoid	Ovoid to sub-spherical	Ovoid to sub-spherical	Ovoidal to sub-spherical
Size	100-130 microns	165-200 microns	50-200 microns	80-200 microns
Macronucleus	Massive ellipsoid	Massive, oval to curved, band-shape	Massive oval to curved band-shape	Massive curved band-shape
Ciliation	45-55 rows (meridians)	Number not known (meridians)	c.50 rows (meridians)	Immature incomplete meridians Adult two girdles
Cyst Physiology	Not known	Temporary and permanent	Temporary and permanent	Permanent
Type of cyst				
Encystment factor		Not known	Not known	Crowding
Excystment factor		Not known	Bacteria	Bacteria
Feeding behaviour	Feeds on algae	Feeds on algae and flagellates	Predatory on trophic <i>Vorticella microstoma</i>	Predatory on trophic ciliates, especially <i>Paramecium</i>
Habitat	Fresh to blackish water	Shallow pools fresh water	Anaerobic meat digester	Fresh water
Ecology	Oligosaprobic to mesosaprobic	Oligosaprobic to mesosaprobic	Polysaprobic	Sapropelic to polysaprobic

This table strongly implies that *Prorodon* and *Didinium* should be included in the same family. It stresses the importance of a complete knowledge of the biology of a species in determining its systematic position. There is also a marked correlation between the behaviour, physiology and ecology of the individual species. For example, cyst physiology is well developed in *Prorodon microstoma* n.sp. and *Didinium nasutum*, which are both absolutely dependent upon a specialized food situation, and in *Prorodon griseus*, whose habitat is subject to periodic desiccation.

DISCUSSION

Lackey (1949) and Rohlick (1949) have recently given a stimulating review and discussion of the place of protozoa in sewage digestion. Hawkes and Jenkins (1951) have also recently reviewed the problem. The process of organic degradation is imperfectly understood. The precise role of the different components of the active flora and fauna is not yet determined (Barker, 1946). The efficiency of degradation appears to be wholly dependent upon the presence of the correct microflora and fauna. The role of the protozoa in this process is greatly debated. Their function seems to be not so much to effect the degradation of the organic substrate, although they may contribute towards this, but rather to prey on the bacterial flora and thereby maintain its efficiency and to assist in flocculation. Work cited by Rohlick and other authors showed that degradation takes place more effectively in the presence than in the absence of protozoa. Satisfactory degradation has been obtained, however, in the absence of protozoa (Jenkins, 1951).

The organisms involved vary from one digestion plant to the next, but certain species appear with greater frequency than others and these are sometimes called anaerobic, although as Lackey points out many of them are truly only facultative anaerobes. The history of the present digester includes only one true anaerobe, *Metopus es*, one of the most common sewage ciliates. The other species occurring in the digester are facultative anaerobes, and it is therefore inferred that for a short time, following the addition of fresh meat waste, aerobic conditions must prevail. It is known that facultative anaerobes cannot divide in the absence of oxygen (Watson, 1944) and further that *Vorticella* normally forms a telotroch when oxygen is removed (Brand, 1946). (The effect of environmental factors, including oxygen lack, upon the life history of *Vorticella microstoma* will be described in a later paper.) It appears that in the digester the vorticellids encyst, due perhaps to intense bacterial decomposition associated with a falling redox potential. The Eh of the digester fluid was about -290mv. whereas the Eh of the oxidation pond was about 200mv. This may also be the case with the other species of facultative anaerobes. Hayes (1938) described encystment of *Dileptus anser* in intense bacterial infusioin. Following aeration the vorticellids excyst. There is no need of further stimulus. *Prorodon* is wholly dependent upon the growth of *Vorticella* and the activity of this ciliate must therefore be confined within the trophic history of the vorticellids. It is interesting to compare the conditions of encystment and excystment of *Vorticella microstoma* and *Prorodon microstoma*. *Vorticella* encysts primarily in response to absence of bacterial food, but under strongly reducing conditions will encyst in the presence of bacteria. It excysts primarily in response to bacteria and oxygen, although better excystment is obtained with fresh medium which suggests the presence in stale medium of an inhibitory factor (Brand, 1923). The life history of *Prorodon*

is determined by very similar factors. It encysts in the absence of food and excysts in the presence of bacteria. Under the present conditions the excystment of *Vorticella* followed within an hour or two of the addition of bacteria but *Prorodon* did not excyst until twenty-four hours or more later. For this reason there was generally a vigorous culture of *Vorticella* to precede the excystment of *Prorodon* when cysts of the two ciliates were in the same drop or culture to which bacteria had been added. Such conditions proved ideal for the development of *Prorodon* for this ciliate cannot be starved indefinitely. Its movements become increasingly sluggish, more like a normal slow swimming holotrich and quite unlike the vigorous darting movement of the normal trophic form. At such a stage it seems unable to attach itself to a vorticellid and so, even if vorticellids are present, it is unable to feed. It is possible that during temporary encystment the ciliate restores its kinetic energy, and when fully active and able to feed breaks out of the cyst membrane. In other words it is suggested that encystment is primarily determined by the energy level of the ciliate. With constant feeding and division, this remains high and encystment does not take place. As the number of vorticellids is diminished, the *Prorodon* encounters fewer food organisms and conversely there is a longer period between each "kill". If this period is too prolonged the ciliate will encyst, provided it is of certain optimum size. It is at this stage that other factors, such as staling, must determine whether a temporary or permanent cyst is formed. In either case the ciliate which subsequently escapes from the cyst membrane is able, once again, to commence that swift darting motion which is essential for its trophic existence.

In its general behaviour and life history *Prorodon* closely resembles two other predacious ciliates, *Didinium nasutum* and *Woodruffia metabolica*, both of which prey largely on *Paramecium*. Structurally it is closely related to *Didinium* and its feeding behaviour is identical (Calkins, 1915). *Didinium* also excysts in response to bacteria although encystment is primarily due to crowding (Beers, 1946, 1947). The cysts of *Didinium*, like the permanent cysts of *Prorodon*, have an ectocyst and an endocyst but *Didinium* also has a thin endocyst which is dissolved after the ciliate has escaped from the outer membranes (Beers, 1945a). In *Woodruffia* there are only the two membranes, as in *Prorodon*, and there are also several types of cyst including permanent and temporary cysts. In *Woodruffia* division also takes place within a cyst membrane, and temporary cysts are formed in food-rich cultures in the same way as with *Prorodon* (Johnson and Evans, 1939, 1940). The chief difference between the cysts of *Prorodon* and *Vorticella* is that in *Vorticella* there is a definite excystment pore, as with *Bursaria* (Beers, 1948), a point not made clear by Brand (1923), although the pore is clearly shown in a drawing by Stein (Kent, 1880-1882). The mechanics of excystment in *Vorticella* are generally similar to those of *Tillina* (Beers, 1945b), in that the build up of hydrostatic pressure accompanying the activity of the contractile vacuole finally ruptures the cyst membrane.

ACKNOWLEDGMENTS

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Scholarship, and is partly included in a thesis submitted for the degree of Doctor of Philosophy.

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